Victims of Play Escalation Rank Below Aggressors in Japanese Macaques (*Macaca fuscata*)

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Abstract

In some rare cases of play fighting, previously shared playful states dissociate, and sessions escalate into overt conflict. We hypothesized that play escalation reflects interindividual differences determined by the dominance rank and development. We observed dyadic play fighting in a group of Japanese macaques (*Macaca fuscata*). When play escalated, we defined the individual expressing negative responses (e.g., screaming and bared-teeth displays) as the "victim" and the other individual as the "aggressor." We found that individuals with a lower dominance rank than their playmates became victims in 12 of 15 escalations in same-age dyads. Furthermore, individuals that were younger than their playmates became victims in 17 of 20 escalations in mixed-age dyads. Individuals that subsequently became aggressors (N = 12) had maintained an advantage for a longer duration during the preceding bout of play fighting compared with individuals that became victims (N = 12). These results suggest that escalation might have occurred because one individual (i.e., a higher-ranked or older individual) held an excessive advantage, and play lost its reciprocity. Overall, our results show that play escalation can reflect interindividual differences determined by dominance ranks and developmental stages. Although our results should be treated with caution because of the small sample size and possible risk of pseudoreplication in the analyses, our findings provide insight into the underlying causes of social interaction failure.

Keywords

Dominance · Peer play · Rough-and-tumble play · Social cognition · Social play

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Introduction

The essence of play behavior is difficult to capture, so it is often described in contrast to so-called "serious" behaviors with clear adaptive functions, such as anti-predator, agonistic, and sexual behaviors (Palagi, 2018; Palagi et al., 2016). However, the boundary between "playfulness" and "seriousness" is not absolute. For example, many motor patterns used in play behavior are borrowed from serious behaviors (Caillois, 1961; Fagen, 1981; Palagi et al., 2016). In addition, in both humans (Cordoni et al., 2016) and nonhuman animals (Pellis et al., 2010), playful interactions can sometimes transform into serious behaviors (Palagi et al., 2016). The phenomenon that best illustrates the transgression of the boundary between playfulness and seriousness is the escalation of play fighting into overt hostility.

Play fighting is a type of social play that is common in immature mammals (Burghardt, 2005) and is generally competitive but nonagonistic. Play fighting can involve motor patterns, such as "biting" and "grabbing," which appear similar to those used in the context of aggressive and predation behavior (Bekoff, 1995; Špinka et al., 2016). Play fighting can be distinguished from agonistic interactions by its affiliative nature and the absence of threats and negative expressions, such as screaming (Fry, 2005; Lewis, 2005). Although animals usually perform these pseudoaggressive motor patterns in a self-handicapping manner to avoid injuring playmates, play sessions can sometimes escalate into overt conflict, presumably because of miscommunication of intent between participants, loss of reciprocity, etc. (Cordoni et al., 2018; Palagi, 2018).

To initiate and maintain play, individuals match each other's playful state. For example, in some birds (e.g., common ravens, *Corvus corax*: Osvath & Sima, 2014; Wenig et al., 2021; keas, *Nestor notabilis*: Schwing et al., 2017), play itself or the behavioral patterns accompanying play (i.e., play-call) exhibited by one individual can induce play in others through play contagion (Adriaense et al., 2020; Held & Špinka, 2011). Likewise, chimpanzees (*Pan troglodytes*) watching a video of other chimpanzees engaging in play exhibited play solicitation behavior and displayed play faces, i.e., a relaxed open-mouth display with a slight upward and backward withdrawal of the lip-corners, to the video monitor (Parr & Hopkins, 2000). In contrast, in calves (*Bos taurus*), the presence of less playful individuals decreased the play level of others (Größbacher et al., 2020).

To sustain play fighting sessions, individuals coregulate each other's behavior, match the intensity of the attacks, and maintain the reciprocity of play (Lampe et al., 2019; Palagi et al., 2016). The "50:50 rule" illustrates how animals sustain play reciprocity by allowing their playmates to counterattack, thus making the interaction balanced and symmetrical (Aldis, 1975; Altmann, 1962; Palagi et al., 2016). This rule indicates that escalation can occur when play loses its reciprocity and becomes unfair (Palagi, 2018; Pellis et al., 2010; Pellis & Pellis, 2017). Indeed, a study using game theory models suggested that deviations from the 50:50 rule could lead to interruption of play and escalation into conflict (Dugatkin & Bekoff, 2003). In addition, observations in degus (*Octodon degus*) suggested that individuals that playfully attack a partner subsequently behave in a way that makes it easier for the partner to have an advantage in the next turn (Pellis et al., 2010).

