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Social interactions and the role of kin recognition within juveniles of a solitary species, the giant panda (*Ailuropoda melanoleuca*)

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Abstract

Kin recognition has been extensively documented in social species, but is less well studied in solitary species, especially in sub-adults. Although giant pandas (*Ailuropoda melanoleuca*) are acknowledged as solitary animals in the wild, in captive settings cubs engage in frequent bouts of affiliative behaviour and evidence suggests that adults are capable of kin recognition. This project examined whether one-year old giant panda cubs displayed kin-biased behavioural interactions based on either genetic relatedness or time spent housed together. Fourteen giant panda cubs were observed at the Chengdu Research Base of Giant Panda Breeding in Sichuan, China during a six-week period in the summers of 2015 and 2016. Focal and instantaneous recording were used to document the behaviour performed by each cub. Neither relatedness nor time spent with other cubs were significant predictors of the amount of time cubs engaged in social interactions. The present study proposes alternatives to explain rates of social engagement of giant panda cubs. Further long-term assessment should be conducted exploring the behavioural impacts of socially housing a solitary species.

Introduction

Kin recognition, the ability to detect related individuals amongst a group, has been exhibited by a range of animal species (Waldman 1987; Holmes and Sherman 1983; Mateo and Johnston 2000; Mateo 2003; Wahaj et al. 2004; Penn and Frommen 2010). Two commonly proposed functional mechanisms for using direct cues to recognise and discriminate kin are prior association and phenotypic matching. Prior association, otherwise known as familiarity, primarily occurs when animals are reared together. During this stage they familiarise themselves with distinctive cues of other animals in their natal range, which are typically kin (Sherman and Holmes 1985; Penn and Frommen 2010). Later in life, animals will identify kin based on the distinguishing characteristics

learned during development, leading to inbreeding avoidance or other non-random social behaviours (Kuester et al. 1994; Komdeur and Hatchwell 1999; Schausberger 2007). The other mechanism, phenotypic matching, arises when animals learn their own distinctive phenotype (the "armpit effect," green beard hypothesis, or self-referent phenotype matching; Dawkins 1982; Mateo 2000; Hauber and Sherman 2001; Mateo 2010). Individuals will use their self-identified phenotype and compare it to unknown individuals' phenotypes to assess if they are kin. This may occur in a variety of modalities, such as olfactory signals in golden hamsters (*Mesocricetus auratus*; Mateo and Johnston 2000), vocalisations in rhesus macaques (*Macaca mulatta*; Pfefferle et al. 2014) or visual cues in peacocks (*Pavo cristatus*; Lacy and Sherman 1983; Petrie et al. 1999).

Using these mechanisms of kin recognition, animals engage in different social behaviours when interacting with kin vs. non-kin. Cooperation with kin members to increase inclusive fitness is well illustrated in the Belding's ground squirrel (*Urocitellus belding*), where an individual will alarm call to relatives when a predator is nearby (Sherman 1981; Mateo 2003). The function of kin biased affiliative interactions has been well documented within social species (see Waldman 1988 for a review), however, it is less common within solitary animals (Eberle and Kappeler 2006; Lizé et al. 2006; Lodé 2008; Flores-Prado and Niemeyer 2010; Kessler et al. 2012). Solitary species interact with siblings on various levels, such as establishing territory (Støen et al. 2005), where kin recognition is advantageous for inbreeding avoidance or to reduce competition with a relative (Simmons 1989; Støen et al. 2005; Fischer et al. 2015).

Although wild solitary species engage in relatively minimal interactions over the duration of their lifespan, captive solitary animals are often socially housed and, as a result, may participate in affiliative interactions more often. Brown bears (*Ursus arctos*) were observed participating in play behaviour more often when housed with another individual than when placed in enclosures by themselves (Montaudouin and Le Pape 2005). As social interactions within wild solitary species are rare, they are difficult to study in situ. Ex situ holdings offer a plausible setting in which to assess what degree kin recognition mechanisms influence social interactions in solitary species.

