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### Are Giant Pandas (*Ailuropoda Melanoleuca*) Averse to Inequity?

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Are giant pandas (*Ailuropoda melanoleuca*) averse to inequity?

by

Miranda Trapani

Submitted in partial fulfillment  
of the requirements for the degree of  
Master of Arts in Animal Behavior and Conservation, Hunter College  
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Date

Dr. Joshua Plotnik

Signature of First Reader

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## Abstract

Inequity aversion, a negative response to situations of unequal reward distribution, is a cognitive trait usually seen in social species. This capacity is thought to regulate cooperative relationships in intelligent, cognitively flexible animals. Giant pandas are a unique case in that wild populations are characterized as nonsocial, however captive populations are socially housed until sexual maturity. This allows for the study of a nonsocial species in a social context and thus the assessment of socio-cognitive flexibility across evolutionarily distant taxa. Here, we assessed whether the giant panda (*Ailuropoda melanoleuca*) displays inequity aversion by testing ten juveniles living at the Chengdu Research Base of Giant Panda Breeding in China. Traditionally in an equity aversion paradigm, the quality or quantity of the reward offered to the subject is less than that offered to the partner. For this study, effort inequity was used instead due to the limited variety in the giant pandas' diet as well as to further verify this less studied kind of inequity. We tested pandas in an effort inequity paradigm by assessing their responses to several testing conditions: social inequity (two pandas, unequal effort, equal reward), social equity (two pandas, equal effort, equal reward), non-social inequity (one panda, unequal effort, equal reward) and non-social equity (one panda, equal effort, equal reward). In the social inequity condition, the partner was given a piece of apple for free before the subject was cued to perform a hind-leg stand in order to receive a piece of apple. Performance was recorded as positive responses to a cue and latency to complete the trained behavior, a hind-leg stand. Rates of frustration-related behaviors displayed during sessions were also recorded to make judgments on the pandas' emotional state in reaction to the situation. We found no statistical significance across conditions, although one panda's performance on inequity trials was suggestive of inequity aversion. Further testing is required to elucidate the context necessary to elicit this response as

well as what individual differences might be involved that influence an individual's propensity to display inequity aversion.

Keywords: giant panda, inequity aversion, social cognition



Are giant pandas (*Ailuropoda melanoleuca*) averse to inequity?

Inequity aversion is a negative response to situations in which assumptions of equity are violated, such as receiving a smaller reward than a partner for equivalent effort (Range, Horn, Viranyi, & Huber, 2009). This capacity may be important for facilitating cooperation as a driving force for unselfish motivated punishment in humans (Range et al., 2009). Recent research has suggested that this is in fact not a uniquely human cognitive capability. These studies have operationalized paradigms which allow animal subjects to make decisions based on perceptions of fairness as a means of expressing this social ideal non-verbally, a necessity if one hopes to learn about social cognition beyond the scope of linguistic paradigms. The first study assessing inequity aversion in a non-human animal focused on capuchin monkeys (*Cebus apella*) and made use of a token exchange paradigm (Brosnan & de Waal, 2003). For this study, Brosnan and de Waal (2003) compared the response of a subject capuchin across several conditions varying in the food reward offered for completing the task as well as the presence of conspecifics. In the test condition, a partner exchanged a token for a piece of grape, a highly prized reward for a capuchin. Immediately after, the subject received a piece of cucumber for the same task, a much less desirable reward. The authors observed in this condition that the subject both failed to return the token as well as refused offered rewards significantly more often than in the control conditions where both partner and subject received the same reward, or the partner was not present. These results support an earlier evolutionary origin for this sensitivity to inequity and counters the previous assumption that this is an exclusively human trait (Brosnan and de Waal, 2003).

Initially, criticism of this study suggested the frustration effect, a refusal to accept a reward simply because a more desirable reward is in view, as an alternative explanation for this ‘aversion’ behavior (e.g., Dubreuil, Gentile, & Visalberghi, 2006). However, follow-up studies incorporating novel conditions to address this have confirmed that the frustration effect is not an alternative explanation, as well as identified that some amount of effort on the animal’s part, such as the performance of a task, is required in order to elicit the inequity response (Van Wolkenten, Brosnan, & de Waal, 2007). Since then, aversive responses to inequity have been identified in social non-human animals including chimpanzees (*Pan troglodytes*) (Brosnan, Schiff, & de Waal, 2005), long-tailed macaques (*Macaca fascicularis*) (Massen, Van Den Berg, Spruijt & Sterck, 2012), corvids (Wascher & Bugnyar, 2013), rats (Oberliessen, Hernandez-Lallement, Schäble, van Wingerden, Seinstra, & Kalenscher, 2016), and dogs (*Canis familiaris*) (Range et al., 2009; Essler, Marshall-Pescini, & Range 2017). Of the studies completed thus far, the prevalent paradigm has compared an animal subject’s response during a token exchange task when a conspecific is given a food that is of higher value than that which the subject themselves receives to their response when both the conspecific and the subject themselves receive the exact same reward. This food quality inequity paradigm was successful in eliciting an aversion response in primates such as capuchins (Brosnan & de Waal, 2003) and chimpanzees (Brosnan et al., 2005), however, for other social species other types of inequity were more successful in eliciting the aversion response.

Two other types of inequity aversion have also been investigated in non-human animals: food quantity inequity and effort inequity. In dogs, food quality inequity did not elicit an aversive response, but food quantity inequity did (Range et al., 2009). The authors found that when one dog received a larger quantity reward for successfully giving their paw when asked

than the subject did for the same behavior, the subject refused to participate earlier in these sessions than in the solo conditions. The subjects also showed increased levels of stress behavior and took longer to respond when they did participate. Following the inequity condition, the subject spent less time near the partner and took longer to approach the experimenter compared to other conditions (Brucks, Essler, Marshall-Pescini, & Range, 2016).

Effort inequity focuses on the disparity in work required for the animal to receive a reward, rather than any differences between rewards afforded to the partner and subject. Effort inequity has primarily been investigated in relation to food quality such that both effort and food vary between conditions (Brosnan & de Waal, 2003; Van Wolkenten et al., 2007; Massen et al., 2012). A recent review of the inequity aversion literature showed that effort inequity was understudied but may be an important way of studying inequity aversion in other species (Vale & Brosnan, 2017). Since then, a study showed that Goffin's cockatoos were less likely to exchange a token for a reward when a visible conspecific had just received that same reward as a gift (Laumer, Massen, Wakonig, Lorck-Tympner, Carminito & Auersperg, 2019). It should also be noted that in dogs, effort inequity also elicited an aversive response (Range et al., 2016). These more recent studies on different inequity situations add to our understanding of what context elicits this socio-cognitive response.

Other factors may modulate aversive responses in different ways across species. The relationship between the subject and partner, for example, may influence responses in chimpanzees (Brosnan et al., 2005) and dogs (Range et al., 2009). In long-tailed macaques however, the authors did not find dominance order between subjects and partners to be influential in inequity aversion responses (Massen et al., 2012). A recent study of four species of parrots (*Psittacine spp.*) tested mated bird pairs that did not show an aversion response to food

quality inequity (Krasheninnikova, Brucks, Buffenoir, Blanco, Soulet & von Bayern, 2019). However, the closely related Goffin's cockatoo (*Cacatua goffiniana*) has shown an aversion to effort inequity (Laumer et al., 2019). Laumer and colleagues (2019)'s study focused on pairs that were not pair-bonded, indicating that perhaps Krasheninnikova and colleagues (2019)'s subjects would have performed differently had those birds not been tested within dependent pair-bonds. The likelihood of cooperation between conspecifics other than with one's mate in the wild may be a mitigating factor in this response for parrots, but this requires further investigation (Krasheninnikova et al., 2019). In other taxa, the modulation of responses by partner relationship is even less well-understood.

