AN INVESTIGATION INTO THE FACTORS THAT AFFECT
PLAY FIGHTING BEHAVIOR IN GIANT PANDAS

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Megan L. Wilson

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An Investigation into the Factors that Affect Play Fighting Behaviors in Giant Pandas

Approved by:

Dr. Terry Maple, Chairman
School of Psychology
Georgia Institute of Technology

Dr. Roger Bakeman
School of Psychology
Georgia State University

Dr. Paul Corballis
School of Psychology
Georgia Institute of Technology

Dr. M. Jackson Marr
School of Psychology
Georgia Institute of Technology

Dr. Rebecca Snyder
School of Psychology
Georgia State University

Dr. Marc Weissburg
School of Biology
Georgia Institute of Technology
Date Approved: April 29, 2005

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SUMMARY

I investigated the effects of sex, partner (dam or cub), and early rearing conditions on play fighting behavior in giant panda cubs by observing video tapes that were recorded at two facilities in China over a three-year period. Two of the three factors, sex and partner, had significant effects on the play fighting behavior of giant panda cubs. I found sex differences in play fighting, with males exhibiting significantly higher rates of biting behavior than females during play bouts with other cubs. This lends support to the motor training hypothesis and suggests that there is a relationship between adult roles and earlier play fighting behavior. Partner had a significant effect on play fighting, in that cubs exhibited significantly higher rates of Bite, Break Away, Paw Swat, and Re-engage behaviors during play bouts with cubs. These differences suggest that cubs and dams might provide different opportunities as partners during play fighting bouts. Because some behaviors occurred at higher rates with dams, it is possible that dams engage in self-handicapping behavior during play fighting bouts with cubs. Early rearing conditions did not have significant effects on behaviors when they were examined by category or by individual behaviors. Similar results were found when cubs that had access to adult females after six months of age were excluded from the analyses. These results suggest that early rearing conditions have little effect on the play fighting behavior of captive giant panda cubs. Certain aspects of giant panda behavioral ecology, however, might contribute to stability in play signals, regardless of early rearing conditions. Future studies of play fighting behavior in bears should further examine these and other factors,

and that data from these studies need to be interpreted in light of the relationship of bears

to other carnivores.

CHAPTER 1: INTRODUCTION

Play is prevalent within the animal kingdom, and is particularly well documented in mammals and birds (Fagen, 1981). Animals engage in solitary play with objects and physical activity play (Power, 2000). Among mammals, physical activity play, including play fighting, is the most common form of observed play (Fagen, 1981). Play fighting in mammals (e.g. marsupials, carnivores, pinnipeds, ungulates, rodents, and primates) includes lunging, pouncing, biting, and pushing (Byers, 1984). Certain carnivores, such as hyeanids, canids, and ursids, also exhibit mouth-to-mouth behavior during play fighting (Power, 2000).

Although recognizable, play is challenging to clearly define in a way that allows it to be placed into a specific behavioral category (Heinrich & Smolker, 1998). Based on existing evidence, Fagen (1981) proposes several characteristics of play that are currently accepted, and these characteristics are "structural" or "functional" in definition. Specifically, the behaviors exhibited in play: 1) are similar to the behaviors exhibited by adults in other functional contexts (functional), 2) appear exaggerated compared to the behaviors exhibited in other functional contexts (structural), and 3) are repeated more often during a play bout than the behaviors exhibited in other functional contexts (structural). If the behaviors are directed toward another living being, these characteristics also define social play (Bekoff & Allen, 1998).

Play Fighting in Animals

Behaviors that comprise play fighting in animals are similar to those seen in aggressive encounters, yet several distinctions can be made between play fighting and

serious fighting. Specifically, play fighting between animals is less intense than aggressive encounters (Croft & Snaith, 1991; Drea, Hawk, & Glickman, 1996; Pellis & Pellis, 1998; Poole, 1966). Additionally, play fighting bouts are usually longer than truly aggressive interactions (Drea et al., 1996; Poole, 1966), and participants are generally not wounded during play fighting bouts (Pellis & Pellis, 1987). Behaviors exhibited during play fighting often resemble behaviors seen during courtship and mating (Allen & Bekoff, 1995). Play fighting in juvenile voles, for example, involves the precocial expression of precopulatory, not agonistic, behavior (Pierce, Pellis, Dewsbury, & Pierce, 1991). Specific vocalizations are also present in play fighting, but not aggressive encounters in carnivores (Bekoff, 1974), primates (Biben & Symmes, 1986; van Lawick-Goodall, 1968; Goedeking & Immelmann, 1986; Masataka & Kohda, 1988; Stevenson & Poole, 1982), and marine mammals (Rasa, 1971).

Proposed Functions of Play

It is generally accepted that organisms incur benefits later in life that result from playing when they are young (Heinrich and Smolker, 1998). This belief is prevalent because play has been documented in the young of a variety of species, despite the fact that play results in costs to the animal. For example, animals expend energy (e.g. Barber, 1991; Bekoff & Byers, 1992; Burghardt, 1984), and might sustain injuries, alert predators, become separated from caregivers, and even die during play (Fagen, 1981).

Engaging in play, however, might also have a number of benefits, such as allowing an organism to practice complex object skills, and facilitating the development of innovative behavior patterns in the organism (see Fagen, 1981). Play fighting in humans provides children with an opportunity to assess, test, and exhibit physical

strength in a safe context (Pelligrini & Smith, 1998), and might also enable children to establish dominance (Smith, 1982). Play fighting in both children and animals might contribute to an organism's ability learn about its social environment (see Fagen, 1981; Power, 2000), serve as aggression training (e.g. "motor training"), aid in aggression prevention or control, provide cognitive stimulation (reviewed by Power, 2000; see also Thompson, 1998), and provide animals with training for unexpected events (Spinka, Newberry, & Bekoff, 2001). All of these functions of play could ultimately contribute to increased survival, and thus be selected for during evolution (see Allen & Bekoff, 1994).

Recent studies on animal play report mixed findings as to whether social play provides animals with the previously mentioned benefits. Sharpe and Cherry (2003) found that social play between pairs of meerkats did not affect subsequent aggressive interactions between the same pairs of animals. Conversely, juvenile squirrels that engage in high rates of social play show greater improvement in motor skills than squirrels that engage in lower rates of social play (Nunes, Muecke, Lancaster, Miller, Mueller, Muelhaus, & Castro, 2004). Additionally, wrestling behavior in marmosets has been shown to facilitate the animals' abilities to negotiate obstacles for food rewards (Chalmers & Locke-Haydon, 1984).