The role of kin recognition is still not entirely understood in the giant panda (*Ailuropoda melanoleuca*; Dungl et al. 2008; Gilad et al. 2016). The giant panda, a solitary ursid, is thought to devote only a small portion of its life to social activities, such as during mating and cub rearing (Schaller et al. 1985). However, outside of the mating season, wild adult giant pandas will share overlapping home ranges, providing opportunities for social interactions between potential kin (Zhang et al. 2014; Hull et al. 2015). Previous studies on kin and individual recognition in giant pandas have investigated the potential of chemo-sensory, acoustic and visual cues, suggesting phenotypic matching and prior association may be mechanisms used by the species (Charlton et al. 2009a; Charlton et al. 2009b; Dungl et al. 2008; Gilad et al. 2016; Liu et al. 2008; Zhan et al. 2007; Zhang et al. 2014). These investigations warrant further questioning on whether these mechanisms facilitate future associations within giant pandas, and at what life stage they develop.

Due to the scarcity of the species and resources available to monitor them, understanding sociality within wild giant pandas has proved challenging. Previous studies have specifically focused on conducting behavioural research on giant pandas within captive settings (Mainka and Zhang 1994; Liu et al. 2003; Liu et al. 2017; Martin-Wintle et al. 2017). However, there remains a lack of exploration surrounding cub social behaviour. Elements of play between mother and cub dyads have been the focus of prior studies (Snyder et al. 2003; Wilson 2005; Wilson et al. 2009), as social play only occurs between a dam and her cub in the wild (Wilson 2005). In captive settings, more than one cub of the same age may be housed with a dam at a time, thus providing an opportunity for differential interactions. When given the opportunity, cubs were found to engage for longer periods of time in play behaviours, such as biting and pawing, with another conspecific than with a dam. Individual differences and the relationship between cubs were not documented (Wilson et al. 2009).

An increased understanding of the social complexity of a naturally solitary creature in captive conditions can be further understood through analysing giant panda cub behaviour. As solitariness is thought to predate sociality (Hamilton 1964a; Hamilton 1964b; Alexander 1974), looking for mechanisms of kin recognition in a solitary species could shed light on how mechanisms emerged and evolved, such as for establishing territory, refraining from parental care, or avoiding inbreeding (Lodé 2008; Kessler et al. 2012; Fischer et al. 2015). The goal of this project was to determine if kin recognition is an underlying factor facilitating interactions within giant panda cubs. The study predicted that affiliative interactions would be influenced by either the degree of genetic relatedness between individuals, i.e. phenotypic matching, or by the amount of prior association amongst the cubs.

Materials and Methods

Animals
A total of 14 giant panda cubs were observed at the Chengdu Research Base of Giant Panda Breeding in Sichuan, China during the summers of 2015 and 2016. Two sets of female twins, three sets of male twins, and four male singletons were differentiated by three observers using visual identifiers, such as ear size and shape of the black eye spots. All cubs were born at the facility and were approximately one year in age during the time of the study (Table 1). Kinship between the cubs was assessed on three levels: (1) full-kin (twins), (2) half-kin (paternally related), (3) non-kin (do not share a mother or father). Information on how long each cub was housed with one another prior to the study was unknown. Thus, the time each cub was housed with one another was noted by the minutes cubs were observed together from the beginning of the data collection period.

Behavioural observations
Groups consisting of three or more panda cubs were observed, to allow cubs opportunities to interact with more than one panda. As there were no observation sessions where three or more pandas had shared kinship, mixed housing situations were the focus for this study. Mixed housing of the pandas indicated there was at least one kin member and one non-kin member amongst the group. Observations of the cubs' behaviour occurred in one outdoor enclosure (400.0 m²) and seven indoor rooms (62.0 m² [2 areas], 135.0 m² [2 areas], 24.2 m² [1 area]), which ranged in size and public viewing access. Enclosures contained bamboo, as well as enrichment, such as slides, toys, boxes and/or crates. Focal and instantaneous recording at one-minute intervals were employed to collect behavioural data performed by a specific cub.

