COOPERATION AND COMPETITION DURING PLAY FIGHTING IN TONKEAN AND JAPANESE MACAQUES: AN EXAMINATION OF JUVENILE BEHAVIOUR WITHIN EGALITARIAN AND DESPOTIC SOCIAL SYSTEMS

CHRISTINE J REINHART
Master of Science, University of Lethbridge, 2005

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Department of Neuroscience
University of Lethbridge
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ABSTRACT

Cooperation and competition during play fighting in Tonkean and Japanese macaques: An examination of juvenile behaviour within egalitarian and despotic social systems

Macaques (*Macaca*) are the most geographically widespread and behaviourally diverse primate genus, and although macaque species share the same basic social structure, they display broad interspecific variation in patterns of social behaviour. 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. In this study, the play fighting of juvenile Tonkean and Japanese macaques was compared to determine whether or not play behaviour co-varies in a manner similar to that of adult social behaviour. As predicted, Tonkean macaques exhibit a relatively cooperative style of play fighting, whereas Japanese macaques exhibit a relatively competitive style of play fighting.

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CHAPTER ONE

General Introduction

1.1 The complexity of social interactions

Animals that live in social groups, especially highly social ones, such as many primates, are constantly faced with the dilemma of striking the right balance between cooperating and competing with those with whom they live. It is important to cooperate with others so as to build and maintain social relationships and reduce tension within the social group. However, at the same time, each individual needs to gain the maximum benefit from its social partners, while paying minimal costs. Complications arise if one individual were to consistently push another too far (i.e., gains become one-sided), in which case, a social interaction can end abruptly and the relationship can be compromised. So how exactly do non-human primates negotiate (behaviourally) the intricacies of complex social interactions? It is likely that there are both genetic and environmental factors that shape how individuals of different species may handle and effectively solve the ‘social challenge’ of balancing cooperative tendencies with competitive drives. At the level of behavioural analysis, one approach that may provide some insight with regard to primate social exchanges is to compare and contrast the dynamics of social behaviour between species that are closely related, but live in social groupings that differ in competitiveness (de Waal & Luttrell, 1989).

1.2 Macaques and differences in social behaviour

Macaques (genus *Macaca*) are the most geographically widespread and behaviourally diverse primate genus, and depending on the classification system to which you refer, there are between 16 and 22 different species of macaques (Delson, 1980; Fooden, 1976; Hoelzer & Melnick, 1996). They share the same basic pattern of organization, in that they all live in multi-male, multi-female groups, and within these groups, females form kin-based subgroups called matrilines (Thierry, 2000). Interestingly, there are dominance hierarchies both within and between matrilines, the ranks of which may fluctuate, thus producing a relatively complex social life for macaques.

Even though macaque species share the same basic social structure, they display broad interspecific variation with regard to patterns of social behaviour (e.g., aggression, reconciliation, dominance, nepotism, socialization, temperament). That is, there are noticeable differences in how different species of macaques manage aggression between individuals, in the degree of mother's permissiveness, and in the degree of dominance and nepotism within the social group (Thierry, 2000). Based on their patterns of aggression and reconciliation, Thierry (2000) proposed arranging macaque species along a 4-grade scale. Species that display high rates of affiliative contacts that reduce social tension and facilitate social contact (e.g., clasps and embraces) are classified as grade 4 (e.g., Tonkean and crested macaques), whereas species that typically have these affiliative behaviour patterns relatively reduced, are classified as grade 1 (e.g., Japanese and rhesus macaques). In grade 1 species, the dominance gradient is steepest; this means that the social life of every individual is governed by strict rules - power asymmetries determine who may interact with whom and how individuals choose partners for proximity, affiliation, and play (Thierry, 2004). Therefore, at one end of this continuum, there are grade 1 species that have social systems that are highly hierarchical and despotic, and at the other end, grade 4 species in which the social system is more relaxed and egalitarian. Furthermore, there are also macaque species whose suite of social behaviours place them somewhere in between these two extremes.

1.3 The *co-variation hypothesis*

According to the *co-variation hypothesis*, a theory that has been applied specifically to macaques (Thierry, 2004), correlated differences in a species' social 'style' that presumably stem from changes in a suite of social behaviours, may be attributed to variation in a single character, such as temperament. A change in temperament can have sweeping effects on social behaviour and social organization in macaques, which could allow species to be broadly categorized as socially 'egalitarian' or 'despotic'. If, during the process of evolution, natural selection acted on response dispositions rather than specific behavioural responses, then this could result in members of different species having different 'modal tendencies' to respond, and these differences would contribute to variations seen on the basic macaque pattern of social organization (Capitanio, 2004). For example, comparative studies of macaques have shown that adult Tonkean macaques have relatively tolerant, relaxed social relationships, whereas Japanese macaques are known to keep rigid dominance hierarchies and are generally more nepotistic in their adult social relationships (Thierry, 2004). That is, because of differences in temperament, these species exhibit contrasting social styles. However, despite the documentation of these species' differences among macaques, if we revert back to the aforementioned complexities of cooperation and competition in social interactions, we do not know whether tolerant species with relaxed dominance hierarchies are particularly cooperative in their social interactions and whether nepotistic species with more rigid dominance relationships behave more competitively in social contexts. Furthermore, it is unclear as to whether these differences - presumably temperamental - are present within the context of interactions that take place between the younger, sub-adult members of each species.

Although the *co-variation hypothesis* seems to hold for adult members of different macaques species, little is known about the behaviour of juvenile macaques. In primate research, the juvenile period has been the most neglected phase of life histories. Indeed, during its first two decades, the field of Behavioural Primatology mainly concentrated on two topics of research: (1) aggression and dominance, and (2) infant development/ mother-infant relations, both of which left juveniles overlooked (Pereira & Fairbanks, 1993). The little information available on juveniles, is primarily focused on social play, interactions with infants and the acquisition of dominance. These data suggested that juvenile modes of behaviour differ substantially from those of mature males and females (Pereira & Fairbanks, 1993). It would thus be an especially important test of the *co-variation hypothesis* to investigate whether the patterns of social behaviour in juvenile-aged macaques do indeed reflect that of adult macaques - particularly in the specific ways that would be predicted for different species.

1.4 Play fighting: An ideal model behaviour

Play fighting, which is observed most frequently during the juvenile stage of development (Pellis & Pellis, 1998a), is an ideal model behaviour with which to examine complex social exchanges because it requires both competition and cooperation (Palagi, 2006; Pellis, Pellis & Reinhart, in press). That is, for a play fight to remain playful, both individuals, while attempting to win, must also cooperate, by alternating between the roles of attacker and defender, which allows each a chance to win. During a play fight, partners compete with each other to gain some advantage, such as contacting a particular part of their opponent's body (Aldis, 1975; Pellis, 1988; Symons, 1978), but unlike serious fighting, in play fighting, the interactants provide their partners with the opportunity to gain an advantage (Pellis & Pellis, 1998b). These characteristic role reversals (i.e., of attacker and defender, or offense and defense), and the delicate balance of cooperation and competition that is maintained between play partners, prevent an interaction from escalating to serious fighting (Dugatkin & Bekoff, 2003). It is also fairly well established that for some lineages, play is a distinct behavioral entity and not simply a juvenile representation of more adult-typical behaviors (Burghardt, 2005; Fagen, 1981; Pellis & Pellis, in press). This means that an examination of play fighting in macaques would be well-suited for testing whether juvenile-aged Tonkean and Japanese macaques differ in species typical ways, with Tonkean macaques exhibiting a more relaxed style of play fighting and Japanese macaques exhibiting a relatively intense/anxious style of play fighting.

Another reason that favours play fighting as a suitable social behaviour with which to examine juvenile macaques, is that the different aspects of play - attack and defense - are dissociable, in that changes in these components can be identified independently. They are clearly dissociable at the behavioral level, and previous studies suggest that attack and defense are also motivationally and genetically independent (Pellis & Pellis, 1991;

Reinhart, McIntyre, Metz, & Pellis, 2006; Reinhart, Pellis, & McIntyre, 2004; Siviy, Love, DeCicco, Giordano, & Seifert, 2003). The *co-variation hypothesis* would predict that all aspects of play should change together in similar manner. That is, if Tonkean macaque play fights are 'easy going' because of the species' relaxed temperament, then these laid-back tendencies should be reflected in both the offensive and defensive components of their playful interactions. In contrast, if Japanese macaque play fights are relatively intense because of their more 'up-tight' temperament, then both the offensive and defensive elements of their play fights should exhibit such qualities. While these intuitive predictions seem reasonable, they also appear rather vague.

From the *co-variation hypothesis*, which is a theoretical context about correlated changes in social behaviour that may be attributed to species differences in temperament, broad predictions about social behaviour can be made. For example, during social interactions, juvenile Tonkean and Japanese macaques should exhibit the same social styles as those of the adults of their respective species. However, within the context of play fighting, one is unable to make more specific predictions from the *co-variation hypothesis* on actual behaviours that could be considered as representative of the different species social styles. Afterall, the more egalitarian social style of Tonkean macaques may permit them to take more, not less, liberties during play fighting, and so, in some ways, be more competitive in their actions compared to Japanese macaques that may be more constrained to follow rigid rules that are sensitive to dominance relationships between the play partners. Alternatively, taking more liberties may allow for more cooperation. Thus, it is unclear as to how the contrasting social styles of Tonkean and Japanese macaques might be behaviourally expressed during play fighting.

1.5 Cooperation and competition in play

In conjunction with the *co-variation hypothesis*, a theoretical context is needed from which predictions about the specific elements of play fighting can be made. The *competition/cooperation model* of play, developed by Pellis, Pellis, and Reinhart (in press), considers aspects that are particularly relevant to mammalian play fighting. This theoretical model takes into account that play fighting needs to incorporate both competition and cooperation, and that for play fighting to be playful, it must have a minimum threshold level of both of these components (Figure 1.1). Without competition, play fighting becomes excessively predictable and so loses its pleasurable quality, and without cooperation, play fighting can escalate into serious aggression. The balance between competition and cooperation may differ across species. When considered in combination, these theoretical viewpoints, the *co-variation hypothesis* and the *competition/cooperation model* of play, can be thought of as complimentary for making specific, testable predictions about play fighting in macaques and in primates more generally.

Considering the tolerant and relaxed temperament of Tonkean macaques, it could be predicted that although they should exhibit some level of competitiveness in their play fights, relative to Japanese macaques, Tonkeans should exhibit more cooperative behaviour. Some examples of cooperative play behaviour include: (1) mainly aiming for

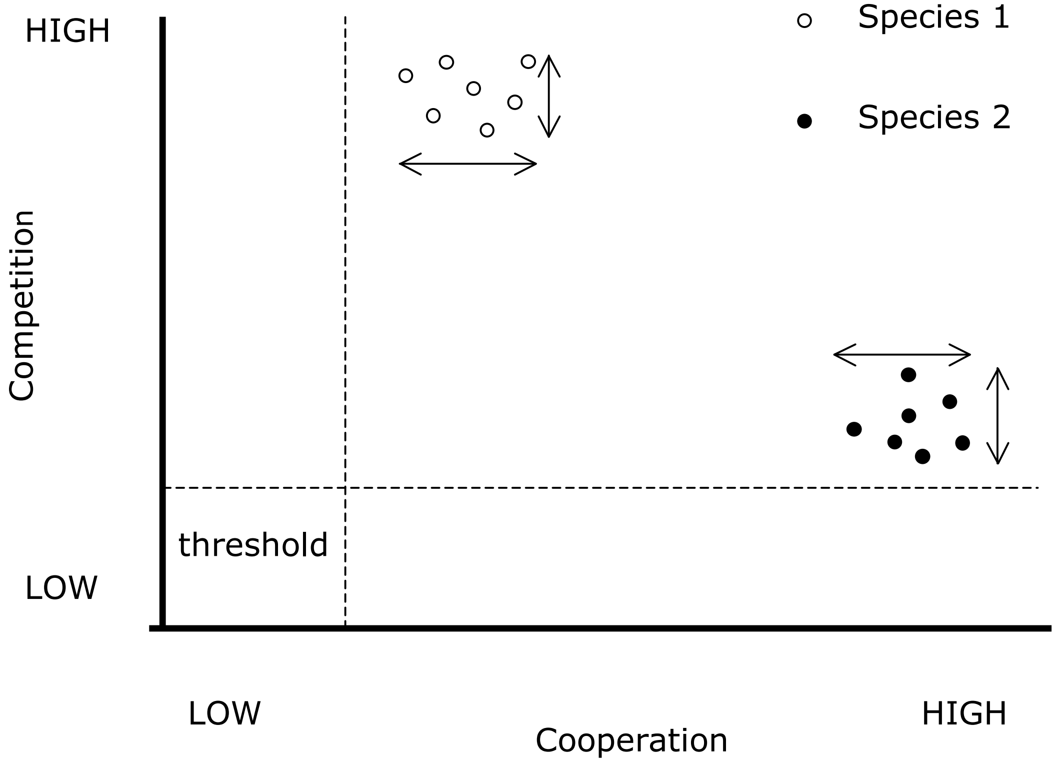


Figure 1.1 *Competition/cooperation model* of play.

the opponent’s play target, rather than agonistic targets, (2) launching playful attacks that do not incorporate a defensive element, (3) exposing your play target to your partner (e.g., putting yourself in a vulnerable position to allow your opponent a potential advantage), (4) engaging in frequent role reversals of attacker and defender during a single play bout or in repeated bouts with the same partner, (5) engaging in play fights with a variety of peers, and (6) participating in prolonged play fights that involve multiple individuals (i.e., polyadic play).

In contrast, it could be predicted that the more dominance oriented Japanese macaques would exhibit a relatively high proportion of some of the following examples of competitiveness during play behaviour: (1) deviating from the opponent’s play target to contact agonistic targets, (2) incorporating a defensive component into playful attacks (e.g., modifying posture or orientation to your partner to prevent yourself from being in a vulnerable position that may provide an advantage to your partner), (3) failing to expose your play target to your partner, (4) resisting or preventing role reversals, and (5) engaging in brief play fights with few partners. Indeed, from the *competition/cooperation model* of play, species-specific predictions can be made with regard to the kinds of observable, measurable behaviours we can expect to be exhibited by each species during play fighting, given their respective social styles. However, is there any evidence to suggest that play fighting patterns in primates are in any way related to species’ social systems?

1.6 Play fighting in primates

Play fighting is one of the most commonly occurring forms of play in mammals (Fagen, 1981), and even though play is common in primates (Pellis & Iwaniuk, 2000; Pellis & Pellis, 1997a), there is a lack of detailed studies of play for most primate species (Fagen, 1993). For primates in general, it has been shown that: (1) high rates of play characterize late infancy and early juvenility (Fagen, 1993), (2) the play patterns observed in non-human primates share several characteristics (e.g., play frequency decreases with increasing age, the play of males is typically more rough and more frequent than that of females) (Petit, Bertrand, & Thierry, 2008), (3) play fighting is observed in the adults of some primate species (Pellis & Iwaniuk, 1999, 2000), and (4) there is some variability between species in how they play (Pellis & Pellis, 1997a). However, age-structured analyses of the quantities and qualities of primate play across the life span are needed to clarify the current understanding of primate play in the ontogeny of primate behaviour (Fagen, 1993).

Given that few studies have focused on analyzing the content of primate play interactions, there is little understanding of the interspecific similarities and differences in patterns of play (for exceptions, see Palagi, 2006; Pellis & Pellis, 1997a; Petit et al., 2008). However, based on the data available, several researchers who have provided empirical information on various species have suggested that play patterns reflect the social organization of a species (Cheney, 1978 (baboons); Flack, Jeanotte, & de Waal, 2004 (chimpanzees); Maestripieri & Ross, 2004 (gorillas); Miller & Nadler, 1981 (orangutans and chimpanzees); Palagi, 2006 (chimpanzees and bonobos); Petit et al., 2008 (macaques); Watts & Pusey, 1993 (great apes); Zucker, Dennon, Puleo, & Maple, 1986 (orangutans). For example, Palagi (2006) found that some aspects of play fighting among adult bonobos (*Pan paniscus*), who live in relatively egalitarian social groups, differed when compared to the play fighting of adult chimpanzees (*Pan troglodytes*), who live in more despotic social groups. The play fighting of bonobos is more 'rough', and the use of play signals (i.e., full play face), particularly during rough play bouts, is relatively exaggerated when compared to the play fights of chimpanzees. Her interpretation is that bonobos may use this particular style of play fighting to enhance their behavioural flexibility, and thus, their ability to negotiate the relatively symmetric social relationships that are characteristic of their more relaxed, less rigidly structured social system. Because the social relationships between adult chimpanzees are relatively more solidified, in that individuals have distinct ranks that are achieved and maintained by the use of unambiguous dominance and subordinate behaviours, the structure of their play fighting is not shaped in such a way as to achieve the same 'goals' as the play fighting of bonobos (Palagi 2007; Palagi & Paoli, 2007).

Although Palagi's findings and interpretations suggest that adult play patterns may be shaped by, and reflective of, a given species' social organization, she did not include in her study analyses of play patterns for juvenile-aged individuals. Petit, Bertrand, and Thierry (2008) examined play fighting in juvenile crested (*M. nigra*) and Japanese macaques, hypothesizing that patterns of play should co-vary with a species' social style. Crested macaques resemble the other species that originate from the island of Sulawesi (e.g., Tonkean macaques) in that their social relationships are not greatly influenced by dominance ranks or strong kin preferences, and their overall levels of tolerance are quite high (Thierry, 2004). The authors found that relative to the more despotic Japanese macaques, play fighting in crested macaques involved (1) more close body contact, (2) more play partners, and (3) wrestling bouts in which partners were likely to move into vulnerable positions, such as lying down. In contrast, Japanese macaques engaged in play fights with fewer partners and usually maintained upright postures that the authors claimed facilitated 'easy escape' from a given interaction.

Their interpretations for these findings suggest that some aspects of juvenile play behaviour may reflect a species' social style in that the crested macaques appear to exhibit a more relaxed style of play, whereas the Japanese macaques seem to prefer more controlled, or less risky, interactions, even within the context of play. However, while some of the data from this study are compelling, the absence of direct information on the dynamics of the interactions between the juveniles of these two species leads to an uncertainty as to the factors producing the species differences found. As explained below, detailed analyses of videotaped data are necessary to identify the bases for these stylistic differences in the play fighting of these species.

1.7 Problems with previous behavioural analyses

Although variations in play fighting patterns have been identified and correlated to species' social systems, for many studies, the interpretations of the data are questionable. One concern is that most studies examine the behaviour of only one troop for a given species. Indeed, caution must be given when generalizing the results from one group to the entire species (Petit et al, 2008). It is important that the behavioural idiosyncrasies of individual populations be teased apart from aspects of behaviour that may be applied to the species more broadly. An additional criticism is that for most studies, the behavioural analyses are derived from tape-recorded data, in the form of pre-defined behaviour units/categories (Pellis, 1989) that are collected during scan sampling or by following focal animals (Altmann, 1974). From such methods, quantitative frequency data can be collected and reported. However, when pre-defined behaviours make up the bulk of the collected data, it is likely that (1) the researcher may overlook potentially important, biologically relevant aspects of behaviour because they were not included, *a priori*, in the list of pre-defined behaviour units, and (2) the subsequent analyses will be left without important qualitative information that pertains not only to the content of an individual's behaviour, but also to the dynamics of the social exchanges taking place between individuals. If there is no account in the primate play literature of what the animals are actually doing within the context of play fights, then it is extremely difficult to pinpoint what may be important for a given species' playful interactions, and what may be contributing to the reported variation in primate play patterns more generally.

Indeed, there are few examples in the primate literature of behavioural analyses that provide an adequate level of detail in terms of describing the content of play behaviour. For example, species-specific play targets have rarely been identified (exceptions: for ring-tailed lemurs, black-handed spider monkeys, and patas monkeys, see Pellis & Pellis, 1997a; for rhesus macaques, see Symons, 1978), and the offensive and defensive components of play fighting have not been independently examined (except for Pellis &

Pellis, 1997a), which, as mentioned previously, is important because they are dissociable and thus may be modified differently, even between closely-related species.

Because play fighting is a complex and dynamic social behaviour, it would be advantageous to make use of observational and analytical methods that afford the observer an opportunity to identify what animals actually *do* during playful interactions. If an accurate, detailed description of behaviour can be generated, then the subsequent interpretations to be derived for that behaviour will be strengthened due to the fact that the behaviour can be considered within the context of several different theories. For example, once the underlying structural organization of play fighting in Tonkean and Japanese macaques has been uncovered, the specific elements of each species' behaviour can be interpreted within the context of the *co-variation* hypothesis, as well as the *competition/cooperation model* of play. For the purpose of this thesis, it was critically important that play fighting be described and analyzed at a level of detail sufficient to appreciate the behavioural differences between individuals, species and troops.

An example that illustrates the importance of avoiding preconceived ideas about the structure of interactions when observing and describing play behaviour comes from Janet Levy and Donald Symons. Symons' book, "Play and Aggression: A Study of Rhesus Monkeys", was published in 1978, and Levy's Ph.D. dissertation, "Play behavior and its decline during development in rhesus monkeys (*Macaca mulatta*)", was completed in 1979. Although these researchers were studying the same behaviour in the same species, and in individuals of the same age, they arrived at completely different interpretations of what the animals were doing. Symons claimed the function of play fighting is to practice and perfect skills needed for predator avoidance and fighting. He noted that the animals aggressively throw each other off balance by pushing, pulling, grasping and grappling, and that partners often try to maintain an ‘on-top’ or ‘behind’ position (which is more advantageous than an ‘on-bottom’ or ‘in-front’ position) during a play fight. Levy, on the other hand, reported that as animals age, there is an increase in the inhibition of rough play, a decrease in the use of speed, and a reduction in the forcefulness of the actions used during play fighting, and, in these ways, she postulated that play fighting functions as a means of developing social cohesion.

While neither of them is wrong *per se*, it is clear that they each focused on different aspects of play fighting. Although Symons went into some detail describing the structure of the play, he was more focused on the competitive nature of play and on the function that this aspect of juvenile rhesus macaque behaviour may serve. Levy focused more on the cooperative aspects of play that she observed throughout development. Both of their interpretations were not as objective as they could have been, and their conclusions were specific only to rhesus macaques, rather than to the genus. Without a descriptive framework to guide decisions as to what to measure and not to measure, what is scored can be arbitrary, making it very difficult to compare across species (Golani, 1976; Pellis, 1989). This problem is further exaggerated when the categories to be measured are selected with a pre-analysis bias as to what functions the observer believes require to be tested (Pellis, 1988). The approach taken in this thesis was to examine and describe play fighting in macaques, while taking into account both the cooperative and competitive aspects of the behaviour, but doing so without attributing functions to the behaviours to be documented. The analytical method that was used to achieve these goals was based on properties of social interactions that are dictated by the animals, not the observer.

1.8 Analysis by synthesis: Targets and tactics

As social behaviours are interactive, the behaviours of both partners must be taken into account in order to understand the structure of an interaction. For example, if animal A does X, then animal B will do Y or Z in response to A's X. That is, to generate an accurate interpretation of the behaviours observed during a social exchange, one must consider how the behaviour of each play partner influences the other, and similarly, that the behaviour of each partner influences its own subsequent behaviour (Lazar & Beckhorn, 1974). When observing juvenile play fights, one needs also to recognize the importance of looking at play from the juvenile's perspective, rather than it being seen as incomplete adult behaviour. Play activities are often inappropriately seen as exaggerated, out of sequence, incomplete or consisting of a mixture of patterns because they are viewed with respect to adult behaviour patterns, but this may misapply adult standards to individuals who are at an earlier, different stage of development (Lazar & Beckhorn, 1974). The components of juvenile play activities are not anomalous versions of adult behaviours, but rather, adult behaviour is likely a product of them (Lazar & Beckhorn, 1974).

Rather than analyzing play fights as a whole, the first goal of this thesis was to break the interactions into their component parts, which could subsequently be recombined to determine if those parts were sufficient to reconstitute the interaction as a whole (an 'analysis by synthesis', Teitelbaum & Pellis, 1992). This approach was used to identify the competitive and cooperative aspects of macaque play fighting and to determine how and why Tonkean and Japanese macaques differ in terms of the frequency with which respective behaviours are used during play fights.

Consistent with this approach, the first task of the analysis is to identify the body targets for which access is competed during play fighting. Once these targets are identified, the movements used by the attacker and the defender to gain access or avoid contact with those targets can be evaluated. Certainly, during serious fighting, most of the movements performed can be interpreted as tactics of offense and defense geared to gain or avoid access to the targets (see Blanchard & Blanchard, 1994; Geist, 1978; Pellis, 1989, 1997). When comparing species, a tactic may be present in some cases and absent in others because the animals have different targets. Alternatively, even with the same target, species may differ because they have alternative tactics. Without knowing the targets, these alternative possibilities cannot be distinguished (Geist, 1971, 1978; Pellis, 1989, 1997). In play fighting, the situation can be more complex.

First, as in serious fighting, species differences in the manoeuvres used during play fighting may arise from differences in the targets over which the animals compete (Aldis, 1975; Pellis, 1988). Second, as already alluded to in the *competition/cooperation model* described above, during play fighting, animals may perform some actions in a manner that facilitates their partner's success rather than their own (Pellis & Pellis, 1998b). That is, some actions performed during play fighting cannot be understood in terms of their value in competing for access to the target (Foroud & Pellis, 2003). Thus, the play fighting of two species may differ because of their preferences for different body targets (Pellis & Pellis, 1997a), and/or because their actions are more closely or more loosely linked to gaining or avoiding access to the target successfully (Pellis, Pellis & Reinhart, in press). Understanding which targets are being competed over during play fighting provides a non-arbitrary framework within which to identify the actions performed. Therefore, the descriptive stance taken in this thesis was to identify the targets attacked and defended during play fighting, and then use those targets to evaluate the monkeys' actions in terms of their tactics of attack and defense, and finally, to use that framework of targets and tactics to determine if there were species differences in their play fighting with regard to facilitating or inhibiting further play.

1.9 The objectives of this thesis

The main goals of this thesis were to characterize the structural organization of play fighting in juvenile Tonkean and Japanese macaques, to determine what the behavioural mechanisms were that were used by each species to facilitate the crucial, but opposing, competitive and cooperative components of social play, so as to determine what aspects of play fighting that may be common, or phylogenetically conserved, to the *Macaca* genus versus idiosyncratic to each species or troop. By using the analytical framework described above, and applying it to a number of different Tonkean and Japanese macaque troops, it was possible to determine (1) if species typical patterns exist, (2) if play fighting co-varies in a manner similar to that which has been shown for other complex social behaviours in macaques (as would be predicted by the *co-variation hypothesis*), and (3) if inter-specific differences in play fighting are stronger than intra-specific variation.

This approach was taken to describe the 'style' of play fighting in both species of macaques so as (1) to identify the offensive and defensive play targets and (2) to describe the tactics of defense used to defend the play targets. Because both species have the same play and agonistic targets, it was possible to make comparisons between the content of their play interactions. Furthermore, having a basic understanding of how the movements of macaque play fighting were organized facilitated the analysis of relatively more complex aspects of macaque playful interactions, such as identifying if there were species differences in play partner preference and how an individual's behaviour may differ in dyadic *versus* polyadic interactions or when playing with same *versus* different aged partners. By using this analytical framework, not only were the important aspects of macaque play fighting identified, but also, objective measures were developed that could be applied more broadly to examine play fighting in other primate species. The findings of this thesis are potentially revolutionary in that they provide a novel way of understanding how cooperative and competitive behaviour during play fighting may be organized and modified under different social systems.

CHAPTER TWO

Targets and tactics of macaque play fighting: Matched-troop comparisons between the Tonkean macaques of Strasbourg Zoo and the Japanese macaques of Paris Zoo

2.1 Introduction

Numerous studies have shown that macaques display broad interspecific variation in patterns of social behaviour. However, it was Thierry (1985a, 1985b) who first undertook a comprehensive comparison of different macaques with respect to agonistic relationships, conflict resolution, and other dispositions. His comparative work on Tonkean, rhesus, and longtailed macaques, revealed dramatic interspecific differences in intensity of aggression, symmetry of contests, amount of appeasement behaviour, reconciliation tendency, maternal restrictiveness, and infant socialization (Thierry, 1985a, 1985b). Furthermore, as de Waal and Luttrell (1989) point out, Thierry hypothesized that there was a causal link between these variables, and that entire sets of social characteristics co-evolved, a theory that would later be introduced as the *co-variation hypothesis* (Thierry, 2004). According to the *co-variation hypothesis*, differences in macaque social style may be accounted for by interspecies differences in temperament. That is, when temperament changes, it is thought that there are sweeping effects on the species' behavioural repertoire.

Some macaque species, such as Tonkean macaques, are known to be relatively tolerant and relaxed in their social relationships, and so have been classified as having an egalitarian social style. Conversely, other species of macaques, such as Japanese macaques, are known to be more dominance-oriented, nepotistic, and are thus classified as having a despotic social style. When the majority of members of a given social group share the same modal tendencies (i.e., they typically behave in similar ways), this creates a social style at the level of the group (Capitanio, 2004). The differences in behavioural tendencies reported for macaques have been recognized within the context of adult social interactions, and therefore, the social styles that have been attributed to each species have been based on the relationships and behaviour patterns of adults. However, little is known about the behavioural tendencies of juvenile-aged macaques.

