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Research Paper

Adult-adult social play in captive chimpanzees: Is it indicative of positive animal welfare?

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ABSTRACT

Play is sometimes considered as an indicator of positive animal welfare. However, it is not yet sufficiently understood whether or not social play among adults can be considered as such an indicator because it is rare in adult animals. This study investigates the factors that influence social play in adult captive chimpanzees in order to discuss its function and use as a welfare indicator. The subjects were 37 adult chimpanzees (17 males and 20 females) living in Kumamoto Sanctuary, Kyoto University, Japan. We completed 367 h of behavioural observation of mixed-sex and all-male groups of chimpanzees between June and July 2014, and December 2014 and March 2015, respectively. We collected data on social play, social grooming (mutual and unilateral grooming), aggressive interactions, self-directed behaviours and abnormal behaviours. We checked the relationship between social play and age, sex, timing, social group formation and different social behaviours. The results reveal that social play increased in males of all-male groups compared to those of mixed-sex groups. Furthermore, we analysed behaviours in individuals from all-male groups and found that social play increased before feeding. In addition, although mutual social grooming showed a negative correlation with aggressive interactions, social play did not show such a relationship. Furthermore, social play and mutual social grooming were negatively correlated. These results suggest that social play may be used as a means to reduce social tension and that it does not necessarily indicate that the individuals formed affiliative social relationships such as mutual social grooming indicates. Therefore, although social play is important to enable the coexistence of multiple adult males who do not always get along well, we need to be cautious when interpreting social play from the view of animal welfare.

1. Introduction

How individuals form social relationships with others is important for the welfare of both human and non-human animals. Studies have shown that close bonds increase the survival rate of infants and lead to longevity (Silk et al., 2003, 2010). A recent study of wild chimpanzees in Budongo forest, Uganda, found that grooming with bonding partners can have a stress reducing effect, as observed in the reduction of the urinary glucocorticoids level after grooming (Wittig et al., 2016). However, social relationships can sometimes have an opposite effect on animal welfare. Increasing social stress is one obvious example. Studies have reported an increase of physiological stress indicators after aggression and with increasing group size in wild chimpanzees (Markham et al., 2013; Wittig et al., 2015). Our previous studies showed that the hair cortisol level (as a physiological index of long-term stress) was higher in captive chimpanzees who received a higher level of aggression, suggesting that social situation affected their stress levels over

long periods (Yamanashi et al., 2013, 2016a). In wild populations of primates, animals have various tactics to reduce the costs of group living. One of these is fission. Another coping strategy is reducing tension and the risk of aggression by engaging in certain affiliative behaviours, such as social grooming and play. Especially in captive situations, where there is not much space for fission, coping by means of this active strategy is important. It has been observed that primates avoid aggression by engaging in affiliative behaviours. Studies have shown that the affiliative behaviours among great apes increased in spatial crowding situations (de Waal, 1989; Nieuwenhuijsen and de Waal, 1982; Ross et al., 2010; Videan and Fritz, 2007).

There are several types of affiliative social behaviours. Among those, social grooming is the most ubiquitous form of affiliative behaviour. Social grooming is considered to be used as a means to establish and maintain social bonds as well as to maintain hygiene. Studies have shown a correlation between grooming interchange and support for agonistic interactions in captive chimpanzees (Hemelrijk and Ek, 1991).

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Mitani (2009) reported that grooming reciprocity occurred between maternal brothers and dyads with strong social bonds. Studies of other primates likewise reported a link between social grooming and affiliative relationships, such as close kin, bond duration and co-feeding (Silk et al., 2006; Ventura et al., 2006). However, compared to the wealth of knowledge concerning social grooming, studies of social play, especially among adults, are scarce. This is because adult-adult social play is rare in non-human animals. For example, Matsusaka (2004) reported that, in a study of wild chimpanzees in Mahale Mountain National Park, Tanzania, only 12 out of 793 bouts of social play occurred between adults, whereas the other 781 bouts occurred including immature individuals. Although many previous studies classify social play and social grooming in the same category of affiliative behaviours, it is not clear whether these two behaviours can be considered identical. It is known that bonobos, a species that is closely related to chimpanzees, are more playful than chimpanzees. Palagi (2006) reported that the rate of social play of adult bonobos increased before feeding rather than control periods. Additionally, Palagi (2006) found that the rate of social play and co-feeding was positively correlated. Tension among group members can be high during the pre-feeding period due to the anticipation for food. Therefore, she concluded that social play between adult bonobos is related to reduce tension between affiliative pairs and hence to reduce aggression. However, the social traits of chimpanzees and bonobos are very different (Hare et al., 2012), and some studies of other mammals failed to find a relation between affiliative relationships and social play (Cordoni, 2009; Sharpe, 2005; Sharpe and Cherry, 2003). Therefore, it is important to understand the details of social play among adults and its relevance to other social behaviours.