Each of the observers watched a randomly selected cub for a 30-minute observation session. Sessions that ended before 30 minutes were classified as incomplete and excluded from the data set. These partial sessions mainly occurred when keepers would remove the cubs from the outdoor enclosure to bring them inside. When a session was unfinished, the observer started a new session, watching the same cub as they had in the incomplete session if it was re-located to another enclosure, disregarding any previous data collected from the incomplete session. If the cub was not identified within any other area, the observer would begin a completely new session, examining a different cub for a complete time frame prior to returning to watching the cub from the previous incomplete session, and again disregarding any previous data collected from the incomplete session. All cubs were observed for one complete session in a randomly determined order before starting another round of observations. Data collection occurred between the timeframe of 8:00–16:00 each day of the week, for six weeks per year from June–August. Interactions between pandas were assessed based on proximity to another panda; proximity was limited to one meter, an estimate of a cub's forelimb reach (Zhu et al. 2001). The initiation of an interaction occurred when the two cubs were within a metre of each other. A modified ethogram, based upon Liu et al. (2003) and Snyder et al. (2003), was created to assess affiliative behaviours (Table 2). Any behaviours that occurred outside of one-meter

Table 1. Identification of one-year old giant panda cubs observed within study. Nicknames were assigned to each cub, dam and sire when applicable. Studbook ID numbers are indicated in parentheses (Zhong 2015). Cubs with the same dam and sire were classified as full-kin, cubs with either the same dam or same sire were identified as half-kin, and any cubs that did not share the same dam or sire were noted as non-kin.

Birth year	Sex	Cub (ID)	Dam (ID)	Sire (ID)
2014	Male	Chen Jiu (917)	Cheng Ji (523)	Qiao Qiao (624)
		Zhen Duo (928)	Qi Zhen (490)	Yong Yong (584)
		Shuang Hao (920)	Da Shuang (453)	Mei Lan (649)
	Female	Qi Qiao (924)	Qi Fu (709)	
		Qi Xi (925)		
2015	Male	Meng Lan (954)	Meng Meng (652)	Mei Lan (649)
		Si Da (961)	Si Yuen (593)	
		Si Xiao (962)		
		Jing Da (963)	Jing Jing (598)	Long Long (831)
		Jing Xiao (964)		
		Qing Da (985)	Qing He (537)	Yong Yong (584)
		Qing Xiao (986)		
	Female	Ke Da (947)	Ke Lin (678)	Qiao Qiao (624)
		Ke Xiao (948)		

proximity to another panda cub were noted as solitary behaviour and not specifically analysed as part of this study.

To determine inter-observer reliability, seven 30-minute video clips were analysed amongst the three observers who collected data. One observer documented behaviour in both 2015 and 2016, and the other two observers each documented behaviour in a single year. Through the usage of Fleiss' alpha, a modified Cohen's kappa specifically for three or more raters (McHugh 2012), a kappa score was calculated in RStudio (version 1.1.442, RStudio Inc., Boston, MA). A kappa score of 0.694 was determined amongst the three observers, indicating fair reliability.

Data analyses

The average percentage of time per session that the cubs spent engaging in social behaviour was calculated and the interactions between the cub pairings were classified by relationship: full-kin, half-kin, or non-kin. A two-way nested ANOVA was used in JMP 14.0 (SAS Institute, Cary, NC) to determine if there was a significant difference in the mean percentage of time cubs interacted per session, and if it was influenced by relationship or behaviour. A linear regression was also performed to examine if there was any influence of time housed on the mean percentage of interactions that occurred between cubs. The amount of time cubs were housed with one another prior to the initiation of the study was not available to be factored into the analysis.

Results

A total of 90 complete behavioural sessions were collected across both years, yielding 45 hours of observational data that the cubs were in a mixed housing situation. On average, cubs spent more time displaying solitary behaviours (85.3%), predominantly resting

alone (57.5%). The most prevalent social behaviours observed on average amongst all cubs were play (4.1%), rest (3.9%) and stationary (1.1%). The social interactions of walk and eat were observed less than 1.0% of time, while groom and climb with other pandas was rarely noted, with mean percentages less than 0.1%.