The matching of individuals' playful states and maintaining play without escalation may be enhanced by rapid mimicry of play signals, which are presumably used to share playful intentions among individuals (Burke et al., 2017; Davila-Ross et al., 2011). Multiple studies have shown that rapid mimicry of play faces, which occurs involuntarily in as little as 1 s, prolongs the duration of play sessions (chimpanzees: Davila-Ross et al., 2011; geladas, *Theropithecus gelada*: Mancini et al., 2013; Tonkean macaques, *Macaca tonkeana*: Scopa & Palagi, 2016; meerkats, *Suricata suricatta*: Palagi et al., 2019). Likewise, rapid mimicry of a relaxed open mouth and play bowing during play in dogs (*Canis lupus familiaris*) functions to sustain play (Palagi et al., 2015). In addition, when

Japanese macaques (*Macaca fuscata*) adopt a face-to-face configuration at the beginning of play behavior, subsequent play sessions are prolonged (Iki & Hasegawa, 2020) and play symmetry is enhanced (Iki & Hasegawa, 2021). When this face-to-face opening is combined with a play face, the duration of play is further prolonged (Iki and Kutsukake, under review). The relationship between play signals and play escalation has been directly examined in laboratory experiments with rats (*Rattus norvegicus*), which indicated that the reciprocal use of ultrasonic calls by rats during play serves to prevent play escalation (Burke et al., 2017). Indeed, when researchers used surgery to render one of the rats in a pair unable to emit ultrasonic calls, the risk of escalation increased (Kisko et al., 2015).

If the initiation and maintenance of play are based on the matching of playful states between individuals, then the breakdown of play can be viewed as a dissociation of these previously matched playful states. In general, processes of so-called "self–other matching," a phenomenon in which observation of others' behavioral, emotional, or physiological states causes congruent states in the observer (Hecht et al., 2012), have received substantial attention as the basis for successful social interaction (Adriaense et al., 2020; Duffy & Chartrand, 2015; Hecht et al., 2012; Hess & Fischer, 2013; Massen & Gallup, 2017; Palagi et al., 2020; Preston & De Waal, 2002; Prochazkova & Kret, 2017; Yamamoto, 2017). Compared with the strong focus on self–other matching, such as behavioral mimicry, emotional contagion, and physiological synchrony, few researchers have examined the process of differentiating previously matched states between individuals, which we define as "self–other dissociation."

Several studies have suggested that self–other matching is facilitated by interindividual similarity (Chartrand & Lakin, 2013; Preston & De Waal, 2002). Extrapolating from this, self–other dissociation, the counterpart of self–other matching, may reflect interindividual differences. In animals with a despotic social structure, group members are differentiated from one another through repetitive dominance–subordination interactions (e.g., Chance, 1967; Thierry, 2000). Interindividual differences determined by dominance cause asymmetric interactions (Drews, 1993; Thierry, 2000) and may affect how previously shared playful states dissociate, i.e., escalate into overt conflict. Regarding the effect of dominance relationships on play fighting, a study showed that dominant dogs delivered a greater proportion of attacks in a play session than subordinates (Bauer & Smuts, 2007). Furthermore, another study designed an experimental situation in which male rats encountered one another and found that individuals that behaved more aggressively when play escalated were dominant (Pellis & Pellis, 1991). In addition, studies involving captive and free-ranging primate groups have suggested that play is more likely to escalate in despotic species than in egalitarian species (chimpanzees vs. bonobos, *Pan paniscus*: Palagi & Cordoni, 2012; Japanese macaques vs. moor macaques, *Macaca maura*: Beltrán Francés et al., 2020). However, it remains unclear whether play escalation reflects dominance relationships between play partners in wild group-living animals.

In addition to dominance relationships, developmental differences may also cause loss of play reciprocity and the dissociation of playful states. A previous study indicated that the degree of play asymmetry is greater in mixed-age dyads than in same-age dyads in wolves, *Canis lupus* (Essler et al., 2016). In pairs of dogs of different ages, older individuals delivered a higher proportion of playful attacks than younger ones (Bauer & Smuts, 2007). However, the effects of age differences on the way play escalates are unclear.