The Structure of Play Fighting

Certain behaviors, or "play signals" that solicit and maintain play fighting are common, and appear to be readily recognized by many species of animals (Fagen, 1981). Play signals that serve to initiate play bouts vary by species. In primates, positive affective signals often precede play fighting in children (see Power, 2000), while chimpanzees tickle (van Lawick-Goodall, 1968) or display facial expressions and body

postures (Hayaki, 1985) to initiate a play bout. Play fighting in captive marmosets often begins with behaviors that involve bodily contact (Chalmers & Locke-Haydon, 1981; Stevenson & Poole, 1982). Rats pounce and bite (Meaney, Stewart, & Beatty, 1981), and carnivores initiate play fighting by rolling on their backs (Biben, 1983; Fagen, 1981; Schenkel, 1966), playwalking (Bekoff, 1974; Biben, 1983; Schaller, 1972), engaging in acrobatics (Fagen, 1981; Bekoff, 1974; Feddersen-Peterson, 1991; West, 1974), or performing the classic canid play bow (Bekoff, 1977). Many carnivores also engage in locomotory patterns (e.g. stalking) prior to the onset of play fighting (domestic cats: Caro, 1981; Fagen, 1981; hyenas: Drea et al., 1996; cheetahs: Caro, 1995; lions: Schenkel, 1966; tigers: Wasser, 1978). This is also true for black bears, which initiate play by first approaching the other animal in a swaggering walk, and then paw at the other individual (Henry & Herrero, 1974). As a general rule, these same behaviors are play signals that serve to maintain play fighting bouts once they are underway (see Power, 2000).

In contrast, play bouts are generally terminated when one of the participants leaves (children: see Power, 2000; rodents: Poole & Fish, 1975; squirrels: Steiner, 1971; bears: Henry & Herrero, 1974). Children (Aldis, 1975; Blurton-Jones, 1967; Fry, 1990; Smith & Lewis, 1985), rats (Hole, 1991), and wallabies (Watson & Croft, 1993) remain in close proximity to each other after the end of a play fighting bout.

It was previously believed that the structure of play, or play sequences, was much more variable than the sequences seen in other functional contexts. Studies have shown, however, that behavioral sequences in play are predictable, and that temporal patterns are evident, particularly in social play (see Hill & Bekoff, 1977, Poole & Fish, 1975,

Leresche 1976, Schoen, Banks, & Curtis, 1976; Latour, 1981). For example, Chalmers and Locke-Haydon (1981) looked at temporal patterns within marmoset play bouts. The authors found that if a play bout contained wrestling, the wrestling started early in the bout. Bekoff (1995) examined the temporal placement of play bows exhibited by canids in infant domestic dogs, infant coyotes, and infant wolves. Specifically, the temporal relationship between play bows and behaviors seen in other functional contexts (biting and head shaking) was examined. The author found that in coyotes, play bows were more likely to occur before or after these common agonistic behaviors, compared to the other two studied species, and thus concluded that bows maintain playful behavior to reduce the likelihood that biting and headshaking behaviors are misinterpreted by some canids as aggression.

Play Fighting in Bears

Although social play has been fairly well documented in certain families of carnivores (e.g. canids, felids, and hyeanids), systematic studies that document play in bears (ursids) are somewhat limited. In a descriptive study on the behavioral development of black bear cubs, Burghardt and Burghardt (1972) reported that the cubs frequently engaged in play fighting. Additionally, Henry & Herrero (1974) found that motor patterns in social play in black bear cubs are similar to the motor patterns observed in other carnivores, namely canids. Play fighting has also been observed in captive sloth bear cubs (Heath & Mellen, 1983), polar bear cubs (Fagen, 1981), and giant panda cubs and subadults (DuBois, Pappas, & Thomas, 1987; Snyder, Zhang, Zhang, Li, Tian, Huang, Lo, Bloomsmith, Forthman, & Maple, 2003; Snyder, unpublished data; Wilson & Kleiman, 1974).

Giant Panda Behavioral Ecology

Giant pandas (*Ailuropoda melanoleuca*) are classified taxonomically in the order Carnivora, family Ursidae (Ewer, 1973; Schaller, Hu, Pan & Zhu, 1985). They are considered largely solitary, except during breeding season and when a female is raising a cub (Schaller et al., 1985). During times at which giant pandas interact, they communicate using visual, auditory, and olfactory signals (Schaller et al., 1985). Giant pandas live within stable, overlapping home ranges, where females concentrate activities in core areas of their ranges and males roam more widely (Schaller et al., 1985). The primary activity of giant pandas is foraging for, and consuming, bamboo (Schaller et al., 1985).

The mating system of giant pandas is considered promiscuous, as both males and females may breed with multiple partners during a breeding season (Schaller et al., 1985). Breeding generally occurs in the spring, at which time males gather and compete for access to estrus females (Schaller et al., 1985). Female giant pandas give birth in the fall in a cave or hollow tree and newborn giant pandas are highly altricial, and remain with the dam in the den for 4- 7 weeks (Schaller et al., 1985). Giant panda cubs remain nutritionally dependent upon their dams for 12- 18 months (Lu, Pan, & Harkness, 1994; Snyder et al., 2003), and are not socially independent until at least 18 months of age (Lu et al., 1994; Schaller et al., 1985). Table 1 summarizes these characteristics, and provides comparisons among giant pandas and other carnivores (adapted from Bekoff, 1974; Biben, 1983; Schaller et al., 1985).

Table 1. Comparisons among giant pandas and other carnivores.

Species	Eyes Open	Weaned	Social Unit	Mating System
Giant Pandas	40- 48 days	46+ weeks	Solitary	Promiscuous
Black Bears	28- 40 days	30+ weeks	Solitary	Polygynous
Grizzly Bears	21+ days	82+ weeks	Solitary	Polygynous
Coyotes	~14 days	28+ days	Mated pair	Monogamous
Maned Wolves	7- 13 days	34+ days	Solitary	Monogamous (remain together for short period of time)
Crab-Eating Foxes	14 days	32+ days	Mated pair	Monogamous
Bush Dogs	1- 17 days	43+ days	Pack	Monogamous

Sources:
Giant pandas, Black bears, and Grizzly bears: Schaller et al., 1985
Coyotes: Bekoff, 1974
Maned wolves, crab-eating foxes, and Bush dogs: Biben, 1983

Thesis Overview

      To date, few studies have been published that examine play fighting in bears. Data exist on the rates of behaviors in giant panda play fighting during dam-cub bouts (Snyder et al., 2003) and cub-cub bouts (Snyder, unpublished data), but these data document only play fighting in giant pandas under one year of age. Further, no published studies exist that systematically document the behavioral sequences or transitions during play fighting in bears, including giant pandas. The present study is a detailed investigation into play fighting in giant panda cubs. The data were obtained from video taped play bouts made on three dams and fifteen cubs housed in two facilities in China. In the second chapter, I examine the effects of sex on play fighting behavior, and find results similar to existing studies that report sex differences in play fighting in other species. In chapter 3, I document the effects of partner on play fighting in giant panda cubs. I found that cubs engaged in significantly higher rates of Bite, Break Away, Paw Swat, and Re-engage during play bouts with cubs when compared to play bouts with dams. I did not find significant differences in the transitions between behavioral categories when I examined them by partner. Chapter 4 examines the effects of early rearing conditions on cub play fighting behavior. Neither categories of behaviors nor individual behaviors differed significantly when examined by early rearing conditions, even when I excluded from the analyses those cubs that had access to adult females after six months of age. I did not find significant differences in the transitions between behavioral categories when I examined them by early rearing conditions. I interpret the results of all of the chapters in light of the current hypotheses about the functions of play,

the relationship of giant pandas to other carnivores, and giant panda behavioral ecology.