Table 2. Modified ethogram of behaviours used for observations. Social behaviours were identified by proximity, as any of the listed actions that occurred within 1m of another panda cub. If these behaviours occurred outside of 1 m, they were noted as solitary actions.

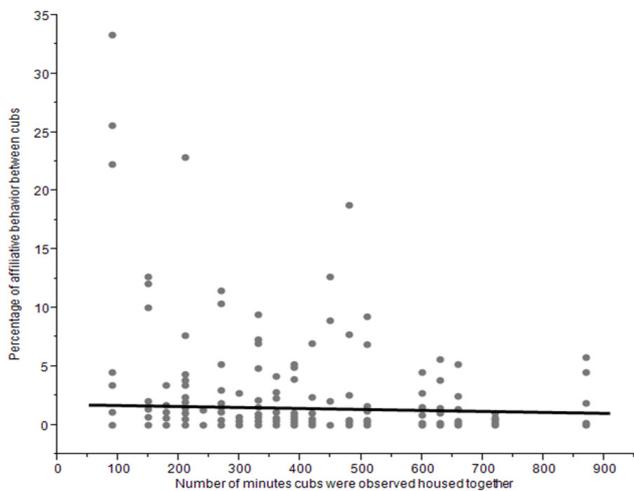| Behaviour	Definition
Climb	Move up or down a climbing structure.
Eat	Put mouth in water; chew, consume, and/or mouth bamboo.
Groom	Lick and/or scratch own fur.
Play	Bite, charge, chew, head-butt, lunge, paw, pull fur, push, sit on, and/or wrestle another panda.
Rest	Lay down with or without eyes closed, unreactive to surroundings.
Stationary	Eyes open in a stationary position, attentive to surroundings.
Walk	Take two or more steps in the same direction.
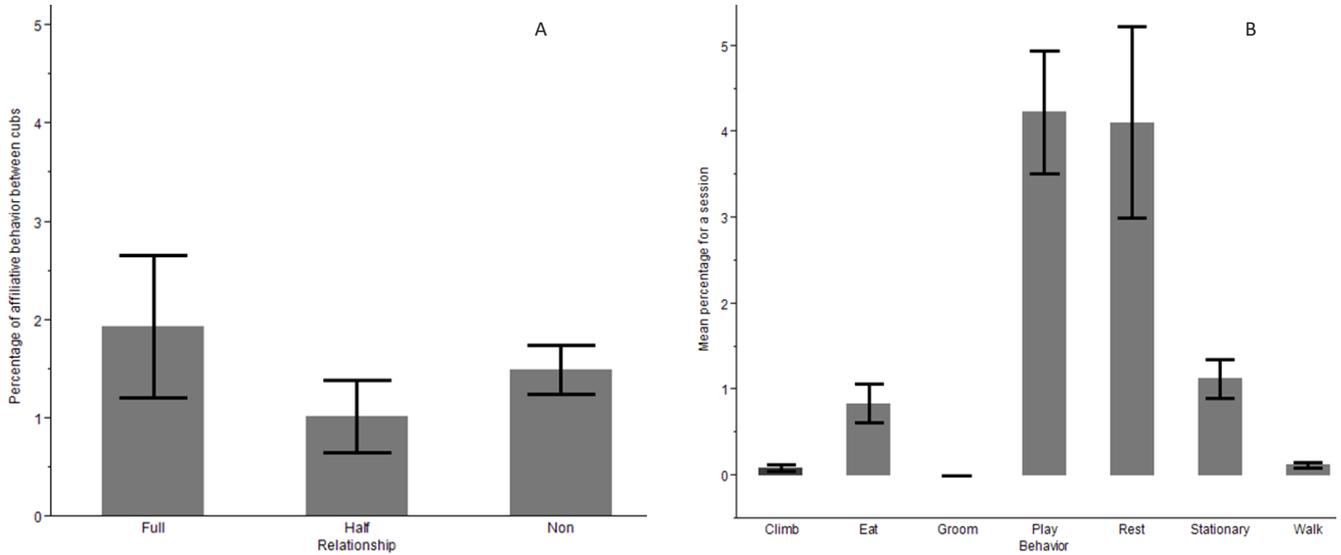
Figure 1. Mean percentage of time full, half, and non-kin spent engaging in affiliative behaviours. There was no significant difference in time spent interacting with cubs based on relationship (A), however there was a difference in observed social behaviours (B) ($F_{6,322}$=5.2, P<0.001*).