Fortunately, play fighting is a complex social behaviour that is commonly observed in primates (Pellis & Iwaniuk, 2000; Pellis & Pellis, 1997a), and particularly in juveniles (Fagen, 1993), making this an ideal social context within which to test whether or not the behaviour of juvenile macaques is shaped by, and representative of, their species' social style. Studies that have looked at play fighting in other primate species have suggested that play interactions can be affected by the behaviour (i.e., the social tendencies) of other group members. For example, Flack, Jeanotte, and de Waal (2004) for chimpanzees and Owens (1975) for baboons, have shown that juveniles learn to modify the roughness of their playful interactions when playing with younger partners. These modifications, however, were more common when the interactions took place in close proximity to the mothers of the younger play partners or near adult males, because when play fights became too aggressive or made a disturbance within the group, individuals were commonly punished. These studies suggest that juvenile chimpanzees and baboons modify their styles of play so as to accommodate and compliment the modal dispositions of adults, and ultimately, to avoid the risk of aggressive interventions. Perhaps, if chimpanzee and baboon mothers were more tolerant, and adult males were less aggressive (i.e., if the environment afforded to juveniles was less socially intimidating), then the patterns of play fighting in these species would be more rambunctious. Whatever the underlying causes, these studies show that some features of juvenile play fighting in chimpanzees and baboons appear to reflect, to some degree, the social styles of the respective species.

It is clear from the examples mentioned above that play fighting is a relatively complex social behaviour. This is because it involves elements of competition and cooperation, both of which must be balanced, so as to prevent social exchanges from breaking down (see the *competition/cooperation model* of play from Pellis, Pellis, & Reinhart, in press, described in Chapter One above). If, for example, a play fight becomes one-sided, and there are no opportunities for alternating the roles of attack and defense, then it is likely that one or both partners will lose interest, and the interaction will end. Therefore, individuals are required to devise a means for obtaining what they want from the interaction, while allowing their play partner the opportunity to do the same. Furthermore, these social negotiations must be carried out within the context of the species' social environment. One can imagine that play behaviours that would be accepted in an egalitarian social group may not be the same as those that are tolerated within the context of a more despotic social environment.

For the present study, juvenile play fighting was examined in two troops of captive macaques with contrasting social styles, using the Tonkean macaque, a relatively egalitarian species, and the Japanese macaque, a more despotic species. These troops 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 (Table 1). By making the observations in similar captive settings, interspecific comparisons could be made, while taking into account the immediate environmental conditions, and eliminating many variables that could confound the interpretation of potential differences among species. Thus, because many of the environmental variables were controlled for, it was likely that, if found, behavioural differences would reflect species-typical dispositions (de Waal & Luttrell, 1989).

The main objective of this study was to characterize the structural organization of juvenile macaque play fighting - to find out whether or not the content of play fights contained differences in elements of behaviour that would be expected, bearing in mind the social styles of Tonkean and Japanese macaques. Based on the *co-variation hypothesis*, it would be predicted that within the context of play fighting, juvenile Tonkean macaques should exhibit relatively tolerant behaviours that facilitate a cooperative style of play, whereas Japanese macaques should exhibit more agonistic behaviours, representative of a more competitive style of play. Preliminary data suggest that play fights last longer, remain gentler, and involve more body contact in Tonkean macaques when compared to Japanese macaques (Thierry, Iwaniuk, & Pellis, 2000; see

Table 1. A comparison of the captive Tonkean and Japanese macaque troops.

Species	Tonkean macaques	Japanese macaques
Geographic location	Strasbourg, France	Paris, France
Captive setting	Orangerie Zoo	Paris Zoo
Cage dimensions	$120m^2$	$300m^2$
Troop size	20	20
Number of adults	7	11
Number of juveniles	10	7
Number of infants	3	2
Season data collected	June-August	August
Time data collected	0900-1800	0900-1800

also Petit et al., 2008, for a comparison of crested macaques with Japanese macaques showing similar differences), implying that there may be species differences in play behaviour. The present study was designed to verify these qualitative impressions about Tonkean and Japanese macaque play fighting, using a method of analysis that would facilitate the examination of more robust, quantitative data.

2.2 Methods

Animals: Tonkean macaques – Orangerie Zoo: Strasbourg, France 2005

Tonkean macaques are found in the central region of the island of Sulawesi, Indonesia (Thierry, Anderson, Demaria, Desportes, & Petit, 1994). However, a group of Tonkean macaques was imported into France (the Landskron Chateau in Southern Alsace) in 1972 and the individuals were released into an area of about 2 acres, with the intention of establishing a new population from eight reproducers (Herrenschmidt, 1977). In 1978, the newly founded breeding population at the Landskron Chateau was divided into two groups, and a main study group was established at the Primate Research Centre of the Université Louis Pasteur in Strasbourg, France (Thierry et al., 1994). Since 1982, another group has been maintained at the Orangerie Zoo of Strasbourg, and this group was used for the present study. The group was housed in a 120m^2 outdoor enclosure that was connected to a 13m^2 indoor shelter. The walls of the outdoor portion of the enclosure were 5m high and the indoor portion, which was cleaned in the morning, 2 times per week, had 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, 4 adult females, 6 juvenile males, 4 juvenile females, and 3 infant females. Ten individuals, between 2 and 5 years old, were included in the study. (For more detailed troop information, refer to Appendix 1).

Observation protocol

I observed this troop of Tonkean macaques over a period of 3 months from June to August, 2005. After 2 weeks of observing the group, I was able to identify all group members consistently, at which time the collection of video data commenced. 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, and approximately 18h of video were obtained.

Animals: Japanese macaques – Parc Zoologique de Paris: Paris, France 1997

In 1985, 10 Japanese macaques (3 males, 7 females) were imported from Nagatoro Monkey Park (Japan), and a captive troop was established at the Parc Zoologique de Paris in Paris, France. The group that was filmed for this study was housed in a 300m^2 outdoor enclosure that was connected to a 20m^2 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, 6 adult females, 3 juvenile males, 4 juvenile females, 1 infant male, and 1 infant female. Eight individuals, between 1.25 and 3 years old, were included in the study. (For more detailed troop information, refer to Appendix 2).

Observation protocol

This troop of Japanese macaques was filmed by Sergio and Vivien Pellis, 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). The animals were filmed only in the outdoor enclosure, and approximately 7h of video were obtained during 30h of observation. Due to lack of time to become familiarized with the troop, the individuals' identities were not recorded at the time of filming. Rather, after the videos were dubbed (see below), a copy was sent to Claude-Anne Gauthier, who was, at the time, the primate curator at the Paris Zoo, who then identified each of the monkeys engaged in the time-coded play fights. The transcripts containing the identity of the animals were then used for subsequent analysis (see below).

Behavioural measures for play fighting

After the video data 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. 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). Prior to the formal scoring, about 30 interactions of 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, 1997a). Nonetheless, it should be the case that 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 make sure that the cross-species comparisons revealed true species biases, rather than byproducts of sampling error (Pellis & Pellis, 1997a).

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 was clearly visible, (3) at least one bite was delivered or an obvious bite was attempted during the interaction, (4) all participants could be identified, (5) no adult participation occurred during the play fight, and (6) the interaction did 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, 1997a): (1) Head/Face (H/F), (2) Neck/Shoulder/Upper Arm (N/S/UA), upper arm being above the elbow, (3) Body (B), including dorsal, ventral and lateral areas, (4) Lower Arm/Hand (LA/H), 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. Previous analyses have revealed that the targeting of retaliatory, or defensive, bites can differ from the targeting of initiating, or offensive, bites (Pellis & Pellis, 1997a), therefore, the offensive and defensive bites were recorded separately. The number of offensive and defensive bites directed to these regions of the body was totalled, and offensive and defensive bite distributions were calculated. A bite was counted not only when actual mouth-to-body contact was made, but also in cases in which there may not have been contact, but it was clear that the attacker had lunged, open mouthed, at a specific target on its opponent's body.

In addition to scoring playful bites, the duration, the initiator and the terminator of each play fight was also noted. A play fight was considered to begin when the animals were no more than 2m apart, and at least one of the participants was advancing toward the other. For example, a play fight could begin with a play chase, or with one individual approaching a stationary individual. The first animal to deliver a bite to its opponent or lunged with an open mouth to bite its opponent was considered to be 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.

One limitation of scoring play fights that at the outset have 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 specific 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 the age, the sex or the species differences involve preferences for different attacking orientations, then by analysing all the available play fight examples, differences in targets could be artificially produced. Therefore, a subset of play fights was extracted for subsequent analyses in which the animals in each encounter began in the same orientation; the context used involved a face-to-face (F-to-F) orientation.

In these play fights, the play partners were facing each other head-on and were in either a sitting, standing, or rearing position (i.e., they were not laying down). In this situation, as both play partners are vertically oriented, they are relatively equal in terms of their opportunities to make offensive playful attacks and defensive movements in response to attacks. For the F-to-F analysis, the specific context could be achieved 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. A total of 252 and 179 F-to-F contexts, for Tonkean and Japanese macaques, respectively, were scored and the number of offensive and defensive bites directed to the various regions of the body were totalled so that offensive and defensive bite distributions could be calculated. When play partners moved out of the F-to-F context (e.g., one or both partners were in a horizontal position, or were standing side by side), the scoring of bites ceased. Consequently, the initiator, but not the terminator of each F-to-F interaction, was recorded following the criterion used for the play fights in general.

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 manoeuvres used, the animals are in a standardized configuration. For example, if defensive manoeuvres 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, in the case of species A, most of the defenses scored arise from a bite to the rump from a rear orientation, whereas most of the defenses from species B arise from bites to the shoulder from a frontal orientation. What is causing the species difference in defensive tactics? 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; Pellis, Pellis, Pierce & Dewsbury, 1992). Therefore, to determine what the macaques do behaviourally, in response to playful bites from their partners, the defensive responses used in the F-to-F contexts when a bite was delivered to the modal target, were analysed. That is, when individuals were bitten on the modal offensive play target, how did they respond?

Again, based on the 30 interactions for each species that were analysed qualitatively, four distinct behavioural options were identified, and then scored quantitatively for 166 and 85 interactions, for Tonkean and Japanese macaques, respectively. These options were: (1) ignoring the attacker (i.e., no response), (2) evading from the attacker, (3) making a movement to break bite contact from the attacker, and (4) combinations of biting the attacker, then moving, or *vice versa*. Once the most common defensive tactics were identified, the responses were broken down into more specific movement categories. These will be described in the Results.

The main objectives of this type of analysis (i.e., identifying the targets and tactics of play fighting, see Pellis, 1989, 1997) are to deconstruct the sequences of movements that take place between individuals, and to identify the species-specific components of play fighting. Subsequently, when the individualized components of the play fight are put back together, integrated patterns of movements are identified and we end up with a more thorough understanding of relatively complex, and dynamic social exchanges (Pellis & Pellis, 1987, 1988, 1998b). In other words, the data extracted from these analyses, when considered in combination, provide the elements necessary to generate a detailed description of play fighting in each species, and more importantly, this particular method of analysis (i.e., analysis by synthesis, see Teitelbaum & Pellis, 1992) makes it possible for the observer to decipher what the animals actually *do* during play fights, and how each member of the interacting pair contributes to the overall structure of the interaction (Pellis, 1989; Pellis, Pellis, Pierce & Dewsbury, 1992).

Statistical analyses

Because the data were collected in a spontaneous, opportunistic manner, and there were no *a priori* assumptions made with regard to the distributions for the behaviours that were measured, it was decided that non-parametric statistical tests would be the most appropriate (as opposed to parametric statistical tests) for analysing the data. In some instances I was working with relatively small sample sizes (e.g., *n* of 7 or 8), and because I was going to be identifying and describing patterns of behaviour that had not been recognized previously, it was imperative to employ robust methods of statistical analysis to be more assured that the patterns that were identified were not showing up by chance. By examining similar data sets, but in different ways, using multiple non-parametric tests, there were many opportunities to potentially falsify the patterns of behaviour observed. For some analyses, pooled troop data were examined, however, when possible, post-hoc analyses (e.g., Wilcoxon matched-pairs-signed-ranks and Mann-Whitney U tests) using individualized data were performed to test whether or not the reported troop patterns held.

Targets: Bite distributions

The 252 and 179 F-to-F contexts that were scored involved 10 juvenile Tonkean and 8 juvenile Japanese macaques, respectively. As mentioned previously, the number of offensive and defensive bites directed to the various regions of the body was totalled 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. The outcomes of these analyses are reported in the Results and the data are represented in subsequent figures to illustrate species-specific patterns in offensive and defensive play targets that were identified in the F-to-F context. However, it can be argued that pooled data may not be representative of true behaviour patterns because the contributions from each individual to the overall data set may not be equal. For example, if one particular individual participated in a large proportion of the play fights that were sampled, then the contribution of that individual to the data set may be over-represented, potentially creating a bias in the patterns reported for the group. Therefore, the offensive and defensive bite distributions for each species were calculated and tested in another way, to verify if the bites delivered by each species to different body areas were randomly distributed or not.

In order to perform a non-biased analysis, a sub-set of the already scored F-to-F contexts was used to calculate offensive and defensive bite distributions for individual animals. However, data could only be included for individuals for whom there were sufficient sample sizes. That is, to be included in the analyses, the individual had to have been involved in 10 interactions in the F-to-F context, and with no more than 5 out of these 10 interactions being with the same play partner. The interactions used to make up each individual's sample were therefore the first 10 recorded for that individual, 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 was found. Consequently, 8 Tonkean and 7 Japanese macaques were included in the subsequent within and between species analyses for bite distributions. To analyse these data, a Friedman ranked-scores analysis of variance was used. For cases where the analysis of variance indicated a significant deviation from random, Wilcoxon matched-pairs-signed-ranks tests were used for follow-up tests. Similarly, for cross species comparisons of specific bite locations, Mann-Whitney U tests were used (Siegel, 1956).

Tactics: Defensive responses

The 166 and 85 defensive responses that were scored involved 10 juvenile Tonkean and 8 juvenile Japanese macaques, respectively. As mentioned previously, once the most common defensive tactics had been identified, the responses were broken down into specific movement categories, and response distributions were calculated for each species. 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. The outcomes of these analyses are reported in the Results and are represented in one of the figures to illustrate the defensive response patterns that were typical for each species. Subsequently, for the reasons mentioned above, non-parametric statistical methods were used to verify if the defensive response distributions reported for each species were random or not.

In order to perform the non-parametric analyses, a sub-set of the already scored defensive responses made in F-to-F contexts was used to calculate defensive response distributions for individual animals. To be included in the analyses, the individual had to have had a minimum of 5 previously documented 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 coming from 8 Tonkean macaques, and 60 responses coming from 7 Japanese macaques, were included in the subsequent within and between species analyses for defensive response distributions.

Play fight durations

When the playful targets and defensive tactics were scored for 200 play fights for each species, play fight durations were also recorded. Thus, contributions to the pooled play fight duration data came from 10 juvenile Tonkean and 8 juvenile Japanese macaques, respectively. The mean durations and 95% confidence intervals for dyadic and polyadic play fights were calculated for each species, and these results were reported. However, because of the potential for reporting species patterns that may be biased by the contributions of one or a few individuals, additional non-parametric statistical methods were performed on individualized data to verify the play duration patterns that were reported for each species.

Because the role of an individual differs between dyadic and polyadic interactions, a different analytical approach was used for each. Mean dyadic play fight durations were calculated for each individual. The durations used to make up each individual's sample were the first 14 recorded for that individual, unless a subsequent interaction had to be included to avoid more than 7 out of the 14 interactions being with the same play partner. A Mann-Whitney U test was then applied to the individualized data to evaluate any species difference in dyadic play fight durations.

Unlike the dyadic play fight durations, however, individual participant scores could not be obtained for polyadic play fight durations, as these involved a shifting number of participants. Within the sample of 200 play fights that was scored for Japanese macaques, there were only 18 polyadic play fights that could be used for analysis. Therefore, the first 18 (out of a possible 62) Tonkean macaque polyadic play fights that were recorded were used so that an equal number of play fights from each species could be compared. Each species' sample of 18 polyadic play fights was then placed into 'bins' for non-parametric analysis. For example, the first 6 polyadic play fight durations for Tonkean macaques were placed into bin #1, the next 6 durations were placed into bin #2, and the final 6 durations into bin #3, the idea being that each bin can be thought of as a random sample. A Kruskal-Wallis one-way analysis of variance was then used to test, within species, whether there were significant differences between bins. In turn, in order to compare dyadic with polyadic interactions, a sample of the first 18 dyadic play fight durations recorded for each species was collected, and as with the polyadic play durations, these dyadic values were placed into bins. Again, a Kruskal-Wallis one-way analysis of variance test was used to compare the 3 bins, within each species.

For cases where the between bin comparisons showed no differences, Mann-Whitney U tests were used to make between species comparisons of the total ‘binned’ data for dyadic and polyadic play fight durations, to test whether or not there were significant between species differences in play fight durations. Finally, Mann-Whitney U tests were used to verify whether or not there were differences between the dyadic and polyadic play fight durations within each species.

2.3 Results

The results are presented in a sequence that follows the path of movements that characterize a dyadic play fight, specifically in the standardized F-to-F context. It is important to note that the movements made during macaque play fights are not rigidly stereotyped. However, to reiterate, the advantage of examining the dynamics of play fights in the F-to-F orientation is that it provides an element of control over the context and ensures that the interactions being compared within and between species are indeed comparable.

The dynamic nature of the interactions and the primary body target around which these competitive interactions were organized is illustrated in Figure 2.1, which shows a

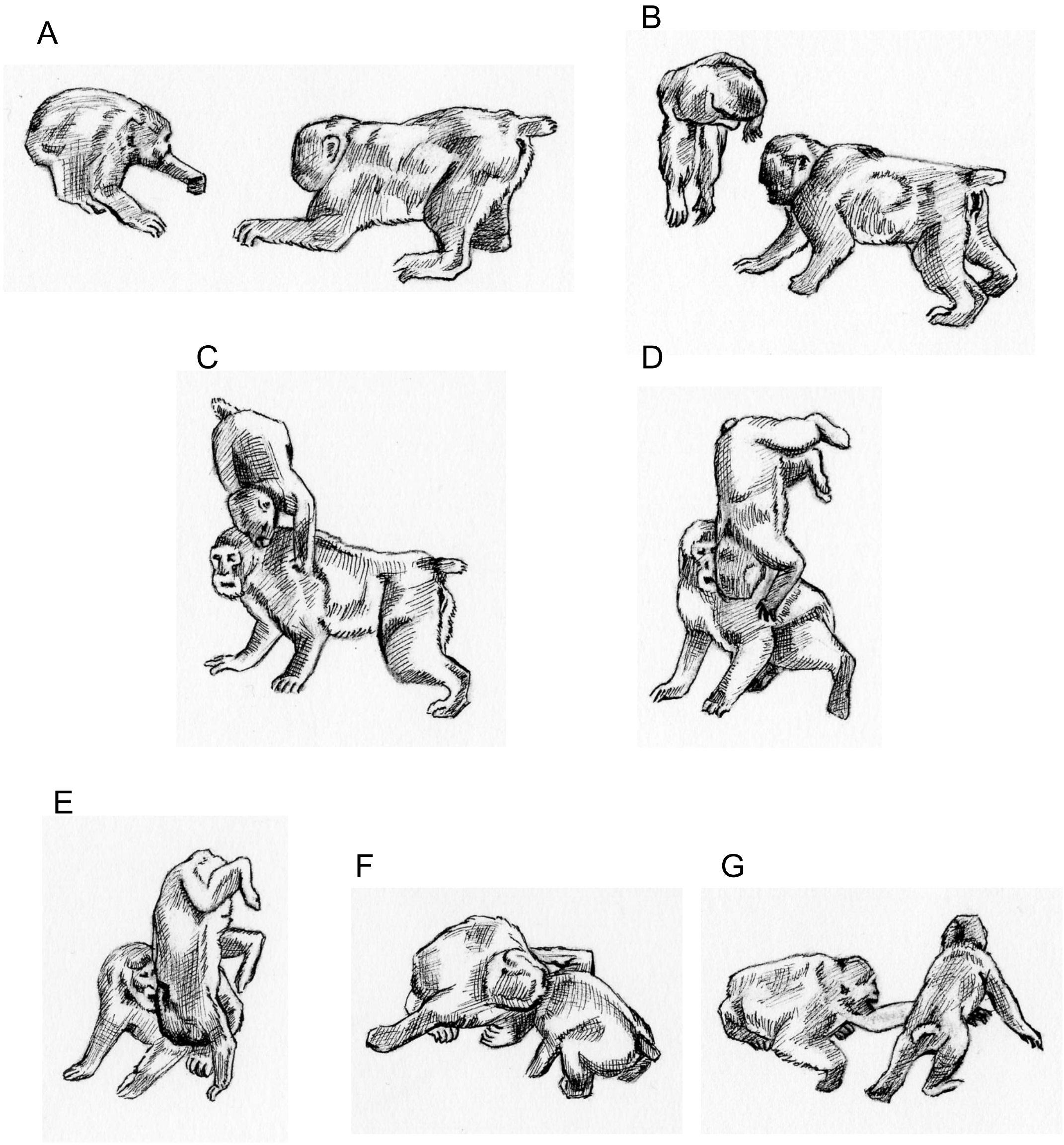


Figure 2.1 A sequence of play fighting by two juvenile Japanese macaques shows a complete encounter starting from F-to-F orientation. Note that both the attacker and defender are targeting the neck/shoulder/upper arm (N/S/UA) region of the body. The illustrations were drawn from videotaped records of the Wakasa B troop that will be described in Chapter Three. See text for play fight description.

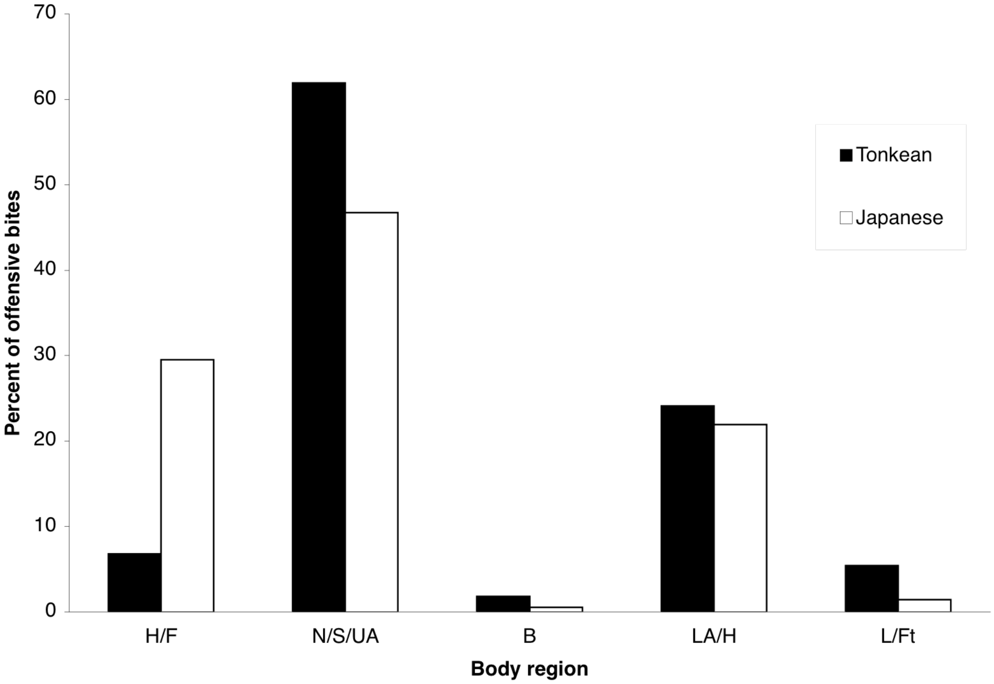
short play sequence in two Japanese macaques, starting from the F-to-F orientation (A). The smaller individual on the left makes a rather acrobatic attack by jumping up into the air and twisting his body (B), while orienting to the play target of the defender on the right (C). As the attacker moves through the air, the defender rotates to face the attacker and delivers a retaliatory/defensive bite to the neck (C – F). As the attacker lands on the ground, the defender continues to bite the back of the neck (F) until the attacker turns away and evades the interaction (G). The play target for macaques is the neck/shoulder/upper arm (N/S/UA) region of the body, and it can be seen that both the attacker and defender adjust their movements so that they are able to contact and bite this area of the body in a playful manner. The quantitative data presented below were used to verify, as predicted, that the N/S/UA was the modal target.

Targets: Bite distributions

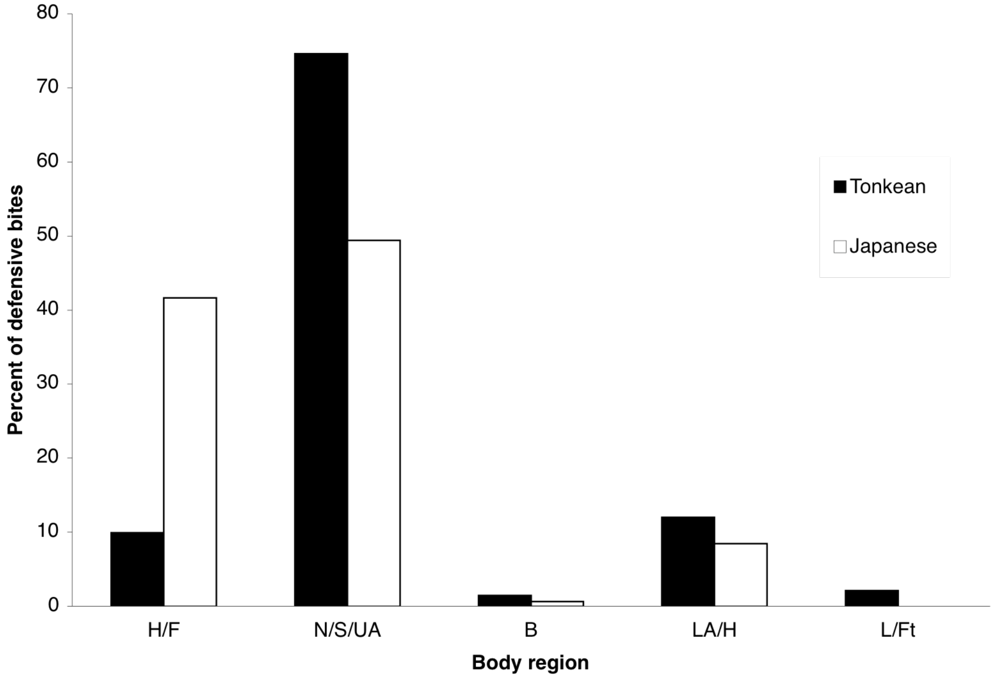
The bite distribution analyses showed that the modal offensive and defensive play target for both Tonkean and Japanese macaques was the neck/shoulder/upper arm (N/S/UA) region of the body, and this pattern was confirmed using multiple statistical tests. Japanese macaques were also found to exhibit a relatively high proportion of defensive bites directed to the head/face (H/F) region, which is known to be an agonistic body target for macaques. The potential importance of species-specific variation on the patterns of playful biting will be discussed below.

A play fight begins when one individual attacks another individual with a playful bite that is usually directed at a specific body target. The pooled F-to-F play fight data for each troop clearly show that the modal offensive play target for both species is the N/S/UA region of the body (Figure 2.2A). Chi-square analyses for each species showed that the distributions of offensive bites delivered to the different regions of the body were not random (Tonkean: $X^2 = 345.7$, $df = 4$, $p < 0.001$; Japanese: $X^2 = 160.8$, $df = 4$, $p < 0.001$). 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 for offensive bites (Tonkean: $X_r^2 = 159.4$, $df = 4$, $p < 0.001$; Japanese: $X_r^2 = 140.4$, $df = 4$, $p < 0.001$). Follow-up analyses using Wilcoxon matched-pairs-signed-ranks tests showed that, in both species, the N/S/UA was bitten significantly more than all other regions of the body (Tonkean: $T\ (8) = 0$, $p < 0.005$; Japanese: $T\ (7) = 2$, $p < 0.05$). 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 each of the different body regions was bitten. That is, Tonkean and Japanese macaques do not differ with regard to offensive targets.

Play fighting involves both offensive and defensive components, and although there were no species differences in offensive targets, for the defensive aspects of their playful interactions, Tonkean and Japanese macaques seem to differ. Again, the pooled F-to-F play fight data for each troop show that the modal defensive play target for both species is the N/S/UA region of the body (Figure 2.2B), further reinforcing the view that the



A. Offensive bite distribution



B. Defensive bite distribution

Figure 2.2 (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).