I conclude this thesis by reviewing my findings, and suggesting topics for future research.

CHAPTER 2

EFFECTS OF SEX ON GIANT PANDA PLAY FIGHTING BEHAVIOR

It is well documented that young male children engage in more play fighting than young female children (Aldis, 1975; DiPietro, 1981; Frey & Hoppe-Graff, 1994; Humphreys & Smith, 1984; Maccoby, 1988; Moller, Hymael, & Rubin, 1992; Pelligrini, 1989; Pelligrini & Smith, 1998). Similar sex differences in play fighting have also been observed in a variety of other species (see Meaney et al., 1985, for review). Male nonhuman primates play more frequently (Beckerman Glick, Eaton, Johnson, & Worlin, 1986) and wrestle more often than females (Biben & Symmes, 1986), and male rats (Pellis, 2002) and red-necked wallabies (Watson & Croft, 1993) engage in more play fighting than females. Male giant panda cubs spend more time engaged play fighting behavior with their dams than do young female cubs (Snyder et al., 2003). An opposite trend has been documented in hyenas, in which young females engage in more play fighting than young males (Pederson, Glickman, Frank, & Beach, 1990).

Males often play more roughly during play fighting bouts than females, especially when playing with other males. Pfeifer (1985), for example, found that play fighting between two males was more intense than play fighting between males and females. More contact play is observed in male Bighorn sheep (Berger, 1980) and nonhuman primates (Berger, 1980). Young male ferrets (Biben, 1982) and young male giant panda cubs (Snyder et al., unpublished data) engage in more biting behaviors than female cubs when playing with their dams. In this same study conducted by Snyder and colleagues

(unpublished data), similar sex differences were not found in paw swatting behavior in giant panda cubs.

The degree of sex differences observed in play fighting is believed to be dependent upon the degree of differences in the adult roles of males and females. For example, few differences are expected in play fighting in young animals in which both males and females exhibit aggressive behaviors for the same functions (Fagen, 1981), such as carnivores, which must capture and subdue prey, and defend territories and offspring (Power, 2000). Additionally, sex differences in play fighting are less prevalent in monogamous species (reviewed by Power, 2000), because intraspecific competition for mates is less important for monogamous species than it is for polygynous species (Smith, 1982). Because of this, sex differences in social play frequency have not been observed in a number of monogomous carnivores, including wolves (Bekoff, 1974; Biben, 1983), coyotes (Bekoff, 1974), foxes (Biben, 1983), and bush dogs (Biben, 1983).

Giant pandas are classified taxonomically as carnivores (Ewer, 1973; Schaller et al., 1985), but nearly all of their diet consists of bamboo branches, stems, and leaves (Schaller et al., 1985), thus they have little use for predatory behavior patterns like other carnivores. Giant pandas can be considered promiscuous, and males gather and compete with each other for access to females during breeding seasons. Incidentally, sex differences have been observed during play fighting bouts between giant panda cubs and their dams (Snyder et al., 2003).

I scored video taped play bouts on 15 giant panda cubs, 7 male cubs and 8 female cubs. All data were scored from play bouts between peers, aged 5- 35 months. I tested the following hypotheses about sex differences in giant panda play fighting:

Hypothesis 1: Male giant panda cubs will engage in significantly higher rates of biting behavior during play fighting bouts with their peers than female giant panda cubs.

Hypothesis 2: No sex differences will be found for paw swatting behavior during peer play fighting bouts.

Hypothesis 3: Male giant panda cubs will play more roughly during play fighting bouts with their peers than female giant panda cubs. Specifically, males will engage in significantly higher rates of the intense contact maintaining behaviors Bite, Bite Pull, and Lunge.

Hypothesis 4: Male giant panda cubs will exhibit significantly higher rates of behaviors that are related to adult giant panda reproductive behavior in play fighting bouts than female giant panda cubs. Specifically, males will engage in significantly higher rates of Climb, Rear Up, and Stand Over.

Table 2. Giant panda cubs studied in Chapter 1, and number of bouts scored on each cub.

Cub ID	DOB	Sex	# of Bouts Scored	# of Minutes Scored
YG	2001	Male	3	4.6
YX	2001	Male	3	5.1
LL	2000	Male	7	12.8
BX	2000	Male	2	4.5
CG	2000	Female	4	8.7
CJ	2000	Female	3	6.4
JW	1999	Female	9	12.7
QZ	1999	Female	9	14.8
LJ	1999	Female	4	8.1
WJ	1999	Female	4	6.4
SS	1998	Male	10	15.1
LunLun	1997	Female	5	12.5
DS	1997	Female	13	43.1
XS	1997	Male	17	49.0
YY	1997	Male	7	17.6

METHODS

Subjects and Data Collection

The Chengdu Research Base of Giant Panda Breeding (Research Base) and the Chengdu Zoo are located in the Sichuan Province of the People's Republic of China. Fifteen giant panda cubs (Table 2) housed at these two institutions were observed for this study. Outdoor areas were naturalistic and contained grass, trees, shrubs, and a pool. Indoor enclosures contained concrete floors and metal bars or glass walls, sleeping platforms, and concrete water troughs. See Snyder et al. (2003) for details about housing conditions.

Data were scored from video taped play bouts between giant panda cubs that were recorded at the Research Base or at the Chengdu Zoo. Play bouts were video taped opportunistically, and thus did not conform to an established observation schedule. Video tapes of play fighting were made from 1998 to 2001, between the hours of 0730 and 1630. Play fighting bouts that began before 1200 were classified as "AM", and play fighting bouts that began after 1200 were classified as "PM". Bouts were fairly equally distributed throughout the day (Figure 1). The video tapes documented play fighting in the same animals during these three years, and some cubs were observed in multiple years. To be included in the study, play bouts had to meet the following criteria: 1) the play bout was classified as play fighting, 2) the play fighting bout was at least 60 seconds long, 3) the play fighting bout consisted of interactions between only two animals (one dam and one cub, or two cubs), and 4) both of the animals in the play bout were not scored as "not visible" during the first 60 seconds of the bout. "Play fighting" was operationally defined as, "interaction between two individuals that resembles real

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fighting, in that each animal exhibits at least one Initiation behavior, or at least one