Full-kin spent approximately 1.9% of their time per session engaging socially, whereas cubs that shared no relationship interacted 1.4% of the time and half-kin 1.0% of the time (Figure 1A). A nested, two-way ANOVA revealed no significant difference regarding relationship and time spent interacting ($F_{2, 258}$=0.51, P=0.61), or effect of specific panda cub pairings ($F_{41, 258}$=1.17, P=0.30). A significant difference was found within types of behaviour performed ($F_{6, 258}$=13.23, P<0.001); a post-hoc Tukey test revealed that cubs spent a significantly larger percentage of their time playing and resting with other cubs over other social actions (Figure 1B), although this did not interact with relationship in any way.

To assess whether non-kin acted differently towards each other across housing types, when kin were present or absent, a nested, two-way ANOVA was performed on mixed and non-kin social behaviours. Again, a difference was observed in the amount of certain types of behaviours being performed ($F_{6,384}$=9.18, P<0.001), but no effect of housing ($F_{1, 384}$=2.38, P=0.13) or of specific panda cub pairings ($F_{63,384}$=0.92, P=0.65), meaning that cubs' interactions with non-kin does not differ across housing contexts.

The amount of time giant panda cubs were housed together varied amongst individual pairings. Some cubs were never seen in the same enclosure; those who were observed together ranged from three to 29 sessions. A linear regression demonstrated that the time giant panda cubs were housed together did not influence the mean percentage of time cubs interacted per session ($F_{1, 306}$=0.45, P=0.50, R^2=0.001; Figure 2).

Discussion

Kin recognition has been well studied in social animals, but its origins and how it develops and manifests in solitary species is not well understood. The aim of this study was to assess whether patterns of affiliative interactions in sub-adults of a solitary species can be explained by kin recognition. While it was observed that cubs spent more time playing and resting near other cubs than other social behaviours, similar to formerly described panda activity budgets (Liu et al. 2003; Snyder et al. 2003), no evidence was found that giant panda cubs display social interactions in a kin-biased manner based on the mechanisms of phenotypic matching or prior association. Cubs interacted socially with kin and non-kin at similar rates, and there was no linear relationship between time observed together and time cubs spent interacting. Furthermore, it was found that the presence of kin does not change the frequency that cubs interact with non-kin. This raises questions about whether recognising kin at a young age confers a

Figure 2. Percentage of time cubs spent interacting over the course of the study. There was no predictive relationship between duration of time panda cubs were observed housed together and time cubs engaged with one another (R^2=0.001).

benefit to giant pandas, and if so, how it is expressed. Alternative explanations are explored below that could account for the lack of difference in social interactions between kin and non-kin in giant panda cubs.

As cubs do not reach sexual maturity until five to six years of age (Zhu et al., 2001), no mating behaviours occurred within this study. It is possible that kin recognition does not manifest in affiliative behaviours within cubs, but rather is only relevant for adults. Kin recognition in adults could occur either through phenotypic matching in a mating context (Liu et al. 2008) or through prior association (Gilad et al. 2016) after dispersal at the onset of territory establishment. The level of inbreeding within giant pandas is particularly high for a solitary mammal (Hu et al. 2017); therefore, as the levels of kin assessment were based solely on parentage, it is also possible that insufficient genetic differences are present in the focal animals to trigger differential behaviour.