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: $X^2 = 271.1$, $df = 4$, $p < 0.001$; Japanese: $X^2 = 172.0$, $df = 4$, $p < 0.001$). 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 each species differed from a random distribution for defensive bites (Tonkean: $X_r^2 = 154.7$, $df = 4$, $p < 0.001$; Japanese: $X_r^2 = 139.7$, $df = 4$, $p < 0.001$). For defensive bites, within species Wilcoxon matched-pairs-signed-ranks tests showed that in Tonkean macaques, the N/S/UA was bitten significantly more than all other regions of the body (T (7) = 0, $p < 0.01$). For Japanese macaques, both the N/S/UA was bitten significantly more than other regions of the body, (T (7) = 0, $p < 0.05$), and the H/F was bitten significantly more than other regions of the body (T (7) = 1, $p < 0.05$); however, the N/S/UA and H/F were not different from each other ($p > 0.05$).

Between species comparisons of the defensive bite distributions 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. Even though Wilcoxon matched-pairs-signed-ranks tests indicated that there were no significant differences ($p > 0.05$) within species, when comparing the number of offensive and defensive bites directed to the same body target (e.g., the percentage of offensive *versus* defensive bites directed to the N/S/UA, within Tonkean macaques), if larger samples size were tested, it would likely be shown that Tonkean macaques bite the N/S/UA more during defense than offense, and that Japanese macaques bite the H/F more during defense than offense. Indeed, the species differences in defensive bite distribution patterns show that Japanese macaques are more likely to deviate from the play target, and that they shift to biting a more agonistic body target, the face (Blanchard, Blanchard, Pank, & Fellows, 1985; Blanchard, Blanchard, Takahashi, & Kelley, 1977; Pellis, 1988, 1993; Pellis & Pellis, 1987), thus suggesting that their particular style of play fighting is relatively more competitive than that of Tonkean macaques. In contrast, Tonkean macaques exhibit a more cooperative style of play fighting by exaggerating the proportion of defensive bites directed toward the play target, which presumably would facilitate prolonged, amicable contact between play partners.

Even though the overall targeting patterns for Tonkean and Japanese macaque play fighting are similar, there is variation in the pattern, particularly for the defensive component of play fights. As will become apparent, the defensive bite distributions provide valuable information about the defensive aspects of macaque play fighting. Once the play target (i.e., the N/S/UA) has been identified, a more thorough and complete description of defense can be generated by examining the defensive tactics or movements the animals make in response to receiving a bite on their play target.

Tactics: Defensive responses

In most instances, the animals respond to N/S/UA bites in a manner that enable 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. These facing defensive responses were grouped into the following categories: (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, staying 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, staying eye level with the attacker, and pushing the attacker away or pulling itself 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 2.3 illustrates three of the tactics (HR, VSELB, VSELPA) that enable the defender to move away from a N/S/UA bite delivered by the attacker.

For both species, the pooled defensive response data showed that the modal response in receiving N/S/UA bites is VSELB (Figure 2.4). Chi-square analyses for each species showed that the distributions of defensive responses were not random (Tonkean: X^2 =

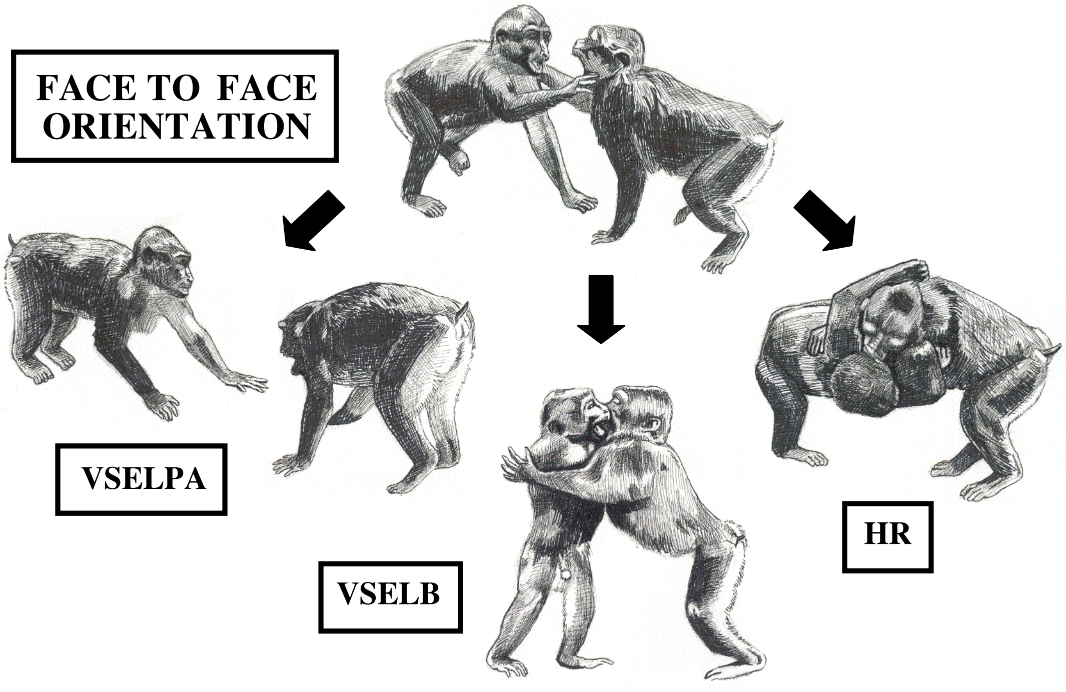


Figure 2.3 Defensive responses of macaques during play fighting in a F-to-F orientation. VSELPA – vertical, stay eye level, push/pull away; VSELB – vertical, stay eye level, bite; HR – horizontal, roll to back/side. The defensive postures represented in the figure were drawn from videotaped records of juvenile Tonkean macaques from the PRC Park 2006 troop that will be described in Chapter Three.

45.3, $df = 4$, $p < 0.001$; Japanese: $X^2 = 111.5$, $df = 4$, $p < 0.001$). 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: $X_r^2 = 146.1$, $df = 4$, $p < 0.001$; Japanese: $X_r^2 = 138.3$, $df = 4$, $p < 0.001$). Wilcoxon matched-pairs-signed-ranks tests were used for within species pair-wise comparisons. For Tonkean macaques, the only significant difference was between VSELB and HR (T (7) = 0, $p < 0.05$), with VSELB being used significantly more often than HR. For Japanese macaques, the VSELB response was significantly more frequent than VSELPA (T (6) = 0, $p < 0.05$) and HR (T (6) = 0, $p < 0.05$). For the other pair-wise within species comparisons, insufficient sample sizes (due to an excess of tied scores) prevented statistical evaluation. Nonetheless, Chi-square analyses of the pooled scores for both species (Figure 2.4) showed that VSELB differs from all other defensive tactics (Tonkean: $X^2 = 15.8$, $df = 1$, $p < 0.001$; Japanese: $X^2 = 50.4$, $df = 1$, $p < 0.001$).

Similar to the bite distributions, Tonkean and Japanese macaques share the same modal tactic of defense (i.e., VSELB). However, comparisons using Mann-Whitney U tests indicated that there were significant between species differences for the frequency with which different defensive responses were used. Tonkean macaques use the following tactics more frequently than Japanese macaques: HR (U (7, 8) = 4, $p < 0.01$),

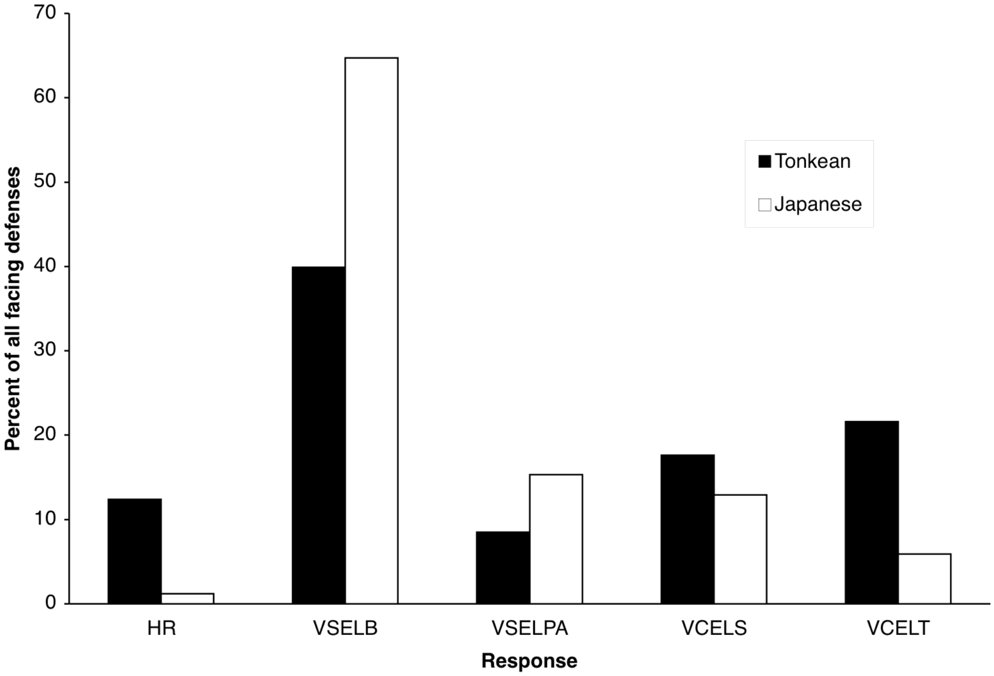


Figure 2.4 Distribution of facing defensive responses to N/S/UA bites delivered in F-to-F contexts. Responses: HR – horizontal, roll to back/side; VSELB – vertical, stay eye level, bite; VSELPA – vertical, stay eye level, push/pull away; VCELS – vertical, change eye level, move downward ('become shorter'); VCELT – vertical, change eye level, move upward ('become taller')

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 stay eye level with their attackers, rather than dropping their heads to 'become shorter' or rearing up to 'become taller' than their play partners. Compared to HR, VCELS, and VCELT, the VSELB and VSELPA tactics of defense allow individuals to execute a wider range of subsequent movements (and bites) effectively in response to the behaviour of their attacking opponents.

It was mentioned in the Methods that defensive responses could include movements that break bite contact, but also ones that have a retaliatory/defensive bite associated with them. Mann-Whitney U tests applied to the individualized data on the percentages of defensive responses that had an associated bite, revealed that Japanese macaques were significantly more likely to deliver a retaliatory bite when making their response to a N/S/UA bite in the F-to-F context (*U* (7, 8) = 7.5, $p < 0.01$). It should also be noted that for the pooled data, 85 defensive responses were scored for Japanese macaques, and in every case, they responded to the attacker (as opposed to ignoring the attacker) and always used a facing defense. In contrast, 166 defensive responses were scored for the Tonkean macaques, 3 of which elicited no response (i.e., the attack was ignored), and there were 10 instances for which non-facing responses (i.e., rotating the body to turn away from the attacker) were used. Therefore, approximately 8% of the Tonkean macaques' responses to N/S/UA bites were either non-responding or non-facing reactions, whereas Japanese macaques executed facing responses 100% of the time. These species differences in behaviour, however subtle, lend further support to the suggestion that Japanese macaques appear to be more competitive in their style of play fighting than Tonkean macaques.

Play partners and play fight durations

Overall, it was found that in both dyadic and polyadic play contexts, the duration of play fights was longer for Tonkean macaques as compared to Japanese macaques. Also, relative to Japanese macaques, Tonkean macaques were shown to engage in a greater proportion of polyadic play fights that involved greater numbers of play partners.

When samples of Tonkean and Japanese macaque play fights were divided into dyadic and polyadic interactions, the proportions with which each species engaged in either type of interaction differed. In a sample of 200 play fights, 63.5% of Tonkean macaque play fights were dyadic, whereas in a sample of 408 Japanese macaque play fights, 88.9% of the interactions were dyadic (Figure 2.5). Because there were only 18 triadic (i.e., 3 play partners) interactions identified within the first 200 play fights scored for Japanese macaques, the sample size for this part of the analysis was doubled, so as to ensure that if polyadic interactions occurred, especially those involving more than 3 individuals they could then be documented. However, despite the enlarged sample size, play fights

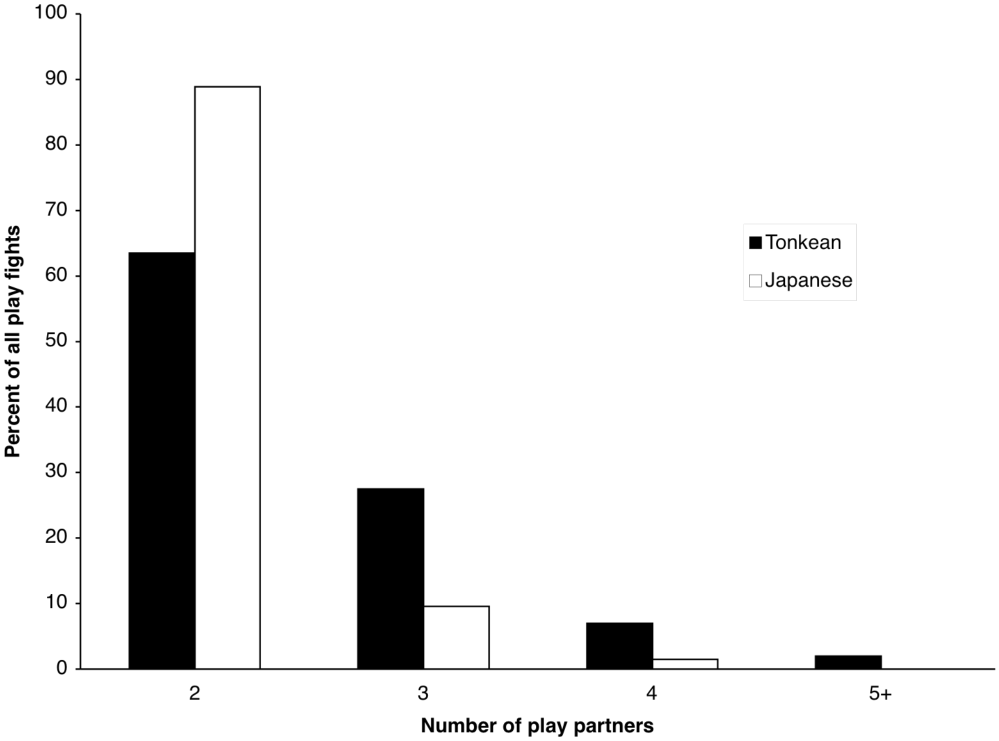


Figure 2.5 Percentage of dyadic and polyadic play fights and number of play partners in Tonkean and Japanese macaques.

involving more than 2 or 3 individuals are rare for Japanese macaques, and this is consistent with earlier studies (e.g., Koyama, 1985; Petit et al., 2008).

In contrast, Tonkean macaques engage in play fights with 3, 4, and even 5+ partners simultaneously, relatively often. Having observed these play fights, I remember masses of black-haired bodies piled on top of one another, and it was difficult to distinguish which arms and legs belonged to which individuals; they remained clumped together, sometimes for minutes, delivering playful bites. However, as previously mentioned, Japanese macaques rarely engage in polyadic play fights, and when they do, they are often very brief and involve only three individuals (Petit et al., 2008). In most cases, the polyadic interactions among Japanese macaques are relatively transient compared to that of Tonkean macaques. That is, 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. Tonkean macaque polyadic play fights appear to be more laid back and prolonged, whereas the polyadic play fights of Japanese macaques seem to be more controlled and rapid in their appearance.

Although the descriptions of polyadic play fights mentioned in this section are anecdotal, statistical evidence for play fight durations provides some support for the contrasting impressions of each species' play style. The pooled play fight duration data show that Tonkean macaques have longer dyadic (Mean ± 95% confidence intervals: Tonkean ($N = 138$): 22.4s ± 2.5; Japanese ($N = 182$): 11.6s ± 1.8), and polyadic (Tonkean ($N = 62$): 41.2s ± 6.7; Japanese ($N = 18$): 16.8s ± 3.5) play fights than Japanese macaques

(Figure 2.6). 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, $p < 0.001$).

As mentioned in the Methods, a different analysis was needed for the polyadic encounters. Samples of 18 dyadic and 18 polyadic play fight durations were obtained and placed into bins, so that further within and between species comparisons could be made. Kruskal-Wallis one-way analysis of variance tests showed that there were no within species differences ($p > 0.05$) between the three dyadic bins and between the three polyadic bins that were compiled for each species. Subsequent Mann-Whitney U tests showed that Tonkean macaques have longer dyadic (U (18, 18) = 89.5, $p < 0.05$) and polyadic (U (18, 18) = 45.5, $p < 0.001$) play fights than Japanese macaques. Within species Mann-Whitney U tests showed that dyadic play fights are significantly longer than polyadic 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 ($p > 0.05$).

Indeed, the species differences in play fight durations compliment the targets and tactics data reported above. That is, the more competitive style of Japanese macaques seems to result in shorter play fights than that exhibited by the more cooperative Tonkean macaques. Furthermore, the more cooperative style in Tonkean macaques seems to permit them to exaggerate the cooperativeness in polyadic encounters and so results in greatly prolonged interactions.

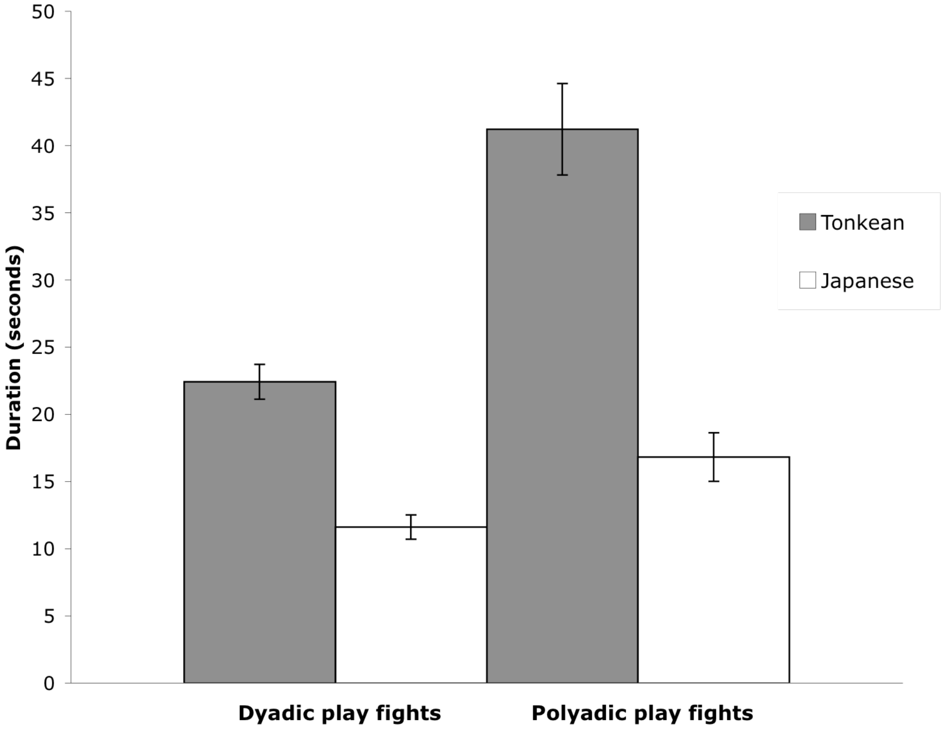


Figure 2.6 Play fight durations of juvenile Tonkean and Japanese macaques (values shown are means ± 95% confidence intervals).

2.4 Discussion

Finding that the N/S/UA region of the body was the modal play target for Tonkean and Japanese macaques is in accordance with what would be expected, based on previous research in other closely related species of non-human primates, especially Old World monkeys. That is, for several different species, the shoulder area has been identified as the region of the body that is commonly targeted during play fighting. Symons (1978) reported that during aggressive play, rhesus macaque bites were generally aimed at the neck or ventral surface of the body. Pellis and Pellis (1997a) similarly showed that a considerable proportion of the initiating play bites delivered during play fights in patas monkeys were directed to the upper arms and shoulders and the sides of the neck and cheeks. Therefore, given the data presented here and the broader evidence from comparative studies, it would seem highly likely that the N/S/UA is the preferred play target for Tonkean and Japanese macaques.

In terms of defensive or retaliatory bites, similar to the offensive bite distribution, Tonkean macaques focus on the N/S/UA as the primary target during play fighting. Although the N/S/UA is also the modal defensive target for Japanese macaques, relative to Tonkean macaques, they tend to deviate from the N/S/UA, in favour of contacting the H/F region. Detailed studies of agonistic interactions in rodents (Blanchard et al., 1977, 1985; Pellis, 1997; Pellis & Pellis, 1988, 1992) and play fighting in rodents (Pellis & Pellis, 1987, 1998a) suggest that bites to the side of the face are defensive, in that they block further attack by the opponent. Shifting to a more agonistic target in the context of defense is not uncommon in primate play fighting. In a comparative study of three different primate species (ring-tailed lemurs, spider monkeys, patas monkeys), Pellis and Pellis (1997a) showed that for all species, retaliatory bites were directed primarily to the head and neck, especially to the sides of the face.

The targeting of defensive bites to specific body areas during play fighting can illustrate important between species differences in social behaviour (Pellis & Pellis, 1998a). During a play fight, the attacker launches an attack at the play target and the defender can then respond by delivering a counterattack (i.e., defensive bite) to the opponent's play target. By contacting the play target reciprocally, the defender facilitates the continuation of the play fight. However, when the defender's counterattack is directed to a more species-typical agonistic target, this is thought to be indicative of an increasing degree of agonism in the play fight. Thus, when an individual delivers a defensive bite to an agonistic body target, there is an increased likelihood that the interaction between play partners will end (Pellis & Pellis, 1998a). In their comparison of 4 different species of rodents, Pellis & Pellis (1998a) found that there were species differences both in the likelihood of launching counterattacks and whether or not those counterattacks were directed to amicable (i.e., play targets) or agonistic targets (i.e., defensive targets that are contacted during serious fighting). Their interpretation was that playful counterattacks may be positively associated with higher tendencies to play and that play fighting may be more congenial in species that tend not to deviate from amicable play targets.

If Pellis and Pellis (1998a) are correct, then the species differences found in defensive bite distributions for Tonkean and Japanese macaques may indicate that play fighting in the former is more amicable (i.e., cooperative) than in the latter macaque species. Close to 75% of the defensive bites delivered by Tonkean macaques were to the play target, and indeed, Tonkeans were also shown to have longer dyadic play fights, as well as longer polyadic play fights and a greater proportion of them than Japanese macaques. These data suggest that the cooperative behaviours of Tonkean macaques may create accommodating social environments that are conducive to prolonged play. In contrast, for Japanese macaques, the defensive bites delivered to the play target were not significantly different (i.e., more frequent) from the overall proportion of bites directed to the agonistic H/F target. Japanese macaques also have shorter play fights and rarely engage in polyadic interactions. Also, when they do engage in polyadic interactions, they are no longer in duration than the dyadic interactions. One interpretation is that the more volatile, despotic temperament of Japanese macaques is reflected in a more competitive pattern of defensive bites, which consequently reduces the duration of their play fights and the number of partners with whom they play.

With regard to the tactics of defense used by Tonkean and Japanese macaques, again, the two species share the same modal defensive response. To defend against bites received on the play target, both species use the VSELB tactic of defense, which allows the defender to maintain an upright body orientation while facing the attacker. The ‘facing’ component of defensive responses seems to be a feature of play fighting that is shared by several primate species. For example, it has been shown that in patas monkeys, the attacker and defender both make movements to maintain F-to-F orientations during play fights (Pellis & Pellis, 1997a). Similarly, in Symons’ study of rhesus macaques

(1978), he reported several tactics that were used to defend against neck bites, all of which were possible because of a tendency for the defender to face the attacker. These include: (1) the defender grabs the back of the biter's head and pull its face away, (2) the defender pushes the biter's face away with its hand or foot, and (3) the defender breaks or avoids bite contact by hunching its shoulders and lowering its chin. Indeed, tactics 1 and 2 are similar to the VSELPA (stay vertical, eye level, and push the attacker/pull yourself away) tactic identified in this study, and tactic number 3 appears similar to VCELS (become shorter). Thus, it can be suggested that there are movement (i.e., response) patterns that can be identified within the context of play fighting, that are typical of the *Macaca* genus.

However, in the present study, species differences in the use of defensive responses were found. Tonkean macaques are more likely than Japanese macaques to use HR, VCELS, and VCELT, tactics that make the defender either shorter or taller relative to one's play partner. In these positions, the play target is not as well protected when compared to vertical responses that keep the defender at eye level with the attacker (i.e., VSELB, VSELPA), which are typical responses of Japanese macaques. It can be argued that defensive tactics that maintain head-on, eye-to-eye orientations with the attacker keep the defender in a less vulnerable position for receiving another bite, and can provide a better opportunity for the defender to make further defensive movements or deliver bites (i.e., counterattacks). This was found to be the case for Japanese macaques, that were shown to be significantly more likely to deliver a defensive or retaliatory bite in conjunction with the actual movement component of the defensive response, which again suggests that they have a higher degree of competitiveness during play fights, particularly in the defensive component of play fights.

In part, the results were as predicted. According to the *co-variation hypothesis* and the *competition/cooperation model* of play, the styles of behaviour that were exhibited by each species within the context of play fighting reflected what would be expected based on the species' social styles. That is, the egalitarian Tonkean macaques exhibit a more cooperative style of play and the despotic Japanese macaques exhibit a more competitive style of play. However, it was unexpected to find that the degree of cooperativeness and competitiveness within the offensive and defensive aspects of play fighting may differ within each species. For example, it was thought that Japanese macaques would be competitive in all aspects of their play interactions, but instead, it was found that they are relatively cooperative in the offensive component of their play fights (based on offensive bite distribution), and highly competitive in defense. However, as mentioned in Chapter One, the attack and defense components of play fighting have been shown to be dissociable at the behavioural level and are also thought to be motivationally and genetically independent (Pellis & Pellis, 1991; Reinhart et al., 2006; Reinhart et al., 2004; Siviy et al., 2003). To make sense of the results of the present study, it is important to bear in mind that play behaviour should be thought of as a mosaic - and one in which not all components necessarily change together in the same way (Pellis & Iwaniuk, 2004).

Further research may indicate that Japanese macaques do indeed exhibit some competitive tendencies during offense. Because the interactions included in this analysis were exclusive to the F-to-F context, the species were being observed from equal starting points, which was important for the reasons mentioned in the Methods. However, I would predict that if the approach angles of each species' play fights were examined (i.e., a measurement of the attacker's initial angle of approach relative to the defender's position), it would be found that Japanese macaques approach play partners from behind - the most advantageous angle for the attacker - more than Tonkean macaques. However, this analysis was not within the scope of this study.

Because macaques arose from a common ancestor, it is likely that they share the same basic 'behavioural tool-kit' (Capitanio, 2004), meaning that different species should be capable of producing the same behaviour patterns. In the context of juvenile play fighting, this suggestion seems to hold. The results from Part I of this thesis, suggest that a 'macaque-typical' pattern of play has been identified (i.e., same modal play target and same modal tactic for defending that target), but because of species differences in temperament, we see some variation on the pattern (i.e., modifications in some aspects of defense, polyadic play fight proportions, play fight durations) when comparing species from contrasting social systems. Tonkean macaques appear to have a more cooperative style of play fighting, whereas Japanese macaques appear to have a more competitive style of play fighting, but there does not seem to be a single, specific behaviour or element of play fighting, displayed by either species, that distinguishes their respective tendencies to be one way or the other.

Indeed, the subtleties, in terms of how each species is able to achieve successful play fighting (i.e., interactions involving some degree of both competition and cooperation), could only be teased out with the depth of analysis that has be used in this study. The individualized data that confirmed the patterns identified using pooled group data, provides future researchers with some confidence that when they use the 'basic measures' that were devised from this analysis (i.e., target of attack, tactics of defense, play fight duration, and proportions of polyadic play fights), even with small sample sizes, they can accurately describe species typical behaviour. Although many aspects of play behaviour were examined and described for this study, it is now clear as to which components of play fighting are genus typical, and what aspects may be species specific. In future studies of primate play, it will be important to bear in mind that there are attack and defense and cooperative and competitive aspects of behaviour involved in play fighting; each must be considered independently and as a part of the behavioural package of the species.

It should be emphasized that broad species assumptions about behaviour should not be based on data from one group (Petit et al., 2008). Although some of the observed differences reported here are probably representative of the two species, considerable intraspecific variation does exist (de Waal & Luttrell, 1989), and thus, a more comprehensive program of comparative studies is needed. As de Waal and Luttrell have pointed out, (1989), the documentation of social dispositions of all macaque species under both captive and natural conditions is more than a single research team can accomplish. In view of considerable intraspecific variation, even under the same conditions, comparisons between different species should ideally involve several groups per species, per type of environment. Chapter Three of this thesis was designed to examine play fighting in additional troops of Tonkean and Japanese macaques to (1) verify whether or not species typical patterns of play fighting have been identified, and (2) identify some of the factors that may contribute to within and between species variation in patterns of play.