Termination behavior, in addition to at least one Contact Maintaining behavior".
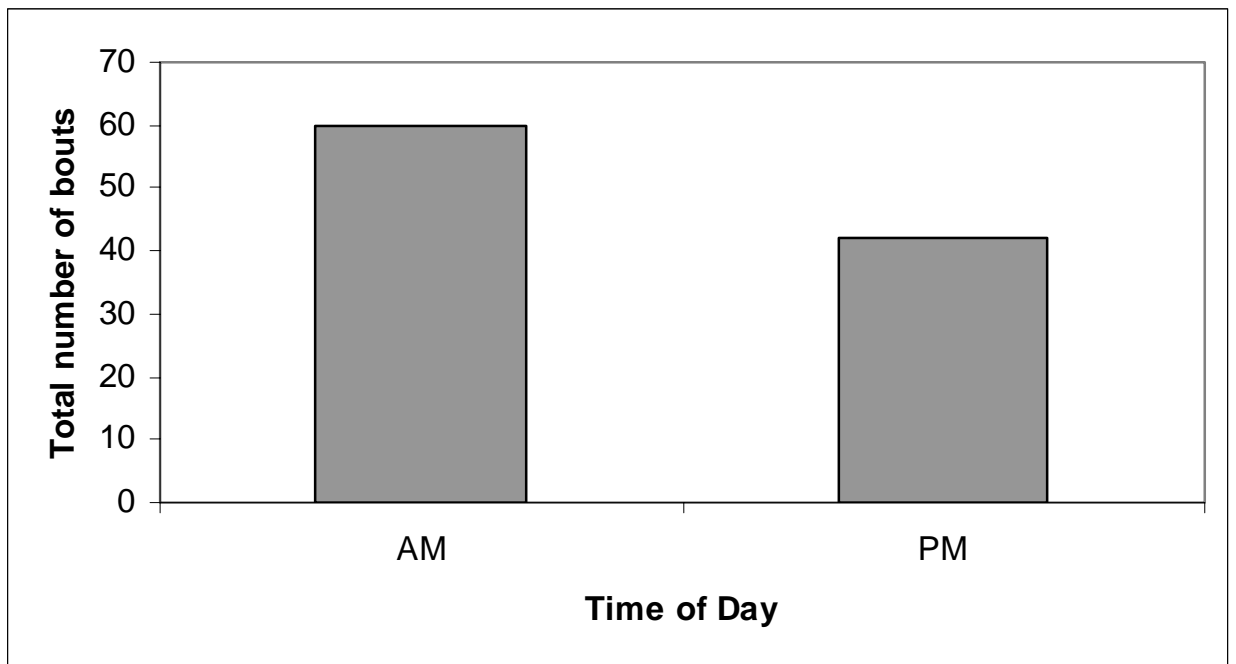
Figure 1. Total number of observations scored in each time period (AM and PM).

Table 3. Ethogram of behaviors.

Initiation Behaviors	
Bite Move (BM)	Incomplete biting action. Mouth open, but not attempting to bite the other animal
Head Shake (HS)	Vigorously shaking head back and forth or up and down, usually while oriented toward another animal
Paw Move (PM)	Incomplete paw swat action. Holding up of paw(s), but not attempting to swat the other animal
Re-engage (RE)	After animal breaks away, reorienting toward animal and continuing in bout
Reproductive Behaviors	
Climb (CL)	At least three paws on another animal, with or without biting
Rear Up (RU)	On hind legs and oriented toward another animal. In contact or in close proximity to the animal
Stand Over (SO)	On hind legs and perpendicular to the other animal's body. In contact with other animal with paws on shoulder or back
Contact Maintaining Behaviors	
Bite (BT)	Mouth is placed on some part of another animal for at least one second
Bite Pull (BP)	Mouth is placed on some part of another animal. Pulling during bite, visibly stretching the animal's skin
Claw (CL)	Vigorously swiping movements at another animal's body with either front or back paws
Lunge (LU)	Rearing on hind legs from stationary position and thrusting body forward and contacting another animal
Paw Swat (PS)	Batting another animal with paw(s), making brief physical contact
Termination Behaviors	
Break Away (BA)	Breaking contact with other animal, and remaining without contact or orientation to the animals for at least five seconds
Head Stand (HS)	Head tucked under the body, with top of head resting on ground. Must last for five seconds, and may be followed by somersault

Table 3 (continued).

Push (PH)	Lifting of one or both hind paws and placing pressure on other animals to break a bite-hold
Somersault (SO)	Rolling headfirst, moving forward, until roll completed
Struggle (SG)	Attempting to break contact with other animal using behaviors not listed on ethogram
Turn (TU)	Twisting and/or rolling to break a bite-hold
Other Behaviors	
Other (OT)	Any behavior not listed on the ethogram
Not Visible (NV)	Focal animal is not visible to the observer
Pause (PU)	Remaining in contact, but not actively participating in bout for at least ten seconds
Sexual (SX)	Mounting, pelvic thrusting, and/or rolling one leg laterally to expose the inguinal region
Stationary (SA)	Out of contact, and not actively participating in a bout for at least five seconds. If animal is stationary for at 20 seconds, the bout is considered terminated

This ethogram (Table 3) was adapted from ethograms developed by R. Snyder (personal communication), Snyder et al. (2003), Henry & Herrero (1974), and Bekoff (1977). In the present study, certain contact behaviors were further defined by intensity (Table 3 in Appendix A). For example, biting behaviors and lunging were considered more intense than paw swatting behavior, because these behaviors require that the animal be in closer proximity to its play partner than does paw swatting. Because of their higher intensity, biting behaviors (Bite and Bite Pull), and Lunge were considered "rough" behaviors that were tested in Hypothesis 3. Climb, Rear Up, and Stand over were classified as "reproductive behaviors" because these behaviors resemble those that are used by adult, male giant pandas for mating. Behavioral codes were scored using all-occurrence sampling (Altmann, 1974), and the sequences of the behaviors were preserved during data collection.

Video scoring occurred on the entire play fighting bout if it met the aforementioned criteria, although the individual video taping the bout occasionally stopped recording before the bout had terminated. Although videos were scored from the beginning of the taped bouts, the play bouts were always in progress prior to taping, and thus data collection was not biased to a certain part of the bout. Generally, video tapes were scored for only one play fighting bout between two particular subjects on a given day. If, however, more than one play bout for two particular subjects had been recorded on a given day, more than one bout was scored if the following criteria were met: 1) the end of the first play bout was at least 120 minutes before the beginning of the second play bout, and 2) the first play bout was recorded during AM sessions (e.g. began before 1200) and the second play bout was recorded during PM sessions (e.g. began after 1200). I

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chose to set the first criteria at 120 minutes to ensure that I distinguished individual play

bouts from sessions of play bouts (see Chalmers & Locke-Haydon, 1981). If the second

play bout did not meet the aforementioned criteria, the longest bout was scored that was

created on that day to maximize the amount of available data.

I conducted reliability testing with one other observer prior to the onset of data

scoring. Portions of existing play bouts that met the previously mentioned criteria were

used for reliability testing. Play bouts used for reliability testing depicted play fighting

between dams and cubs, and play fighting between two cubs. The two observers

obtained a kappa of .8657 for cub behavior and a kappa of .85 for dam behavior during

play bouts (Martin & Bateson, 1993) prior to the onset of data collection. I scored all of

the data for the study.

During scoring, 8mm videotapes were played on a video camera that was

connected to a television, so that play bouts appeared on the television screen. Each play

bout was coded twice. That is, one subject was the focal animal the first time the bout

was scored, and the other subject was the focal animal the second time the bout was

scored. For some bouts, only one panda was observed as the focal animal, because some

subjects were video taped more frequently than others. This was done to try to obtain a

fairly equal number of bouts for each subject that was also equally distributed among the

ages. It should be noted the data used in this study violate the assumption of

independence, and significant p values should be interpreted with caution.