It is important to note the duration of observations for this study occurred in the same season and six-week time span. It is possible that giant panda cubs are basing their social behaviours on kin recognition and this study was too short to detect differences, or that differences are only present in certain seasons, as is the case for adult males (Liu et al. 2008). Longer studies conducted continuously across seasons, such as in predatory mites (*Phytoseiulus persimilis*; Schausberger 2007) and barbary macaques (*Macaca sylvanus*; Kuester et al. 1994), may reveal different patterns within panda cub social interactions, although studies on zebra finch (*Taeniopygia guttata*) fledglings detected kin-recognition behaviour in less than 25 days (Krause et al. 2012). As noted, prior association primarily takes place when animals are raised together in a cohort (Penn and Frommen 2010), which relies heavily on time for repeated encounters. The amount of time cubs were kept together preceding the project was not available to be incorporated into the analysis. Cubs may have been housed with specific kin or non-kin for varying periods; however, record of this was unknown. Giant panda cubs may use prior association, but to definitively elucidate this, the time cubs are housed with one another must be varied and documented.

It is also possible that giant panda cubs do not employ kin recognition and social interactions are random, or are governed by other aspects such as personality or sex. Personality was not a focus within this study, but could yield information as to why specific individuals engage more often with one another (Weinstein et al. 2008). Defining differences in panda personalities has been of interest for mate selection pairings (Powell and Svoke 2008; Martin-Wintle et al. 2017). Exploring personality characteristics in juveniles can provide information as to which individuals are more likely to engage in affiliative social behaviours and can further improve captive breeding, management and welfare of certain species, including the giant panda. Furthermore, within this study, there were no kin that were of mixed sex. Previous literature has noted that both kinship and sex can bias interactions between organisms (Kappeler 1993; MacCormick et al. 2012; Morton et al. 2015). Female rhesus macaques were more affiliative with female half-kin than non-kin (Widdig et al. 2001). Future studies should also focus on how sex and relationship can facilitate interactions within giant panda cubs and other solitary animals.

Lastly, recognition mechanisms could be in place in the giant panda, but cubs may overall fail to recognise kin in the housing and husbandry model observed in this study, possibly due to the Westermarck effect (Westermarck 1891). The current techniques implemented in rearing giant panda cubs within zoological institutions is distinct from how a dam would raise a cub in the wild. Although approximately 60% of the time dams give birth to twins, they will allocate their care towards only one individual, abandoning the other cub (Li et al. 2017). In captive settings, the amount of time each cub spends with its actual dam

is varied, as infant twins are rotated between different mothers and incubators to increase the survival rate of both twins (Zhu et al. 2001; Swaisgood et al. 2003; Edwards et al. 2006). For the first few months of its life, during the time a cub is not with a mother, it is placed into an incubator to receive care from the staff. When the cub becomes old enough, it is introduced to a group of other cubs of the same age and development, presenting opportunities to engage in various social behaviours. Foster mothering, as well as mixed kin housing at an early age, may have confused and prevented kin recognition from developing appropriately. If this were the case then cubs would show no difference in their social preferences because they falsely believe all of the cubs are kin.

Based on this study, it is suggested to continue researching to elucidate if giant panda cubs are capable of kin recognition. If cub interactions are random and not governed by other factors, then follow-up studies to determine if kin recognition behaviour develops during sexual maturation would shed light on whether social housing practices should be reviewed. Given the species' poor history of natural mating in captivity (Zhang et al. 2004), it is possible that mating pairs that were socially reared together, or shared the same foster mothers, may falsely believe they are kin and fail to show appropriate breeding behaviours. If prior association in females is the main force dictating kin recognition, then a mixed-sex, mixed-kin social group of cubs could lead to potential difficulties in the captive breeding program. Long-term investigations on the affiliative behaviour of young solitary animals housed in mixed-kin social groups could reveal vital information towards future management of giant pandas and provide insight on captive management of other solitary species.

Acknowledgements

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