Japanese macaques are considered a valuable model for examining the influence of interindividual differences determined by the dominance rank and development on play escalation. Among the species in the genus Macaca, which exhibit a variety of matrilineal dominance styles, Japanese macaques have one of the strictest dominance hierarchies (Thierry, 2000). In immature

Japanese macaques, there are clear physical differences between individuals of different ages (Fooden & Aimi, 2003; Hamada, 1994). Play fighting in Japanese macaques involves aggressive motor patterns, such as biting, grabbing, slapping, and wrestling (Petit et al., 2008; Reinhart et al., 2010). Japanese macaques often use play faces (Scopa & Palagi, 2016) but do not use play vocalizations. Sessions that remain playful do not show any sign of negative emotions, but when a session escalates into overt conflict, one of the players expresses negative responses (e.g., screaming, bared-teeth displays).

In this study, we examined whether play escalation reflects interindividual differences determined by the dominance rank and development by analyzing data on play fighting in juveniles in a free-ranging provisioned group of Japanese macaques. We hypothesized that deviations from the 50:50 rule caused by interindividual differences lead to escalation into conflict. Specifically, we tested the following predictions.

Prediction 1 is relevant to dominance relationships. We defined an individual that expressed negative responses (e.g., screaming) when play escalated as the "victim," and the individual that provoked such responses in the partner as the "aggressor." We predicted that when escalation occurs in same-age dyads (Prediction 1a) or mixed-age dyads (Prediction 1b), individuals ranked higher than their playmates are more likely to be the aggressors, whereas individuals with lower ranks are more likely to be the victims.

Prediction 2 is relevant to developmental differences between individuals. We predicted that when escalation occurred in mixed-age dyads, individuals older than their playmates would be more likely to be the aggressor, and individuals younger than their playmates would be more likely to be the victim.

Prediction 3 is relevant to play reciprocity and unfairness. In play fighting, players compete for an advantage over their play partners by attacking them without being attacked. We predicted that individuals that subsequently became aggressors would maintain an advantage for a longer total duration compared with individuals that subsequently became victims.

Prediction 4 is relevant to the influence of a dominance relationship on postescalation behaviors of the victim. If dominance relationships affect the way previously shared playful states dissociate, the behavior of individuals immediately after escalation may vary according to the dominance relationship. We predicted that a victim with a higher rank than the aggressor would be more likely to counterattack the aggressor, whereas a victim with a lower rank than the aggressor would be more likely to avoid the aggressor.

Methods

Study Site and Subjects

We studied a free-ranging provisioned group of Japanese macaques in Shiga-Heights, Nagano Prefecture, Japan. S.I. made behavioral observations from July to October of 2018 and from July to September of 2019. S.I. observed the group between approximately 09:00 and 17:00 almost every day, resulting in a total observation time of approximately 1,008 h. Demographic records have been kept since 1962, and all individuals are identifiable. As tourists regularly visit the study site, the study group is fully habituated to humans. Park staff give the group barley, soybeans, and apples four times daily (09:00, 12:00, 15:00, and 16:30). Our study group is the only group of macaques that regularly visits the park, and other groups rarely approach the park. Although it was not possible to determine the exact number of individuals in the group, because mature Japanese macaque males migrate between groups and some individuals were located at the periphery of the group (Sprague et al., 1998), the group size was approximately 240 individuals. We determined individuals' age based on

the demographic records. In September 2019, there were 82 adult females (>4 years old), approximately 20 adult males (>4 years old), approximately 110 juveniles (1–4 years old), and 32 infants (<1 year old).