I scored videos from 15 giant panda cubs, 7 males and 8 females (Figure 2), during video taped play fighting bouts. I scored 49 bouts on males and 51 bouts on females, for a total of 100 scored bouts. The number of play bouts from which the rates were derived is listed in Table 2. The studied cubs ranged in age from 5- 35 months.
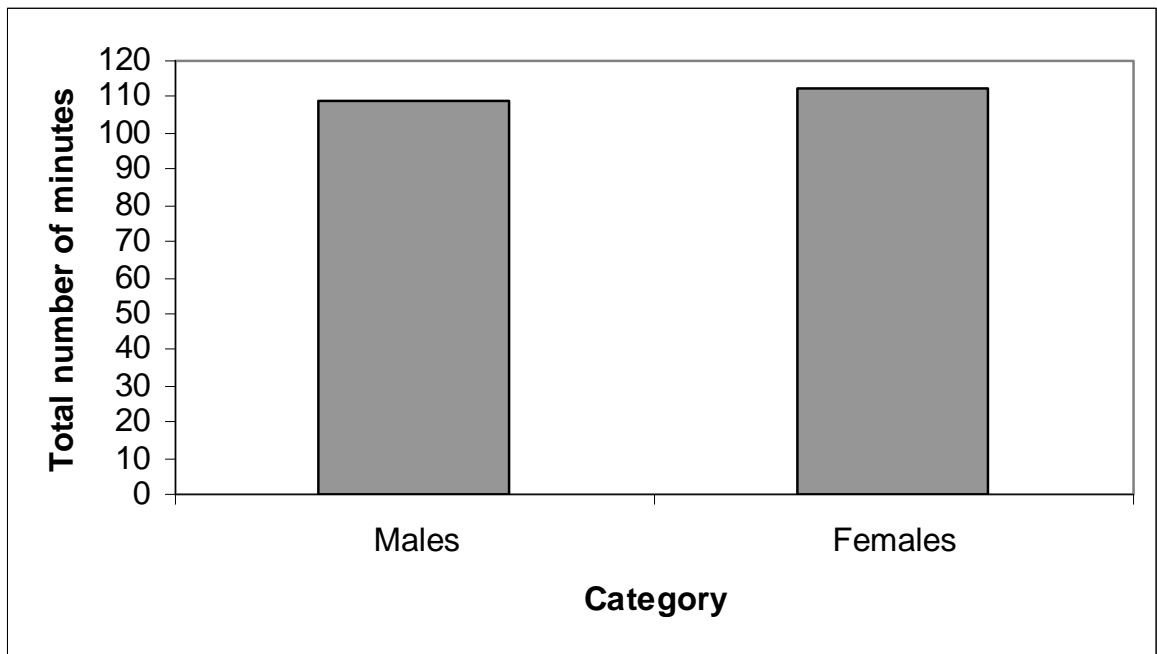
Figure 2. Total minutes of observation on male and female cubs.

Statistical Analyses

I calculated a rate per minute for the following behaviors for each giant panda cub to test the hypotheses: Bite, Bite Pull, Paw Swat, Lunge, Climb, Rear up, and Stand Over. Rates were obtained for each cub by first calculating the total amount of time cubs engaged in play fighting during a particular bout. The total time was obtained by subtracting the time the cub was "not visible" from the total time the subject was observed during that particular bout. Rates were obtained by dividing the total time spent engaged in play fighting by 60, and dividing the frequencies of the behaviors by this number.

I used Statistica 6.0 to obtain descriptive statistics for all of the categories of behaviors and individual behaviors. Due to the small sample size included in this study, and because the data appeared skewed upon visual inspection, I tested all hypotheses with Mann-Whitney U tests (Sheskin, 2004). After arranging all of the scores in order of magnitude, I assigned each of the scores a rank. I computed the sum of the ranks for each group (male and female) and determined the U values for each group using the following equations:

$$U_1 = n_1 n_2 + \frac{n_1(n_1+1)}{2} - \sum R_1$$

$$U_2 = n_1 n_2 + \frac{n_2(n_2+1)}{2} - \sum R_2$$

I used the smaller of the two values as my Mann-Whitney U test statistic, and interpreted the U value based on a table of critical values on page 1151 in Sheskin (2004). Because Hypotheses 1, 3, and 4 were directional hypotheses, I evaluated them with one-tailed tests. Hypothesis 2 was nondirectional, and I evaluated this hypothesis

with a two-tailed test. I calculated Cohen's *d* indices of effect sizes. Although I used

nonparametric statistical tests, I reported means, as these values are more meaningful to

the reader than ranks. Table 4 lists the means tested for each of these hypotheses, and

corresponding effect sizes.

Table 4. Mean rates tested for effects of sex examined in Chapter 2.

Hypothesis	Means for Males	Means for Females	ES_d
Hypothesis 1: Biting	5.51	3.12	1.98
Hypothesis 2: Paw swatting	.91	1.05	.35
Hypothesis 3: Rough play	1.90	1.08	.37
Hypothesis 4: Reproductive play	.04	.01	.60
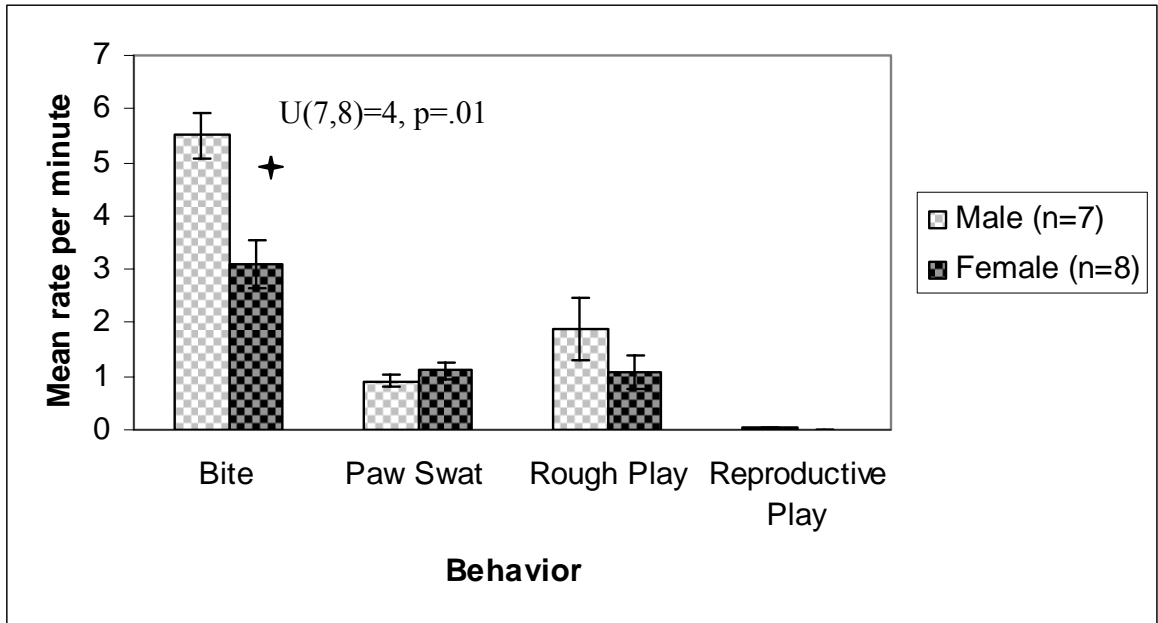
Figure 3.   Sex differences in behaviors (mean $\pm$ SEM) during cub-cub play fighting bouts

RESULTS

Sex Differences

I found evidence for sex differences in biting behavior, but similar differences did

not exist for paw swatting behavior, rough play, or reproductive play behavior (Figure 3).