Through the study of socio-cognitive traits like inequity aversion, comparisons across species are made possible that inform our understanding of the evolutionary origins of social cognition. The primary hypothesis of the phylogenetic origin of social intelligence, the adaptive specialization hypothesis, states that through living in social groups, social learning and socio-cognitive traits such as inequity aversion have been evolutionarily favored in these species (Klopfer, 1961). However, this social/nonsocial dichotomy is too simplistic and not reflective of the true continuum observed in social behavior across species (Doody, Burghardt and Dinets, 2012). As an alternative explanation, Heyes (2003) argues that observed variation in cognition is not a product of exclusively phylogenetic changes to cognitive mechanisms themselves, but can be due to any of four different "routes" of both ontogenetic and phylogenetic influence to either the input into the mechanism or the mechanism itself. Through this theory it is suggested that superior performance on social cognition tasks by social species is instead a product of those individuals having increased interaction with conspecifics, thus increasing the salience of social cues and facilitating learning in social contexts (Wilkinson, Kuenstner, Muller, & Huber 2010;

Dolman, Templeton & Lefebvre, 1996). In a similar vein, Vonk & Beran (2012) argue that “demonstrating that a non-social mammal that faces significant foraging challenges exhibits the same sorts of cognitive abilities as more social species within the same order may indicate that adaptive problems faced in the physical environment, such as with foraging, is a better predictor of these kinds of cognitive traits, than is social-living” (pg. 2). It is reasonable to consider that the relationship between socio-cognitive traits and nonsocial or physical cognitive traits is not dichotomized by a phylogenetic origin as previously thought.

While this alternative explanation of the evolutionary origins of social cognition has yet to be experimentally investigated at length, support has been found in the observations of true nonsocial species expressing socio-cognitive skills through social learning. It has been shown that a truly solitary reptilian species, the red-footed tortoise (*Geochelone carbonaria*) is capable of learning to solve a task by observing a conspecific successfully complete that same task (Wilkinson et al., 2010). This suggests a capacity for social learning, a cognitive skill previously expected to be unique to social species, exists in a nonsocial species. Social interactions have been observed as early as gestation; for instance, egg-hatching is often coordinated between siblings in egg-laying species (Doody et al., 2012). Conspecific signaling, courtship dances, cooperative hunting, and socially-cued aggression have also been observed across nonsocial reptilian species (see Doody et al., 2012 for a review). These emerging studies on social behaviors in reptiles, the majority of which are precocious at hatching and live solitary lives, indicate a conflict with the assumption that social learning evolved because of social living and highlight the dichotomous misrepresentation of the label nonsocial versus social. This supports the alternative hypothesis for the evolutionary origins of social cognition suggested by Heyes (2003), however, further comparisons across species that range in their socio-cognitive

phylogeny and ontogeny, particularly ontogenetic variance within a species, is necessary to further support this theory.

The socio-cognitive skills of mammalian carnivores other than the domestic dog (*Canis familiaris*) have not yet been investigated at length (Lea & Osthaus, 2018). Bears pose a unique case as they carry some traits associated with high social intelligence such as large brain size and yet lack the highly social group dynamics of other widely investigated taxa such as canids and pinnipeds (Vonk & Johnson-Ulrich, 2014), indicating that further research is warranted. To my knowledge, there is one social cognition study focused on a bear species. A comparative study between chimpanzees and American black bears (*Ursus americanus*) investigating their social and nonsocial category discriminations required a chimpanzee and three black bears to categorize items using the mother/offspring category for the social condition and the food category for the nonsocial condition (Vonk & Johnson-Ulrich, 2014). For the mother/offspring category, this was done by providing all subjects with images depicting conspecifics that were either a mother with her offspring or some conspecifics without a clear parental bond, such as one or two adult individuals, and rewarding the animal for choosing the image of the mother and offspring. For the food category, the comparisons were food items and nonfood items. During test trials, the images depicted were novel ones not yet experienced by any test subject to ensure that correct responses were not a reflection of learning which pictures were “correct” but an expression of the underlying concept representation guiding that choice. While the bears did not show responses indicative of having a mother/offspring concept representation, one did perform above chance when provided with novel examples for the nonsocial category, indicating a food concept representation (Vonk & Johnson-Ulrich, 2014). Additionally, the authors point out that the bears’ ability to form abstract social concepts cannot be ruled out as this study was on a small

number of individuals (Vonk & Johnson-Ulrich, 2014). More research is necessary to determine what socio-cognitive traits bears express and in what capacity to allow for comparisons across taxa that will further contribute to our understanding about the evolutionary origins of social cognition.

More broadly, research on bears has been limited. Cognition studies published to date have focused on, for instance, picture recognition in black bears, suggesting that bears can successfully recognize physical characteristics of objects from 2D photos (Johnston-Ulrich, Vonk, Humbyrd, Crowley, Wojtkowski, Yates & Allard, 2016), and a capacity for relative quantity judgment when comparing arrays of moving dots (Vonk & Beran, 2012). Ecology studies have found that black bears display social behaviors such as maintaining kin relationships as they will continue to be observed in the vicinity of parents even into adulthood (Rogers, 1987). Brown bears (*Ursos arctos*) will cooperatively divide up access to resources through social hierarchies when gathering to access highly valued resources such as during the yearly salmon run (Egbert, Stokes, & Egbert, 1976; Stonorov & Stokes, 1972). In this context, aggressive behaviors between brown bears were displayed less often during a more prolific salmon run than a year with less salmon (Egbert et al., 1976), indicating that environmental context modulates these social behaviors. Thus, even though bear species tend to lead predominantly solitary lives, their nonsocial cognitive capacities and capabilities for social communication and behavior in wild populations suggest it necessary to determine whether they express socio-cognitive traits and in what contexts.

Giant pandas (*Ailuropoda melanoleuca*), like other bears, are largely solitary animals in the wild (Schaller, 1985) and are considered nonsocial. Although giant panda group dynamics are similar to those of nonsocial species, they do frequently communicate through scent

markings and vocalizations (Swaisgood, Lindburg, White, Zhang & Zhou, 2004). Males will also travel great distances to find, court, and engage with multiple females and compete with rival males (Wei et al., 2015). Additionally, in captivity pandas are often housed in social groups until sexual maturity, unlike in the wild. For captive pandas maintaining and regulating social bonds with non-kin conspecifics may be important and may evoke social behaviors and increase the salience of social cues in ways not seen in wild populations.

Observations of brown bears negotiating access to communal resources also indicate that even primarily nonsocial bears can negotiate for limited resources. Similarly, anthropogenic influences on panda habitat has led to new situations where wild pandas may also be negotiating finite resources. Human encroachment through the clearing of bamboo and old-growth forests to access new arable land (Zhang, Daszak, Huang, Yang, Kilpatrick, & Zhang, 2008; Peng, Jiang, & Hu, 2001; Liu, Linderman, Ouyang, An, Yang, & Zhang, 2001) has led to a fragmentation of suitable habitat and exacerbated isolation in wild giant panda populations (O'Brien, Wenshi, & Zhi 1994). Wild pandas are also in closer proximity now as they are forced to converge on smaller habitats with higher densities than seen previously (Zhang et al., 2008). Another influence on resource availability has been the simultaneous flowering and die off of multiple bamboo species in the Min mountains in the mid 1970's and then again in the Qionglai mountains in 1983 creating subsequent periods of food shortage (De Wulf, Goossens, MacKinnon, & Cai, 1988; Zhang et al., 2008), an impact that has likely been exacerbated by isolation due to habitat fragmentation preventing pandas from traveling to suitable foraging opportunities (Peng et al., 2001). The next bamboo flowering of the Min and Qionglai mountains is expected to occur in 2020 and it is suspected this will pose a serious threat to wild populations in the next 10 years (Tian et al., 2019). This convergence of populations in decreasingly suitable



habitat coupled with expected food shortages due to projected bamboo flowerings will likely increase conspecific interactions and resource negotiation, as has been seen in brown bears. These environmental stressors warrant investigation into how pandas might cope to manage diminishing resources effectively.

The giant panda living in captivity is an ideal candidate for a social cognition study due to the social housing of captive juveniles despite the nonsocial characterization of wild populations. This offers the opportunity to investigate whether increased exposure to conspecifics can elicit a socio-cognitive skill in a nonsocial species. Comparative cognition studies, especially those in evolutionarily distant species, allow us to examine the environmental pressures that shape the evolution of similarities in complex cognition across taxa. Here, success in an inequity aversion paradigm would indicate that social cognition is a more generalized trait and not evolved in social species exclusively. Assessments of the behavioral flexibility of captive pandas in an inequity setting also allows for a potential framework for predicting the behavior and needs of wild populations as they cope with diminishing food and habitat resources. A negative reaction to inequity would be valuable when needing to divide up resources fairly as a way of modulating energy expenditure in situations that provide poor returns. For the pandas, this is relevant due to the negative pressures of diminishing resources on wild populations. Finally, captive pandas are housed with both kin and nonkin which allows for comparisons that may inform our understanding of how inequity responses are modulated by conspecific relationships.