Data Collection

We conducted behavioral observations of agonistic interactions and play fighting sessions and recorded their outcomes and the participating individuals. To assess the dominance ranks, we observed 1,112 unidirectional agonistic interactions using ad lib sampling (Martin & Bateson, 2007). We considered a unidirectional agonistic interaction to have occurred when individual A approached individual B, and the latter exhibited submissive behavior (e.g., bared-teeth displays and screaming) or fled, or when A unilaterally attacked B. We only recorded unidirectional interactions in dyads of adult females. As the Japanese macaque is a highly despotic species, almost all agonistic interactions are completely unidirectional (Thierry, 2000). Therefore, it was easy for the observer to discern the winner and the loser of aggressive interactions. In Japanese macaques, offspring inherit their mother's dominance rank (Chapais, 1988; Kutsukake, 2000). Hence, we considered immature players to have the same ranks as their mothers. A study of rhesus macaques, *Macaca mulatta*, which are close to Japanese macaques phylogenetically and have a similarly despotic society, provided a plausible justification for assigning immature offspring the same rank as their mothers (Berman, 1980). That study showed that the infants of high-ranked mothers were less likely to be threatened or attacked by other group members than the infants of low-ranked mothers. As Japanese macaques form linear matrilineal dominance hierarchies (Chaffin et al., 1995), we indexed dominance using an ordinal rank based on the outcomes of these unidirectional interactions by assigning an ordinal rank value of 1 to the highest-ranked adult female, a value of 2 to the next-highest-ranked adult female, and so on.

To examine the escalation of play fighting, we observed play fighting sessions and recorded data on the outcome of the sessions (i.e., whether they escalated), the identities of the two individuals participating in the sessions, and their behavior after the escalation. To collect these data, the observer stood in specific positions in the park, from which almost all members of the group could be observed, and recorded all visible play fighting sessions between juveniles using a digital video camera (HDR-TD10 211; Sony, Tokyo, Japan). To observe as many incidents of escalation as possible, we used event sampling (Altmann, 1974; Martin & Bateson, 2007). If several bouts coincided, we focused on the dyads with the smallest number of observations. To avoid observation bias, the observer regularly altered their standing position. We did not observe animals 30 min before or after feeding times. We did not use focal sampling because only ~3% of all play sessions escalate in primates (chimpanzees and lowland gorillas, *Gorilla gorilla*: Cordoni et al., 2018; bonobos and chimpanzees: Palagi & Cordoni, 2012; moor macaques and Japanese macaques: Beltrán Francés et al., 2020). We defined the beginning of each bout of play fighting as the point at which an individual directed any playful attack (i.e., biting, grabbing, wrestling) at a partner, and the end as the point at which both individuals of the dyad stopped playing for at least 10 s. A play session that proceeds without escalation usually ends with individuals staying close together or moving away from each other (Reinhart, 2008). There were no "winners" or "losers" in the sessions that remained consistently playful, at least not obviously (Bekoff, 2014; Burghardt, 2005). In contrast, a session that escalates into overt conflict ends with negative responses (i.e., screaming, bared-teeth displays, grimacing) by one of the players. We defined the individual that expressed the negative response as the victim and the partner as the aggressor. To precisely determine the victim and aggressor roles, we only analyzed cases in which only one individual was in physical contact with a victim when the escalation occurred. To exclude cases of affiliative but nonplayful physical contact, only bouts that included at least one instance of biting were analyzed. We did not analyze data from cases in which the first contact between

individuals resulted in overt conflict.

We classified the behavior of each victim immediately after escalation into two categories: retaliation and avoidance. We defined retaliation as instances in which the victim lunged, threatened, bit, or grabbed the aggressor within 5 s of the occurrence of the escalation. We defined avoidance as instances in which no retaliation occurred within 5 s of the escalation, and the victim moved away from the aggressor or maintained negative responses (i.e., screaming, bared-teeth displays, grimacing). There were no cases in which individuals resumed play immediately after escalation.

In total, we recorded 578 cases of dyadic play fighting sessions that proceeded without escalation and 39 cases of escalation of play fighting that met the above criteria. These cases involved 41 juveniles (10 females, 31 males) as aggressors or victims. Each individual was involved in a mean of 1.9 ± 1.3 cases (range 1–7) of escalation. The difference in the number of males and females in our dataset may reflect the fact that immature Japanese macaque males play more frequently than immature females (Eaton et al., 1986). Two of these sessions occurred between siblings. To exclude confounding effects due to sibling relationships, we excluded these cases from our analysis. Two dyads were included in the dataset twice, and the other dyads were included once. To ensure data independence, we randomly selected one session for each of the former two dyads and omitted them from the analysis. Of the 35 remaining cases, 15 were escalations that occurred in same-age dyads (13 cases in dyads of 1-year-old individuals and 2 in dyads of 2-year-old individuals), and 20 cases occurred in mixed-age dyads (11 cases in dyads with an age difference of 1 year, 8 cases with an age difference of 2 years, and 1 case with an age difference of 3 years). We used the former dataset to test Prediction 1a and the latter to test Predictions 1b and 2. For the dataset used for Prediction 3, see the "Video coding" section. Immediately after escalation, a victim's behavior may be affected by confounding effects related to the presence of third parties, such as potential allies. To rule out this confounding effect, we excluded cases in which siblings, mothers, and other playmates were within 5 m of the aggressor and victim at the time of the escalation from our analysis. As a result, 19 cases of escalation were used as the dataset for testing Prediction 4.