As hypothesized, male giant panda cubs engaged in significantly higher rates of biting

behavior (Mann-Whitney U test: U(7,8) =4, one-tailed p=.01). Female giant panda cubs

engaged in higher rates of paw swatting behavior, but these differences were not

statistically significant (Mann-Whitney U test: U(7,8)=23, two-tailed p>.05). Male giant

panda cubs engaged in higher rates of rough play (U(7,8)=12, one-tailed p>.05) and

reproductive play behavior (Mann-Whitney U test :U(7,8)=18.5, one-tailed p>.05), but

these differences were not statistically significant.

Because biting behavior occurred at significantly higher rates in males than

females, I also examined whether males engaged in significantly higher rates of biting

behavior with other male cubs. I tested the rates of biting behavior with a Wilcoxon

signed-ranks test (Shekin, 2004). I calculated a difference score (D) for each subject, and

then I ranked the absolute values of these scores. I then placed the sign of each

difference score in front of its rank, and calculated sums for ranks with both positive and

negative signs. I used the absolute value of the smaller of the two values as my Wilcoxon

T test statistic, and interpreted the T value based on a table of critical values on page

1138 in Sheskin (2004). Only four subjects were included in this study, because these

were the only cubs for which data from male-male bouts and male-female bouts were

available. A critical T value did not exist for such a small sample size. I was able to

conclude, however, that male cubs engaged in higher rates of biting behavior with female

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cubs, but the difference was not statistically significant (Wilcoxon signed-ranks test: T=1,

N=4, p>.10) (Figure 4).
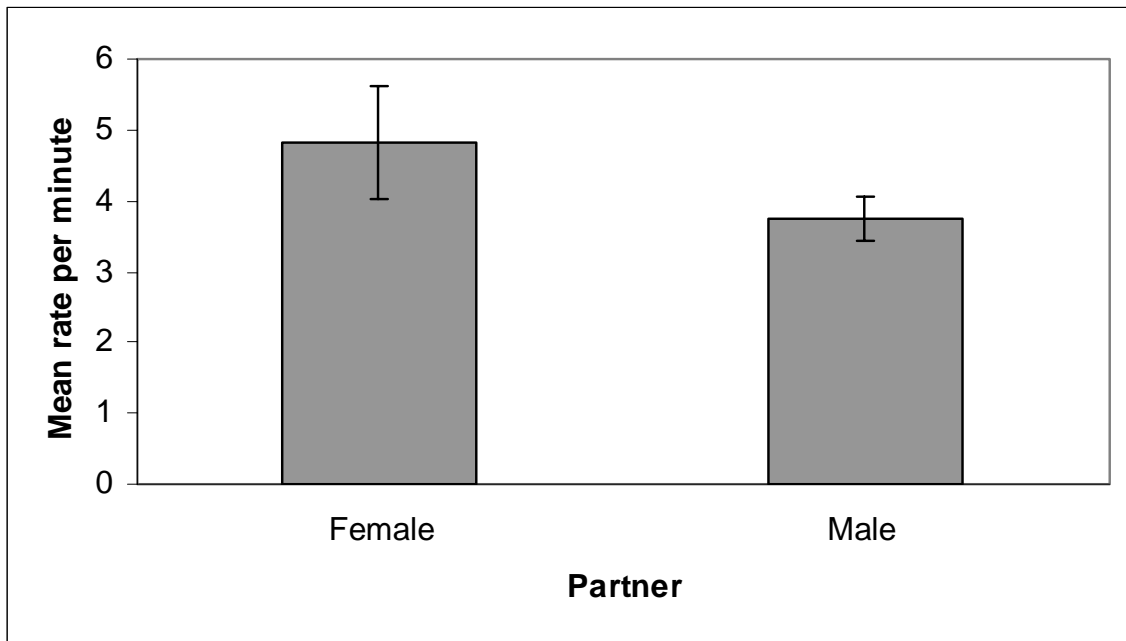
Figure 4. Sex differences in biting behavior (means $\pm$ SEM; n=4) by male cubs during play fighting bouts based on partner.

DISCUSSION

Sex Differences and the Motor Training Hypothesis

The purpose of this study was to assess whether sex differences existed in certain play fighting behaviors exhibited by giant panda cubs, and to determine how these findings support functional hypotheses about play fighting. I found significant sex differences in play fighting behavior, with males exhibiting significantly higher rates of biting behavior than females when playing with peers (Hypothesis 1). Similar sex differences in biting behavior have been found in giant panda cubs less than one year of age during play bouts with their dams (Snyder et al., unpublished data). Taken together, the results of these two studies on giant panda play fighting behavior suggest that this is a robust finding that is observed regardless of play partner (e.g. dam or cub) and, to a certain extent, the age of the cub.

It has been argued that sex differences in play fighting behavior are closely tied to the reproductive strategy of the species (Byers, 1980). Many carnivore species are monogamous, which requires less intraspecific competition than other mating systems (e.g. polygynous, polyandrous, and polygynandrous mating systems). Giant pandas employ a promiscuous mating system. Because adult male giant pandas must compete to have access to females prior to other males during breeding seasons, one would predict that sex differences would exist in play fighting behavior in these animals (see Smith, 1982). This prediction is supported by the data in the present study, which indicate that males engage in biting behavior at significantly higher rates than females during play fighting bouts with other cubs. The prevalence of sex differences in biting behavior in giant panda cubs lends support to the belief that there is a relationship between adult roles

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and earlier play fighting behavior. Further, the results of this study provide evidence to support the "motor training hypothesis", which states that play fighting allows young animals to improve their motor performance through exercise, physical training, or practice (Bekoff & Byers, 1981).

Significant sex differences in paw swatting behavior were not found in this study (Hypothesis 2), female cubs engaged in slightly higher rates of paw swatting behavior than male cubs. In many carnivore species, adult males and females use aggression to defend territories, capture and subdue prey, and protect offspring. Currently, little evidence exists that suggests either male or female giant pandas are territorial (see Schaller et al., 1985), and there is virtually no need for giant pandas to capture and subdue live prey. Female giant pandas, however, do need to protect their offspring from predation, and thus it is important for them to possess at least some degree of proficiency at fighting during aggressive encounters. This places giant pandas in an interesting niche in terms of carnivores. While the promiscuous mating system of giant pandas predicts that sex differences would be expected, the fact that adult males and females must both use aggression predicts that sex differences would not be expected in the play fighting behavior of giant panda cubs.