The current study tests pandas in an inequity aversion paradigm to assess the expression of socio-cognitive skills in a generally non-social mammal. I tested pandas in an effort inequity paradigm by assessing their responses to several testing conditions: social inequity (two pandas,

unequal effort, equal reward), social equity (two pandas, equal effort, equal reward), non-social inequity (one panda, unequal effort, equal reward) and non-social equity (one panda, equal effort, equal reward). An effort inequity paradigm was chosen over the traditional food quality paradigm due to the fact that I could not define a clear food preference in this panda population. In other words, the pandas did not consistently prefer one food reward over another in any preference test, and thus I chose to proceed with this study using an effort inequity approach.

### *Hypotheses*

I predicted that the subject panda would refuse to perform a hind-leg stand significantly more often in the social inequity condition than in any other condition.

I predicted that the subject panda would exhibit behaviors that were indicative of frustration (muzzle licks, bites, foot scrapes) significantly more often in the social inequity condition than in any other condition.

I predicted that frustration behaviors and cue refusals observed would be significantly more frequent in non-kin than kin pairs.

Specifically, I predict that the socially-housed pandas studied will display an aversive reaction to the social inequity condition, when a partner conspecific is given an apple immediately prior to the subject being asked to perform a hind leg stand for that same reward. I also predict that the subject panda will display greater rates of behaviors associated with frustration during the social inequity condition as compared to their behavior in the other conditions.

This work aims to contribute to our understanding of the evolution of social cognition across evolutionarily distant species and how socio-cognitive abilities may evolve in non-social species navigating difficult natural environments.

## **Methods**

### *Subjects*

The subjects of this study were ten three-year-old pandas born between June – August, 2016 at the Chengdu Research Base of Giant Panda Breeding in Chengdu City, Sichuan Province, P.R. China (N=5 males and 5 females). All were reared by their mother except for one male that was hand-reared. Three sets of pandas were twins, a F x F pair, a M x M pair, and a M x F pair. The pandas were assigned to 2 of 9 pairs (with the exception of two who were part of 1 pair) such that 5 of the twins were in a pair with their kin and with another non-kin panda. The final could not be paired with a non-kin panda due to husbandry constraints. Thus, there were 3 M x M pairs, 2 F x F pairs, and 4 M x F pairs. All subjects were naive to this study at the beginning of testing, but all had prior husbandry training and were familiar with the hind-leg stand task.

### *Ethical approval*

This study was reviewed and approved by the Hunter College Institutional Animal Care and Use Committee (Protocol: JP-Giant Panda 12/21).

*Experimental design & Procedures*

Testing occurred in an enclosure with two adjacent cages (depicted in Figure 1) such that the pandas could see and smell each other, and touch to some extent, through the bars of the connecting side. The experimenter (me) oriented herself directly in between the two cages. On either side of the experimenter were two large, clear buckets, depicted in Figure 2. Each bucket had a layer of sand at the bottom approximately 3 cm deep to anchor it and held 10 bamboo skewers with a cube of apple, approximately 3 cm diameter in size, depicted in Figure 2. The experimenter and buckets were on the concrete floor approximately an arm's length back, close enough that the experimenter could comfortably reach the pandas with the extended bamboo skewers, but far enough that the panda could not reach the experimenter and that both pandas could see the contents of both buckets. Each bucket was oriented in front of one panda. Both buckets were present in both one-panda and two-panda conditions. This set-up was the same for all sessions, regardless of condition.

The pandas at the Research Base had already been trained to stand up on their hind legs. This behavior required some effort from them and they appeared reluctant to do it. The experimenter cued the panda to stand on their hind legs by extending both hands as fists so she was at eye level with the panda, then raised both arms over her head. If the panda was not attending to the experimenter – determined by whether the panda was facing her – the experimenter first got the panda's attention by calling their name. The experimenter repeated the cue no more than twice, ensuring that eye contact was made both times, and held the cue for 5 seconds before moving on. If the panda did not maintain eye contact for a cue, it was repeated a third time only. If the panda wandered away or was not sitting up against the bars facing the experimenter, the panda's name was called and the panda had 15 seconds to approach. If the

panda walked away, the experimenter called their name repeatedly for no longer than 15 seconds before moving on. After successfully performing a hind leg stand, the panda received the food reward of apple offered on a bamboo skewer extended through the bars of the cage. If any animal failed to perform a hind-leg stand and the experimenter was confident the cue was observed, she moved on to the other panda. A trial included an interaction with each panda and always began with the partner. A session consisted of 10 trials regardless of participation, unless both pandas had wandered away and were completely unresponsive.

The study included four conditions: a nonsocial equity condition, a social equity condition, a nonsocial inequity condition, and a social inequity condition. In the social equity condition, all pandas were cued to perform a hind-leg stand before receiving an apple cube. The partner was always fed first. The nonsocial equity condition was the same, except only one panda was present. The experimenter still cued the empty cage, paused briefly, and then placed the apple in the cage where the partner panda would have been by dragging the skewer across a horizontal bar and allowing the apple to slide off. This motion was similar to the act of removing the stick from the panda's mouth after they had grasped the apple. The equity conditions served as a baseline to measure 1) the propensity of a panda to perform the hind leg stand and 2) the latencies in performance of the behavior after the cue to rule out any possible influence on the subject's behavior by simply having a partner present. In the nonsocial inequity condition, the partner was not present, and the apple was placed into the empty cage without presenting the cue to hind-leg stand in the same manner as in the nonsocial equity condition. The nonsocial conditions aim to account for the frustration effect by controlling for the panda's reaction to seeing apple but not receiving it, the movement of the food from the container to the panda area (both with and without a cue to stand preceding it), as well as the influence of the partner

panda's presence. In the social inequity condition, the partner received a cube of apple without having to perform the hind-leg stand. The partner was always fed first. This condition aimed to assess the subject's response to the presented inequity, by comparing any differences in the performance and latency in the performance of the behavior and the rejection/acceptance of the reward, as compared with the other conditions

For the nonsocial conditions, 5 of the pandas received all sessions of nonsocial trials at the start of the study, before all social condition trials, and the other 5 received all nonsocial trials at the end, after all social condition trials. This was to control for a possible order effect and thus to make sure that the presentation of nonsocial and social conditions was balanced. Pandas were divided within these two groups to balance the number of males and females such that 2 females and 3 males experienced nonsocial trials before social trials, and 3 females and 2 males experienced nonsocial trials after social trials. Kin pairings were also established so that one individual in each pairing had experienced nonsocial trials before the other to counterbalance against any influence that having already experienced the nonsocial trials may have on performance in the social trials.

For the social conditions, the 10 pandas were divided into 9 combinations, with most pandas being matched up with two partners throughout the study except for two that were only paired with one. This was due to the limitations of the pandas being divided between two enclosures with no feasible way of creating pairs with pandas from both. Pairs were either kin or nonkin, and all pandas tested with kin were also tested with nonkin. The combinations were organized such that three consisted of two females, three of two males, and four of one female and one male. There were three related and six unrelated combinations. In total, there were 17

pairings, considering that a single match-up could be considered two pairings depending on which panda was subject and which was partner.

A session consisted of 10 trials of the same condition, with a single trial including interactions with both pandas (or one panda and an empty cage in nonsocial conditions). A panda or pair, depending on whether the conditions were nonsocial or social, received two sessions in the morning, with a short break in between. Occasionally, a pair might receive another two sessions in the afternoon if the Research Base limited testing time to finish a particular pair based on husbandry needs. Once a pairing completed its four sessions, the partner/subject roles were reversed, and four more sessions were run. Thus, a panda pair completed all eight of their sessions (four with one panda serving as subject and four with the other as subject) before the next pair was tested. This avoided any potential confounds due to the possibility that the pandas behaved differently with one partner before and after experiencing a condition with a different partner.