Video Coding

To compare the amount of time during which individuals that subsequently became aggressors and victims held the advantage over their partner during the prior play bout, we conducted frame-by-frame video analyses (30.3 FPS) using ELAN software (Lausberg & Sloetjes, 2009). Following previous studies (Bauer & Smuts, 2007; Biben, 1986; Iki & Hasegawa, 2020; Pellis & Pellis, 1997), when a player attacked her/his partner unidirectionally or pinned down her/his partner, we defined that player as having the advantage. An attack was defined as unidirectional if an individual grabbed or bit their partner without being grabbed or bitten by their partner. A player was determined to have pinned down their partner if they stood or sat with their weight on their partner, causing the partner to lie down in a prone, supine, or lateral position. We calculated the proportion of time during which each individual maintained the advantage by dividing the total duration during which each individual maintained the advantage by the total duration of the play session. Following previous studies (Iki & Hasegawa, 2020; Reinhart et al., 2010), we only included play bouts that met the following criteria in the analysis to control for confounding factors: the individuals did not use objects such as stones and branches, the entire bout took place on relatively flat ground and not in a three-dimensional environment, including fences or trees, and the play bout lasted for more than 5 s. Fourteen cases of play bouts met the above conditions and escalated to overt conflicts. The mean duration between the start of play and the escalation of play was 21.5 ± 21.4 (range 5.4–89.6) s. We used these cases as the dataset to test Prediction 3. A separate coder checked the dataset to assess interobserver reliability. The resulting Cohen's kappa values were 0.91 for cases in which the player held an advantage, 1.00

when the player became the victim, and 0.89 when the victims counterattacked or evaded aggressors.

Statistical Analysis

We randomly labeled one of the two individuals involved in the escalation as the "subject player" and the other as the "subject's partner." Fisher's exact test was used to examine whether higher-ranked and older subject players were more likely to be aggressors than lower-ranked and younger ones (Predictions 1 and 2; Table I) and whether postescalation behaviors of the victim varied according to the dominance relationship with the aggressor (Prediction 4; Table I). To compare the proportions of time during which individuals that subsequently became aggressors and those that subsequently became victims maintained the advantage (Prediction 3; Table I), Wilcoxon rank-sum test was performed. We conducted analyses using R ver. 4.0.5 (R Core Team, 2021) and created figures using the ggplot2 package (Wickham, 2016). We set the alpha value at 0.05.

To reassess the results in light of Predictions 1 and 2, we conducted follow-up analyses. We evaluated the correlation between the outcome of play escalation and the rank or age difference by calculating point-biserial correlations using the cor.test function in R. We coded the outcome of play escalation dichotomously according to whether a subject player became the aggressor (1) or the victim (0). We calculated the rank and age differences by subtracting the absolute rank and age of the subject's partner from those of the subject player. Note that our data were pseudoreplicated because the same individuals contributed to multiple dyads. Due to the small sample size, we did not use mixed model analyses, and therefore care is required in interpreting the results.

Ethical Note

This study was observational and noninvasive. All study protocols followed the SOKENDAI ethical guidelines for animal research. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. The authors declare that they have no conflicts of interest to report.