Because giant pandas are unique carnivores, the effect of sex on play fighting is not entirely clear. It could be that paw swatting during play fights allows female cubs to practice a behavior that they will later use in aggressive encounters as adults. Further, paw swatting behavior does not require the same level of contact as does biting behavior, and potentially poses less risk for injury. Whereas biting implies that close physical contact has been made and aggression has escalated, paw swatting behavior might be

used by adult females to thwart an approach by a predator or conspecific. According to Power (2000), little attention has been paid to defensive tactics used in play fighting, and studies on play fighting must consider both offensive and defensive strategies. These data on paw swatting behavior in male and female giant panda cubs provide the initial step on which to base a detailed investigation into offensive and defensive play fighting behaviors used by this species.

The fact that significant sex differences were not found in paw swatting behavior might also have alternative explanations. First, Henry and Herrero (1974) propose that bears initiate play fights by pawing at their play partners. In this study, I classified paw swatting as a behavior that serves to maintain contact during a play bout. Paw swatting behavior in female giant pandas might instead serve as a signal to play partners that initiates a play bout, which might have affected the results. Because I analyzed play bouts that were already in progress, determining the behaviors that initiate play fighting bouts in giant panda cubs was not possible in this study. Second, sex differences in young animals emerge in part through social interactions with adults, including their dams (Meaney et al., 1985). In the present study, rearing conditions differed among the cubs, and some of the cubs were "dam-reared" and some were "peer-reared". It is possible that there is a relationship between early rearing conditions and the development of sex differences in the play fighting behavior of the giant panda cubs observed in this study. The effects of early rearing conditions on the play fighting behavior of giant panda cubs are discussed in Chapter 4 of this document.

Rough and Reproductive Play

I did not find significant sex differences in the rates at which males and females engaged in rough play (Hypothesis 3) or reproductive play behavior (Hypothesis 4). In general, play fighting in animals peaks in the juvenile periods, and then decreases as the animal ages (Power, 2000), but the relationship between age and certain characteristics of play fights is unclear. For example, in primates (Baldwin & Baldwin, 1978: Van Lawick-Goodall, 1968) and rodents (Poole & Fish, 1976; Meaney & Stewart, 1981) roughness of play fighting increases with age. Further, play in older ground squirrels contains more aggressive behaviors than does play in younger ground squirrels (Waterman, 1987). In contrast, the proportion of high-intensity play fights in wallabies declines with age, which results in gentler play fighting bouts in older animals (Watson & Croft, 1993).

Skill in play fighting is perfected over a long period of time, in small increments (Fagen, 1981), and captive giant pandas continue to play until at least three years of age (Wilson & Kleiman, 1974). I documented play fighting behavior in cubs from five months to nearly three years of age, but it is possible that developmental changes that result in increased roughness or intensity are not evident in giant pandas until later in life. Further, giant pandas are not sexually mature until approximately 5 years of age (Schaller et al., 1985). Therefore, the propensity for males to show significantly higher rates of reproductive play behavior might not yet be apparent during the age range of the subjects in this study. Unfortunately, my data did not allow me to examine age as a variable, because most of the scored bouts on cubs over one year of age were recorded on three male cubs (YY, QM, and SS) and one female cub (QF).

It should be pointed out that although this study did not experimentally examine the effects of age on play fighting, the age of the cubs is one variable that could have prevented me from finding significant differences in rough and reproductive play behavior. A second factor that must be considered is the potential effect of play partners. Previous studies have found a relationship between the intensity of play fighting bouts and the characteristics (e.g. sex) of the play partners. In oryx, for example, play fights of the highest intensity occur between two males, whereas play fights betweens males are females are less intense (Pfeifer, 1985). In this study I did not find similar significant differences, and males did engage in more biting behavior when playing with female cubs. Although this is an interesting trend, the small sample size makes if difficult to draw firm conclusions about the effects of partner on sex differences in giant panda play fighting behavior. The available play partners of the studied animals might explain why significant differences in play fighting roughness and reproductive play behaviors were not found in males and female giant panda cubs. I scored nearly twice as many play bouts between a male and a female cub, as play bouts between two male cubs.

CHAPTER 3

EFFECTS OF PARTNER ON GIANT PANDA PLAY FIGHTING BEHAVIOR

Social play between parents and offspring, such as play fighting, has been documented in a variety of animals (humans: see Power, 2000; nonhuman primates: Hoff, Nadler, & Maple, 1981; van Lawick-Goodall, 1968; Bard, 1994; Enomoto, 1990; Biben & Suomi, 1993; carnivores: Drea et al., 1996; Bekoff, 1978; Heath & Mellen, 1983; Fagen, 1981; Snyder et al., 2003; also see Kleiman & Malcolm, 1981). Existing studies on play fighting between carnivore dams and their offspring, however, report differences in this type of play. For example, coyote dams wrestle and play fight with their pups, but they do not initiate these types of playful interactions with them (Bekoff, 1978). In contrast, Heath and Mellen (1983) found that a captive female sloth bear not only engaged in play fighting with her cubs, but also initiated much of the observed play bouts with her cubs. Polar bear dams (Fagen, 1981) and giant panda dams (Snyder et al., 2003) also initiate social play with their cubs.

When adults play with offspring, they appear to play differently than their younger partners. Snyder and colleagues (unpublished data), for example, found that giant panda cubs engage in more biting and paw swatting behaviors than giant panda dams during dam-cub play bouts. In addition, existing data indicate that other young carnivores might play differently, depending upon available partners. For example, single kittens direct more playful behavior toward their dams than do kittens with siblings (Mendl, 1988). Additionally, young hyena cubs engage in more social play with siblings, when available, than they do with their dams (Drea et al., 1996). Conversely, young

giant panda twins engage in more play fighting with their dams than they do with their siblings (Snyder et al., 2003).

I scored play bouts on 9 giant panda cubs, aged 5- 35 months, during bouts with both dams and other cubs. Because previous work has been done on specific giant panda play fighting behaviors (see Snyder et al., 2003), and in order to assess whether differences exist in the behavior of cubs based on partner (e.g. dam or cub), behaviors were examined individually, in addition to categorically. I did this to specifically identify the behaviors that differed based on play partners. All of the tested behaviors were classified as behaviors that serve to initiate a play fighting bout, maintain contact during a play fighting bout, or terminate a play fighting bout. I categorized Bite Move, Head Shake, Paw Move, and Re-engage as Initiation behaviors. These behaviors either did not involve actual physical contact with the play partner, but did involve orientation toward the play partner (Bite Move, Head Shake, Paw Move), or appeared to "restart" play (Re-engage). Contact Maintaining behaviors included Bite, Bite Pull, Claw, Lunge, and Paw Swat. I categorized these behaviors as Contact Maintaining behaviors because they required the subject to be in close proximity to, and in contact with, the play partner. I categorized Break Away, Struggle, and Turn as Termination behaviors. These behaviors either did not involve actual physical contact with the play partner and orientation toward the play partner (Break Away), or appeared to be used to end play (Push, Struggle, and Turn). I tested the following hypotheses about the effects of partner on giant panda play fighting:

Hypothesis 1a: The rate of Initiation behaviors exhibited by cubs when playing with dams will differ significantly from the rate of Initiation behaviors exhibited by cubs when playing with cubs.