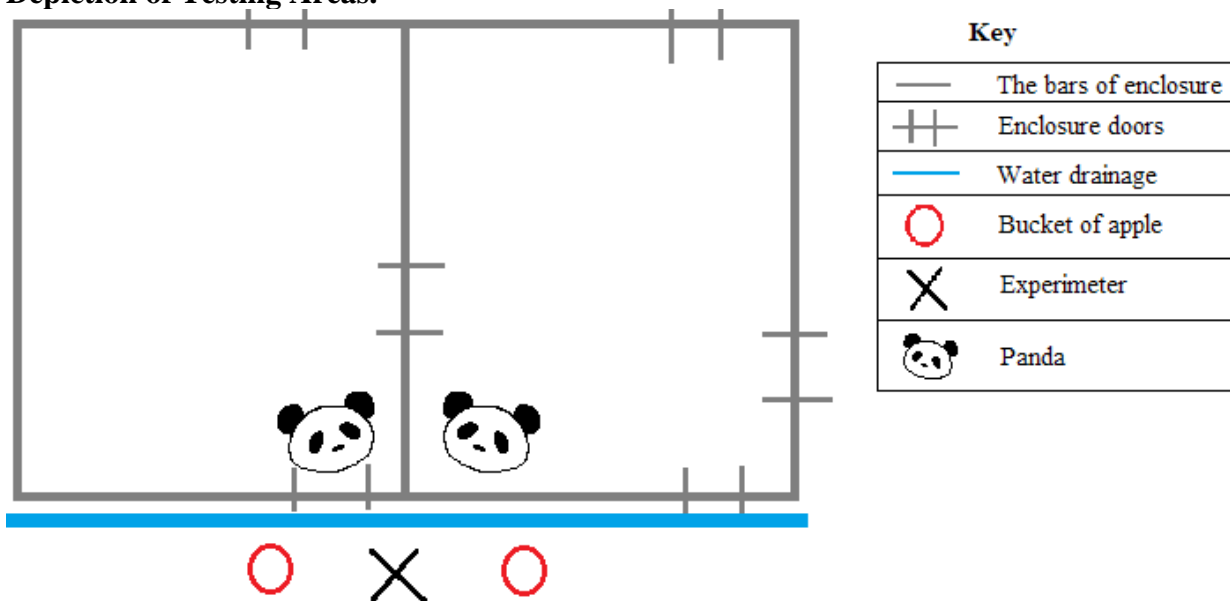
For a given pairing or individual panda, the order of conditions followed one of three patterns. For the first pattern, day 1 consisted of one equity session followed by one inequity session and day 2 was the same. For the second pattern, day 1 consisted of two inequity sessions and day 2 consisted of two equity sessions. For pattern 3, day 1 consisted of two equity sessions and day 2 consisted of two inequity sessions. One of these patterns was randomly chosen for each panda's nonsocial testing, as well as for all the pairs involved in social testing. If a given combination/pairing followed one pattern with one panda as subject, that combination followed a different pattern when the other was subject. Patterns were randomly distributed across the pairs so that all three were used as close to equally as possible. The order of testing across pandas can be found in Table S1 in the appendix. There were no days in which an inequity session was

immediately followed by an equity session. This was to avoid the possible situation where the panda in the partner role might reject apple because they had come to expect apple for no effort after the first session that day.

All sessions occurred on weekdays in the morning, with the exception of eight afternoon sessions, between the months of April and June, 2019. Session duration ranged from two and a half minutes to about eight minutes long with most sessions falling in the three- to four-minute range.

Figure 1:

**Depiction of Testing Areas.**



*Figure 1. Depiction of the set-up in one of the enclosures (not drawn to scale). The other enclosure had minor differences in placement of doors along back and side walls. Water drainage refers to small ditches in the floor around enclosures. For enclosure 1, the two rooms were 12.2 meters squared and the other 12.6 meters squared. For enclosure 2, both rooms were 11.7 meters squared.*



Figure 2:

**Depiction of Experimental Materials.**

*Figure 2. Depiction of container of apple slices. One was situated in front of each enclosure for all sessions, regardless of whether the partner was present.*

*Data Collection and Analysis*

All sessions were videotaped. Behavioral responses to the offering of a reward were recorded on a Sony HDR-CX405 HD Handycam mounted on a Sony VCT-R640 Lightweight Video Tripod and saved to a microSD card. Video recordings of sessions were analyzed on BORIS, a free event-logging software (Friard & Gamba, 2016), according to an ethogram of panda behavior adapted from Sandhaus (2004) and shortened to fit the needs of this study. All behavioral analyses were conducted after data collection. The frequency of positive responses to the cue (pandas standing following the two cue presentations per trial) were calculated. The latency of the panda to stand, measured from the moment the cue began to the moment that the

panda's hind legs were fully extended vertically, was recorded in milliseconds for each trial. All expressions of frustration-related behaviors, namely door-directed behaviors such as muzzle pushes, biting directed at the bars of the enclosure, licking directed at either the bars of the enclosure or the mouth, and foot scrapes directed at the ground while the panda is at the spot where testing occurred, were also recorded for each trial. These behaviors have been previously reported to be signs of frustration or discontent in giant pandas (Sandhaus, 2004; R. J. Snyder, personal communication, September 27, 2019). These behaviors, along with the desired standing hind-leg behavior and instances where the pandas walked away from the testing area, account for all behaviors observed throughout the experiment, with the exception of one trial where a panda splashed a bucket of water several times. Vocalizations were not considered in this study as it was impossible for the experimenter to determine which animal was producing them in social trials. All statistical analyses were run using Jeffrey's Amazing Statistics Program (JASP) version 0.14 (JASP Team, 2020).

In total, there were ten subjects, five female and five male pandas all born in the 2016 birthing season. They were organized into 17 pairings. Of these pairings, six consisted of sibling pandas and 11 consisted of unrelated pairings. A total of 107 sessions were conducted overall (19 = nonsocial equity, 20 = nonsocial inequity, 34 = social equity, and 34 = social inequity). For one panda, Fu Shun, one nonsocial equity session had to be disregarded due to his lack of interest. As discussed previously, each pair experienced two sessions of each condition, so for all analyses, the mean across both sessions was calculated. For latency to stand, the median was calculated as well. This worked out to an N of 17 for all variables, with one exception that will be discussed below.

The average session was 4 minutes and 40 seconds long. The longest trial was 8 minutes and 39 seconds. The shortest trial was only 2 minutes and 9 seconds long.

I did not perform any analyses comparing performance between subjects or pairs due to the high variability in the pandas' responses. In addition, the focus of this study was on the expression of inequity aversion and whether the pandas' behavior differed between social and nonsocial conditions, and thus all analyses were done within-subjects.

## Results

### *Interrater Reliability*

Interrater reliability was performed by providing 20% of the videos to another individual, a fellow graduate student, unfamiliar with the experiment. He was first trained using a small subset of videos (not included in the analyzed 20%) on the panda ethogram, and on measuring time latencies. He also used BORIS for all video coding. An intraclass correlation (ICC) comparing the rates of behaviors showed a high degree of correlation; the average measure of ICC was .945 with a 95% confidence interval from .918 to .963 ( $F(91,92) = 35.1, p < .001$ ). The ICC for the panda's latency to stand also showed a high degree of correlation; the average measure of ICC was .784 with a 95% confidence interval from .729 to .829 ( $F(229,230) = 8.28, p < .001$ ). These data showed high interrater reliability, and thus the final analysis was conducted on the experimenter's coding of the dataset.

### *Positive Responses to Cues*

For each pairing, the percent ratio of positive responses (standing after the cue) by the subject in the social inequity condition was compared to the percent ratio of positive responses

by the subject in the social equity condition, nonsocial equity condition, and social inequity condition. There was no significant difference between the ratio of positive responses across conditions (Friedman's ANOVA:  $X^2(3) = 0.886$ ,  $p = 0.829$ ). The ratio of positive responses to total trials for each individual panda can be seen below (Table 1). Additionally, post-hoc comparisons using Wilcoxon signed-rank tests across conditions were run. The values of these tests were also not significant and can be seen in Table 2 below.