Table I Overview of data on play escalation by Japanese macaques at Shiga-Heights, Japan (July–October 2018 and July–September 2019)

Dataset	No. of escalations	Total individuals	Mean	SD	Min	Max	Category		
							Subtotal no. of individuals	Sex	Birth year
Prediction 1a	15	14 (subject player)	1.07	0.27	1	2	3	Female	2018
							2	Male	2016
							2	Male	2017
							7	Male	2018
Prediction 1b, Prediction 2	20	16 (subject player)	1.25	0.45	1	2	1	Female	2014
							2	Female	2016
							3	Male	2016
							5	Male	2017
							5	Male	2018
Prediction 3	14	12 (aggressor)	1.17	0.39	1	2	1	Female	2018
							1	Male	2015
							6	Male	2016
							4	Male	2018
		12 (victim)	1.17	0.58	1	3	1	Female	2016
							2	Female	2018

Dataset	No. of escalations	Total individuals	Mean	SD	Min	Max	Category		
							Subtotal no. of individuals	Sex	Birth year
							1	Male	2016
							3	Male	2017
							5	Male	2018
Prediction 4	19	16 (victim)	1.19	0.40	1	2	1	Female	2014
							1	Female	2016
							1	Female	2017
							3	Female	2018
							2	Male	2016
							3	Male	2017
							5	Male	2018

Mean, the mean number of escalations in which each individual participated

Data Availability The data analyzed in this study can be accessed at https://bit.ly/3DTwVO9.

Results

For escalations that occurred in dyads of the same age, individuals with a higher rank than their playmates were more likely to be aggressors when escalation occurred (Table II; Prediction 1a supported). However, for escalations that occurred in dyads of different ages, the likelihood of becoming an aggressor did not differ significantly between a subject player with a higher rank than the partner and one with a lower rank than the partner (Table II; Prediction 1b not supported). In contrast, individuals older than their playmates were more likely to be aggressors when escalation occurred (Table II; Prediction 2 supported).

The follow-up analyses using point-biserial correlations corroborated the results. For the escalation that occurred in same-age dyads, we detected a significant correlation between the outcome of play escalation and the rank difference (point-biserial correlation: rpb = −0.63, df = 13, P = 0.012), suggesting that the higher the rank of the subject player relative to their partner, the more likely the subject player was to be the aggressor. In contrast, the correlation between the outcome of play escalation and the rank difference was not significant for escalations that occurred in mixed-age dyads (point-biserial correlation: rpb = −0.19, df = 18, P = 0.426). For those cases, the correlation between the outcome of play escalation and the rank difference was significant (point-biserial correlation: rpb = 0.63, df = 18, P = 0.003), suggesting that the older the subject player was relative to the partner, the more likely the former was to be the aggressor.

With respect to the proportion of time during which each player maintained an advantage over their partner, a player that subsequently became the aggressor maintained an advantage in the preceding play session for a greater proportion of time than a player that subsequently became the victim (Wilcoxon rank-sum test: W = 167.5, P < 0.001; Fig. 1; Prediction 3 supported).

Table II Number of play escalations in which a subject player was the aggressor or victim among Japanese macaques at Shiga-Heights, Japan (July–October 2018 and July–September 2019)

Dataset	No. of escalations	P value*	Relative rank/age of the subject player	Outcome	
				Victim	Aggressor
Prediction 1a	15	0.041	Higher	2	6
			Lower	6	1
Prediction 1b	20	1.0	Higher	7	3
			Lower	7	3
Prediction 2	20	0.007	Older	2	5
			Younger	12	1

*Two-tailed Fisher's exact test

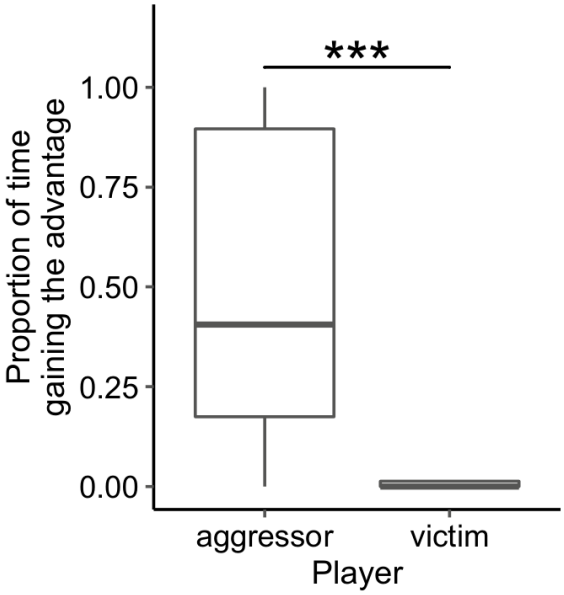


Fig. 1 The proportion of time during which the aggressor or victim maintained the advantage over their partner during the play session in Japanese macaques at Shiga-Heights, Japan (July–October 2018 and July–September 2019). The boxes represent the upper and lower interquartile ranges (IQRs), the horizontal lines indicate the median, and the whiskers represent 1.5 times the upper and lower IQRs. We obtained the P-value by two-tailed Wilcoxon rank-sum test. Sample size: 14 escalations involving 12 individuals that were subsequently aggressors and 12 individuals that were subsequently victims. ***P < 0.001.