CHAPTER THREE

Comparisons of juvenile play fighting between multiple troops of Tonkean and Japanese macaques: Confirming species-specific patterns of play fighting and accounting for variability

3.1 Introduction

As was mentioned in the Discussion of Chapter Two, it is important to recognize that broad conclusions about a species' behaviour based on data from a single group of animals may be inappropriate (Petit et al., 2008). Thus, it is important to study several different groups of the same species to confirm whether or not there are species typical patterns in behaviour, and to determine what aspects of the behaviour may be susceptible to intraspecies variation. To establish a more thorough understanding of the structural organization (i.e., content) of play fighting in juvenile macaques, a method called analysis by synthesis (described in Chapter Two) was used to identify, and then describe, species typical patterns of play fighting for Tonkean and Japanese macaques. It was found that for both species, the N/S/UA region was the modal offensive and defensive play target, and that VSELB was the modal tactic of defense. However, Tonkean macaques targeted the N/S/UA region to a greater extent than Japanese macaques, and the latter species was more likely to utilize the VSELB tactic of defense than the former. Thus, although a macaque-typical pattern of play was identified, there also appears to be between species variations on that pattern.

Previous research has shown that both social and contextual factors can influence the quality and quantity of play in primates. Gard and Meier (1997) found that in sub-adult rhesus monkeys, the activity level of the group was positively correlated with most categories of play, whereas a negative correlation was found between the frequency of vocalizations and amount of play. In another study on rhesus macaques, Meier and Devanney (1974) found that play was not observed during times when there was aggression in the group. Taken together, these findings suggest that activity levels and vocalizations (which are assumed to be indices of group tension), as well as the presence of overt aggression within the troop, can affect the amount and content of juvenile play behaviour. Temperature and seasonal factors have also been shown to influence macaque play fighting. For example, Bernstein & Mason (1963) found that in rhesus macaques, the amount of time spent resting (i.e., time not spent engaged in play fighting) within the troop increases with a rise in temperature. That is, when the temperature is high, then the level of troop activity, including play, is likely to be low. Bernstein (1993) also showed that there are seasonal influences on play in rhesus macaques, in that mature males were observed to play more in the spring - the non-breeding season - whereas younger males and females played more in the fall - the breeding season. Similar seasonal and contextual influences on the performance of play have been reported for many species of primates (e.g., squirrel monkeys, Baldwin & Baldwin, 1974; gelada baboons, Barrett, Dunbar & Dunbar, 1992; squirrel monkeys, Stone, 2008).

Although the interpretations as to why these various social and contextual factors may have a particular influence on play behaviour may be of value for understanding species specific behaviour, for the purposes of this thesis, the relevance of these data lay in the fact that the content of playful interactions, even within the same species, may vary depending on many different factors. With these studies borne in mind, it was deemed necessary that in order to be confident about the within species patterns that were proposed in Chapter Two, it was essential that the content of play fights be examined in multiple troops of Tonkean and Japanese macaques. That is, it had to be verified whether or not the patterns reported for play fighting were indeed representative of each species, rather than being idiosyncratic to the individual troops from which the patterns were derived.

The ‘basic measures’ of play fighting that were described in Chapter Two (i.e., play targets, tactics of defense and play fight durations) can be thought of as comprising two kinds of measures, qualitative and quantitative. Consider a furnace regulated by a thermostat: both the temperature set on the thermostat and the duration of bouts of activity by the furnace may be measured as behavioural properties of the system – but they are fundamentally different. The temperature set on the thermostat regulates the behaviour of the whole system, whereas the length of time the furnace is running may merely reflect local weather conditions. If, for example, the thermostat is set at 20 degrees Celsius and the temperature outside the room is lower than 20, the furnace will be running, but if the temperature outside the room is above 20 degrees, the furnace will not be in operation. Similarly, two furnace-thermostat systems, both with their temperature set at 20 degrees, operating in different rooms in different parts of the world, should still have ‘working to maintain 20 degrees’ as the qualitative commonality, even though how long and how hard each furnace works may vary.

Applying this logic to play fighting, it should be the case that the species-typical target over which the animals compete should remain constant from context to context, but the frequency with which they engage in play fighting and the length of time of individual play bouts are likely to vary. Comparative studies have shown that species can differ in the targets competed over (e.g., Aldis, 1975; Pellis, 1988), and that within a species, irrespective of age, sex, strain and experimental manipulation, the target remains the same, even though frequency and duration can vary dramatically (for rats, see Field & Pellis, 1994; Foroud & Pellis, 2002; Pellis & McKenna, 1992; Pellis & Pellis, 1987, 1990, 1997b; Reinhart et al., 2004, 2006). For example, when the social dynamics of a group are tense, the play fights should be furtive and are likely to be of shorter duration than when the group is not stressed. However, in both cases, the same targets are attacked and defended (e.g., Pellis, 1981). The tactics used to gain access to the body target and those used to defend against such contact should, using the thermostat analogy, be highly variable, but in practise, they are not. It seems that, out of all the options available, species will use preferred manoeuvres, with these preferences reflecting either mechanical or neural efficiency – that is, the tactics used are the ones that are the most effective and efficient (Pellis, 1989, 1997). While there are preferred species tactics, contextual factors may affect whether less preferred ones are used in a specific case. It should also be remembered, that unlike serious fighting, when animals engage in play fighting, they have species typical ways to maintain reciprocity, and this difference may, in turn, affect the choice of tactics used (Pellis, Pellis & Reinhart, in press). I would therefore expect that all troops of the same species should compete for the same play target, that the duration of bouts of play fighting should be highly variable, and that the preferred tactics of attack and defense should show an intermediate level of variability.

The objective for Chapter Three of this thesis was to determine whether a macaque-typical pattern of play could be identified, and if interspecies style differences in play were upheld regardless of the sample population. The troops that were included for the subsequent analysis of juvenile play fighting will be fully described in the Methods section. Briefly, however, the study included two Tonkean macaque troops that were housed in a ‘semi-free’ park environment, and one juvenile-only Tonkean troop (i.e., there were no adults or infants in the group) that was housed in a relatively small indoor/outdoor cage. The two Japanese macaque troops that were included in the study differed in terms of the number of troop members and the age of those members - both, however, were housed in relatively large, outdoor enclosures within a large primate research institute.

If there are true species-typical patterns for juvenile play fighting in Tonkean and Japanese macaques, then it is likely that within species, the content of playful interactions - the play targets and tactics of defense - should be relatively stable across troops. In contrast, it is more likely that the quantitative aspects of play should exhibit fluctuations, depending on troop-specific contextual variables such as the time of day or year, and the number of play partners available when the data were collected. That is, the core content of play fighting should be relatively stable, and play fight durations should be more labile. For the purposes of Chapter Three of this thesis, *what* each species did within the context of a play fight was of greater interest than *how often* each species engaged in play fights.

First, the targets, tactics and durations of dyadic play fights for all troops were analysed, and then within species troop comparisons were made to find out if the patterns from the Zoo troops of Chapter Two were able to predict these variables in the additional troops observed. The additional troops conformed, to varying degrees, to what was predicted. As indicated above, given that context can influence the choice of tactics, some of the variation found in the use of tactics was explainable by troop differences in demographics. Therefore, for reasons that will be made clear in the Results, age comparisons were conducted to examine whether or not age could account for the observed within species variations. Gard and Meier (1997), for example, showed that, in sub-adult rhesus monkeys, age was an important factor that affected the content and frequency of play, with 2 year olds playing the most. Furthermore, Meier and Devanney (1974) have reported that the form and complexity of social play in rhesus macaques is related to what an individual of a particular age is capable of doing physically, and that the physical distance between the individual and its mother can have an profound influence on the play, with the latter likely being due to varying degrees of permissiveness by the mothers.

There are known temperamental differences between Tonkean and Japanese macaques that pertain specifically to maternal restrictiveness and infant socialization (Thierry, 2000). From Thierry's 4-grade classification of macaques, it is known that, in Japanese macaques, which are a grade-1, despotic species, the mothers are more protective than grade-4, egalitarian Tonkean macaque mothers (Thierry, 2004). Thus, an examination of age as a potential factor that influences the structural organization of play fights was indeed justified. It should be noted that the troop of isolated, juvenile Tonkean macaques was omitted from this portion of the analysis because this group differed from the others in too many variables (e.g., they were housed in a relatively small and novel environment, all individuals were of the same age and there were no infants or adults present in the troop).

3.2 Methods

Animals: Tonkean macaques – Primate Research Centre; Strasbourg, France 1996 (PRC Park 1996)

Tonkean macaques are found in the central region of the island of Sulawesi, Indonesia (Thierry et al., 1994). However, a group of Tonkean macaques was imported into France (the Landskron Chateau in Southern Alsace) in 1972 and the individuals were released into an area of about 2 acres, with the intention of establishing a new population from eight reproducers (Herrenschmidt, 1977). In 1978, the newly founded breeding population at the Landskron Chateau was divided into two groups, and the main study group was established at the Primate Research Centre (PRC) of the Université Louis Pasteur in Strasbourg, France (Thierry et al., 1994). The group under study was maintained at PRC and was housed in a 2-acre wooded enclosure containing an indoor shelter (cleaned in the morning 3 times per week), surrounded by a fence electrified at the top (Thierry et al., 1994). Monkey pellets, fresh fruits, and vegetables were provided daily and water was available *ad libitum*. At the time of the study, the group contained 24 individuals: 2 adult males, 9 adult females, 7 juvenile males, 1 juvenile female, 2 infant males, and 3 infant females. Juveniles were considered to be between 1.5 and 5 years old. One of the 4 year old juvenile males of this group was not included in the analysis because he was not a frequent participant in the play fights that were included in the analysis. (For more detailed troop information, refer to Appendix 3).

Observation protocol

Sergio and Vivien Pellis filmed this troop over a period of 2 weeks in July, 1996. Data were collected from 1000 - 1200, and 1400 - 1700: 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 et al., 1990). The animals were filmed only in the outdoor enclosure, and approximately 6h of video were obtained. Due to a lack of time to become familiarized with the troop, the individual's identities were not recorded at the time of filming. Rather, after the videos were dubbed (see below), a copy was sent to Bernard Thierry at PRC, who then identified each of the monkeys engaged in the time-coded play fights. The transcripts containing the identity of the animals were then used for subsequent analysis (see below).

Animals: Tonkean macaques – Primate Research Centre; Strasbourg, France 2006 (PRC Park 2006)

As mentioned previously, two groups of Tonkean macaques were maintained in Strasbourg, France, with the main study group at PRC and another group at the Orangerie Zoo of Strasbourg. The group under study was maintained at PRC, and was constituted in December 2002. The adult male (Gaëtan) came from the Orangerie Zoo to join four adult females (Jeanne, Lady, Néréis, Olga) and one infant (Patsy), who were from the initial PRC group. The group was housed in a 2 acre wooded enclosure containing an indoor shelter (cleaned in the morning 3 times per week), surrounded by a fence electrified at the top (Thierry et al., 1994). Monkey pellets, fresh fruits, and vegetables were provided daily and water was available *ad libitum*. At the time of the study, the group contained 13 individuals: 1 adult male, 4 adult females, 3 juvenile males, 1 juvenile female (not filmed), 2 infant males, and 2 infant females. Juveniles were considered to be between 1.5 and 5 years old. The 4 year old juvenile female of this group was not included in the analysis because she was never observed to engage in play fighting during the observation period. (For more detailed troop information, refer to Appendix 4).

Observation protocol

I observed this troop of Tonkean macaques over a period of 4 weeks from April to May, 2006. After 2.5 weeks of observing the group, I was able to identify all group members consistently, at which time the collection of video data commenced. Data were collected between 0930 and 1500: all play fights involving juvenile members of the group (with the exception of the 4 year old female), 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 et al., 1990). The animals were filmed only in the outdoor enclosure, and approximately 3.5h of video were obtained over 15 days of observations.

Animals: Tonkean macaques – Primate Research Centre; Strasbourg, France 2006 (PRC Isolated Juveniles)

This group of Tonkean macaques, also maintained at PRC, was comprised of 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 group was housed in a 14.4m^2 outdoor wire-mesh enclosure containing a 4m^2 indoor shelter. Both sides of the enclosure were 3m high and the indoor portion was cleaned in the morning, 3 times per week. Monkey pellets, fresh fruits, and vegetables were provided daily and water was available *ad libitum*. (For more detailed troop information, refer to Appendix 5).

Observation protocol

I observed this troop of Tonkean macaques over a period of 5 weeks from May to June, 2006. After 2 weeks of observing the group, I was able to identify all group members consistently, at which time the collection of video data commenced. Data were collected from 0930 - 1630: all of the group's play fights 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 et al., 1990). The animals were filmed only in the outdoor enclosure, and approximately 10h of video were obtained over 19 days of observations.

Animals: Japanese macaques – Primate Research Institute; Inuyama, Japan 2007 (Takahama B+)

This captive group of Japanese macaques was introduced to the Primate Research Institute, Kyoto University from Takahama in Fukui Prefecture, Japan, in 1970 and 1971. The troop was maintained in a 960-m^2 open-air enclosure surrounded by a 5m high concrete wall topped with an electric fence. Monkey chow was provided each day, several kinds of fruit and vegetables were given occasionally, and water was available *ad libitum*. At the time of the study, the group contained 51 individuals: 7 adult males, 14 adult females, 9 juvenile males, 9 juvenile females, 3 infant males, and 9 infant females. Individuals between 1 and 5 years old for males, and between 1 and 4 years old for females were included in the study. (For more detailed troop information, refer to Appendix 6).

Observation protocol

I observed this troop of Japanese macaques over a period of 10 days in November, 2007, and approximately 2.25h of video were obtained during 39.5h of observation time.

Data were collected between 0800 and 1600: all play fights involving juvenile and ‘older’ infants in the group (judgment of age based on body size and hair colour), were filmed using a Sony Digital Video Camera (model no. DCR-PC9). The identity of specific individuals was not known. Nonetheless, when possible, the approximate age and the sex of the individuals were noted.

Animals: Japanese macaques – Primate Research Institute; Inuyama, Japan 2007 (Wakasa B)

Wakasa is the name of a township on the western coast of Japan in Tottori Prefecture. The original Wakasa troop of Japanese macaques (n = 21) were likely captured from the mountains on the edge of Tottori City and were brought to PRI on March 21, 1974. (M. Huffman, personal communication). In November 2007, when the data were collected, the troop was split up into different groups, and the Wakasa B troop was observed for the present study. The troop was maintained in a 524-m^2 open-air enclosure surrounded by a concrete wall topped with an electric fence. Monkey chow was provided each day, several kinds of fruit and vegetables were given occasionally, and water was available *ad libitum*. At the time of the study, the group contained 37 individuals: 2 adult males, 14 adult females, 3 juvenile males, 6 juvenile females, 4 infant males, and 8 infant females. Individuals between 1 and 5 years old for males, and between 1 and 4 years old for females were included in the study. (For more detailed troop information, refer to Appendix 7).

Observation protocol

I observed this troop of Japanese macaques over a period of 12 days in November 2007, and approximately 2.2h of video were obtained during 43.25h of observation time. Data were collected between 0800 and 1600: all play fights involving juvenile and 'older' infants in the group (judgment of age based on body size and hair colour), were filmed using a Sony Digital Video Camera (model no. DCR-PC9). The identity of specific individuals was not known. Nonetheless, when possible, the approximate age and the sex of the individuals were noted.

Behavioural measures for play fighting

After the video data were collected, the digital video 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. The same analytical methods that were described in Chapter Two (analysis by synthesis) were used to score a sample of play fights for each of the Tonkean and Japanese macaque troops described in Chapter Three. That is, from each troop's sample of scored play fights, F-to-F contexts were identified and the offensive and defensive bite distributions, as well as the defensive responses to bites received on the modal play target, in the F-to-F context were scored (Table 2). After the play targets and tactics of defense had been identified for each troop, non-parametric statistical analyses were used to verify the species' patterns that were reported in Chapter Two. For

Table 2. The number of play fights, F-to-F contexts, defensive responses, and dyadic play fight durations analysed for Tonkean and Japanese macaque troops.

Troop	Play fights	F-to-F contexts	Defensive responses	Dyadic play fight duration
Tonkean macaques				
PRC Park 1996 (7)	50	44	31	42
PRC Park 2006 (3)	50	38	21	43
PRC Iso Juves 2006 (5)	100	48	39	92
Japanese macaques				
Takahama (15*)	55	54	31	49
Wakasa (8*)	62	32	17	42

Note: Because individual identities were not known for the Takahama and Wakasa troops, the approximate number of juvenile-aged animals that could have been included in the play fighting analyses are reported.

each troop's sample of scored play fights, dyadic play fight durations were also recorded so that comparisons with the respective Zoo troops could be made.

Statistical analyses

Troop comparisons

Chi-square analyses of the pooled raw scores for each of the Tonkean and Japanese macaque troops described above were performed to test whether the modal patterns found for each troop (i.e., modal offensive and defensive play targets in F-to-F context, and the defensive responses to N/S/UA bites in F-to-F context) could be predicted from the species-specific patterns found in Chapter Two for the Tonkean macaques of the Orangerie Zoo and the Japanese macaques of the Paris Zoo. Because for each troop there was greater than 30 data points for dyadic play fight durations, this allowed for a normal distribution to be assumed, and so permitted the use of parametric statistics. Therefore, one-way ANOVAs were used for each species to compare the duration of dyadic play fights with the two troops studied in Chapter Two.

Age comparisons

A sub-set of the data were analysed to test whether or not age effects could account for within species deviations from the expected modal patterns. That is, within each troop (except for the PRC Isolated juveniles), the offensive and defensive bite distributions, and defensive responses, were calculated for young individuals playing with young (i.e., same age) partners, and for old individuals playing with old partners. Individuals included in the 'Young' category were 2 years old or less, and individuals included in the 'Old' category were 3 years old or more. Thus, when possible, there were (1) offensive target, (2) defensive target, and (3) defensive tactic distributions calculated for Young and Old juveniles within each troop. Within each species, the Young and Old data sets from each troop were then collated, resulting in Young Tonkean, Old Tonkean, Young Japanese, and Old Japanese groups that were then compared. Chi-square analyses of the pooled raw scores for the Young Tonkean and Old Tonkean data sets were performed to test if the offensive and defensive bite distributions, and the defensive responses for Old Tonkean macaques could be predicted from the patterns found for Young Tonkean macaques. The same analysis was performed to test if the patterns observed in Young Japanese macaques could predict the patterns observed in Old Japanese macaques.

In cases where Young and Old within species comparisons were not significantly different, the Young and Old categories were collated, resulting in Tonkean and Japanese macaque data sets, which were both comprised of interactions that were only between same-age play partners. Subsequently, Chi-square analyses of the pooled raw scores for the collated Tonkean and Japanese macaque data sets were performed to test if the offensive and defensive bite distributions, and the defensive responses found for Tonkean macaques, could predict the patterns found for Japanese macaques.

3.3 Results

Troop comparisons

Chi-square analyses of the pooled raw scores for each of the Tonkean and Japanese macaque troops showed that most of the modal patterns found for each troop (i.e., modal offensive and defensive play targets in F-to-F context, and the defensive responses to N/S/UA bites in F-to-F context) could be predicted from the respective species patterns reported in Chapter Two (Table 3). For each troop, the N/S/UA was the modal offensive and defensive target. For one troop, the N/S/UA was attacked more often than expected during offense and, in another troop, less often than expected for defense. Similarly, the VSELB tactic was the modal one for all troops, although for one, it was used less frequently than predicted. Even though some troops significantly varied in frequency, in all cases, the targets and tactics presented in Table 3 were the modal ones for all troops.

With regard to durations, there were no significant group differences for the troops of Japanese macaques (F (2, 123) = 0.85, $p > 0.05$). For the Tonkean troops, there was a significant difference between groups (F (3, 164) = 12.60, $p < 0.001$). Post-hoc tests showed that the Orangerie Zoo and PRC Park 2006 troops were different to the PRC Park 1996 and PRC Isolated juvenile troops ($p < 0.05$), but they were not different from each other ($p > 0.05$). The 2 troops with the lowest durations were not significantly different from one another ($p > 0.05$). Indeed, comparison of the lowest scoring troop of Tonkean macaques with the Paris Zoo troop of Japanese macaques showed a significant difference (t (82) = 2.32, $p < 0.05$). That is, some troops of Tonkean macaques can have durations that are even less than those of Japanese macaques. As predicted then, targets and tactics were relatively stable across troops, while measures such as duration, were not.

As shown in Table 3, from a total of 15 within species comparisons for targets and tactics that were made for the 5 different troops, there were 3 patterns of behaviour that

Table 3. A comparison of the modal offensive and defensive targets, defensive responses, and dyadic play fight durations for Tonkean and Japanese macaques.

Troop	Offensive N/S/UA bites	Defensive N/S/UA bites	VSELB responses	Play fight durations
Tonkean macaques				
PRC Park 1996	69.4% (same)	82.9% (same)	53.3% (same)	14.5s (less)
PRC Park 2006	56.1% (same)	38.5% (less)	28.6% (same)	25.2s (same)
PRC Iso Juves 2006	75.9% (more)	78.6% (same)	52.6% (same)	9.4s (less)
Japanese macaques				
Takahama	58.1% (same)	46.7% (same)	61.3% (same)	14.2s (same)
Wakasa	51.4% (same)	42.3% (same)	23.5% (less)	12.2s (same)

Note: The N/S/UA bites are shown as percentages of the total number of offensive and defensive bites delivered in the F-to-F context. VSELB responses are shown as percentages of total facing responses. The dyadic play fight durations reported are mean values for each troop. In brackets, it is indicated whether the percentage or duration found for each troop, was the same as, less than, or more than what was predicted based on the data reported in Part 1 for the respective Zoo troops.

were not as expected: (1) PRC Isolated juveniles showed higher than expected levels of offensive bites directed to the N/S/UA ($X^2 = 4.5$, $df = 1$, $p < 0.05$), (2) PRC Park 2006 juveniles showed lower than expected levels of defensive bites directed to the N/S/UA ($X^2 = 17.9$, $df = 1$, $p < 0.001$), and (3) Wakasa juveniles showed lower than expected levels of VSELB responses ($X^2 = 12.7$, $df = 1$, $p < 0.001$). My level of familiarity with these troops led me to generate specific hypotheses with regard to potential factors that may have been responsible for producing each of the observed deviations from the proposed, species typical patterns of behaviour.

The PRC Isolated juveniles exhibited an exceptionally high level of offensive N/S/UA bites, relative to the other Tonkean macaque troops, however, many contextual factors made this group different from the others. These juveniles were removed from their home troop on April 6, 2006, and moved into their permanent housing environment on April 10, 2006. During their first 2 weeks in this new environment, random observations were made and notes were taken regarding the animals' behaviour. My records indicate that during the first week, all individuals were clearly anxious in their new surroundings, and although they seemed to become increasingly comfortable in the new environment as time passed, for several weeks, they continued to be easily startled by human voices and unfamiliar sounds that they experienced from the confines of their new cage.

Data collection for the Isolated juveniles commenced approximately 5 weeks after their removal from their home troop, and despite having had some time to habituate to the novel surroundings, it is highly likely that these juveniles were still adjusting not only to the new housing conditions, but also to the alteration of their social group. The exaggerated offensive targeting of the N/S/UA could be a byproduct of the high levels of stress that the individuals in this group were likely experiencing. That is, because they were highly anxious, their play fighting may have been more stereotyped (as evidenced by their extreme adherence to the play target), in order to facilitate exceedingly cooperative social interactions within a context that was still relatively ambiguous to them. However, despite the distinct differences in social and environmental variables that were inherent to this group, it is important to note that for the most part, their patterns of play fighting conformed to what would be predicted as species-typical for juvenile Tonkean macaques.

The PRC Park 2006 juveniles exhibited a lower than expected level of defensive N/S/UA bites relative to the other Tonkean macaque troops, and there may be a plausible explanation that relates to symmetry (or lack thereof) between play partners. From the 38 F-to-F contexts that were scored for this troop, 74% of the interactions took place between asymmetrical play partners. Because there were relatively few play partners available within this troop (i.e., only 3 juveniles), most of the documented play fights took place between the 3 year old and the two 2 year olds, and so between partners of different ages and sizes. During play fights between unevenly matched play partners, it is likely that the smaller/younger individual would be less able to contact preferred body targets effectively and execute preferred defensive tactics to protect those targets.

Therefore, with regard to this troop's deviation from the expected level of defensive N/S/UA bites, perhaps the defensive bites of younger individuals were being directed to alternate play targets (e.g., LA/H - lower arm and hand), which in turn, biased the troop's pooled data set. A comparison of play patterns that emerge when evenly matched 'younger' or evenly matched 'older' play partners interact, may clarify whether or not this interpretation could account for the observed variation in the species typical pattern of defensive targeting found for this troop.

The Wakasa troop juveniles exhibited a lower than expected level of defensive VSELB responses, and similar to the explanation provided above for the Park troop of Tonkean macaques, play partner asymmetry may account for the observed deviation in the defensive behaviour of Wakasa juveniles. This troop of Japanese macaques was comprised of 9 individuals that ranged in age from 2 to 5 years old, and 12 individuals that were 1 year old or less - a relative abundance of infants. Based on casual observations, infant-infant interactions seemed to be much more frequent than juvenile-juvenile interactions. Because the identities of individual animals were not known for this troop it is likely that the sample of play fights that were collected and analysed for this troop, included a relatively high proportion of play fights that involved some of the older infants (i.e., individuals who, based on body size, were older than 1 but less than 2 years old). As mentioned previously, it is possible that even within the same species, play patterns of younger individuals may differ from the play patterns exhibited by older individuals. Therefore, for both Tonkean and Japanese macaques, age comparisons were made to test whether or not age effects could possibly account for within species deviations from the expected modal patterns.

Age comparisons

Chi-square analyses of the pooled raw scores for the Young Tonkean and Old Tonkean data sets showed that all of the modal patterns for targets of attack and tactics of defense for Old Tonkean macaques could be predicted from what was found for the Young Tonkean macaques ($p > 0.05$). The same result was found for Japanese macaques. That is, the modal targets and tactics found for Old Japanese macaques were not significantly different from those found for Young Japanese macaques ($p > 0.05$).

Because the Young and Old within species comparisons were not significantly different, the Young and Old data sets were collated for each species. Chi-square analyses of the pooled raw scores for the collated Tonkean and Japanese macaque data sets showed that the modal patterns found for Tonkean macaques did not predict the patterns found for Japanese macaques (Figure 3.1). That is, Japanese macaques showed lower levels of offensive N/S/UA bites ($X^2 = 17.8$, $df = 1$, $p < 0.001$), lower levels of defensive N/S/UA bites ($X^2 = 52.5$, $df = 1$, $p < 0.001$) and higher levels of VSELB responses ($X^2 = 9.1$, $df = 1$, $p < 0.01$), when compared to Tonkean macaques. Although there were some age changes in the modal play patterns for each species, the changes were not significant, and there were no age x species interactions, suggesting that species differences in these patterns were maintained throughout development. The age effects contributing to the deviations in Table 3 may then not be due to age itself, but by animals

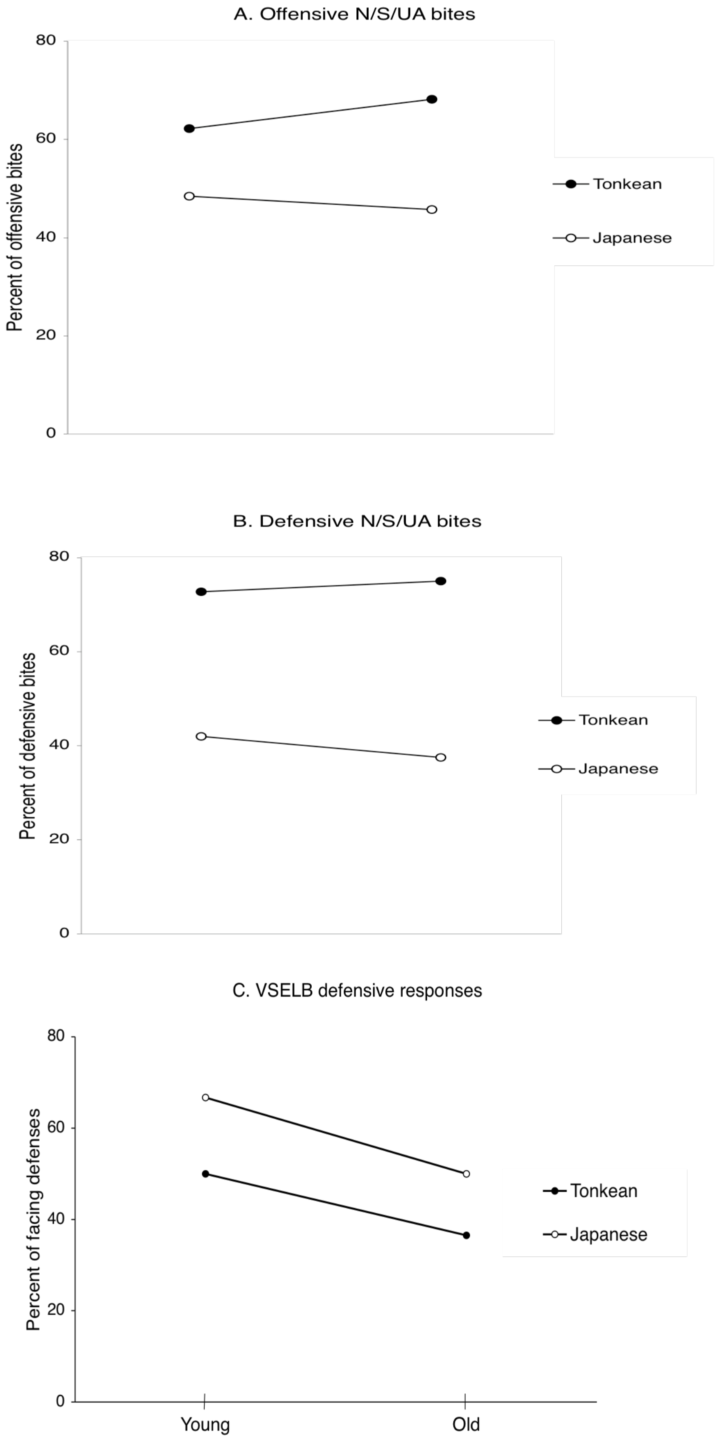


Figure 3.1 A comparison of modal play targets and tactics of defense in Young and Old Tonkean and Japanese macaques, when paired with play partners of the same age. Data has been collapsed within species and across troops to show percentages of (A) Offensive N/S/UA bites, (B) Defensive N/S/UA bites, and (C) VSELB tactic of defense.

of different ages interacting. This possibility will be explored in Chapter Four.