While as a group the pandas did not appear to show inequity aversion responses, one panda's behavior is worth describing in detail. Cheng Shi's first experience in the study was the first two sessions of social equity with his first partner, Wen Wen. For this first day, he stood for all 10 trials the first session, and all but the final trial in the second session. This level of participation is very similar to what we saw for the other pairings. However, three days later during the two social inequity sessions for this pairing, Cheng Shi refused to stand in 13 out of 20 trials in the social inequity condition. In the first session of the day, he stood for 5 trials, and then refused to stand for the last 5. After the 15-minute break, the second session began. This time, he stood for the first two trials and then refused to for the last 8. Cheng Shi also refused to stand in 9 out of 20 trials in the social inequity sessions in his second pairing (with Yuan Yue as his partner). For this latter pairing, Cheng Shi experienced both social inequity sessions the same day and stood much less often in the second session. For the first, he refused to stand only for the 8<sup>th</sup> and 9<sup>th</sup> trials, however for the second session he refused to stand on the 2<sup>nd</sup>, 3<sup>rd</sup>, 5<sup>th</sup>, and final 4 trials. On the very next day of the Cheng Shi – Yuan Ye pairing, Cheng Shi stood for only three trials in the first session of social equity but stood for all 10 in the second session.

Table 1:

**Demographics and positive cue responses across subjects**

Panda	Code	Sex	Age	Kin?	Pos NE	Pos NI	Pos SE	Pos SI
Ya Yun	Y	F	3	Yes	18/20	20/20	37/40	35/40
Ya Zhu	Z	F	3	Yes	14/20	19/20	39/40	39/40
Yuan Yue	U	F	3	No	20/20	19/20	40/40	38/40
Cheng Shi	C	M	3	No	20/20	20/20	32/40	18/40
Wen Wen	W	M	3	No	20/20	20/20	40/40	40/40
Mao Dou	D	M	3	Yes	20/20	20/20	39/40	40/40
Mao Tao	Y	M	3	Yes	18/20	19/20	36/40	40/40
Fu Shun	S	M	3	Yes	8/10	17/20	18/20	19/20
Fu Lai	L	F	3	Yes	20/20	20/20	17/20	20/20
Qi Yi	Q	F	3	No	20/20	20/20	20/20	20/20

*Table 1. Table of all subjects. Columns from left to right are name, the single letter code used to identify each individual during analysis, sex, age, whether they are housed with a sibling, and raw number of positive responses to cue for Nonsocial Equity (NE), Nonsocial Inequity (NI), Social Equity (SE), Social Inequity (SI) for all total sessions that panda is a subject in, regardless of partner. Note Cheng Shi's performance in social inequity, highlighted.*

Table 2:

**Ratio of positive cues post-hoc analysis**

Conditions compared	W	p
SE x SI	21.500	0.725
SE x NE	38.000	0.823
SE x NI	21.000	0.298
SI x NE	29.500	1.000
SI x NI	17.500	0.809
NE x NI	5.000	0.121

*Table 2. Wilcoxon signed-rank tests were run as post-hoc tests comparing percent ratio of positive cues for all conditions. W and p values are listed as they appeared in JASP for all comparisons. Condition key: Nonsocial Equity (NE), Nonsocial Inequity (NI), Social Equity (SE), Social Inequity (SI)*

*Latency to Stand*

Both mean and median latencies to stand across trials within each session for each pairing were calculated in milliseconds. The median calculations were used to better account for the trials in which the pandas refused to stand and thus a latency could not be recorded. This was done by setting an arbitrarily high value for any trial where the panda did not stand. Trials where the panda refused to stand could not be considered in mean calculations so analyzing both allowed me to consider latency data with all trials considered and with only the trials where the panda stood considered. The raw latency score for all trials used to calculate these scores can be found in the appendix, Table S2. There was no significant difference between latencies to stand between conditions using mean values (Friedman's ANOVA:  $X^2(3) = 5.19$ ,  $p = 0.16$ ). Post hoc-

comparisons were performed using Wilcoxon signed-rank tests on all possible condition pairing, and none were significant. These comparisons can be found below, in Table 3.

Using median latencies, there was a significant difference between conditions (Friedman's ANOVA:  $X^2(3) = 9.60$ ,  $p = 0.02$ ). Post-hoc analyses were run by performing Wilcoxon signed-rank tests for all possible comparisons. The Wilcoxon signed-rank tests did not yield any significant pairings. These values can be found below in Table 4.

In the case of Cheng Shi, the median latency to stand for the social inequity condition was missing a value, as he did not stand in enough trials to calculate a median value when he was paired with Wen Wen (pairing CW).

Table 3:

**Mean latency to stand post-hoc analysis**

Conditions compared	W	p
SE x SI	72.000	0.854
SE x NE	38.000	0.071
SE x NI	43.000	0.120
SI x NE	44.000	0.132
SI x NI	48.000	0.190
NE x NI	102.000	0.236

*Table 3. Wilcoxon signed-rank tests were run as post-hoc tests comparing mean latency to stand across all conditions. W and p-values are listed as they appeared in JASP for all comparisons. Condition key: Nonsocial Equity (NE), Nonsocial Inequity (NI), Social Equity (SE), Social Inequity (SI)*

Table 4:

**Median latency to stand post-hoc analysis.**

Conditions compared	W	p
SE x SI	67.000	0.980
SE x NE	51.000	0.243
SE x NI	48.000	0.190
SI x NE	38.000	0.130
SI x NI	39.000	0.144
NE x NI	91.000	0.506

*Table 4. Wilcoxon signed-rank tests were run as post hoc comparing median latency to stand for all conditions. W and p values listed as they appeared in JASP for all comparisons. Condition key: Nonsocial Equity (NE), Nonsocial Inequity (NI), Social Equity (SE), Social Inequity (SI)*

*Frustration Behaviors*

For the four behaviors listed previously (muzzle pushes, licks, bites, and foot scrapes), all were scored individually for each session. The rates of behaviors were calculated per minute to account for variability in session length. A Friedman's ANOVA was run to compare the total counts for frustration behaviors across conditions; this was not significant ( $X^2(3) = 0.94, p = 0.82$ ). Post-hoc comparisons were made using Wilcoxon signed-rank tests on all possible condition pairings, none of which were significant. These values can be found below in Table 5.

Here, Cheng Shi was observed behaving differently in the social inequity condition compared to the other conditions. He was first tested with Wen Wen as subject, and both social inequity sessions occurred on the same day. During the first session, he stood for the first five trials but then began walking around the enclosure. He refused to return to the testing area after several calls. Between sessions, there was always an approximately 15-minute time period in



which I prepped the testing setup for the next session. During this time, panda staff (J. Ayala) remained at the enclosure and was able to coax Cheng Shi back to the testing area and successfully cued Cheng Shi to stand again. During the second social inequity session, the panda began pacing the enclosure shortly after the session began. He did not behave in this way for nonsocial sessions or during his social equity sessions with Wen Wen. When paired with Yuan Yue, Cheng Shi did not pace as frequently. Instead, he sat at the testing area and maintained eye contact with the experimenter's hands as the cue was given while refusing to stand. The day following social inequity sessions, Cheng Shi received his social equity sessions with Yuan Yue. During the first session, he refused to stand for the majority of trials. However, for his second session he stood for all 10 trials.

Table 5:

**Frustration behavior post-hoc analysis**

Conditions compared	W	p
SE x SI	46.000	0.980
SE x NE	78.500	0.243
SE x NI	67.000	0.190
SI x NE	95.000	0.130
SI x NI	85.000	0.144
NE x NI	55.000	0.506

*Table 5. Post-hoc Wilcoxon signed-rank tests were run comparing the rates of all frustration-related behaviors for all conditions. W and p-values are listed as they appeared in JASP for all comparisons. Condition key: Nonsocial Equity (NE), Nonsocial Inequity (NI), Social Equity (SE), Social Inequity (SI)*

*Kin Comparisons*

Four of the pandas served as subjects in two pairings: one with a sibling, the other with nonkin. Unfortunately, due to changes in husbandry protocol and time constraints, the third pair of twins (Fu Shun and Fu Lai) could not complete trials with a nonkin partner.

Three Wilcoxon signed-rank tests were run to compare performance between kin and nonkin in the social inequity condition. The first compared the subject's mean latency to stand, measured in milliseconds, when partnered with kin ( $M = 2664.100$ ) to the subject's mean latency to stand when partnered with nonkin ( $M = 3752.450$ ); this comparison was not statistically significant ( $W = 1.000$ ,  $p = 0.250$ ). The second test compared the subject's median latency to stand, measured in milliseconds, when partnered with kin ( $M = 2406.750$ ) to the subject's median latency to stand when partnered with nonkin ( $M = 3436.375$ ); this was also not significant ( $W = 4.000$ ,  $p = 0.875$ ). The final test compared the subject's rate of frustration related behaviors per minute when partnered with kin ( $M = 5.640$ ) to the subject's rate of frustration related behaviors per minute when partnered with nonkin ( $M = 7.617$ ). This result was also not significant ( $W = 1.500$ ,  $p = 0.269$ ).