With regard to postescalation behaviors, victims with higher rankings than aggressors were more likely to retaliate immediately after the escalation, whereas those with lower rankings than aggressors were more likely to avoid the aggressors (Table III; Prediction 4 supported).

Table III Number of play escalations by Japanese macaques at Shiga-Heights, Japan (July–October 2018 and July–September 2019) in which the victim exhibited retaliation or avoidance

Dataset	No. of escalations	P-value*	Relative rank of the victim	Victim's behavior	
				Retaliation	Avoidance
Prediction 4	19	0.01	Higher	5	2
			Lower	1	11

*Two-tailed Fisher's exact test

Discussion

Overall, our results show that play escalation can reflect interindividual differences between play partners. Specifically, in dyads of the same age, individuals with a lower rank than their playmates were more likely to be victims during play escalation (Prediction 1a supported). The results of our

field observations are consistent with the findings of a laboratory study showing that dominant rats behaved more aggressively when play escalated (Pellis & Pellis, 1991). Many studies have identified social factors affecting the process of self–other matching, such as behavioral mimicry (yawning: Campbell & de Waal, 2011; vigilance: Iki & Kutsukake, 2021; scratching: Laméris et al., 2020), emotional contagion (Bourgeois & Hess, 2008; Weisbuch & Ambady, 2008; for a review, see Hess & Fischer, 2013), and physiological synchrony (Feldman et al., 2011). However, whether self–other dissociation, which is the counterpart of self–other matching, is associated with social factors remains unclear. Our results indicate that interindividual differences determined by dominance relationships may influence the way previously shared playful states dissociate. Follow-up analyses also indicated that the higher the rank of the subject player relative to the partner, the more likely the subject player was to be the aggressor. This result further supports the interpretation that interindividual differences may affect play escalation.

Our results also showed that play escalation reflects developmental/physical differences between individuals. In play escalation that occurred in dyads of different ages, those that were more likely to express negative responses (i.e., victims) were younger than their playmates (Prediction 2 supported). As there are clear physical differences between juvenile Japanese macaques of different ages (Fooden & Aimi, 2003; Hamada, 1994), attacks by an older/larger individual might have caused the play breakdown. In contrast to escalations that occurred in dyads of the same age, the relatively higher-ranked individuals in dyads of different ages were not significantly more likely to become aggressors during escalations than the relatively lower-ranked individuals (Prediction 1b not supported). This indicates that the dissociation of playful states between individuals of different ages may follow a pattern that reflects developmental differences, but not rank differences. The follow-up analyses using point-biserial correlations were consistent with the above results, indicating that for escalations in mixed-age dyads, the age difference was more influential than the rank difference. In addition, it remains possible that body size differences might influence the outcome of escalation even in same-age dyads. Offspring of higher-ranked mothers may be able to gain more weight than those of lower-ranked mothers (rhesus macaques: Bercovitch et al., 2000; although Hinde et al., 2009 found no effect of mother's rank on infant weight in rhesus macaques). Hence, there may be a link between offspring body size and maternal rank. To examine the influence of rank while controlling for physical differences, future studies need to collect data on body size and/or weight.

Individuals that subsequently became aggressors maintained an advantage for significantly longer during the preceding play compared to individuals that subsequently became victims (Prediction 3 supported). This implies that escalation might have occurred because one individual held an excessive advantage, and play lost its reciprocity. This is consistent with previous studies that indicated that asymmetry in the chances of gaining an advantage between players can cause play escalation (Dugatkin & Bekoff, 2003; Palagi, 2018; Pellis & Pellis, 2017). As other researchers have noted, maintaining play reciprocity may be important for continuing to share a playful state (Lampe et al., 2019; Palagi et al., 2016). If so, to elucidate how play escalates into overt conflict, it is important to clarify the relationship between the level of advantage held by each individual and their relative age and rank. Indeed, in some species, dominant individuals are more offensive than subordinate ones during social play (dogs: Bauer & Smuts, 2007), and the degree of play asymmetry is greater in mixed-age dyads than in same-age dyads (wolves: Essler et al., 2016). According to the data used for Prediction 3 ($N = 14$), six escalations occurred in same-age dyads and eight in mixed-age dyads. Due to this small sample size, we did not perform further statistical analyses to clarify the relationship between the level of advantage and each individual's relative age/rank. Future studies with larger sample sizes are needed to address these issues.