3.4 Discussion

In Chapter Three of this thesis, the between troop comparisons of the content of juvenile play fighting in the F-to-F context were able to confirm two claims that were made in Chapter Two. First, there seem to be macaque-typical patterns of play that are maintained in all contexts. That is, for every troop that was examined, the modal offensive and defensive target was the N/S/UA and the modal tactic of defense was VSELB. Second, because the within species content of play fights was the same across different troops, this suggests that there are species-specific styles of play. Tonkean macaques tend to be more cooperative in that they target the N/S/UA to a greater extent than Japanese macaques, and Japanese macaques exhibit a more competitive style of play by using the VSELB tactic of defense more than Tonkean macaques. An additional, although expected finding, was that species patterns of play appear to be somewhat flexible in different environments. However, the behaviour exhibited within the context of symmetrical play fights (i.e., play fights between individuals of the same age) does not seem to account for the variations observed in the play patterns of juvenile macaques.

It is also important to note that the qualitative variables around which play fights revolve, that is, the targets and tactics, are stable across troops living under varying conditions, and so these are the optimal measures for cross species comparisons of play (see also Aldis, 1975; Pellis, 1988). Other measures, such as duration, seem more subject to the effects of local contextual conditions. Therefore, for species comparisons using either free-living animals or animals living under captive conditions over which the observer has little control, measures such as duration are likely of poor value for species comparisons. Such measures are likely most useful when animals can be tested under controlled conditions that are optimal for all species compared. Under such controlled laboratory conditions, for example, rats have been shown to have play fight durations of little over 3 seconds, whereas Syrian hamsters have durations of 15 seconds or more (Pellis & Pellis, 1987, 1988). Similarly, the data presented in Chapter Two show that when troops of Tonkean and Japanese macaques are closely matched for demographics, space and weather conditions, the Tonkean macaques have dyadic play fights that last significantly longer. Therefore, it is highly likely that Tonkean macaques have longer lasting play fights under the appropriate conditions. Nonetheless, as shown in this chapter, under some conditions, Tonkean macaques may play with durations that are significantly shorter than those of Japanese macaques.

Because the content of play fighting in both macaque species was found to be consistent regardless of context or sample population, this suggests that the patterns reported in Chapter Two are indicative of species-typical behaviour, rather than being idiosyncratic to those particular troops. The implications of this finding are that for future studies, when making between species comparisons of play fighting, using behavioural measures that focus on the content of play fights may be the most accurate and informative method for identifying and characterizing species typical behaviour, especially when data may only be available for a single troop of a given species. Using the method of analysis by synthesis to understand the underlying structural organization of play fighting, seems to be a technique that can be used to examine, describe, and compare play behaviour effectively not only in other species of macaques, but more broadly, in other non-human primates.

Indeed, it would have been ideal to complete these analyses using both individualized and pooled data sets. For most of the troops included in this study, having more individualized data that included different combinations of play partners (i.e., same and different ages), and a sample of play fights that spanned a wider range of developmental stages would have been beneficial. However, the time that would be required to collect and analyse this kind of information was outside the scope of this study. To conduct a more thorough analysis of the developmental patterns of play fighting in each species, future (longitudinal) studies that include the behaviour of juveniles, as well as infants, need to be done conducted. For example, it is unknown whether or not the infants of different macaque species start out playing the same, and then their behaviour patterns diverge later in life, or if species differences are evident from the time when play behaviour is first exhibited. There is some evidence to suggest the latter hypothesis may be correct. In an examination of the development of peer-mate relationships in Japanese macaque infants, (Norikoshi, 1974) it was found that dominance behaviours were exhibited within the first few weeks of life, suggesting that infants growing up in different social environments may be different from birth, as opposed to having to 'grow into' species specific behavioural styles through socialization.

Because the Young and Old juveniles within each species were not significantly different from one another, the behaviour patterns that were observed between same-age play partners could not account for the between troop variability in patterns of play. Therefore, in Chapter Four of this thesis, the content of juvenile play fighting will be examined in another way. Stemming from a new foundation of knowledge about: (1) the content of Tonkean and Japanese macaque dyadic play fights (particularly between same-age partners), and (2) the specific hypotheses generated from the *co-variation hypothesis* and *cooperation/competition model* of play (i.e., that temperament influences the relative levels of cooperativeness and competitiveness reflected in the play fighting of each species), the behavioural analyses to be made in Chapter Four will test these theories by making several predictions about different aspects related to the content of play fights. The next step in the characterization of Tonkean and Japanese macaque play fighting will utilise scan sampling data, polyadic play fights, asymmetrical play fights and the means used to terminate interactions, to make specific predictions about how each species would be expected to behave in different types of playful situations. For example, how might the targets and tactics of play fighting for each species be altered when individuals are interacting outside of the highly controlled, dyadic contexts that have been previously described?

CHAPTER FOUR

Predicting species differences in play fighting: Tonkean macaques are more cooperative and Japanese macaques are more competitive

4.1 Introduction

In Chapter Two, species typical styles of play fighting were shown to be consistent with predictions derived from the *co-variation hypothesis* and *cooperation/competition model* of play. In Chapter Three, the respective styles that had been proposed for Tonkean and Japanese macaques in Chapter Two were confirmed by behaviour patterns that were consistently observed in multiple troops of each species. Based on the patterns identified and the core theoretical contexts within which play fighting has been interpreted for this thesis, additional predictions on the content of their playful interactions, that have not yet been considered, were made for each species. That is, *with whom* are you going to play, and *how* are you going to play with them? In Chapter Four of this thesis, I will examine scan sampling data, polyadic play fights, asymmetrical play fights and the means used to terminate interactions, so as to test specific predictions about how each species should be expected to behave in these situations - all of which are different to the F-to-F interactions previously examined.

It has been previously mentioned that adult Tonkean macaques have relatively relaxed, symmetrical social relationships, whereas adult Japanese macaques exhibit asymmetrical social relationships that are more heavily influenced by dominance rank and kinship (Thierry, 2004). Although data pertaining to juvenile social relationships are relatively scarce, it has been well documented that kinship greatly affects play partner preferences in Japanese macaques (Hayaki, 1983; Imakawa, 1990; Koyama, 1985). In Koyama's study (1985) of juvenile Japanese macaques, he found that related individuals played 6.9 times as frequently as unrelated individuals. Similarly, in the troop of Japanese macaques that he observed, Hayaki (1983) found that all pairs of siblings interacted more frequently than would be expected, were they not siblings. That is, Japanese macaques tend to show high degrees of nepotism when choosing play partners, which would indeed be predicted by the *co-variation hypothesis*.

In contrast, because of the more cooperative temperament and egalitarian style of Tonkean macaques, from the *co-variation hypothesis,* it would be predicted that when choosing play partners, their juveniles should show less of a preference for close kin. That is, Tonkean macaques should play as equally with kin (siblings) as with non-kin (non-siblings). This prediction was tested in the present study using scan sampling data from the Orangerie Zoo troop of Tonkean macaques. Although scan sampling data was not collected for any of the Japanese macaque troops described in this study, the patterns of play partner preference have already been established by multiple studies on juvenile Japanese macaques (Hayaki, 1983; Imakawa, 1990; Koyama, 1985). Thus, results for the Tonkean macaques from this study were compared to the findings on play partner preferences previously reported in the literature for Japanese macaques.

Subsequent to identifying whether or not there were particular play partner preferences in Tonkean macaques, the next objective was to make predictions about, and examine the qualities of, different types of play fights. That is, relative to dyadic F-to-F play fights between evenly matched partners, how does the content of play fighting change when the number of simultaneous play partners is increased (i.e., polyadic play fights)? As with the previous analyses of F-to-F contexts, offensive and defensive bite distributions were calculated to identify the modal targets and tactics of defense used within the context of polyadic play fights. Within species comparisons were made to test whether or not the species typical F-to-F (dyadic) patterns of behaviour could predict the polyadic play patterns, and between species comparisons of the polyadic patterns were made to determine if Tonkean and Japanese macaques exhibit different polyadic play styles.

Based on the results shown in Chapters Two and Three, it is known that Japanese macaques exhibit a more competitive style of play in the F-to-F context, whereas Tonkean macaques exhibit a more cooperative style of play. But how would each species behave in polyadic interactions? Indeed, when several individuals are simultaneously playing together, it becomes increasingly difficult for them to contact the preferred targets of an opponent. For example, if two individuals are play fighting in an upright, F-to-F orientation, as the third play partner, where are you going to direct your attack? If you were a macaque, would you attempt to bite the preferred N/S/UA region, which in this scenario, would likely to be rather difficult to contact, or would you direct your bite in a more opportunistic manner? That is, the third play partner could go for an easy-to-reach target such as the body (e.g., middle of the back) or an exposed leg or foot (Pellis, 1984; Pellis & Pellis, 1998a). Whether a species' temperamental tendency in social contexts is to be more intense and competitive or more relaxed and cooperative, would likely influence the specific behaviour (i.e., the body regions toward which the attacks are launched) that would be expressed in this situation.

I predict that Japanese macaques should maintain the same, or close to the same, level of competitiveness during polyadic interactions as that observed during dyadic play fights. That is, although it may be difficult to accomplish when interacting with multiple partners, Japanese macaques should show little deviation from their preferred offensive and defensive play targets. Their more rigid pattern of play fighting should be expressed through consistent offensive and defensive targeting of the N/S/UA, and, to some extent, the H/F. In contrast, Tonkean macaques have been shown to exhibit a more cooperative style of play, and although they tend to target the N/S/UA to a greater extent than Japanese macaques during F-to-F interactions, their more relaxed, tolerant and seemingly flexible social demeanour, would suggest that as opposed to the Japanese macaques, Tonkean macaques should not be as rigidly bound to their play target. That is, they should show a more even distribution of bites across body regions that are not necessarily preferred, modal play targets (e.g., body, leg/foot).

If these predictions about polyadic patterns of play for Tonkean and Japanese macaques are true, they would concur with what Petit and colleagues (2008) reported in their study of juvenile crested and Japanese macaques. These authors predicted that in juvenile Japanese macaques, a species for which the social relationships are characterized by a strong degree of dominance asymmetry, play patterns should be less relaxed, and the individuals at play should take fewer risks than the more socially tolerant crested macaques. Their results suggested that Japanese macaques preferred more controlled social interactions (i.e., relatively structured dyadic interactions *versus* more anarchical polyadic interactions) that facilitate easy escape, whereas crested macaques preferred more 'risky' play fights, which involve closer physical contact and multiple play partners. The results presented in Chapter Two of this thesis showed that Tonkean macaques engaged in a greater proportion of polyadic play fights than Japanese macaques and that the durations of these multiple partner interactions in the former species are longer than those observed in the latter. Thus, the next step was to determine whether or not there were species differences in the content of polyadic play fights, and if within species polyadic play patterns could be predicted from the species typical play patterns that were identified within dyadic contexts.

It was established in Chapter Three of this thesis that in the dyadic interactions of both Tonkean and Japanese macaques, when play fights were examined between same age Young and Old play partners, that the within species play patterns did not differ. Young Tonkean macaques played in a similar manner to Old Tonkean macaques when interactants were the same age, and the same was true for Japanese macaques. However, it remains to be determined how the species specific content of play fighting may change when the partner with whom one is playing is different in age/size (i.e., asymmetrical play fights).

Levy's (1979) study of rhesus macaques (which are categorized as a grade 1 species on Thierry's 4-grade scale) reported that older juvenile males begin to assert their developing rank within the context of play fighting, in that they monopolize opportunities to perform in particular roles (i.e., the attacker), and make quasi-aggressive movements that Levy called 'mock attacks', which make it difficult for them to attract play partners and maintain interactions. She also found that as both males and females of this species aged, there was an increased avoidance of play fighting, presumably because of (1) an inability of older juveniles to accept mock attacks from subordinates, and (2) the lack of reciprocity that resulted when play partners insisted on solely playing the role of the attacker. In contrast, Bertrand's (1969) findings for play fighting in stumptail macaques (a grade 3 species), showed that rank order was ignored and subordinates were able to perform behaviours that were not normally tolerated by dominant juveniles outside of play, and 'self-handicapping' by stronger/older individuals (in the form of playful wrestling that involved them lying on their backs) was often observed. Thus, it appears that species' social styles may indeed be reflected within the context of asymmetrical play fights between juveniles, with despotic species behaving more competitively, and egalitarian species behaving more cooperatively.

Pereira & Preisser (1998) point out that although there have been many anecdotal accounts of self-handicapping during mammalian play fighting, it is extremely difficult, if not impossible, for a researcher to measure a subject's individual competitive capacities or levels of physical restraint objectively. That is, how can one quantify whether or not an older play partner is 'holding back' when interacting with a younger play partner? Indeed, it would be difficult to determine if a relatively advantaged (i.e., older/stronger/larger) play partner voluntarily places itself in a vulnerable physical position to afford a less advantaged play partner an opportunity to succeed in a play fight. However, by continuing to concentrate on the content of play fights and considering the interactions within the theoretical contexts proposed by the *co-variation hypothesis* and *competition/cooperation model* of play, several predictions can be made as to how the older and younger partners of each macaque species could modify their targets of attack and tactics of defense when playing with a different age partner.

In Chapter Three, there were two deviations from the expected modal play patterns that could not be explained by age effects *per se*, but were hypothesized to be accounted for by animals of different ages interacting. The PRC Park 2006 Tonkean macaque troop showed lower than expected levels of defensive N/S/UA bites, and the Wakasa Japanese macaque troop exhibited lower than expected levels of the VSELB tactic of defense. Because there was a high proportion of asymmetrical play fights in the former troop, and an abundance of yearlings in the latter, the bite and defensive response distributions may have been biased by the behavioural contributions of younger animals when they were interacting with older play partners. That is, when playing with larger/older partners, smaller/younger individuals may not be able to contact the preferred play targets or execute the preferred tactics of defense, due to their smaller size and lesser physical ability (or opportunity) to do so. Then, instead of biting the N/S/UA, as a larger partner would be predicted to do, smaller animals should bite targets to which they have access, such as the LA/H, whereas in terms of defense, larger individuals should continue to use

VSELB and the smaller partners should use HR or VCELS to defend their play target effectively.

The predicted play patterns for larger and smaller partners should be applicable to both Tonkean and Japanese macaques. Regardless of species, the larger play partner should continue to contact the modal play target and use the modal tactic of defense, and the smaller play partners should exhibit deviations from the modal targets and tactics. Because of their cooperative nature, Tonkean macaques should be more accommodating, and although larger individuals may target the N/S/UA and use VSELB tactics with smaller play partners, it should be to a lesser degree than that observed for larger Japanese macaques playing with smaller partners. If larger Japanese macaques do maintain a high level of competitiveness, even with smaller play partners, then the smaller juveniles should be relatively constrained to targeting the LA/H region and using HR or VCELS responses (more so than their smaller Tonkean macaque counterparts).

If Tonkean macaques are more cooperative in their play and Japanese macaques are more competitive, then how they terminate play fights should also differ. Given the greater competitiveness of play in Japanese macaques, they should have more abrupt and clearer endings to their play fights, to limit the risk of escalation to more serious combat (Hayaki, 1985). Petit and colleagues (2008) showed that relative to crested macaques, Japanese macaques prefer to be in contexts that allow ‘ease of escape’ during play fights, and they achieve this by engaging in more chase/escape bouts, rather than play fights that involve close physical contact, and by maintaining sitting positions during wrestling, as opposed to defenseless lying positions that would leave them more exposed, and make it difficult for them to escape. In contrast, when Tonkean macaques terminate a play fight, they should do so in a more relaxed and drawn out manner, reflecting the cooperative content of their interactions (see Chapter Two for an anecdote describing the laid back and prolonged appearance of Tonkean macaque polyadic play fights). Rather than quickly leaping or running away from a play partner, the individual terminating the bout may move away slowly, or stay in close proximity to the other individual, which allows for the possibility that the play fight will continue or resume. Thus, the end of a Tonkean macaque play fight should be more drawn out and ambiguous - particularly when one partner is persistent to continue the interaction - than those observed in Japanese macaques. Furthermore, in asymmetrical play fights, larger and smaller Tonkean macaque partners should be equally likely to terminate play fights, whereas in the more competitive Japanese macaques, because larger juveniles would be expected to uphold their relative advantage as much as possible, the smaller individual would be expected to evade (i.e., terminate) a play fight more often than the larger individual.

4.2 Methods

Observation protocol for scan sampling

In addition to filming play fights at the Orangerie Zoo, 5 days of scan sampling (Altmann, 1974) were conducted on this troop of Tonkean macaques in August, 2006. Scans were taken of all troop members from the left to the right of the cage, every 15 min from 0900 to 1800, generating a total of 185 scans per individual. In rare cases when individuals were not observable (i.e., they were inside of the indoor portion of the enclosure), they were assumed to be eating. For every scan, one of the following behaviour categories was recorded with a pencil and paper for each member of the troop: social play (included play fighting and play chase), solitary object play, solitary locomotor play, huddling or resting, grooming, eating, locomoting, exploring, and auto-grooming. When the focal individual was observed to be involved in social play, the identity of the partner(s) interacting with that focal individual was recorded. For the purpose of this study, only the social play data (n = 349 interactions) for juveniles will be reported.

Behavioural measures for polyadic and asymmetrical play fights

After the video data were collected, the digital videocassettes 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. The same analytical methods that were described in Chapter Two (analysis by synthesis) were used to score samples of polyadic and asymmetrical (i.e., interactions between different age partners) play fights for each of the Tonkean and Japanese macaque troops described in Chapters Two and Three. That is, the offensive and defensive bite distributions, as well as the defensive responses (for asymmetrical, but not polyadic play fights) were scored.

Behavioural measures for play fight terminations

Thirty dyadic play fights in the Tonkean macaques, where the ending could be clearly discerned, were analysed, frame-by-frame, to identify the ways in which they could end. From these, a pattern emerged as to how endings could unfold. Essentially, the play fights could end in one of two major ways: (1) By both subjects ceasing the interaction and simply staying, usually sitting, in the same location, either remaining in body contact or a body length or so apart. (2) One or both subjects could move away from one another, either doing so rapidly, by leaping or running, or more slowly, by walking. If a subject ran away, this could lead to a chase by the other. For both types of ending, one partner could keep grasping and biting the other, with the partner seemingly ignoring the contact, or a play fight was considered to have resumed when the intermission between play partners was no longer than 10 seconds. Video from the Orangerie Zoo Tonkean macaque troop and the Paris Zoo Japanese macaque troop was used to quantify play fight endings. The videos were examined from beginning to end for play fights, and those where the endings were present and the actions of the monkeys discernible, were scored. Only dyadic encounters were used. Of the play fights found, 182 for the Tonkean macaques and 161 from the Japanese macaques fitted the criteria for inclusion into the analysis.

Statistical analyses

Scan sampling data

All 10 juveniles from the Orangerie Zoo troop were arranged on a focal individual/social partner matrix that resulted in 45 possible pairs of play partners. Each cell of the matrix contained the number of social play interactions that were observed for each individual, and each of its 9 possible play partners. However, only half of the table was used because it was the total number of *interactions per pair* that was of interest, rather than from whom the focal data points were coming. For example, Achille and Charles were observed playing together 9 times. Three of the play fights between Achille and Charles came from the scans of Achille, and the other 6 interactions between these individuals came from Charles' sample of scans. The question of interest was, did Achille and Charles play together the same as, more than, or less than expected? The scores were then collated, resulting in raw scores for the number of interactions observed per pair. A Chi-square analysis was performed for the entire matrix, as well as for each of the 45 possible pairs to test whether or not different pairs played together more or less than expected.

In addition to the matrix analysis, calculations were completed for each individual to determine the number of social play interactions that each individual had with partners who were either siblings (same mother) or non-siblings (different mother). Of course, some pairs that were considered non-siblings were likely half-siblings due to having the same father. However, it is known that the social organization of macaques is highly structured around the formation of kin-bonded sub-groups called matrilines (Thierry, 2004). That is, females remain in their natal groups, whereas most males leave their natal groups at maturation (or in captive situations, the adult males are often removed from their natal troops). In his study of Japanese macaque social behaviour, Imanishi (1957) proposed that both mature and immature group members identify other young members of the troop with their mothers. Although Chauvin and Berman (2004) point out that

Imanishi's hypothesis was never thoroughly tested, they also bring attention to the fact that the tendency for animals to form preferences for familiar conspecifics, and engage in frequent interactions with those preferred partners, has been well documented in a variety of taxa. Therefore, for the purpose of this study, individuals with the same mother were classified as siblings, and those with different mothers as non-siblings.

The individualized scores for the number of play interactions with siblings and non-siblings were controlled for the number of possible siblings or non-siblings with whom each individual had to play. For example, Bob had 31 interactions with siblings and 26 interactions with non-siblings. Because Bob had 3 siblings and 6 non-siblings in the troop, his score for sibling interactions was 10.3 (31 interactions divided by 3 siblings) and for non-sibling interactions, 4.3. These 'controlled' scores were calculated for 9 of the juveniles (there was one 3 year old male with no siblings in the troop and so he could not be included in this analysis), and a Wilcoxon matched-pairs-signed-ranks test was used to test if the number of interactions that individuals had with siblings was significantly different from the number of interactions they had with non-siblings.

Polyadic play fights

The two Zoo troops from Chapter Two were used as the focal troops for the first part of the polyadic play fight analysis, so 18 polyadic play fights were scored for each species. The number of offensive and defensive bites directed to the various regions of the body was totalled, and bite distributions were calculated for each species. 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 differed from random.

Unlike the F-to-F play fights, however, individual participant scores were not appropriate for polyadic play fights, as these involved a shifting number of participants who likely contribute disproportionately to each play fight. Similar to the polyadic play fight durations that were analysed in Chapter Two, the polyadic offensive and defensive bites for each species' sample of 18 polyadic play fights were placed into bins for non-parametric analysis, the idea being that each bin can be thought of as a random sample. 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 a bin could no longer 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 than the sample available for offensive bites. In total, there were 9 offensive and 4 defensive bins for Tonkean macaques, and 8 offensive and 6 defensive bins for Japanese macaques. Friedman ranked-scores analysis of variance tests were performed to test whether or not the offensive and defensive polyadic bite distributions for each species were different from random across bins. For cases inwhich the analysis of variance indicated a significant deviation from random, and when there were sufficient data, Wilcoxon matched-pairs-signed-ranks tests were used to determine which body regions, within species, were targeted most frequently.

After the polyadic play patterns had been examined within each species, it was important to make within species comparisons of those patterns, with the F-to-F bite distribution patterns reported in Chapter Two. 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 each species' F-to-F bite distributions. The same non-parametric tests were also used to compare the F-to-F modal play targets (i.e., N/S/UA in offense and defense for both species, as well as the H/F in defense for Japanese macaques), with the polyadic bite distributions. For example, in Tonkean macaques, can the observed F-to-F distribution of offensive N/S/UA bites predict the offensive N/S/UA distribution in polyadic play fights? By making these within species comparisons, it was possible to identify the similarities and differences exhibited by each species in their respective dyadic and polyadic play styles. As a follow-up, Mann-Whitney U tests were used to compare, within species, whether or not individualized data on offensive N/S/UA bites from the F-to-F context was significantly different from the binned offensive N/S/UA data obtained from polyadic fights. Mann-Whitney U tests were then applied for cross species comparisons of specific bite locations.

Finally, it was important to verify whether or not the patterns reported for polyadic play fighting were indeed representative of each species, rather than being idiosyncratic to the focal troops. Therefore, within species comparisons were made for all of the troops described in Chapter Three. That is, Chi-square analyses of the pooled raw scores for each troop were performed to test whether or not the distributions of F-to-F offensive

N/S/UA bites and polyadic offensive N/S/UA bites could be predicted from the data reported for each of the respective focal troops. For example, could the offensive N/S/UA bites in F-to-F and polyadic contexts for PRC Park 1996, PRC Park 2006 and PRC Isolated juveniles, be predicted by the offensive N/S/UA bites of the Orangerie Zoo Tonkean macaques?

Asymmetrical play fights

A sub-set of the data were analysed to test whether or not partner effects could account for within species deviations from the expected modal patterns. That is, within each troop (except for the PRC Isolated juveniles), the offensive and defensive bite distributions, and defensive responses to N/S/UA bites, were calculated for larger individuals playing with smaller partners (i.e., asymmetrical), in the F-to-F context. Thus, when possible, there were (1) offensive target, (2) defensive target, and (3) defensive response distributions calculated for 'Larger' and 'Smaller' play partners within each troop. Within each of the Zoo troops, the Larger and Smaller offensive and defensive bite, and defensive response distributions were compared, as these were the troops for which there were the most data available for analysis. Chi-square analyses of the pooled raw scores for each of the Zoo troops were used to test if the offensive and defensive bite distributions, and the defensive responses for Smaller Tonkean macaques could be predicted from the patterns found for Larger Tonkean macaques. The same analysis was performed to test if the patterns observed in Larger Japanese macaques could predict the patterns observed in Smaller Japanese macaques.

Next, between species comparisons were made using Chi-square analyses of the pooled raw scores for the Larger and Smaller data sets from each species. These tests were used to determine whether or not the offensive and defensive bite distributions and the defensive responses for Larger and Smaller Japanese macaques, could be predicted from the patterns found for Larger and Smaller Tonkean macaques, respectively. By making these comparisons, it was possible to identify between species similarities and differences in patterns of play for Larger and Smaller play partners of the two species. It could be determined, for example, if Smaller Tonkean macaques show the same or different play patterns as Smaller Japanese macaques, within the context of asymmetrical play fights.

As with the polyadic play fights, it was again important to verify whether or not the patterns reported for asymmetrical play fighting were representative of each species, rather than being idiosyncratic to the focal troops. Therefore, within species comparisons of Larger and Smaller juveniles were made for all of the troops (except for the PRC Isolated juveniles) described in Chapter Three. That is, Chi-square analyses of the pooled raw scores for each troop (for Larger and Smaller play partners separately) were performed to test whether or not the distributions of offensive bites, defensive bites, and defensive responses could be predicted from the data reported for each of the respective focal troops. For example, could the offensive bite distributions for Larger partners in the PRC Park 1996, and PRC Park 2006 troops be predicted by the offensive bite distributions of the Larger Orangerie Zoo Tonkean macaques, when comparing behaviours observed during asymmetrical play fights?

Play fight terminations

Given that the transcripts involved sequentially recorded endings with individuals contributing to differing numbers, the transcripts were divided into bins of 10 as they emerged in the sequence of recordings. In this way, the placement of individual scores into particular bins was not biased in any systematic manner. For making cross species comparisons, the proportion of occurrence within bins was used to examine the distribution of proportions across bins within the species and with those across species. To test this statistically, a test of significance of difference between two proportions was used, which yields a z score. A calculated z score greater than 1.96 or less than –1.96 is considered significant at the .05 level, using a two-tailed test, and plus or minus 1.65, for a one-tailed test (Bruning & Kintz, 1987). An alternative method for some measures where sufficient scores for individual animals were available, involved using species values derived from individual animals, and comparing these using the Mann-Whitney U test. Where neither the bin, nor the individuals' scores approach could be used, the data were simply pooled and within and between species differences were tested using Chi-square analyses.

4.3 Results

Scan sampling data

A Chi-square analysis of the play partner matrix showed that the 349 social play interactions were not randomly distributed ($X^2 = 246.5$, $df = 8$, $p < 0.001$). From the 45 possible pairs, 11 pairs played more frequently than expected, but only 2 of those pairs were siblings, and 2 pairs that played less than expected, were non-siblings (Figure 4.1).