**Discussion**

Overall, the subject pandas' behavior did not differ significantly across the four conditions, nor was their behavior impacted by the partner with whom they were paired. While only descriptive, the one panda that performed markedly differently from the others was Cheng Shi. His performance with his partner Wen Wen, another male, seemed to indicate that he may be averse to inequity. This pairing followed a testing schedule by which day one consisted of two sessions of social equity and day two consisted of two sessions of social inequity. Initially,

Cheng Shi stood willingly when cued. For the social equity conditions with Wen Wen, he stood in all but one trial; the final trial of the day he refused to stand. It was somewhat common for a panda to refuse to stand for one or two trials, so this behavior was not extraordinary. When tested in the social inequity condition, he stood for the first five trials in the first session, and then refused to stand for the final five trials. Instead, he began walking in circles around the enclosure and refusing to come when called. All pandas had been trained to approach when called by name so we can be confident that he knew the experimenter was calling for him to approach. Between sessions while the test set-up was being reset, a Research Base staff member (J. Ayala) that had not participated in giving any cues during trials came over, called Cheng Shi and requested he stand. In response to J. Ayala requests, Cheng Shi came over when called and readily stood. J. Ayala never participated in testing (I was the only experimenter) and these requests occurred in-between trials (and thus never in relation to equity or inequity testing). When the experimenter returned and began the second session, approximately 15 minutes after the first one ended, Cheng Shi stood for only the first two trials and then began to pace the enclosure again. The fact that Cheng Shi stood consistently for J. Ayala in-between inequity trials as well as for me during all other conditions when I was the experimenter suggests that his rapid decline in responding consistently in inequity trials was due to his aversion to inequity.

Cheng Shi's first pairing was tested relatively early in the study. Towards the end of the study, he was tested again with a different partner, Yuan Yue. In this pairing, Cheng Shi experienced social inequity immediately prior to social equity. Both sessions of a single condition were run on the same day. Again, he stood much less often during the second social inequity session than the first and overall stood much less often in this condition than the others. It is also interesting that the next day following the inequity sessions, when tested in the social

equity condition with Yuan Yue, he also refused to stand for seven of the ten trials in the first session. For the second session of social equity, however, he stood for all trials. This behavior suggests that perhaps Cheng Shi had developed an initial expectation for the session and altered his behavior once he recognized that the session contingencies changed. Perhaps, with the inequity experience still a recent memory as it was just the day before, he was expecting inequity for that first session and behaved accordingly. This would also explain his performance in social inequity sessions during which he tended to stand more often in the first session of the day and less often during the second. This was true for both pairings in which he was a member.

The pandas in this study were socially housed very early in their lives, sharing time between their mothers and each other for most of their three years. This is very different from what they might experience in the wild, where their only contact with pandas in these early years is familial (their mother or sibling if they are a twin). While the fact that these pandas are socially housed – a situation that differs significantly from the wild – may be a factor in their heightened sensitivity to socio-cognitive tasks such as this one, it is also possible that this close proximity led the pandas to form strong social bonds with each other that weakened any possible inequity aversion response, as has been suggested for chimpanzees (Brosnan et al., 2005) and dogs (Range et al., 2009). In the future, this paradigm might elicit different results when comparing pandas that did not grow up together, but that did grow up socially with others. Unfortunately, this was not possible for this study due to the logistics of having to relocate pandas from different enclosures, which would have been necessary to make this comparison. Additionally, further testing comparing wild-caught pandas to captive-born pandas may also produce interesting results. Wild-caught pandas may have first-hand experience negotiating their

limited wild resources and be better able to identify differences in reward availability or equity or be more likely to respond to social situations or norms due to that experience.

One interesting confound in this study may relate to the issue of food choice. Typically, an inequity aversion paradigm involves differences in food reward rather than in effort. Prior to the beginning of trials, pre-testing was done using dichotomous food choice tasks to determine possible foods that would suit a food quality or food quantity inequity paradigm. These included a comparison of apples to pears, apples to bamboo, apples to honey, and honey-covered apples to regular apples. In all cases, either a slice or cube of fruit or cube of bamboo of approximately the same size were compared. For the honey, a chopstick was mixed into the jar and either slathered somewhat generously on the apple or the panda was offered the opportunity to lick the honey off the chopstick. In all comparisons, the experimenters could not find two foods where one was consistently preferred over the other but both always still resulted in the standing behavior. Instead, either the pandas did not reliably choose one or the other or the pandas would refuse to stand for the offered reward, as was the case with bamboo. Other foods such as squash and carrot were offered freely prior to be used as a reward for standing, however, some of the subjects refused to consume these foods at all. Cheng Shi was the only panda willing to try any food offered to him.

I then decided to test whether the pandas reliably chose a greater amount of apple over a smaller amount, in an effort to use a food quantity inequity paradigm. The pandas did not reliably choose a larger piece of apple nor a greater number of apple cubes in this scenario. Anecdotally, I noticed a potential side bias but I did not continue this paradigm and thus did not test for one. Given observations of Cheng Shi's behavior as well as the pandas' observed behaviors during food choice tasks in pre-testing, one potential influencing factor may be the

giant pandas' vision. While pandas most likely have comparable vision to other diurnal carnivore species (Kelling et al., 2006), the giant panda's vision is likely poor (Chorn & Hoffmann, 1978). Poor vision is a possible explanation for Cheng Shi's behavior in the first session of a new condition following the completion of a different condition; he tended to behave similarly between conditions and only adjusted his behavior to the new condition later in it. Similarly, we observed that during the dichotomous food choice task, the pandas tended to focus on only one of the offered options and ate whichever one it seemed they noticed first. Indeed, at one point, I tried putting no reward on the stick situated on whatever side that particular panda seemed to be favoring, and found that the panda tried to eat from the empty stick first. They only looked for the other option after realizing it was empty. Further research on giant panda vision and how much the species truly relies on their visual sense would be important for future panda cognition research, particularly if those assessments require visual interactions with the physical or social environment.

The reliance on vision in animal cognitive tasks has a potentially confounding effect that is certainly not unique to pandas. For example, elephants prioritize auditory and olfactory over visual information in social contexts, although there is variability between species (Jacobson & Plotnik, 2020). As the panda is a primarily solitary species (Brambell, 1976) that lives in a densely forested habitat and relies on understory vegetation (Linderman, Bearer, An, Tan, Ouyang & Liu, 2005), it is likely they do not prioritize visual information in social contexts. In fact, it is likely that pandas rely heavily on chemosensation in social contexts such as communicating sexual status and dominance long range (Swaigood, Lindburg, White, Zhang & Zhou, 2004) as they can discriminate between the odor of kin and non-kin (Gilad, Swaigood, Owen & Zhou, 2016). It is not surprising that a species that rarely spends time in close proximity

with conspecifics would rely on chemosensation to communicate important information over long distances or across territories. For these reasons, a cognitive task – particularly one that relies on the animal making assessments in a social context or being informed by social information such as the one in the current study – that centers on vision may in fact be setting non-visual species up for failure. It is important that multi-modal sensory information is provided or available so that fair comparisons of socio-cognitive abilities can be made across species.

The selection of the food reward is crucially important for the design of inequity studies, and the choice of apple here was important, as the participation of the pandas remained consistently high throughout the study. Traditionally, the food rewards in an inequity aversion study are treats that are not a staple part of the subject's diet. However, the pandas do receive apples as part of their diet and outside the context of this study. Cheng Shi, the panda that seemed to show an aversive response during the social inequity condition, was also observed to be more food motivated than the others, as indicated by his willingness to eat all offered foods during pre-testing. His keepers also confirmed this based on their own experience working with him. It is possible that the pandas' motivation for apples during the study was tempered to some extent by the fact that apples are a larger part of their diet and thus were not unique to this study. If this is the case, it would make sense that individual differences in food motivation may affect the pandas' aversion to inequity. Cheng Shi, being so food motivated, may have been more attuned to the rewards conspecifics were receiving. This may also explain why it took time for him to express aversion to inequity; he was initially motivated to eat the apples but this motivation waned once he recognized the partner was getting the same reward for no effort. The yet unanswered question of course is why the other pandas did not respond differently to equity and inequity situations. This indifference to inequity may be due to differences in food

motivation, a lack of interest in or saliency of the partner's behavior, or a confound of the available sensory information. It is also possible, of course, that solitary animals do not show an aversion to inequity or that their response to inequity is far less pronounced than that observed in social species. As this is the first study of panda inequity aversion and one of the first on their social tendencies in general, further research is clearly needed to better understand the socio-cognitive capacities of the giant panda.