Even if it is true that unfairness causes the breakdown of play, it is difficult to determine based on our data whether the aggressor or victim directly triggered the escalation. It is difficult to imagine that the benefits, if any, of turning play into overt conflict would outweigh the costs. Hence, it is unlikely that the aggressor willingly assumes the risk of escalation. Rather, it may be that a victim that reacts negatively to deviation from 50:50 fairness is the direct cause of the escalation. To address this question, it might be helpful to compare the level of advantage each individual maintains during escalated sessions with that in sessions that remain playful to the end.

The postescalation behaviors of victims varied according to the dominance relationship with the aggressor. Victims with a higher rank than their aggressors were more likely to counterattack their partners immediately after escalation, whereas victims with a lower rank were more likely to evade their partners (Prediction 4 supported). In despotic species, such as Japanese macaques, it may be especially inappropriate for lower-ranked individuals to provoke a negative response from higher-ranked ones. One can speculate that to reform and reverse this incorrect relationship, higher-ranked victims may retaliate. This study only focused on victim behavior within 5 s after the escalation to investigate whether a counterattack took place immediately after the play fighting turned into overt conflict. However, given that an individual's emotional state can persist for several minutes (Ioannou et al., 2014), play escalation may affect an individual's behavior beyond the 5-s time window. How play escalation affects subsequent long-term relationships between individuals is an interesting topic for future studies.

The main limitation of our study was the small sample size. As we treated dyads as independent and the same individuals contributed to multiple dyads, a risk of pseudoreplication and possible type I error should be considered. Accordingly, although we found support for Predictions 1 to 4, the results should be treated with caution. As many studies have indicated (Palagi & Cordoni, 2012; Cordoni et al., 2018; Beltrán Francés et al., 2020), play fighting rarely escalates. Therefore, small sample size is an inevitable limitation when studying play escalation based on observational data from wild animals. In addition, as this study included a sample from a single group, our results should not be generalized too hastily to all Japanese macaques.

It would be interesting to determine whether play fighting is more likely to escalate in dyads that play infrequently than in dyads that play frequently. Several species preferentially choose same-age and same-sex partners for play (Boulton, 1991; Thompson, 1996). In long-tailed macaques (*Macaca fascicularis*), whereas the offspring of high-absolute-rank mothers preferentially play with one another, the offspring of low-absolute-rank mothers do not exhibit such rank preferences (Fady, 1976). To examine the effects of partner preference on play escalation, the frequency with which each individual chooses specific partners should be recorded. As we did not use focal sampling, we were unable to collect data on partner preferences, and further detailed studies are needed to address this issue.

Although this study did not focus on this particular topic, it is also possible that how the play begins can influence the outcome (i.e., whether and how it escalates). There are several patterns in which Japanese macaques begin play fighting (Iki & Hasegawa, 2020, 2021). One pattern involves a single play initiator. In this case, play is initiated by one individual making a surprise attack from behind on a partner. In other cases, there is no clear initiator of play, such as when both individuals form a face-to-face configuration and then begin to play together or when individuals continuously transition from other types of social interactions (e.g., grooming and mounting) to play. When there is a single play initiator, it would be interesting to find out whether the initiator is more likely to become an aggressor in play escalation than its partner. In Japanese macaque play fighting, cases with a single initiator are rarer than cases without one (Iki & Hasegawa, 2021). In the dataset used for Prediction 3,

there were only four cases with a clear play initiator. Due to this small sample size, we did not examine whether play initiators were more likely to be aggressors.

Conclusions

This study highlighted the escalation of play fighting into overt conflict as an incidence of self–other dissociation. Our results suggest that the dissociation of playful states may follow interindividual differences determined by the dominance rank and development. To understand how and why play fighting escalates and how animals prevent this from happening, future studies should compare escalated sessions and sessions that remain playful from the beginning to the end. We hope that the results of this study will provide a foundation for such a comparison.

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