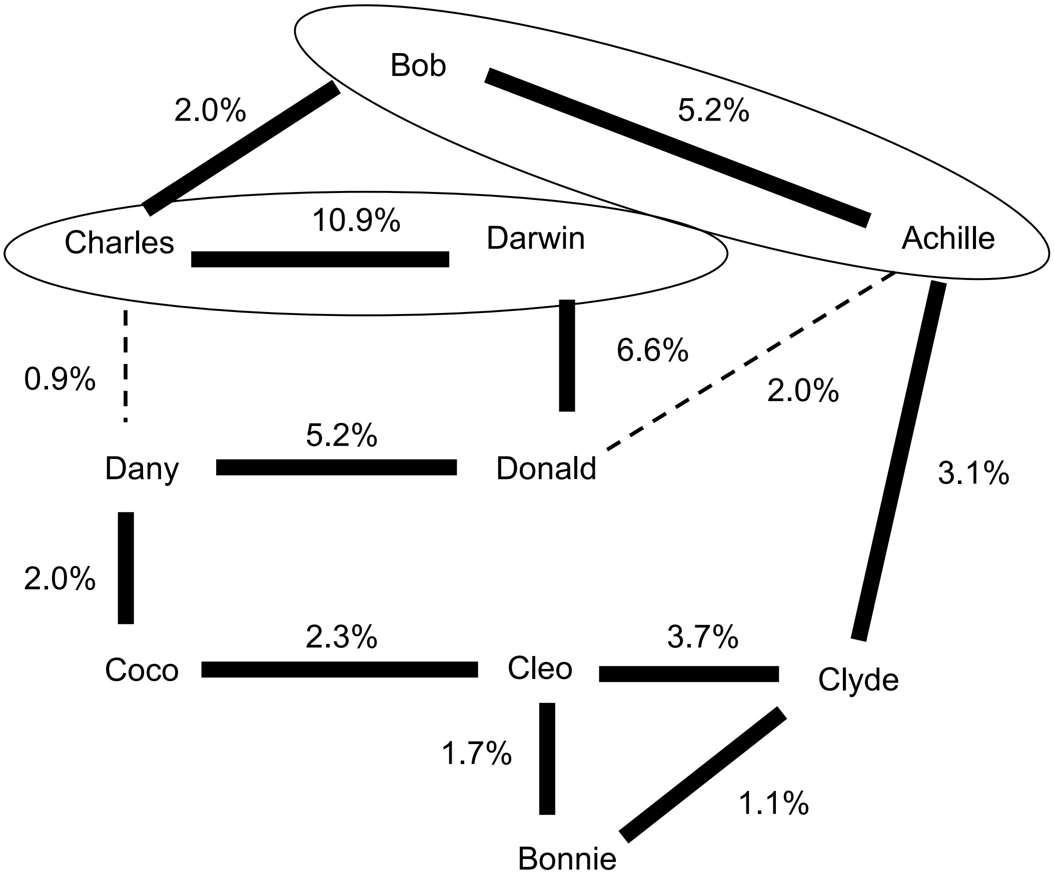


Figure 4.1 Sociogram of play partners in the Orangerie Zoo Tonkean macaques. Pairs that played more than expected (*n* = 11) are connected with thick lines, and pairs that played less than expected are connected by dashed lines (*n* = 2). Pairs that are circled are siblings, and all other pairs are non-siblings. Percentages represent the percent of play interactions that were observed between each pair, in relation to the total number of play interactions observed for the entire troop (*n* = 349 play interactions).

The Wilcoxon matched-pairs-signed-ranks test showed that Tonkean macaques played equally with siblings and non-siblings (T (9) = 3.0, $p > 0.05$) (Figure 4.2), suggesting that strong kin preferences do not influence an individual's choice of play partners in this species. Indeed, play between related individuals was about 1.5 times as frequent as play between unrelated individuals, but this was non-significant, and relative to Japanese macaques, for whom it has been shown that relatives are 6.9 times more likely to play than unrelated partners (Koyama, 1985), the Tonkean macaques do not appear to exhibit high levels of nepotism when choosing play partners. In accordance with data shown in Chapters Two and Three, these data suggest that Tonkean macaques are likely to incorporate cooperative elements into their play fights, in this case, by playing equally with peers, regardless of respective matrilines and dominance ranks.

Polyadic play fights

- Identifying species-specific polyadic play patterns

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: $X^2 = 41.3$, $df = 4$, $p < 0.001$; Tonkean defensive: $X^2 = 15.5$, $df = 4$, $p < 0.001$; Japanese offensive: $X^2 = 58.1$, $df = 4$, $p < 0.001$; Japanese defensive: $X^2 = 43.3$, $df = 4$, $p < 0.001$) (Figure 4.3). When bite distributions were calculated for the binned data, within species Friedman ranked-scores analysis of variance tests confirmed that each species differed from a random distribution for offensive and defensive bites (Tonkean offensive: $X_r^2 = 168.9$, $df = 4$, $p < 0.001$;

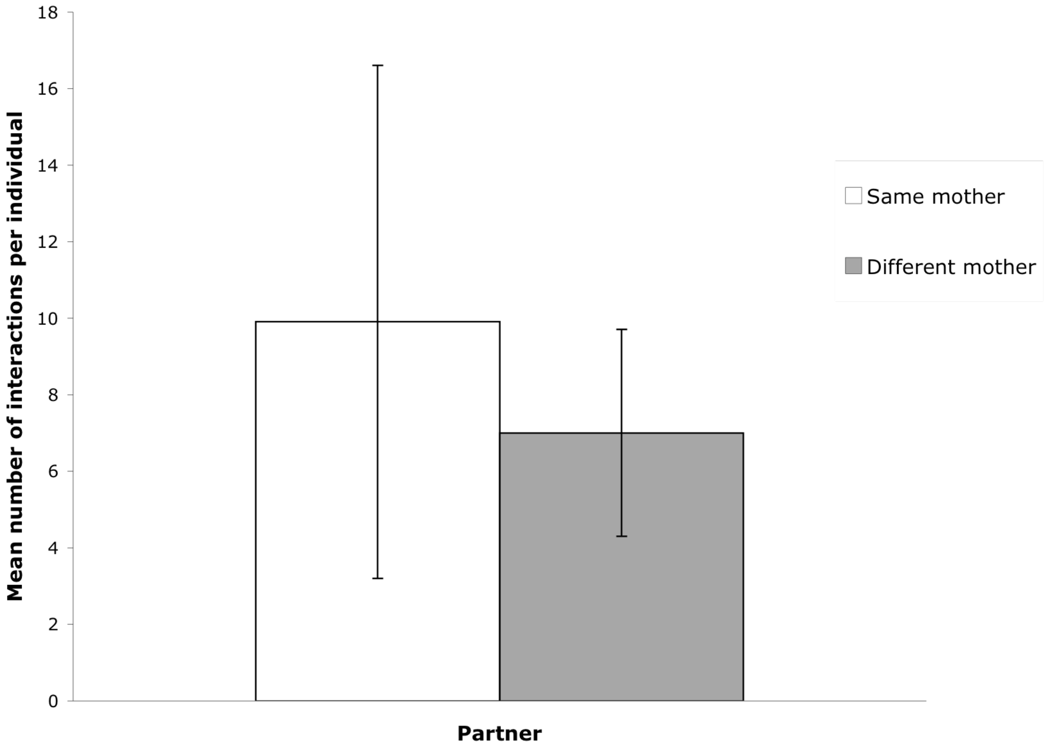
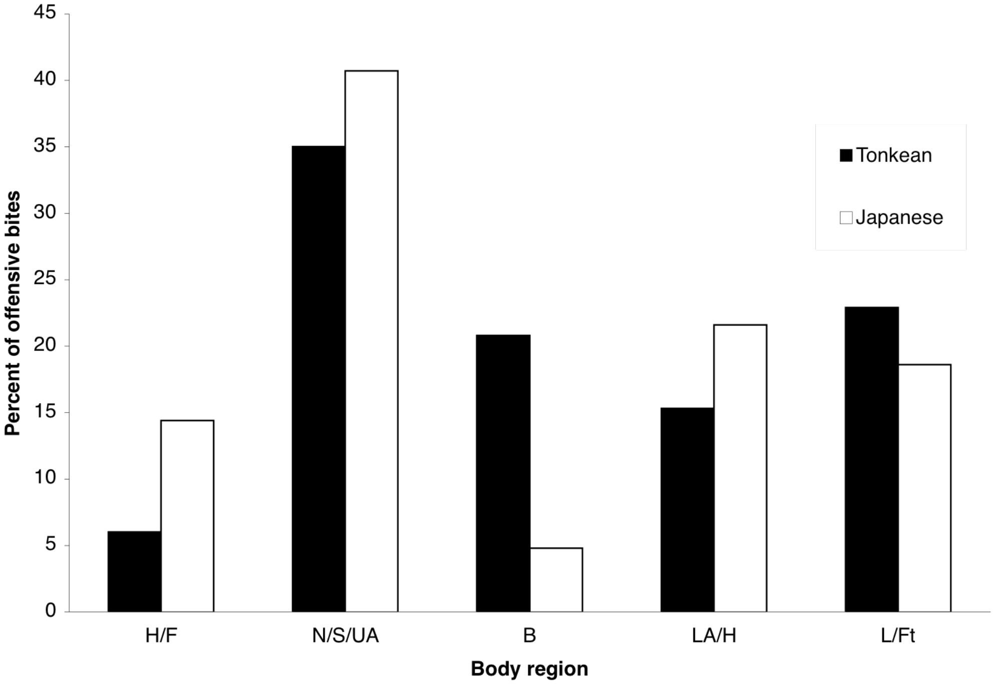


Figure 4.2 Play partner preferences in juvenile Tonkean macaques of the Orangerie Zoo (values shown are means ± 95% confidence intervals).

A. Offensive bite distribution



B. Defensive bite distribution

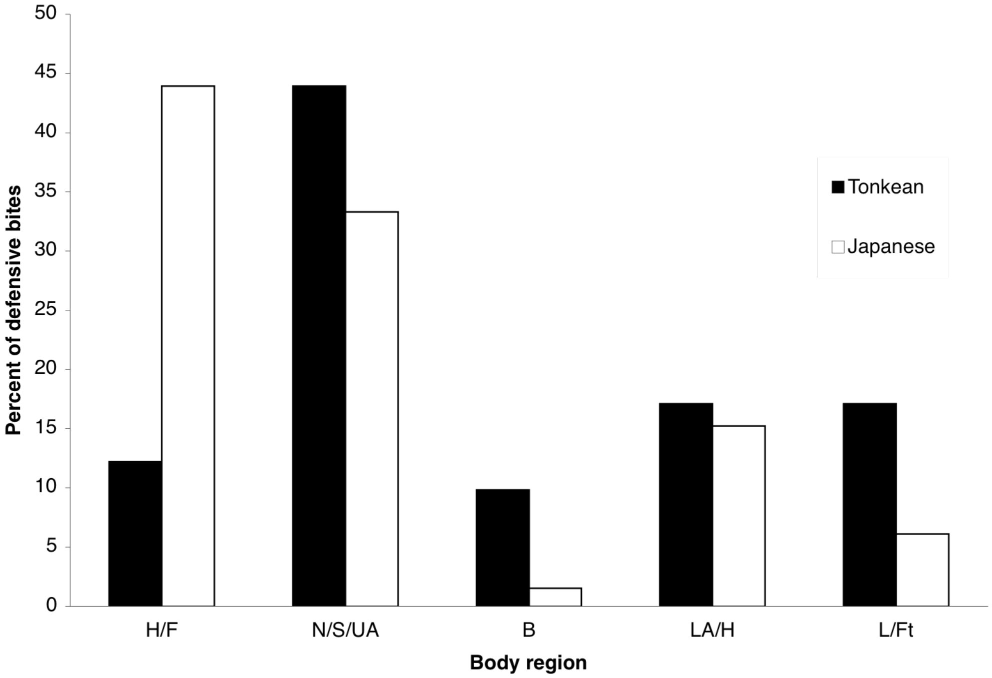


Figure 4.3 (A) Offensive and (B) defensive bite distributions during polyadic play fights. Body regions: Head/Face (H/F), Neck/Shoulder/Upper arm (N/S/UA), Body (B), Lower arm/Hand (LA/H), Leg/Foot (L/Ft). (Total number of offensive bites: Tonkean 183, Japanese 167; defensive bites: Tonkean 41, Japanese 66.)

Tonkean defensive: $X_r^2 = 63.4$, $df = 4$, $p < 0.001$; Japanese offensive: $X_r^2 = 156.18$, $df = 4$, $p < 0.001$; Japanese defensive: $X_r^2 = 103.4$, $df = 4$, $p < 0.001$).

Follow-up analyses using Wilcoxon matched-pairs-signed-ranks tests using the binned data, showed that for offense, Tonkean macaques bit the N/S/UA significantly more than LA/H (T (9) = 5.5, $p < 0.005$) and H/F (T (8) = 0, $p < 0.005$), whereas for Japanese macaques, the N/S/UA was bitten more frequently than all other regions of the body (T (8) = 2, $p < 0.01$). Although the sample sizes for defensive bites were not sufficient to perform statistical analyses, with more data, it would likely be shown that similar to the F-to-F defensive bite distributions, during polyadic play fights, Tonkean macaques would bite the N/S/UA more than all other body regions. With respect to polyadic defensive bites for Japanese macaques, I would predict that with more data, it would be shown that both the N/S/UA and the H/F would be bitten significantly more than other regions of the body, but the N/S/UA and H/F would not differ from each other. It should be noted that for polyadic play fights, the modal defensive target for Japanese macaques was the H/F, rather than the N/S/UA, suggesting that within the context of polyadic interactions, this species retains a high level of defensive competitiveness.

- Comparing polyadic patterns with F-to-F patterns of play

Additional Chi-square analyses were performed on the pooled raw scores to determine whether or not the offensive and defensive bite distributions observed in polyadic play fights could be predicted by each species' respective F-to-F bite distributions. For Tonkean macaques, both the offensive and defensive polyadic bite distributions differed significantly from what was predicted from the F-to-F bite distributions (offensive: $X^2 = 498.1$, $df = 4$, $p < 0.001$; defensive: $X^2 = 67.0$, $df = 4$, $p < 0.001$), suggesting that Tonkean macaques are targeting different regions of the body in polyadic play fights, as compared to F-to-F contexts. In contrast, for Japanese macaques, although the offensive F-to-F bite distribution could not predict the offensive polyadic distribution ($X^2 = 426.3$, $df = 4$, $p < 0.001$), F-to-F and polyadic defensive bite distributions were not significantly different ($p > 0.05$). That is, although the offensive behaviour of Japanese macaques appears to differ when comparing dyadic and polyadic play fights, for the defensive component of play fighting, they seem to retain the same behaviour patterns in both contexts.

With regard to modal play targets, for Tonkean macaques, the percentage of offensive and defensive N/S/UA bites delivered during F-to-F play fights could not predict N/S/UA bites in polyadic interactions (offensive: $X^2 = 56.24$, $df = 1$, $p < 0.001$; defensive: $X^2 = 20.5$, $df = 1$, $p < 0.001$). That is, as predicted, Tonkean macaques targeted the N/S/UA less during offense and defense in polyadic play fights, as compared to F-to-F contexts, suggesting that they must be biting other regions of the body when playing with multiple play partners. For Japanese macaques, the offensive N/S/UA bites delivered in F-to-F did not differ from those observed in polyadic interactions ($p > 0.05$), meaning, that during polyadic play fights, they continue to contact the preferred offensive play target. In terms of defense, the polyadic distribution of N/S/UA bites was not predicted by the F-to-F N/S/UA distribution ($X^2 = 6.8$, $df = 1$, $p < 0.01$). That is, the N/S/UA was contacted less during polyadic play fights as compared to dyadic play fights. However, when comparing defensive H/F bite distributions, the distribution observed in the F-to-F context did not differ from that observed in polyadic play fights ($p > 0.05$), meaning, that as predicted, even when playing with multiple play partners, Japanese macaques continue to exhibit a relatively high level of defensive competitiveness through their adherence to an agonistic body target.

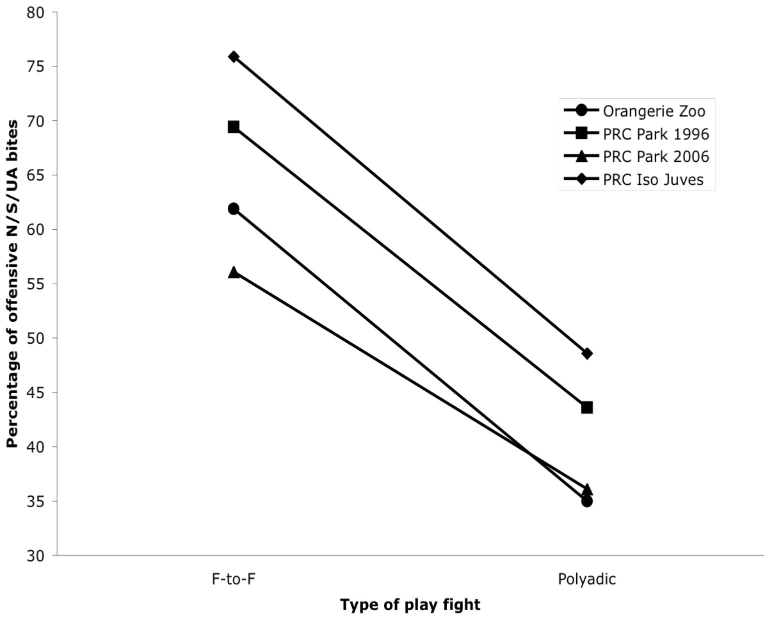
Follow-up analyses using Mann-Whitney U tests showed that Tonkean macaques differed significantly when comparing individualized F-to-F offensive N/S/UA distributions (from Chapter Two of this thesis) with 'binned' polyadic offensive N/S/UA distributions, (U (8, 8) = 8.0, $p < 0.005$), whereas for Japanese macaques, individualized F-to-F offensive N/S/UA distributions did not differ from 'binned' polyadic offensive N/S/UA distributions ($p > 0.05$). These data suggest that the offensive polyadic play patterns of Tonkean macaques (specifically with regard to the modal play target) differ from their offensive dyadic play patterns. In contrast, Japanese macaques tend to maintain relatively consistent play patterns across dyadic and polyadic contexts.

- Interspecies comparisons

Between species comparisons of the offensive and defensive bite distributions using Mann-Whitney U tests, indicated that there were significant between species differences for: (1) offensive B bites (U (8, 9) = 6.5, $p < 0.05$), with Tonkean macaques biting this region more than Japanese macaques, and (2) defensive H/F bites (U (4, 6) = 1.5, $p < 0.05$), with Japanese macaques biting the H/F region more than Tonkean macaques. Indeed, these between species differences in specific body regions targeted during polyadic play fights were predicted in the Introduction, and the data support the proposal that in Japanese macaques, polyadic play fights resemble dyadic ones in their level of competitiveness. In contrast, during polyadic encounters, Tonkean macaque play partners shift from biting the dyadic play target, and will bite one another indiscriminately, on various parts of the body, and will do so without regard for protecting their own play targets. In this way, the cooperative tendencies of Tonkean macaques afford multiple animals to remain locked in playful contact for relatively prolonged periods, as reflected in the play fight durations reported in Chapter Two.

As mentioned, it was important to verify that patterns reported for polyadic play fighting were indeed representative of each species, rather than being idiosyncratic to the focal troops. Chi-square analyses of the pooled raw scores for each troop showed that the distributions of F-to-F offensive N/S/UA bites and polyadic offensive N/S/UA bites could be predicted from the data reported for each of the respective focal troops ($p > 0.05$) (Figure 4.4). That is, the PRC Park 1996, PRC Park 2006 and PRC Isolated juvenile troops, were not significantly different from the Orangerie Zoo Tonkean macaques and the Takahama and Wakasa troops were not significantly different from the Paris Zoo Japanese macaques. It can be seen in Figure 4.4 that, although the absolute level of N/S/UA bites within species may vary slightly, the overall dyadic and polyadic bite patterns are conserved. As was predicted, Tonkean macaques deviate from the play target in polyadic fights and shift to biting other areas of the body, whereas Japanese macaques seem to be more rule-bound in their patterns of play fighting, sticking to their play target regardless of the context.

A. Tonkean macaques



B. Japanese macaques

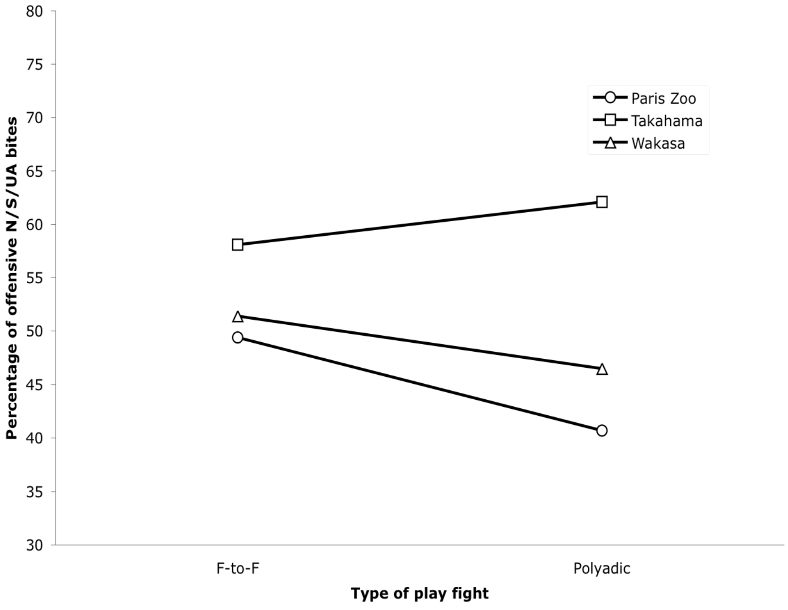


Figure 4.4 Percentage of offensive N/S/UA bites delivered in F-to-F *versus* polyadic play fighting contexts for (A) Tonkean macaques, and (B) Japanese macaques.

Asymmetrical play fights

Chi-square analyses of the pooled raw scores for Tonkean macaques showed that Larger and Smaller juveniles were different for the offensive bite distributions ($X^2 = 13.7$, $df = 4$, $p < 0.01$), and defensive responses ($X^2 = 37.0$, $df = 4$, $p < 0.001$), but not for the defensive bite distribution ($p > 0.05$) (Figure 4.5A and C). When looking at the Chi-square values for each body region and defensive response within the respective distributions, the differences between Larger and Smaller partners become evident. Smaller partners offensively target the L/Ft more than Larger partners, however, this appears to be the only significant deviation between partners. That is, despite the significant difference reported for the offensive bite distributions, Larger and Smaller partners seem to follow relatively similar biting patterns (Figure 4.5A), suggesting that even within the context of asymmetrical play fights, Smaller partners are still able to contact their preferred play target. As predicted, for the defensive responses, Larger partners use the VSELB tactic more than Smaller partners, whereas the latter use the HR and VCELS tactics more than Larger partners (Figure 4.5C). By using the HR and VCELS tactics, the Smaller individuals seem to be exaggerating their existing level of vulnerability to Larger partners. That is, because of their size, Smaller partners are already relatively disadvantaged as compared to Larger partners, and, by using these horizontal/lowered defensive tactics, they move into positions from which it is difficult to defend the play target and launch counterattacks. It appears that similar to the other play fighting contexts that have been examined, during asymmetrical interactions, both the Larger and Smaller partners exhibit behaviours that continue to facilitate a style of play fighting that is relatively cooperative. Indeed, the choice of more vulnerable defensive

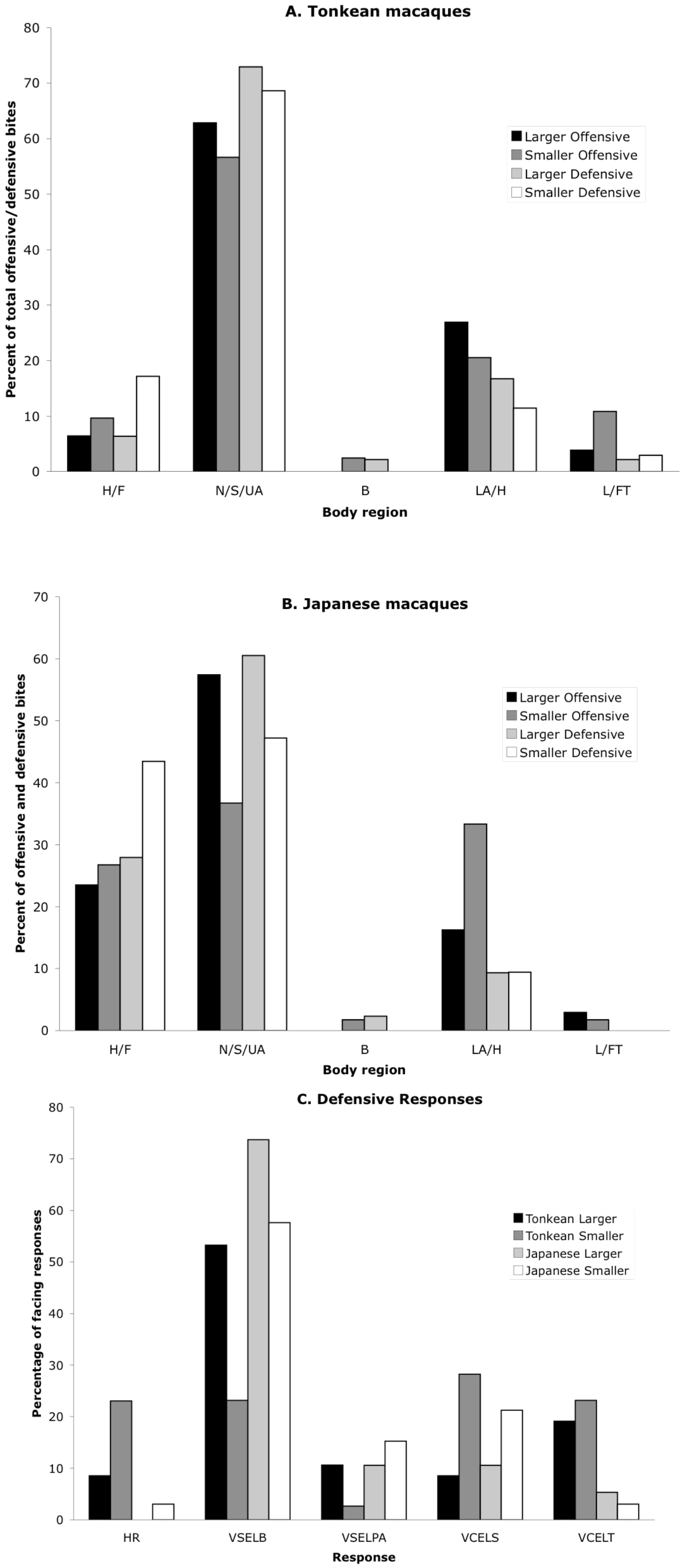


Figure 4.5 Play targets and tactics of defense in asymmetrical play fights. (A) Tonkean macaque bite distributions, (B) Japanese macaque bite distributions, and (C) defensive response distributions for Tonkean and Japanese macaques.

tactics by the Smaller partner likely explains the deviation in offensive targets. By rotating to an on-side or fully recumbent position, or by lowering the body vertically, the area of the Larger partner's body closest to the Smaller partner is the lower legs and feet. By making the first offensive lunge after evading a bite from the Larger partner, a highly likely contact area would be a bite to the feet or lower legs (L/Ft).

For Japanese macaques, Chi-square analyses showed that Larger and Smaller partners were different for the offensive ($X^2 = 16.0$, $df = 4$, $p < 0.01$) and defensive bite distributions ($X^2 = 17.9$, $df = 4$, $p < 0.01$). However, they did not differ for defensive responses ($p > 0.05$) (Figure 4.5B and C). Again, the differences between Larger and Smaller partners become clear when the Chi-square values for each of the body regions are examined. As predicted, the N/S/UA continued to be the primary offensive and defensive play target for Larger partners. In contrast, Smaller Japanese macaques exhibited lower levels of N/S/UA bites for offense and defense, higher levels of offensive LA/H bites, and higher levels of defensive H/F bites, as compared to Larger Japanese macaques. Most of the deviation in targeting appears to be accounted for by a shift in the behaviour of Smaller partners, suggesting that (1) Larger partners may not be accommodating to Smaller partners, and (2) Smaller partners may be hyper-defensive (as per their targeting of the agonistic H/F region). The latter claim is supported by the fact that Larger and Smaller partners did not differ for the defensive responses, indicating that Smaller partners continue to use the preferred, more competitive VSELB tactic, even when playing with Larger partners. As observed previously in the other contexts of play fighting, Japanese macaques appear to exhibit a style of play fighting that is relatively more competitive than that observed in Tonkean macaques.