### *Conclusion*

Further studies on inequity aversion in pandas would benefit from an increase in sample size, and more attention to variability in kin and non-kin, familiar and unfamiliar pairings. It would also be interesting to introduce pairs of wild-caught pandas to the inequity paradigm to see whether variability in experience affects their responses. Additionally, observing the pandas' social interactions in a more natural setting could inform our understanding of the situations in which an inequity response would be most pronounced. Dogs spend less time interacting with their partners as well as the experimenters during the time following a social inequity session compared to the time following a social equity session (Brucks et al., 2016), suggesting that responses to inequity may be more subtle than expected.

This study also highlights interesting areas for future research. There is remarkably little research on panda social behavior because they are generally regarded as a solitary animal. However, further research on how pandas recognize their kin and distinguish between kin and non-kin would be crucially important for future panda socio-cognitive investigations. Variability in panda personality may also inform our understanding of differences in cognitive abilities between pandas, and may help explain why the pandas in this study varied in their behavior (i.e.,



standing and frustration) and why pandas in captivity vary in their propensity for expressing stereotypies. The findings of this study and potential future research on panda behavior have the potential to not only inform our understanding of the evolution of social cognition across evolutionarily distant species, but also how it may be expressed in species where social interactions are relatively rare.

In addition, this research has important implications for panda conservation. As an endangered species, understanding how pandas behave and the flexibility of behavior in social situations could help inform future reintroduction or habitat preservation efforts. Closer examination of panda behavior could improve resource management and habitat protection efforts. Understanding panda social and foraging behavior, for instance, could aid in the appropriate selection of optimal forest habitat to ensure that these areas remain suitable for wild populations, an issue that is currently of concern (Vina et al., 2007; Zhang, Luo, Mallon, Li, & Jiang, 2017; Tian et al., 2019). Human-wildlife coexistence requires that both human and non-human animal perspectives are considered (Mumby & Plotnik, 2018), and thus this study and future attention to controlled studies on panda physical and social cognition could play an important role in their conservation.

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## Appendix

Table S1:

**Randomized scheduling of sessions**

Social			Nonsocial			
Pairing	Day 1	Day 2	Panda	Day 1	Day 2	Pre/post
SL	SI, SI	SE, SE	Fu Shun (S)	NE, NI	NE, NI	Pre
LS	SE, SI	SE, SI	Fu Lai (L)	NI, NI	NE, NE	Post
DT	SI, SI	SE, SE	Mao Dou (D)	NE, NE	NI, NI	Pre
TD	SE, SE	SI, SI	Mao Tao (T)	NE, NI	NE, NI	Post
DS	SE, SI	SE, SI	Qi Yi (Q)	NE, NE	NI, NI	Post
QT	SE, SI	SE, SI	Ya Zhu (Z)	NI, NI	NE, NE	Pre
TQ	SI, SI	SE, SE	Ya Yun (Y)	NE, NE	NI, NI	Post
ZY	SE, SI	SE, SI	Wen Wen (W)	NE, NI	NE, NI	Pre
YZ	SE, SE	SI, SI	Yuan Yue (U)	NI, NI	NE, NE	Pre
ZW	SE, SE	SI, SI	Cheng Shi (C)	NE, NI	NE, NI	Post
WZ	SE, SI	SE, SI				
YU	SI, SI	SE, SE				
UY	SE, SI	SE, SI				
WC	SI, SI	SE, SE				
CW	SE, SE	SI, SI				
CU	SI, SI	SE, SE				
UC	SE, SE	SI, SI				

*Table S1. Table of social session scheduling for all pairings, as well as nonsocial session scheduling for individuals. The pairing column lists the single letter code of each panda in a pairing, with the subject always listed first. Day 1 and Day 2 testing were always conducted chronologically. The final pre/post column refers to whether that panda received their nonsocial sessions before or after all social sessions were conducted.*



Table S2:

**Latency to stand for all trials**

Date	Panda(s)	Condition	Trial 1	Trial 2	Trial 3	Trial 4	Trial 5	Trial 6	Trial 7	Trial 8	Trial 9	Trial 10
2019.5.16	S	NE	Refuse	Refuse	Refuse	Refuse	Refuse	Refuse	Refuse	Refuse	Refuse	Refuse
2019.5.16	S	NI	6750	Refuse	7999	6237	18252	15000	3999	5753	2750	4749
2019.5.16	Z	NI	26499	13500	5501	3250	2500	3249	4250	2000	8750	4250
2019.5.16	Z	NI	9499	16500	1750	7250	2002	5750	Refuse	20498	29501	34253
2019.5.17	S	NE	5250	9502	15751	14003	Refuse	3250	5001	Refuse	7000	3251
2019.5.17	S	NI	5751	3002	15543	2999	Refuse	19251	Refuse	Refuse	8000	11000
2019.5.17	Z	NE	2750	8751	Refuse	2749	4007	8250	Refuse	3250	Refuse	Refuse
2019.5.17	Z	NE	24746	14251	Refuse	44250	22750	12751	Refuse	94748	10002	3750
2019.5.20	D	NE	2749	1999	2250	2000	2248	2241	2752	2999	2000	6246
2019.5.20	D	Ne	2499	4253	2252	4001	2001	4002	2001	3501	7000	1501
2019.5.20	W	NE	13999	9750	6568	18251	9740	4750	13750	11000	13000	13252
2019.5.20	W	NI	8491	4249	10751	10501	5250	7752	30750	3000	3499	21500
2019.5.21	D	NI	2250	1998	2250	2502	1749	1745	2003	2250	1752	2500
2019.5.21	D	NI	1750	1249	1750	5250	1750	1752	1759	1752	2250	1997
2019.5.21	W	NE	7250	4499	2749	3000	4750	2750	10501	8499	2249	2501
2019.5.21	W	NI	3249	4001	5252	3739	3249	3252	3500	2250	2500	3002
2019.5.22	SL	SI	3499	3628	8000	2001	2000	6000	4759	6000	3501	1749
2019.5.22	SL	SI	2751	4248	4748	15750	6250	3752	Refuse	6003	14499	Refuse
2019.5.22	U	NI	6000	9248	2748	2497	4003	4248	1747	4749	2296	2749
2019.5.22	U	NI	5263	Refuse	3000	12796	14500	2500	2249	1749	1998	1750
2019.5.23	U	NE	3254	1996	2248	1752	1750	1750	1998	2002	1252	1997
2019.5.23	U	NE	8750	3499	1978	3254	2249	7502	3250	2753	2500	2498
2019.5.24	LS	SE	2750	2750	3002	2500	Refuse	Refuse	Refuse	8000	2250	2321
2019.5.24	LS	SI	6248	3878	2250	1998	4248	15749	6751	4500	6748	7001
2019.5.24	CW	SE	2251	2251	2251	2749	8001	5002	4249	4000	2251	2500
2019.5.24	CW	SE	2486	7738	7250	2000	2501	4251	6371	6500	2998	Refuse
2019.5.27	LS	SE	10501	12746	8500	14752	3500	2750	7251	3248	3750	3999
2019.5.27	LS	SI	7249	3249	4501	5250	4751	4250	23750	6250	3749	5252