Understanding what type of social relationship social play reflects is also important from the perspective of animal welfare assessment. Attention for positive animal welfare has been increasing, and play is sometimes considered as a positive indicator of welfare (Boissy et al., 2007; Held and Špinka, 2011). This is because play is often observed when animals are without chronic stress (Graham and Burghardt, 2010) and is often accompanied by signs of pleasure (Held and Špinka, 2011). In addition to such immediate benefits, play also has delayed benefits and is important for the socio-cognitive development of immature animals (Shimada and Sueur, 2014). A recent study showed that social play during juvenile periods correlated with future copulation behaviours in American minks (Ahloy Dallaire and Mason, 2017). Locomotor play facilitates motor skill acquisition in Assamese macaques (Berghänel et al., 2015). Therefore, increasing the level of play among immature animals can be important from the perspective of animal welfare. Nevertheless, it is controversial whether play, especially social play, which is the most prevalent form of play after maturation (Pellis and Iwaniuk, 2000), can be considered as a positive indicator of welfare (Blois-Heulin et al., 2015). Age, sex and species differences are often associated with the level of social play (Burghardt, 2005). In addition, social play of adult non-human primates is also frequent in contexts of heightened tension, such as pre-feeding time for bonobos (Palagi et al., 2006) and in contexts of group encounter for Verreaux's sifaka (Antonacci et al., 2010). Furthermore, the above-mentioned study of immature Assamese macaques (Berghänel et al., 2015) also reported a negative correlation between physical development and locomotor play rate, which suggests energy-demanding aspects of play. Therefore, it is under debate how we should deal with social play from the perspective

This study investigates the factors that influence social play in adult captive chimpanzees by using unique captive settings to discuss the function of social play. First, we describe the influence of age, sex and group formation on social play levels in chimpanzees living in mixed-sex and all-male groups. Then, we investigate the time distribution of social behaviours, the association among three social behaviours (social play, social grooming and aggressive interaction) in all-male groups of chimpanzees. We also examined the association between social play and abnormal and self-directed behaviours because these behaviours

have been frequently used as indicators of animal welfare (Baker and Aureli, 1997; Duncan and Fraser, 1997). If social play used as a means to reduce social tensions among individuals, social play among adult chimpanzees can increase during times of heightened tension, such as pre-feeding time. Furthermore, we predicted that social play is higher in males than in females and can be increased in all-male groups with many adult males coexisting in a closed environment. If social play can be considered as a means to form and maintain social bond, social play can be an indicative of affiliative relationships similar to how mutual grooming was observed to be (Fedurek and Dunbar, 2009). We predicted that social play can be observed between dyads of affiliative social relationships with high levels of social grooming and low levels of aggressive interaction. Based on these findings, we will discuss the use of social play as an indicator of positive welfare.

2. Methods

2.1. Subjects and housing

The subjects are 37 adult chimpanzees (17 males and 20 females) living in Kumamoto Sanctuary, Wildlife Research Center, Kyoto University (KS). The subjects were divided into several social groups which include both all-male groups and mixed-sex groups (Table 1). In the case of males, we collected data from 11 all-male group chimpanzees and six mixed-sex chimpanzees. Two out of five mixed-sex groups have two males, while other groups have only one male in a group. However, one male from a mixed-sex group with two males moved to another zoo for breeding during the study (September 2014). Therefore, only data from the six males in the mixed-sex group was included. Three to six females lived with those males. The members of the allmale groups changed periodically as described in the Supplementary Table. All individuals were above nine years old, and the details of their profiles and social structures are supplied in the Supplementary 1. Males in the all-male groups of chimpanzees were biologically unrelated except for one dyad that had an uncle-nephew relationship.

Established in 2007, KS was the first chimpanzee sanctuary in Japan (it was renamed from Chimpanzee Sanctuary Uto (CSU) in 2011 when the institution was passed from Sanwa Kagaku Research Institute onto Kyoto University). For more information, see (Morimura et al., 2010). KS accommodates ex-laboratory chimpanzees and chimpanzees that are considered surplus in Japanese zoos. It promotes the social life of chimpanzees. Three types of social groups have formed within KS: allmale groups; one-male and multi-female groups; and multi-male, multifemale groups. The members of the all-male groups are changed periodically to provide social stimulation and prevent escalated aggression, especially directed toward immigrant individuals. All individuals had access to both indoor and outdoor enclosures, most of which are cage style (i.e. a building with a roof), although one outdoor enclosure (approximately 270 m² in area) has no roof. The outdoor cages range in size from approximately 70 m² in area and 5.4 m in height to about 120 m² in area and 12 m in height. All these outdoor cages are connected to other cages. During wintertime, some of the outdoor cages were covered with plastic sheeting so that the chimpanzees could avoid cold temperatures. Passages that connect several cages within KS were introduced, totalling 150 m in length, and groups of chimpanzees could access these passages for exploration in turn. They had free access to

Table 1
Information of observed social groups.

Group type	Number of groups	Number of males	Number of females	Age range
All-male group Mixed-sex group	2 5	11 6	0 20	15–40 9–43

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