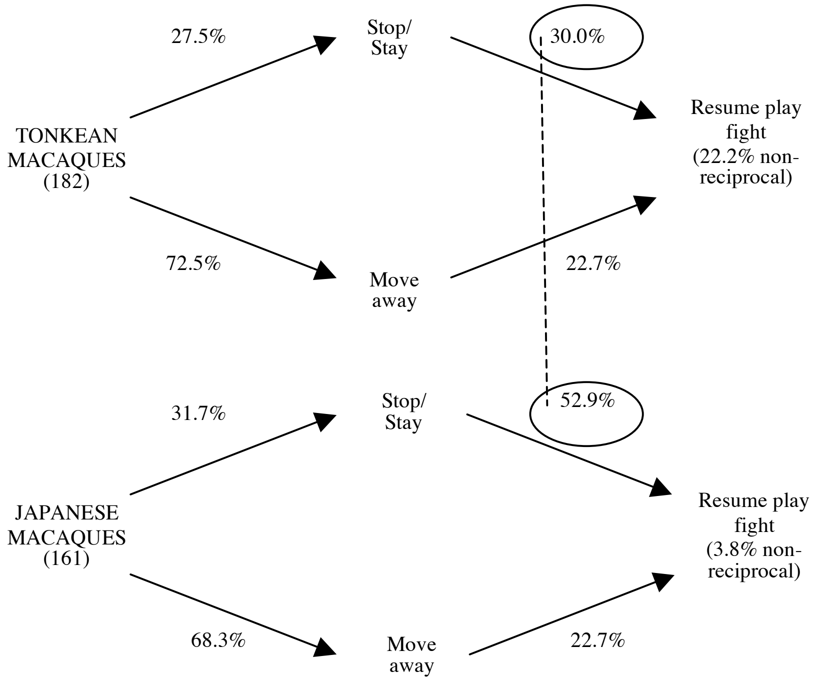
Between species comparisons using Chi-square analyses of the pooled raw scores for the Larger data sets from each species showed that Larger Tonkean and Larger Japanese macaques differed for offensive ($X^2 = 35.2$, $df = 4$, $p < 0.001$), and defensive bites ($X^2 = 35.3$, $df = 4$, $p < 0.001$), but were not different for defensive responses ($p > 0.05$). When the Chi-square values for each of the body regions were examined the significant between species difference was for offensive and defensive targeting of the H/F region, with the Larger Japanese macaques biting this area more than Larger Tonkean macaques. Smaller Tonkean and Japanese macaques were found to be different for offensive bites ($X^2 = 31.9$, $df = 4$, $p < 0.001$), defensive bites ($X^2 = 26.5$, $df = 4$, $p < 0.001$) and defensive responses ($X^2 = 47.8$, $df = 4$, $p < 0.001$). As was shown for the between species comparisons of Larger partners, Smaller Japanese macaques exhibited higher levels of offensive and defensive H/F bites as compared to Smaller Tonkean macaques. The significant difference in defensive responses was reflected in the higher use of the VSELB and VSELPA tactics by Smaller Japanese macaques. To summarize then, during asymmetrical play fights (1) Larger and Smaller Japanese macaques tend to bite, more frequently, agonistic body targets (i.e., H/F) during offense and defense, than Tonkean macaques, and (2) after they have been attacked, Smaller Japanese macaques are more likely to use defensive tactics that allow them to uphold relatively competitive upright postures, whereas Smaller Tonkean macaques use a wider range of defensive responses that are relatively more cooperative.

Finally, the patterns reported for asymmetrical play fighting in the focal troops were compared within species to test whether or not the bite distribution and defensive response patterns were conserved across troops. For Tonkean macaques, Chi-square analyses of the pooled raw scores for the Larger and Smaller play partners in each troop showed that for most comparisons, the troops did not differ from the Orangerie Zoo troop ($p > 0.05$). The only exception was that PRC Park 1996 Smaller partners showed more VSELPA defensive responses than expected ($X^2 = 29.6$, $df = 4$, $p < 0.001$). For Japanese macaques, Chi-square analyses of the pooled raw scores for the Larger and Smaller play partners in each troop showed that there were no differences in offensive bites ($p > 0.05$), and only 1 deviation from expected for defensive bites. The Smaller Wakasa partners showed higher than expected levels of defensive LA/H bites ($X^2 = 39.2$, $df = 4$, $p < 0.001$) relative to the Paris Zoo troop. However, as mentioned in Chapter Three, the Wakasa troop had a high proportion of yearlings, whose behaviour may account for the deviation. For defensive responses, the Larger Takahama partners differed from expected ($X^2 = 9.0$, $df = 4$, $p < 0.05$), however, there was only one defensive response available for the troop to contribute to the distribution. The Smaller Wakasa partners also deviated from expected for defensive responses ($X^2 = 26.8$, $df = 4$, $p < 0.001$), using HR more than expected, but as mentioned, the high number of yearlings may account for this variation. It will be important for future studies to examine the content of play fighting in infants (i.e., individuals less than 2 years old), to confirm whether or not the targets and tactics of play fighting in yearlings differ from that observed in juvenile aged individuals. However, for the purposes of this thesis, it is important to recognize that the species-typical patterns of asymmetrical play are, for the most part, conserved across troops.

Play fight terminations

The two species of macaque were very similar in their patterns of ending play fights, with both about 2 times more likely to move away from the partner than to remain in close proximity (Figure 4.6A). A couple of species-level differences were present, however. Japanese macaques were more likely to resume play fighting after ceasing a play fight, and if the play fight ended with them remaining near one another. A test of difference of proportions showed a significant species difference ($z = 2.58$, $N = 5, 5$, $p < 0.001$). Most critically, with the predicted species differences, while both species were equally likely to move away from the partner at the end of the play fight, Japanese macaques were more likely to leap or run away than were Tonkean macaques (Japanese macaques = 84.5%; Tonkean macaques = 52.3%) (Figure 4.6B). That is, while Tonkean macaques were equally likely to move away from the partner slowly or quickly, virtually all of the departures by the Japanese macaques were rapid ones. A statistical test of proportions showed that the Tonkean macaques were significantly more likely to move away from a partner slowly than were Japanese macaques ($z = 3.39$, $N = 13, 11$, $p < 0.001$). Of all the possible comparisons, the only one for which sufficient scores for individual animals could be obtained was in comparing the proportion of slow withdrawals compared to all withdrawals (i.e., slow plus quick). For seven individuals for each species, the proportion of slow withdrawals was calculated (based on greater than or equal to 6 scores per individual) and compared with a Mann-Whitney U. Tonkean macaques were significantly more likely to withdraw slowly than were Japanese macaques ($U\ (7, 7) = 0$, $p < 0.05$). Therefore, different analyses appear to point to the same conclusion: Japanese macaques break playful contact more rapidly.

A. Relative proximity



B. Relative velocity

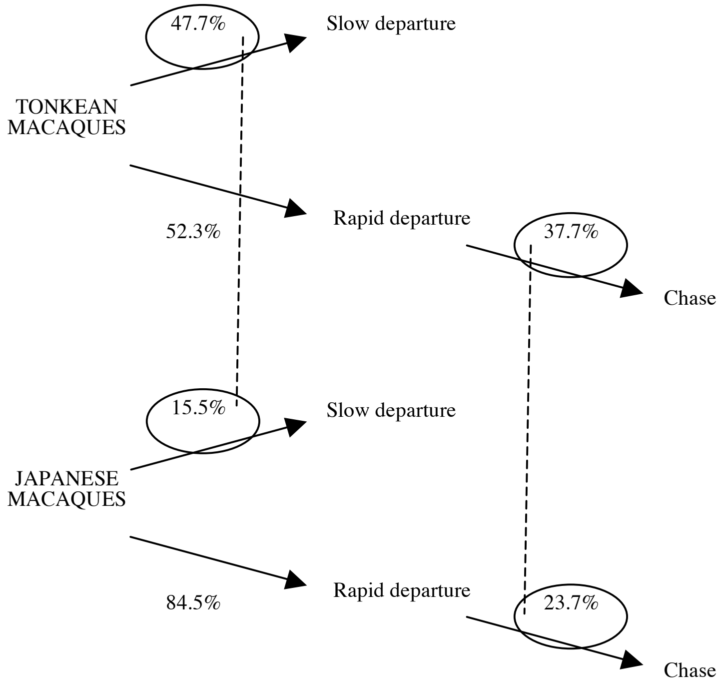


Figure 4.6 Termination styles of Tonkean and Japanese macaques.

A clue as to why such a species difference exists is provided by the fact that if they stay in close proximity at the end of a play fight, Japanese macaques are more likely to resume play fighting (Figure 4.6A). Therefore, it was hypothesized that, for Japanese macaques, a slow departure would increase the risk of resuming play fighting. If so, the likelihood of resuming play fighting should be greater following a slow departure than a fast departure in Japanese macaques, but not different in Tonkean macaques. A test of difference in proportions for within species differences revealed that, indeed, for Japanese macaques, play fights were more likely to resume if the subject departed slowly ($z = 1.69$, $N = 9, 3$, $p < 0.05$), but not for Tonkean macaques ($z = 1.04$, $N = 7, 6$, $p > 0.05$). That is, for Japanese macaques, there is a significant increase in the likelihood of resuming a play fight following a slow departure, jumping from 20.6% to 35.3%. In contrast, the change in the Tonkean macaques is non-significant (18.3% *versus* 25.8%). This interpretation is reinforced by two other species differences.

First, while a proportion of the instances when a partner runs away involve a chase, Tonkean macaques are more likely to do so (37.7% *versus* 23.7%). A test of difference of proportions shows that this species difference is significant ($z = 2.51$, $N = 9, 7$, $p < 0.001$). Therefore, staying or moving away slowly leaves the Japanese macaques more vulnerable to play fights resuming, and running away is less likely to maintain the interest of the partner to follow. Second, if play fights do resume, they are more likely to involve unidirectional mouthing and grappling in Tonkean macaques than in Japanese macaques (22.2% *versus* 3.7%). Although the frequency of occurrence was too low to allow statistical analysis, this possible difference further suggests that if play fights are resumed in Japanese macaques, they involve the full-blown reciprocal exchange.

Finally, when the data were broken down for asymmetrical pairs into whether the younger or the older monkey terminated the play fight, there was a species difference. For these data, given the limited number of animals, all instances were pooled. Once terminated, play fights were more likely to be restarted by the older partner in Japanese macaques ($X^2 = 7.1$, $df = 2$, $p < 0.05$), whereas in pairs of Tonkean macaques, younger partners were just as likely as older ones to restart the play fight ($X^2 = 1.11$, $df = 2$, $p > 0.05$). That is, the percentage of greater re-onsets of play fighting by the older partner doubled in Japanese macaques (17.3% *versus* 8.8%). To supplement these data, 112 Japanese macaque and 83 Tonkean macaque asymmetrical play fights (again from the Zoo troops) were examined, and it was found that in the former species, 67.9% of the play fights were terminated by the older partner, which was significantly more than that of the younger partners ($X^2 = 14.2$, $df = 1$, $p < 0.001$). However, for Tonkean macaques, older partners terminated 53% and younger partners 47% of the interactions, with Chi-square analysis confirming that partners were equally likely to terminate asymmetric play fights ($X^2 = 0.4$, $df = 1$, $p > 0.05$).

4.4 Discussion

The objectives of Chapter Four of this thesis were to generate, based on the behaviour patterns previously identified and the theoretical contexts of the *co-variation hypothesis* and *competition/cooperation model* of play, species specific predictions about play partner preferences and how the content of play fighting may change when the interactions between juvenile macaques are no longer dyadic and/or symmetrical. Numerous predictions about the behaviour expected for each species were presented and between-troop comparisons of the content of play fighting in polyadic and asymmetrical contexts tested these predictions. Indeed, the results reported in Chapter Four appear to support the overall hypothesis for this thesis, that Tonkean macaques are more cooperative and Japanese macaques are more competitive during play fighting.

Previous studies on different species of macaques that exhibit tolerant social styles (including Tonkean macaques) have reported that formal indicators of subordination are relatively rare and that the proportion of friendly interactions among non-kin is quite high, as compared to species that have more despotic social styles (Butovskaya, 2004). For example, in socially tolerant social systems, lower ranking females have a higher diversity of choices for partner affiliation and as such, relative to individuals living in despotic social systems, their social networks are more broad and incorporate individuals from different matrilines (Butovskaya, 2004). For Tonkean macaques specifically, it has been shown that there are no significant kin-preferences in grooming or in aggressive and affiliative support (Butovskaya, 2004). Therefore, to find that juvenile Tonkean macaques showed no strong preference for playing with related or non-related peers is in accordance with the species typical behaviour observed in social contexts involving adults. To play equally with all peers could be considered indicative of cooperativeness, in that regardless of rank or matriline, playful interactions are tolerated and acceptable. In contrast, for Japanese macaques (and as mentioned previously for rhesus macaques), even within the context of play, dominance rank and relatedness heavily influence the combinations of social partners. Perhaps Tonkean macaque juveniles are more willing to potentially ‘lose face’ during a play fight, and for Japanese macaques it may be more important to uphold the ‘social rules and regulations’ of the species, no matter the circumstance.

The final point made above, seems to be supported in many ways by the species differences that were found within the context of polyadic play fights. During multi-partner play, although the N/S/UA was the modal offensive and defensive play target for Tonkean macaques, relative to Japanese macaques, they directed significantly more offensive bites to the B, and directed significantly more defensive bites to the L/Ft. That is, Tonkean macaques deviated from the preferred play target when playing with more than one individual. Their polyadic bite distribution patterns were not only shown to be significantly different from their F-to-F bite distributions, but they were also conserved within species when compared across Tonkean macaque troops. These data suggest that when Tonkean macaques are no longer interacting within a dyadic context, the ‘rules’ of play fighting can be modified, and this is likely attributable to their more relaxed and tolerant temperament. Cross-species comparisons also show that for other hyper-social animals, targeting can deviate to body locations distant from the dyadic play target (Pellis, 1984 (otters); Pellis & Pellis, 1997a (3 primate species); Pellis & Pellis, 1998a (otters and rats).

For Japanese macaques, however, the behaviour patterns exhibited in polyadic play fights were similar to their F-to-F play patterns, and perhaps the former play fights were even more competitive. In polyadic play fights, the N/S/UA was the modal offensive play target, and although this area was bitten often in defense, the H/F (an agonistic target) was the modal defensive target. Importantly, the overall patterns reported for the Paris Zoo Japanese macaques were conserved across troops, meaning that the relatively competitive polyadic bite distribution patterns reported for the focal troop are not idiosyncratic to the troop. Indeed, the rule-bound structure of Japanese macaque social interactions appears to be upheld not only within the context of juvenile dyadic encounters, but also to a large degree in encounters that involve multiple individuals (see also Petit et al., 2008). Knowing that the content of polyadic interactions in Japanese macaques is relatively competitive, now provides an interpretation as to why, in chapter Two, it was found that this species engages in fewer and shorter polyadic play fights than Tonkean macaques.

Within the context of asymmetrical play fights, Tonkean macaques again seem to be more cooperative and Japanese macaques more competitive. When looking at the bite distributions for Larger and Smaller Tonkean macaques, they were found to be statistically different for offensive bites, but not for defensive bites. Despite the reported difference in offense, when considering the content of play fighting more broadly, the differences between Larger and Smaller partners were rather negligible. That is, regardless of partner asymmetry, the overall patterns appear to be highly similar to one another and both partners seem to have access to the play target, suggesting that Larger partners may be facilitating cooperative interactions with Smaller partners by allowing them access to the play target. In turn, Smaller partners tend to reciprocate with relatively cooperative behaviour through their use of particular tactics of defense. Smaller partners were shown to use 4 out the 5 defensive responses relatively equally, but specifically, their use of HR and VCELS tactics suggest that they are willing to move in to positions that reduce their ability to retaliate against a play partner. And, indeed, using these tactics likely influences the change in offensive targets. Therefore, it is the use of tactics that facilitate more, not less, playful contact that lead to targeting differences between Larger and Smaller partners. This is very different from the situation in Japanese macaques.

The differences in bite distributions for Larger and Smaller Japanese macaques were more dramatic than that observed in Tonkean macaques. Typical of the species, Larger Japanese macaques displayed high levels of offensive and defensive N/S/UA bites, as well as relatively high levels of offensive and defensive H/F bites. In contrast, Smaller partners showed lower levels of offensive and defensive N/S/UA bites, and consequently, shifted to biting the LA/H more on offense and the H/F on defense. These patterns suggest that similar to the other play fighting contexts, asymmetrical play fights in Japanese macaques continue to be relatively competitive. It is possible that on the one hand, Larger partners may not be accommodating to Smaller partners by blocking access to the preferred play target, and on the other hand, despite being relatively disadvantaged and unable to reach the play target, Smaller partners persist in biting the regions to which they can get access. More likely, the shift to bites to the LA/H reflect defensive, rather than offensive, bites by the Smaller partner, as in the F-to-F context, a common starting position is to grab each other's arms, and a bite to the hand is one way to induce the partner to let go (Pellis & Pellis, 1997a). So, a combination of the Larger partner limiting access to the preferred target and the Smaller partner attempting to break free from the partner's hold, may account for these targeting changes by the Smaller partner.

The competitive tendency of both partners is also reflected in the defensive tactics they use. Larger and Smaller partners were not shown to differ for defensive responses, meaning that they were both using the preferred VSELB tactic to a great extent. When between species comparisons of Larger and Smaller macaque partners were made, it was found that Larger and Smaller Japanese macaques bite the H/F more than Tonkean macaques, and that Smaller Japanese partners use VSELB and VSELPA more than Smaller Tonkean macaques, suggesting that the overall style of asymmetrical play for Japanese macaques is more competitive than that of Tonkean macaques. Furthermore, the asymmetrical play patterns were conserved when compared with troops for both species, supporting the conclusion that these are species typical behaviour patterns.

An examination of the means for terminating play fights provided further insight into the ways in which Tonkean macaques could exhibit more cooperative behaviour and Japanese macaques more competitive behaviour during play fights. In dyadic interactions, both species were more likely to move away from their play partner, rather than stop the play fight and remain close by. However, when individuals remained close to their play partner, it was more common to see a resumption in play between Japanese macaques. This may seem counterintuitive, but if Japanese macaques have the same motivation as Tonkean macaques to engage in playful interactions, then this may be a means by which they can achieve adequate levels of play. By taking brief pauses in between play fights, rather than having prolonged interactions as observed in Tonkean macaques, Japanese macaques are able to prevent their highly competitive interactions from carrying on too long and reaching a point of aggressive escalation.

Another species difference that was detected with regard to the termination of play fights was the relative speed with which each species tended to end their interactions. Tonkean macaques were equally likely to terminate their interactions with either slow (walking) or fast (running or leaping) departures, whereas Japanese macaques were more likely to exhibit a rapid departure. Furthermore, when an abrupt departure was employed, Tonkean macaques were more likely to be chased by the play partner from whom they evaded. These patterns suggest that the endings to Japanese macaque play fights are more abrupt, and that if an individual moves away quickly; that the play fight is considered by both partners to be over. During asymmetrical interactions in Japanese macaques, play fights appear to be relatively more contingent on the behaviour of the Larger partner, in that play fights are more likely to be resumed and terminated by the Larger partner rather than the Smaller partner. In Tonkean macaques, however, both partners are equally likely to resume or terminate a play fight, which seems to reflect the social symmetry that is typical of this species.

In every context that was examined, Tonkean macaques consistently exhibited more cooperative behaviour than Japanese macaques, and, in contrast, the latter species appeared to behave in a more competitive manner. There are several potential underlying factors that may be responsible for creating and/or maintaining these seemingly, species-typical differences in patterns of juvenile social behaviour, and some of the plausible causes will be discussed in the chapter to follow. To my knowledge, the level of analysis that was applied to the examination of play fighting in these two species was the first of its kind, therefore, the implications for the results of this study will be considered in terms of not only what they can contribute to our understanding of macaque play fighting, but also, the benefits inherent to the analysis by synthesis method for characterizing complex social behaviours in general.

CHAPTER FIVE

General Discussion

The main goals of this thesis were to use the method of analysis by synthesis to examine the content of juvenile play fighting, and as such, characterize the structural organization of this dynamic and complex social behaviour in Tonkean and Japanese macaques. By using this methodological approach for analysing the content of play fights, and applying it to a number of different Tonkean and Japanese macaque troops, it was possible to determine (1) if species typical patterns exist, (2) if play fighting co-varies in a manner similar to that which has been shown for other complex social behaviours in macaques (as would be predicted by the *co-variation hypothesis*), and (3) if inter-specific differences in play fighting are stronger than intra-specific variation. Furthermore, with the *competition/cooperation model* of play borne in mind, I focused specifically on how the competitive and cooperative components of play fighting were organized and modified under each species' social system. It was hypothesized that the more egalitarian Tonkean macaques should exhibit a relatively cooperative style of play fighting, whereas the more despotic Japanese macaques should exhibit a relatively competitive style of play fighting. Specific predictions were made with regard to the patterns of behaviour that were expected to be found for each species, and indeed, these predictions were tested and confirmed not only for various features of play fighting, but also across multiple troops of each species.

5.1 Identifying and interpreting species-specific patterns in play fighting

In Chapter Two, within the context of dyadic play fights, when the partners were facing one another (F-to-F), it was found that Tonkean and Japanese macaques shared the same modal offensive and defensive play target – the neck, shoulder and upper arm area (N/S/UA) – as well as the same modal tactic of defense when bitten on the play target – that of staying vertical, facing the opponent at the same eye-level, while delivering a retaliatory bite (VSELB). That is, a ‘macaque-typical’ pattern of play fighting was identified. However, one strength that is inherent to the method of analysis by synthesis is that play targets and tactics of defense can be examined independently, therefore making it possible to recognize more subtle, but significant, between-species differences in the structure of play fighting. Because Tonkean and Japanese macaques had the same play and agonistic targets, between species comparisons of the modal patterns for offensive and defensive behaviour were made and species-specific deviations from those patterns were identified.

Tonkean macaques tended to contact the play target during offense and defense to a greater extent than Japanese macaques, meaning that the counterattacks of the former species were relatively cooperative. Consequently, the cooperative structure of Tonkean macaque play fights seemed to facilitate their more prolonged dyadic and polyadic interactions as compared to Japanese macaques. In contrast, Japanese macaques bit the N/S/UA less often than Tonkean macaques during offense and defense, and directed a relatively high proportion of their bites to the head and face (H/F), which is an agonistic target. The launching of defensive retaliatory bites toward an agonistic body target suggests an increasing level of agonism and, perhaps, competition in a play fight, and this interpretation was supported by shorter play fight durations and fewer polyadic play fights exhibited by Japanese macaques. Regarding the tactics of defense, when bitten on the play target Tonkean macaques were more likely than Japanese macaques to respond in a manner that allowed the play target to be exposed and that reduced the defender's ability to launch counterattacks. Tonkean macaques appeared to allow themselves to be vulnerable, often by lowering themselves toward the ground in a crouched position or by rolling onto their sides or backs. Japanese macaques, however, used defensive tactics that kept the N/S/UA region well protected in that they maintained upright postures that enhanced their ability to launch defensive counterattacks toward their play partners. Even though a macaque-typical pattern for play fighting was identified, the results of Chapter Two suggest variation on that pattern is present across species - most critically, that species-level variation is consistent with the social style of each species.

Based on the descriptions of the content of each species' dyadic interactions, it is clear that Tonkean macaques seem to engage in behaviours that are more cooperative, and that allow for both play partners to be successful (i.e., contact the play target) during a bout of play. But when two Japanese macaques are playing, they tend to behave in ways that appear to be 'less giving', as each individual tries to maintain a competitive advantage over their partner during the interaction. In Chapter Three, these species differences in the relative levels of cooperativeness and competitiveness exhibited during dyadic play fighting were confirmed when multiple troops of each species were examined; supporting the claim that these truly are species-typical behaviour patterns that were not unique to the focal Zoo troops of Chapter Two. Regardless of the sample population being observed, the macaque-typical modal targets and tactics of defense were consistent and the species-typical patterns of play fighting were conserved across troops. Although some features of play (e.g., play fight durations) were highly variable among troops for both species, the modal targets and tactics varied to a lesser degree. Furthermore, and as predicted, the inter-specific differences in patterns of play fighting were indeed stronger than the observed intra-specific variations.

The topic of developmental stability of species-typical behaviour patterns was given some attention by Symons (1978) in his comprehensive study of aggressive play in rhesus macaques. Symons referred to a review done in 1975 by Seay and Gottfried that focused on the development of rhesus macaque behaviour in environments with varying degrees of impoverishment. This review reported that in a great variety of social and physical environments, species-typical behaviour patterns were maintained, although the frequency of performance of those behaviours was highly variable across contexts. Symons quotes Seay and Gottfried: “Across many environments, almost identical behavioral repertoires develop in conspecific animals; only in extremely, unfavorable environments will the behavioral repertoire of the species fail to appear” (p. 133). The developmental studies on rhesus macaques seem to support the methodological approach that was employed in this thesis, and in part justifies the importance of studying the content of playful interactions, rather than focusing exclusively on how frequently behaviours occur or how long they last. For example, while the absolute frequency with which the play target is attacked may vary, the relative proportion of it being attacked relative to other body areas remains stable.

The analysis of play fighting in the PRC Isolated juvenile troop of Tonkean macaques was well suited for testing whether or not the content of play behaviour would be preserved across different environments because relative to all of the other troops, the PRC Isolated juvenile troop had a social and physical environment that by far made them ‘the outliers’. Despite their abnormal social demographics, novel housing situation, and generally anxious/stressed state, the pattern of their play fights conformed to what was expected for the species, supporting the proposal that, when conducting comparative studies, it is important, to use detailed behavioural measures that represent the actual content of interactions. Without having a thorough understanding about the underlying structure of complex social exchanges (such as play fighting), it is difficult to identify and account for group and species differences in patterns of behaviour. In Chapter Four of this thesis, I continued to focus on comparing the content of play fights, but in this section I examined aspects and contexts of play fighting that were not subjects of analysis in Chapters Two and Three. Rather, based on the conclusions about species typical behaviour patterns drawn from those earlier sections, I made specific predictions about how the two species should behave in these contexts.

Given the greater cooperativeness of Tonkean macaques during dyadic play, I predicted that Tonkean macaques, unlike Japanese macaques, should show little if any bias for preferring to play with siblings. Similarly, I predicted that during polyadic play, Tonkean macaques should be less fixated on the modal play target, be more accommodating when playing dyadically with a smaller partner, and finally, have a more relaxed style for terminating play fights.

To summarize Chapter Four, in all contexts, the behaviour observed for Tonkean macaques was relatively more cooperative than that of Japanese macaques. As predicted, Tonkean macaques were shown to play equally with siblings and non-siblings, suggesting that factors such as dominance rank and kinship affect their playful interactions to a lesser degree than that observed in the more despotic, hierarchical, and nepotistic Japanese macaques (Hayaki, 1983; Imakawa, 1990; Koyama, 1985). When compared to F-to-F bite distributions, the polyadic bite distributions for Tonkean macaques were more widely distributed across the body, especially on the lower parts of the body and feet. The tendency to alter their dyadic pattern of play when interacting with multiple individuals further supports the conclusion that Tonkean macaques are more cooperative in their play fights. In contrast, the polyadic play of Japanese macaques was the same as that of their dyadic play.

In asymmetrical play fights, smaller Tonkean macaques were more likely to adopt defensive tactics that led to them being recumbent and shifting to biting body areas distal to the modal play target – this enabled prolonged contact during such play fights. In contrast, even though less successful in gaining access to the modal play target, smaller Japanese macaques continued to use the same modal defensive tactics. Thus, the asymmetrical play fights of Japanese macaques retained the same competitive quality as symmetrical ones. Larger Japanese macaque partners were also more likely than smaller partners to resume and abruptly terminate interactions, whereas for Tonkean macaques, both partners were equally likely to resume interactions and more casually terminate play bouts. To reiterate, in multiple contexts, and across multiple troops, the style of play fighting was more cooperative in Tonkean macaques and more competitive in Japanese macaques.

It is important to note that the level of detail for which the between-species behavioural comparisons were made was essential for making it possible to identify and understand the distinctive play patterns of Tonkean and Japanese macaques. The method of analysis by synthesis allows the different components of play fighting (i.e., offense/attack, defense) to be teased apart, and as such, each component can be evaluated in terms of how it may be modified in a species-specific manner. It is known from previous research that attack and defense are dissociable and can be modified independently in play fighting (Pellis & Iwaniuk, 2004; Pellis & Pellis, 1991; Reinhart et al., 2004, 2006), thus, an examination of these aspects of play fighting in macaques was necessary and justified. Indeed, the respective cooperative and competitive ‘styles’ that characterize Tonkean and Japanese macaque play patterns could only be differentiated by examining the offensive and defensive components of play separately.

It should also be noted that species differences are relative. For example, because there is a macaque-typical pattern of play, a naïve observer could watch a few bouts of play fighting in both macaque species used in this study (and likely any other species from the *Macaca* genus) and they would likely be unable to detect any noticeable differences between the species with regard to the overall appearance of their playful interactions. It is the proportional distribution of bite targets and defensive tactics that reveal that Tonkean macaques have a more cooperative style of play *as compared* to Japanese macaques, and Japanese macaques have a more competitive style of play *as compared* to Tonkean macaques.

A recent comparative study by Thierry and colleagues (2008) examined conflict resolution in various groups of different macaque species and found that there was a broad range of inter-group variation in conciliatory tendencies and proportions of counter aggression between unrelated individuals. However, there were no significant differences between groups of the same species, and substantial differences between species. Similar to what I have proposed in this thesis, the authors propose that their results demonstrate how detailed data on behavioural interactions can be used in comparative studies to identify subtle, but important and consistent species differences that may not be detected when making comparisons of more broad categories of behaviour, as is typically done. The results of Thierry and coworkers' (2008) study suggest that traits (i.e., expressions of social behaviour) are correlated with the species' social organization, and the results of this thesis lend further support for this proposal, specifically with regard to juvenile behaviour (see also Petit et al., 2008). Once such persistent species differences have been descriptively characterized and confirmed, the question can shift to identifying the causal processes that generate and maintain them. There are several, potential underlying factors that may be responsible for creating and/or maintaining the species-typical differences in patterns of juvenile social behaviour, and I will examine some that I view as most plausible below.