2019.5.27	CW	SI	12752	4500	1500	35500	2263	Refuse	Refuse	Refuse	Refuse	Refuse
2019.5.27	CW	SI	28752	4751	Refuse	Refuse	Refuse	Refuse	Refuse	Refuse	Refuse	Refuse
2019.5.28	SL	SE	2500	1251	2998	4502	1998	3751	3749	1751	10752	8751
2019.5.28	SL	SE	4501	3500	2500	2750	12240	2751	Refuse	3500	2250	10001
2019.5.28	WC	SE	3250	10252	1502	1749	1999	1751	1500	1502	2000	1750
2019.5.28	WC	SE	5251	2750	2500	2751	3001	2250	3249	2000	2750	2000
2019.5.29	TD	SI	2002	2500	3751	1750	4251	3250	4499	2001	2000	3500
2019.5.29	TD	SI	2249	3501	3239	2250	2501	2000	2498	1999	2249	3501
2019.5.29	TD	SE	1751	1750	1742	2999	3499	4249	3249	8250	2300	4011
2019.5.29	TD	SE	10752	3000	3750	3001	Refuse	7251	6502	Refuse	Refuse	Refuse
2019.5.19	WC	SI	2250	2500	2001	2000	1500	1750	2250	1499	1500	1750
2019.5.19	WC	SI	2250	1999	750	1796	1250	1750	1751	1750	1749	1251
2019.5.30	WZ	SE	1250	1502	2001	5328	3277	2750	3000	1500	1985	1250
2019.5.30	WZ	SI	1989	1512	4249	1500	2750	3501	1500	2501	4500	1752
2019.5.31	DT	SE	9508	1249	1499	1501	1001	1257	2000	1499	3250	1500
2019.5.31	DT	SE	1250	1250	1500	1502	2000	1751	Refuse	3000	1500	1498
2019.5.31	DT	SI	2250	999	1000	1259	1501	1250	1500	1501	1749	1250
2019.5.31	DT	SI	1252	1005	1001	1235	1001	1500	1732	1500	13250	1749
2019.5.31	WZ	SE	2749	2498	1751	2500	2000	1251	1500	1750	2001	2777
2019.5.31	WZ	SI	3250	2251	3001	8249	2000	2002	11751	1998	2251	3500
2019.6.3	QT	SE	2498	2001	1264	2000	1999	1500	1751	1999	2250	9750
2019.6.3	QT	SI	2001	2257	2500	2000	1750	11249	9752	2251	2000	2751
2019.6.3	ZW	SE	2749	3498	3249	3002	4502	3999	3249	2251	4752	2252
2019.6.3	ZW	SE	3000	4249	Refuse	10249	3501	12249	2251	9500	2750	4499
2019.6.4	QT	SE	2000	2250	2000	2000	1999	2252	2249	2002	4502	2500
2019.6.4	QT	SI	2250	3250	2499	2989	2306	2262	2000	4247	1748	3250
2019.6.4	ZW	SI	2248	2515	3999	4749	3999	3499	7499	2248	3494	Refuse
2019.6.4	ZW	SI	5999	3250	3751	3001	2253	2750	2999	3000	2499	7250
2019.6.5	YU	SI	2499	9722	2501	6748	4394	Refuse	3250	3249	8001	Refuse
2019.6.5	YU	SI	4249	Refuse	12751	8997	2748	4499	Refuse	3001	10250	Refuse
2019.6.6	TQ	SI	1489	1500	1751	1502	15499	1506	1251	1501	1751	3032
2019.6.6	TQ	SI	1748	1503	1752	2749	4251	5249	14487	2750	4251	15498

2019.6.6	YU	SE	4500	14999	Refuse	21000	4001	Refuse	Refuse	15258	12623	13252
2019.6.6	YU	SE	4750	5249	2751	3248	3749	4000	16753	3070	12499	13750
2019.6.7	TQ	SE	1751	1250	1750	2499	2751	1748	1499	1499	7752	3498
2019.6.7	TQ	SE	2252	2001	1499	1749	2000	2001	2251	2000	1749	1751
2019.6.7	UY	SE	10274	1585	2226	4751	1999	2000	22750	1753	1748	2000
2019.6.7	UY	SI	13751	1750	2750	7251	1499	1500	1252	1499	1501	1500
2019.6.10	DS	SE	1501	1250	999	1000	1249	750	1000	1001	1249	1251
2019.6.10	DS	SI	1498	1501	1248	1250	750	1248	1000	1251	1751	999
2019.6.10	UY	SE	1752	1249	1501	1501	1500	1513	1000	1499	1499	2499
2019.6.10	UY	SI	1252	1249	1498	1500	1501	1500	1500	1749	1250	1500
2019.6.11	DS	SE	1751	1002	999	1000	999	1249	999	1499	751	2000
2019.6.11	DS	SI	1000	1000	751	1000	1249	1247	1001	1249	1001	1500
2019.6.11	YZ	SE	2983	2018	2498	2250	3000	2750	1751	2500	2250	2500
2019.6.11	YZ	SE	2341	9748	11720	3748	6248	3250	2503	2502	3250	4000
2019.6.12	YZ	SI	2500	2751	3011	4750	2750	3252	3999	3749	2749	3000
2019.6.12	YZ	SI	2750	3498	2749	3000	3999	2750	2133	3749	2999	2751
2019.6.13	ZY	SE	2250	2252	2750	2499	2499	2252	2000	2249	2251	4248
2019.6.13	ZY	SI	2751	2503	1999	4499	2999	2501	2749	3509	2748	3750
2019.6.14	ZY	SE	1501	2252	8501	4000	2324	20249	2752	3000	3250	2252
2019.6.14	ZY	SI	752	3001	3000	2751	2251	3251	2749	2499	2502	2501
2019.6.17	UC	SE	2250	1501	1251	2252	1252	1500	1500	1501	1752	1499
2019.6.17	UC	SE	1749	1500	1248	1498	1500	1501	1598	1499	1749	2000
2019.6.18	Q	NE	2501	1750	1490	1751	1499	1499	1999	1499	1501	1516
2019.6.18	Q	NE	2016	1500	2249	2499	1749	1500	1500	2502	1999	1750
2019.6.18	UC	SI	3000	1499	3999	1751	1750	1501	1499	1750	1750	1491
2019.6.18	UC	SI	Refuse	1594	2501	1248	908	1499	12061	1500	1931	Refuse
2019.6.19	Q	NI	1750	1749	1500	2250	1249	3015	2001	1751	2750	3001
2019.6.19	Q	NI	1502	3002	2500	1749	2999	1499	1250	2501	2999	5249
2019.6.19	CU	SI	3749	2258	2500	9001	2267	1500	2000	Refuse	Refuse	9250
2019.6.19	CU	SI	1498	Refuse	Refuse	9000	Refuse	2501	Refuse	Refuse	Refuse	Refuse
2019.6.20	T	NE	2500	2503	3251	9000	3148	2748	8119	2087	2002	Refuse
2019.6.20	T	NI	1748	3003	2502	4000	3000	2689	Refuse	2498	4750	3001

2019.6.20	CU	SE	2248	Refuse	Refuse	Refuse	Refuse	3749	Refuse	Refuse	Refuse	3500
2019.6.20	CU	SE	2998	2247	2749	9749	12250	14499	12512	2999	1500	3501
2019.6.21	T	NE	2000	13750	1500	1999	25999	1752	13511	1752	1999	Refuse
2019.6.21	T	NI	4000	2002	1749	1750	1751	2252	4797	4251	4500	11000
2019.6.21	Y	NE	2501	Refuse	3750	Refuse	10000	2750	3751	13500	3500	3250
2019.6.21	Y	NE	3251	3988	2751	2500	10751	2500	2750	2250	2251	2350
2019.6.24	L	NI	4499	5503	2998	4500	5000	3249	2750	3750	2247	2005
2019.6.24	L	NI	4253	3248	5000	3499	3123	4750	4501	3751	6508	4252
2019.6.24	Y	NI	2252	6000	3249	3251	9000	11749	11250	3000	3002	3252
2019.6.24	Y	NI	2000	12748	2250	1750	2749	1751	1509	2249	2250	3251
2019.6.25	L	NE	2250	4753	3744	4503	2245	3001	3251	2501	2002	6252
2019.6.25	L	NE	2500	4749	11500	3501	4106	3249	4500	9001	3499	4250
2019.6.25	C	NE	2500	5010	2251	2252	1750	1000	1500	14750	5000	1751
2019.6.25	C	NI	19500	3496	3750	2748	5001	1250	2249	1999	2500	6501
2019.6.26	C	NE	2000	1751	2229	1747	2001	2498	1751	2000	1753	1751
2019.6.26	C	NI	1250	2012	2250	1999	1752	1749	10251	2999	1001	1749

*Table S2. The raw latency to stand score for each trial. Refusals are noted in appropriate cells. Conditions included are NE (Nonsocial Equity), NI (Nonsocial Inequity), SE (Social Equity), and SI (Social Inequity). Pandas are listed by their single letter code. For social conditions the two letters represent the two pandas, with the subject panda listed first. Single letter codes are referenced in Table 1.*