5.2 What shapes play behaviour?

There are likely both genetic and environmental factors that shape how individuals of different species may handle and effectively solve the 'social challenge' of balancing cooperative tendencies with competitive drives, and it is clear from the results of this thesis that juvenile Tonkean and Japanese macaques appear to negotiate the elements of cooperation and competition inherent to play fighting in very different ways. One possible explanation for species differences in social behaviour was mentioned briefly in Chapter One. It was suggested that changes in temperament may have sweeping effects on social behaviour, and, if this is true, then differences in the temperament of macaques may account, at least in part, for the observed species-level variation of the macaque-typical play pattern. For example, the more relaxed temperament of Tonkean macaques could be expressed as higher degrees of cooperativeness, particularly in polyadic and asymmetrical play fighting, and the more reactive temperament of Japanese macaques could be expressed as higher degrees of competitiveness, particularly in the defensive aspects of their play fights.

Although temperament may be a main factor that influences the modal behavioural tendencies in each species, the social organization/style of a particular group/species will also likely influence patterns of social behaviour by either facilitating or inhibiting the expression of certain behaviours. That is, because of a species' social style, some forms of behaviour may be tolerated, but in another group, with a contrasting social style, those same behaviours may be punished. Therefore, the between species variability in patterns of play behaviour found for juvenile Tonkean and Japanese macaques may have been potentially shaped by both temperament (arguably, a biological factor) and social context (an environmental factor). The potential influence of these factors – temperament and social context – will be considered in greater detail below.

The roles of temperament and context

First, it seems important to acknowledge that theoretically speaking, temperament, social organization, and social context may each have influences on social behaviour, but they may also have influences on one another (Figure 5.1). As mentioned previously, temperament refers to behavioural styles or tendencies (rather than distinct behaviours/actions) that can be identified early in life, and that show continuity over time (Clarke & Boinski, 1995). It is commonly believed that temperament is based on biological underpinnings and that certain temperamental qualities may be heritable (Clarke & Boinski, 1995), meaning that individuals can have different behavioral dispositions due to genetic differences. The expression of an individual's behavioural tendencies will surely influence the content of social exchanges (Figure 5.1A), and when these interacting individuals live in a social group, then the accumulation of various dyadic relationships should result in a group that can be recognized as having modal behaviour patterns (B). Taken a step further, the modal tendencies of one group can be compared with the modal tendencies of another group, and when differences arise, it could be said that each group has a particular social 'style' (i.e., one group is despotic or

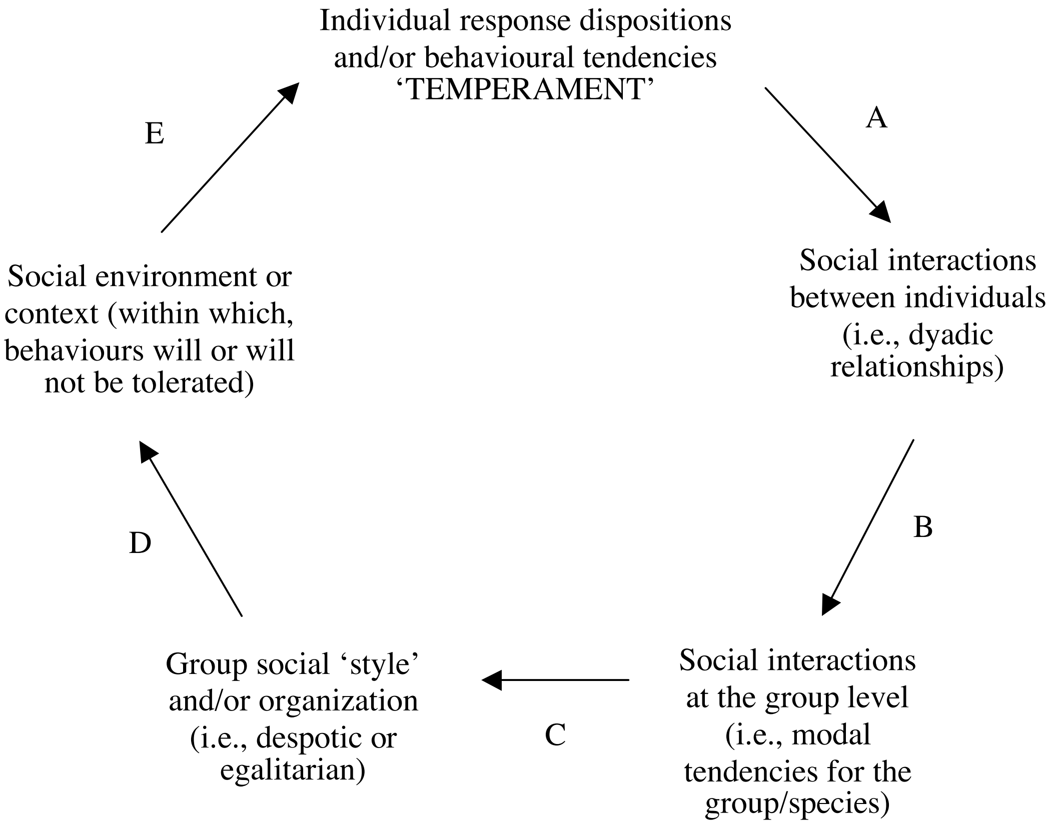


Figure 5.1 Theoretical feedback loop of temperament, social organization, and social context.

egalitarian relative to another group) (C). Therefore, although the individual members of a group will have similar modal tendencies based on temperament, the behaviour of the group as whole will act to foster the maintenance of the species-typical social style further.

As mentioned above, if you are an individual living in an egalitarian social group, within your own group, you would likely be ‘permitted’ to behave in ways that would be considered ‘unacceptable’ if performed within the context of a despotic social group. For example, in a more egalitarian social group, a low ranking female may be allowed to hold the infant of a higher ranking female, whereas in a more despotic group, this type of behaviour may not be tolerated and the higher ranking female may show aggression towards the lower ranking female if she attempts to contact the infant (Thierry, 2000, 2004). The content of these social exchanges creates a ‘social context’ that facilitates or inhibits certain behaviours within the group (D). Even though it is argued that contrasting temperament styles may stem from differences in the species’ physiological organization (which in turn affects its behavioural responsivity), various lines of research suggest that temperament can also be influenced by environmental experiences (Clarke & Boinski, 1995) (E). In summary, it is possible that the influences of temperament (biological/genetic factor) and social context (environmental factor), which are part of a self-perpetuating feedback loop that influence one another, maintain species-specific behavioural dispositions/styles generation after generation, and they may play a strong role in shaping the play behaviour of Tonkean and Japanese macaques. Although this systems way of thinking may be criticized for seeming circular, it is a well acknowledged fact that social organization is made up of multiple feedback loops (Thierry, 2004), thus, to consider any one factor as being more important than the others for shaping the structural organization of social behaviour seems erroneous.

Because macaques arose from a common ancestor and likely share the same basic 'behavioural tool-kit' (Capitanio, 2004), it is most parsimonious to expect that there are no fundamental differences between macaque species in terms of their behavioural repertoires. Rather, species differences in aspects of social behaviour can be thought of as variability in modal tendencies for acting in particular ways, and these tendencies represent different points on the same behavioural continuum. For example, it was shown that there is a macaque-typical pattern for play fighting (common play targets and tactics of defense), which suggests that both Tonkean and Japanese macaques have the same abilities for producing these behaviours within the context of play fighting. However, it was also shown that the macaque-typical pattern can be modified in different ways in each species. The *co-variation hypothesis* states that suites of behaviour change as a unit (Thierry, 2004), and it is possible that a change in temperament may account for the species-level differences found in this study.

One line of research examining the roles of serotonin (5-HT) levels and rearing environment on the development of social behaviour in rhesus macaques, may provide some insight with regard to how a specific neurochemical mechanism that affects temperament, in combination with atypical rearing experiences, may influence play behaviour. Young rhesus macaques with reduced levels of serotonin (i.e., carriers of the ‘short’ 5-HT transporter allele) that grow up with only peer-aged conspecifics, show deficits on various measures of social competency, including infant social play (Barr et al, 2003). Barr and colleagues’ (2003) preliminary work on play fighting and aggression in young rhesus macaques that were either peer-reared (PR) or mother-reared (MR), and either homologous (l/l) or heterogeneous (l/s) for the 5-HT transporter alleles (rh5-HTTLPR), showed that in the context of social play with age-matched peers, all MR animals played less than PR animals, and PR animals carrying the short rh5-HTTLPR allele (l/s) played less than PR l/l individuals.

To explain the lower levels of play in MR animals, the authors suggest that because these individuals have been reared with their mothers, the infants are relatively inexperienced socially. However, more interesting is the argument that l/s infants, because of their genotype, are socially withdrawn regardless of rearing condition. Furthermore, because aggressive behaviour in rhesus macaques typically begins to develop during the second year of life, the authors subsequently reported the mean rates of juvenile aggression in these subjects. PR animals with the l/s genotype exhibited high levels of aggressive behaviour compared to all other groups, and to explain this behaviour, the authors suggest that low activity of the short variant of rh5-HTTLPR (i.e., reduced serotonin) may augment the influence of early maternal absence, resulting in an increased frequency of aggressive behaviour. In summary, l/s infants appear to be socially withdrawn, but then become extremely aggressive as juveniles, and so exhibit a more competitive style of play fighting.

Another example supporting the contention that social context can influence the expression of social behaviour is a study conducted by de Waal and Johanowicz (1993) in which rhesus and stumptail juvenile macaques were co-housed for 5 months so that cross-species influences on behaviour could be examined. They found that in mixed-species groups, play interactions were primarily intraspecific in that the dyadic play rate was between 2-11 times higher among members of same species than between different species, and that the bias for conspecific play did not decrease with time. Because the authors did not report specific details that pertained to the content of the within, and albeit rare, between species play fights, it is unclear whether or not these species differed in their respective styles of play, or if there appeared to be cross-species influences on the patterns of play.

However, it was found that during the co-housing period, rhesus juveniles showed an increasing tendency to reconcile serious fights with conspecific opponents, and the authors propose that this modification of the rhesus macaques' behaviour was a result of having been exposed to the more conciliatory stumptail macaques. In this example, it appears that the characteristics of a particular social environment may have influenced the expression of patterns of social behaviour. However, it is also probable that the specific social context of these cross-species social groups was influenced by species differences in temperament. That is, according to Thierry's classification system (Thierry, 2004), rhesus macaques are categorized as Grade-1 macaques, and stumptails are categorized as Grade-3 macaques, meaning that the former species is known to be relatively more despotic and the latter species more egalitarian. Therefore, the results suggest that the more tolerant and conciliatory behaviours that were exhibited by stumptail juveniles, because of their species-typical temperament, may have influenced the social context of the group, and consequently, the behaviours that were expressed by rhesus macaque juveniles were modified. In fact, it was noted that the changes in the rhesus macaques' conciliatory behaviour were sustained during a 6 week observation period after the species were housed separately, which again illustrates the feedback relationship between temperament and social environment/experience, and their cumulative effects on the expression of social behaviour.

Similar to the serotonergic studies mentioned above, a recent study by Wendland and colleagues (2006) attempted to elucidate, specifically, the genetic basis of social behaviour by comparing two genetic polymorphisms (rh5-HTTLPR and MAOALPR) involved in serotonin and dopamine pathways among 7 different species of macaques. Respectively, these neurochemicals are thought to be associated with anxiety- and depression-related traits as well as aggressive behaviours in humans, and studies suggest that orthologous polymorphic regions identified in rhesus macaques may contribute in a similar manner to the expression of aggressive/anxious social behaviour (Wendland et al., 2006). The authors hypothesized that these specific genetic polymorphisms contribute to the well-documented variability in species-level behaviour within the *Macaca* genus.

The results of their study showed that for four species of macaques that were classified as either a Grade 3 or 4 species, there was only one instance of within species variation detected in the two genotypes that were examined (Tonkean macaques were shown to have two versions of the MAOALPR allele). In contrast, all of the highly intolerant and more hierarchical Grade 1 and 2 macaque species were shown to be polymorphic at one or both loci. This study suggests that within the *Macaca* genus, cross-species variations in temperament may arise from differences in serotonin- and dopamine-related genetic polymorphisms, and an extension of this interpretation would be the prediction that the spectrum of behavioural variability/flexibility in macaque play fighting may correlate with such genotypic variability. If this is true, then there should be greater behavioural variability in rhesus macaques than in other species of macaques, because the former have been shown to exhibit greater genotypic variability (Wendland et al., 2005). However, it is possible that there may be a density dependent effect – if, for example, the proportion of the polymorphism that 'makes' an individual relatively anxious or aggressive is higher in one species than another, then through the combined effect on the overall group interactions, different species may promote and maintain more competitive social styles. Again, this suggests that the effects that temperament and social environment have on social behaviour may be part of the same positive feedback loop.

Despite having contrasting temperaments and social styles, juvenile Tonkean and Japanese macaques both seem to exhibit elements of flexibility in their play, however, the expression and 'type' of behavioural flexibility exhibited by each species seems to differ. Because the 'social rules' for Tonkean macaques seem to be relatively less rigid within the context of play than that observed for Japanese macaques, the former species seem to be permitted to behave in ways that may not necessarily follow the rules of a standard play fight. For example, regardless of the play context or particular individuals involved in the play fight, bite targets can be modified and a variety of defensive responses may be executed. In contrast, Japanese macaques appear to be socially-obligated to adhere to the rules more strictly, suggesting that the amount of flexibility that is afforded by a social context may be species specific, and if so, this means that particular social styles may confound the ways in which individuals are able to generate and express variability in behaviour.

Although there was no formal analysis of this aspect of play fighting, Japanese macaques were able to demonstrate a rather impressive form of behavioural flexibility that allowed them to achieve success in play fighting without breaking the species-typical ‘play fighting protocol’. I can recall a couple of different tactics that were employed by the attackers that allowed them to improve their relative advantage for accessing the play target of the soon-to-be opponent. That is, Japanese macaques would often use approach angles that either came from behind their partners, or orientations that would allow them to launch ‘acrobatic attacks’ (recall Figure 2.1) where they could bounce off of walls or logs to get around the opponent and into a better position to deliver a bite to their neck.

Based on the studies described above and the anecdotal evidence provided, it appears that the social constraints imposed on individuals by their social groups may influence not only the opportunities for interactions between particular play partners, but also the degrees of cooperation and competition that make up the content of those interactions. In her study of play in vervet monkeys, Fedigan (1972) points out that “in play an individual must know at exactly what point a play bite or mouthing is considered severe enough to be a real bite by each individual, how close an infant is to its high-ranking mother when he attempts to play with it, how watchful the mother is, who amongst partners and adults is irritable that day, and so forth" (p. 361). Indeed, the social exchanges that take place between juvenile primates within the context of play fighting likely require a delicate balance that satisfies the playful motivations of the individual partners and, at the same time, adheres to the social rules and behaviour patterns deemed acceptable for the particular social group. For these reasons, play fighting, a behaviour in which animals readily engage and so is readily accessible in captive and free-living troops, may be an ideal window into studying the dynamic interaction between individual temperament and social organization.

5.3 Understanding the organization of play fighting

The species differences between the two species of macaques were quite subtle, and so the analyses of the videotaped sequences needed to discover them were, admittedly, rather arduous. Nonetheless, they were a necessary first step for identifying the core behavioural measures that may be most fruitful for future comparative studies of primate play. Furthermore, it was shown, again and again, across many statistical comparisons, that data derived from scores from individual animals yielded the same results as when data were pooled for the troop as a whole. These findings should give future researchers confidence that when they use measures that focus on the content of social interactions, that even with small sample sizes, species-typical behaviours can be accurately described. Indeed, the analytical framework and the specific behavioural measures that were used to make within and between species comparisons in this thesis could be applied more broadly to describe and compare play fighting in other primates.

A suitable candidate for testing the utility of this method of analysis and the behavioural measures derived from it would be to follow-up on a line of research that has been carried out in the laboratory of Stephen Suomi. Suomi (2005) has shown that in rhesus macaques, many behaviour patterns and tendencies that distinguish impulsively aggressive monkeys from others in their social group initially appear in late infancy and remain consistent throughout development. As young infants, such individuals are socially withdrawn and inactive, however, as juveniles, these individuals exhibit behaviours that have been labelled agitated and hyperactive (Suomi, 1991). Interestingly, young monkeys growing up in field settings who exhibit such patterns, initially do so in the context of rough-and-tumble play with peers (Suomi, 2005). That is, their play tends to be excessively aggressive, and often escalates inappropriately to exchanges that involve actual physical attack. However, it is unclear as to what exactly is happening behaviourally in such instances. What behaviours precede or take place during interactions that become escalated, causing them to break down? Are certain individuals overly competitive or do they behave too intensely? Are biting and other forms of physical contact not restrained, suggesting that some individuals may be playing too competitively? The analytical method and behavioural measurements that I have employed would be valuable for analysing and comparing the content of playful interactions for these different ‘types’ of rhesus macaques, and may provide some insight as to what the animals may be doing behaviourally to cause the social exchanges to break down. Specifically, individual differences in degree of competitiveness should be revealed by modifications in the modal targets attacked and in the modal defensive tactics used, as revealed in this thesis for species differences.

The *competition/cooperation model* of play could also be applied more broadly because it provides a theoretical context from which specific predictions can be made about species-typical behaviours that would otherwise not be obvious. In combination with the behavioural measures devised in this thesis, a more thorough and comprehensive understanding of how the competitive and cooperative components of play fighting can be organized and modified under different social systems in a range of non-human primates could be achieved. In light of the results reported in this study, a revised version of *competition/cooperation model* of play has been proposed, showing that although there is a macaque-typical pattern of play, because of between species variations that seem to depend on the species' social system, each species' pattern can deviate from the average macaque pattern in different directions (Figure 5.2). The more egalitarian, Grade-4 Tonkean macaques show a shift toward the cooperative end of the continuum, whereas the more despotic Grade-1 Japanese macaques show a shift toward the competitive end. It would be predicted that species classified as Grades 2 and 3 would lie somewhere in between these two extremes. In addition, the model could eventually include another dimension. That is, knowing that the different components of play fighting – offense and defense – may be modified in different ways, its possible that two macaque species may be equally cooperative on offense, but that one species may be significantly more competitive than the other in terms of defensive behaviour. The application of the

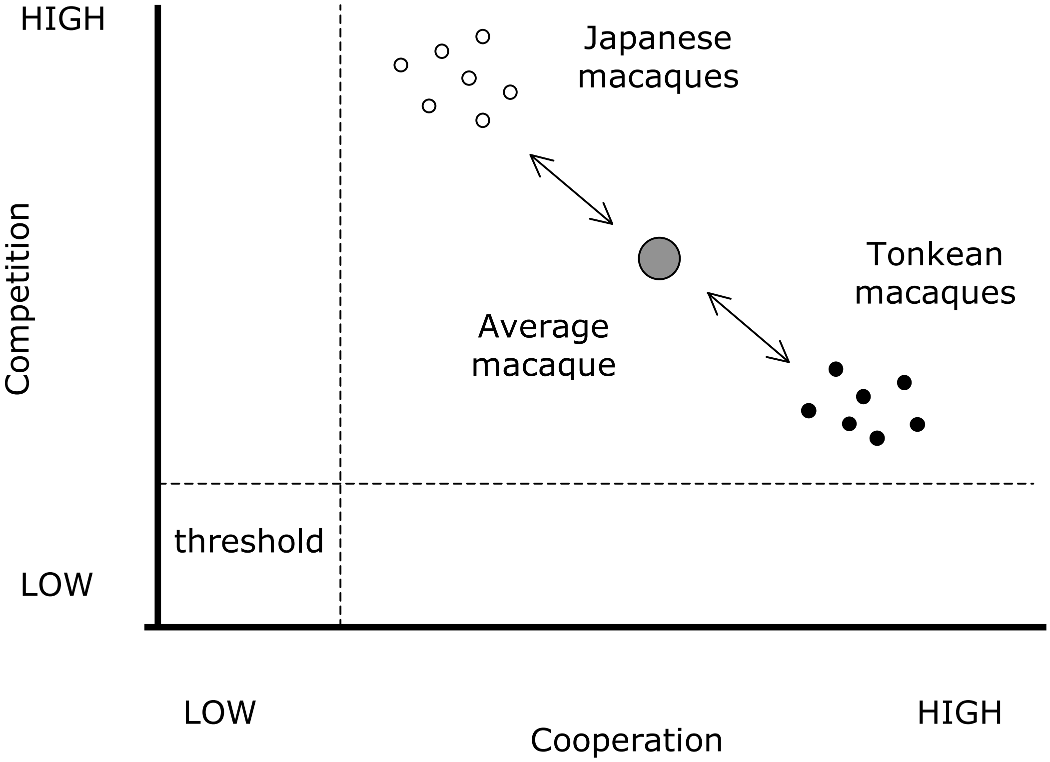


Figure 5.2 A modified version of the *competition/cooperation model* of play, initially described in Chapter One.

analytical techniques described in this thesis and the theoretical framework provided by the *competition/cooperation model* of play, provide the tools for gaining new, and perhaps, revolutionary insights into subtle, but important, species differences in play fighting, and more broadly, how the various aspects of play fighting may be organized and modified throughout the Primate Order.

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APPENDICES

Appendix 1: Troop demography for Tonkean macaques of the Orangerie Zoo (Strasbourg, France 2005)

Name	Sex	Age Group	Age (yrs)	DOB	Mother
Gaston	M	adult	14	14-08-1991	M1 (died)
Greg	M	adult	11	23-08-1994	M2 (died)
Leo	M	adult	8	07-09-1997	Gilette
Gilette	F	adult	17	22-08-1988	M1 (died)
Guilaine	F	adult	10	13-05-1995	Gilette
Amy	F	adult	11	17-10-1994	M1 (died)
Lili	F	adult	8	18-07-1997	M2 (died)
Achille	M	juvenile	5	10-03-2000	Amy
Bob	M	juvenile	4	11-02-2001	Amy
Bonnie	F	juvenile	4	03-01-2001	Guilaine
Charles	M	juvenile	3	23-06-2002	Guilaine
Clide	M	juvenile	3	12-06-2002	Lili
Cleo	F	juvenile	3	28-05-2002	Amy
Coco	F	juvenile	3	16-01-2002	Gilette
Darwin	M	juvenile	2	15-08-2003	Guilaine
Donald	M	juvenile	2	23-07-2003	Gilette
Dany	F	juvenile	2	18-06-2003	Amy
Esther	F	infant	1	23-07-2004	Lili
Eve	F	infant	1	02-09-2004	Amy
Fleur	F	infant	<1	01-06-2005	Guilaine

Appendix 2: Troop demography for Japanese macaques of the Parc Zoologique de Paris (Paris, France 1997)

Name	Sex	Age Group	Age (yrs)	DOB	Mother
Paolo	M	adult	21	02-1976	N/A
Carry	M	adult	20	02-1977	N/A
Willy	M	adult	17	02-1980	N/A
Lima	F	adult	18	02-1979	N/A
Mona	F	adult	17	02-1980	N/A
Kama	F	adult	16	02-1981	N/A
Ella	F	adult	10	08-1987	Kama
Danny	M	adult	9	06-1988	Mona
Claudia	F	adult	9	07-1988	Bima (died)
Rudy	M	adult	9	07-1988	Noa (died)
Olga	F	adult	7	06-1990	Lima
Groseille	F	juvenile	5	05-1992	Ella
Moka	M	juvenile	3	05-1994	Mona
Idra	F	juvenile	3	06-1994	Lima
Clyde	M	juvenile	2	05-1995	Claudia
Jennie	F	juvenile	2	06-1995	Lima
Jessie	F	juvenile	2	06-1995	Olga
Elli	M	juvenile	2	07-1995	Ella
Kenya	F	infant	1	07-1996	Ella
Grizou	M	infant	1	07-1996	Groseille

Appendix 3: Troop demography for Tonkean macaques of the Primate Research Centre - Park (Strasbourg, France 1996)

Name	Sex	Age Group	Age (yrs)	DOB	Mother
Nemo	M	adult	20	1976	N/A
Bulle	M	adult	8	21-08-1988	Bouboule
Vera	F	adult	26	1970	N/A
Bouboule	F	adult	18	?-10-1978	Vera
Julie	F	adult	17	15-10-1979	Mamie (died)
Marie	F	adult	14	23-07-1982	Mamie (died)
Veronique	F	adult	14	10-08-1982	Vera
Daisie	F	adult	7	13-08-1989	Marie
Dilie	F	adult	7	28-01-1989	Julie
Erike	F	adult	6	08-11-1990	Veronique
Elodile	F	adult	6	14-09-1990	Bouboule
Vaclav	M	juvenile	4	10-10-1992	Vera
Vorik	M	juvenile	4	10-01-1992	Veronique
Gemule	F	juvenile	4	06-02-1992	Bouboule
Victor	M	juvenile	3	08-04-1993	Veronique
Milos	M	juvenile	2	12-10-1994	Marie
Janek	M	juvenile	2	11-12-1994	Julie
Virgile	M	juvenile	2	09-09-1994	Veronique
Bemol	M	juvenile	2	17-04-1994	Bouboule
Volodia	M	infant	1	08-12-1995	Veronique
Jeanne	F	infant	1	14-12-1995	Bouboule
Kronos	M	infant	<1	18-04-1996	Marie
Kishar	F	infant	<1	04-05-1996	Erike
Kali	F	infant	<1	12-05-1996	Elodile

Appendix 4: Troop demography for Tonkean macaques of the Primate Research Centre - Park (Strasbourg, France 2006)

Name	Sex	Age Group	Age (yrs)	DOB	Mother
Gaëtan	M	adult	10	07-03-1996	N/A
Jeanne	F	adult	11	14-12-1995	Bouboule
Lady	F	adult	9	11-10-1997	N/A
Néréis	F	adult	7	15-01-1999	N/A
Olga	F	adult	6	25-08-2000	N/A
Patsy	F	juvenile	5	24-08-2001	N/A
Shan	M	juvenile	3	09-09-2003	Lady
Tao	M	juvenile	2	13-03-2004	Néréis
Ulysse	M	juvenile	2	08-01-2005	Jeanne
Ujung	F	infant	1	14-03-2005	Lady
Uhlrich	M	infant	1	05-10-2005	Olga
Uruk	M	infant	1	29-12-2005	Néréis
Baby V	F?	infant	<1	07-04-2006	Lady

Appendix 5: Troop demography for Tonkean macaques of the Primate Research Centre – Isolated Juveniles (Strasbourg, France 2006)

Name	Sex	Age Group	Age (yrs)	DOB	Mother
Tancrède	M	juvenile	2	02-06-2004	Marie
Tethys	F	juvenile	2	10-05-2004	Fannie
Thor	M	juvenile	2	20-11-2004	Daisie
Thulé	F	juvenile	2	22-10-2004	Vero
Tanya	F	juvenile	2	17-10-2004	Gemule

Appendix 6: Troop demography for Japanese macaques of the Primate Research Institute – Takahama B+ (Inuyama, Japan 2007)

Sex	Age (yrs)	Age Group	Sex	Age (yrs)	Age Group
F	27	adult	M	5	juvenile
F	25	adult	F	4	juvenile
F	24	adult	F	4	juvenile
F	19	adult	F	4	juvenile
F	18	adult	M	4	juvenile
F	16	adult	M	4	juvenile
F	14	adult	M	3	juvenile
F	12	adult	M	3	juvenile
M	12	adult	F	2	juvenile
F	11	adult	F	2	juvenile
F	11	adult	F	2	juvenile
M	11	adult	M	2	juvenile
M	11	adult	M	2	juvenile
M	10	adult	F	1	infant
M	9	adult	F	1	infant
F	8	adult	F	1	infant
F	7	adult	F	1	infant
M	7	adult	F	1	infant
F	6	adult	F	1	infant
F	6	adult	M	1	infant
M	6	adult	M	1	infant
F	5	juvenile	M	1	infant
F	5	juvenile	F	< 1	infant
F	5	juvenile	F	< 1	infant
M	5	juvenile	F	< 1	infant
M	5	juvenile			

Appendix 7: Troop demography for Japanese macaques of the Primate Research Institute – Wakasa B (Inuyama, Japan 2007)

Sex	Age (yrs)	Age Group	Sex	Age (yrs)	Age Group
F	23	adult	F	3	juvenile
F	21	adult	M	3	juvenile
F	20	adult	F	2	juvenile
F	17	adult	F	2	juvenile
F	13	adult	F	2	juvenile
F	12	adult	M	2	juvenile
F	11	adult	F	1	infant
F	10	adult	F	1	infant
M	10	adult	F	1	infant
F	9	adult	F	1	infant
F	9	adult	F	1	infant
F	8	adult	F	1	infant
F	8	adult	F	1	infant
M	8	adult	M	1	infant
F	7	adult	M	1	infant
F	6	adult	F	< 1	infant
F	5	juvenile	M	< 1	infant
M	5	juvenile	M	< 1	infant
F	3	juvenile			