Hypothesis 1b: Cubs will exhibit significantly different rates of the following behaviors when compared by partner: Bite Move, Paw Move, and Re-engage. This hypothesis tests differences of individual Initiation behaviors.

Hypothesis 2a: The rate of Contact Maintaining behaviors exhibited by cubs when playing with dams will differ significantly from the rate of Contact Maintaining behaviors exhibited by cubs when playing with cubs.

Hypothesis 2b: Cubs will exhibit significantly different rates of the following behaviors when examined by partner: Bite Pull, Bite, Lunge, and Paw Swat. This hypothesis tests differences of individual Contact Maintaining behaviors.

Hypothesis 3a: The rate of Termination behaviors exhibited by cubs when playing with dams will different significantly from the rate of Termination behaviors exhibit by cubs when playing with cubs.

Hypothesis 3b: Cubs will exhibit significantly different rates of the following behaviors when examined by partner: Break Away, Push, Struggle, and Turn. This hypothesis tests differences of individual Termination behaviors.

In addition to the aforementioned hypotheses tested on rates of behaviors, I also examined transitions between the three categories of behaviors to determine whether certain transitions were more characteristic of cubs during play bouts with dams or during play bouts with cubs. I tested the following hypotheses about the effects of partner on behavioral transitions in giant panda play fighting:

Hypothesis 4a: Cubs will exhibit significantly different transitions between Initiation behaviors and other categories of behaviors (Initiation, Contact Maintaining, and Termination) when examined by partner.

Hypothesis 4b: Cubs will exhibit significantly different transitions between Contact Maintaining behaviors and other categories of behaviors (Initiation, Contact Maintaining, and Termination) when examined by partner.

Hypothesis 4c: Cubs will exhibit significantly different transitions between Termination behaviors and other categories of behaviors (Initiation, Contact Maintaining, and Termination when examined by partner.
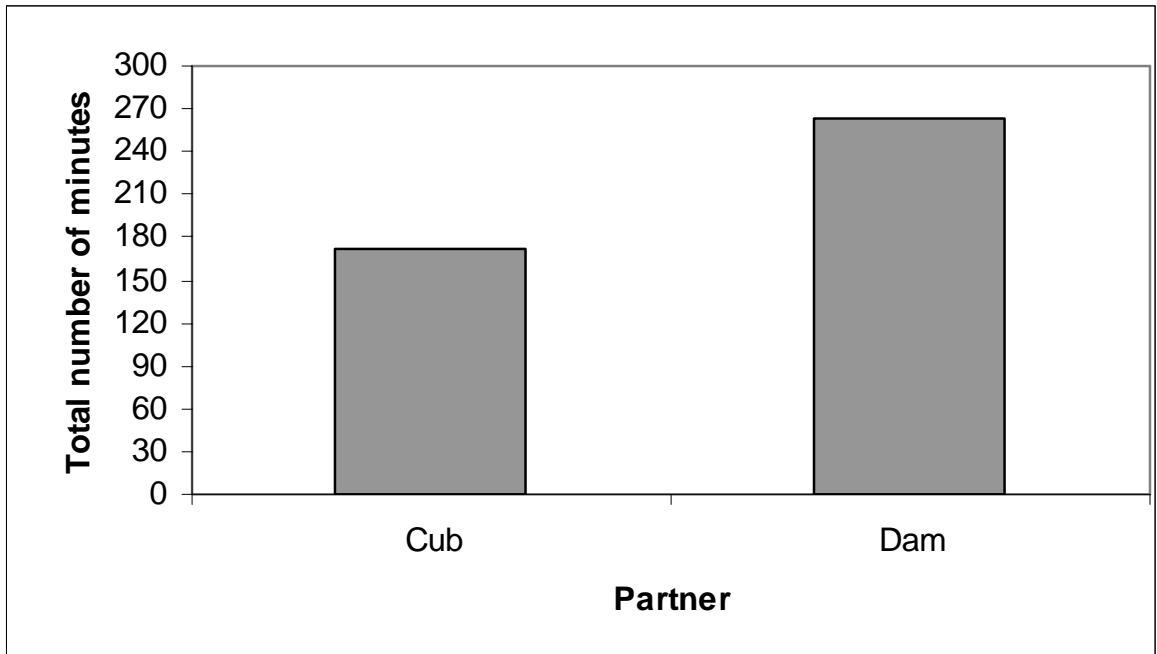
Figure 5. Total minutes of observation on cubs by partner.

METHODS

Subjects and Data Collection

I scored video on 9 cubs playing with other cubs, and also scored video on these same cubs playing with dams (Figure 5). Table 5 list the cubs included in this study. I scored a total of 75 play bouts of cubs playing with other cubs, and 76 play bouts of cubs playing with dams. Of the 76 bouts I scored on cubs playing with dams, 39 bouts were scored on cubs with YaYa, 20 bouts were scored on cubs with QQ, and 17 bouts were scored on cubs with CC (Table 6). The cubs ranged in age from 5- 35 months. Details about the methodology used for data collection can be found in Chapter 1 of this document.

Statistical Analyses

I used Statistica 6.0 to calculate descriptive statistics for all categories of behaviors and individual behaviors. Due to the small sample size included in this study, and because the data appeared skewed upon visual inspection, I tested all hypotheses using Wilcoxon signed-ranks tests (Sheskin, 2004). I calculated a difference score (D) for each subject, and then I ranked the absolute values of the differences scores. I then placed the sign of each difference score in front of its rank, and calculated sums for ranks with both positive and negative signs. I used the absolute value of the smaller of the two values as my Wilcoxon T test statistic, and interpreted the T value based on a table of critical values on page 1138 in Sheskin (2004).

Table 5. Giant panda cubs studied in Chapter 3.

Cub ID	DOB	Sex	# of Bouts Scored (Cub)	# of Bouts Scored (Dam)	# of Minutes Scored (Cub)	# of Minutes Scored (Dam)
BX	2000	Male	2	3	4.5	5.6
JW	1999	Female	9	2	12.7	7.4
QZ	1999	Female	9	1	14.8	1.7
LJ	1999	Female	4	9	8.1	15.3
WJ	1999	Female	4	11	6.4	27.6
SS	1998	Male	10	14	15.1	53.7
DS	1997	Female	13	8	12.3	18.7
XS	1997	Male	17	12	49.0	61.9
YY	1997	Male	7	16	17.6	71.2

Table 6. Giant panda dams studied in Chapter 3.

Dam ID	DOB	Maternal History	# of Bouts Scored	# of Cubs Scored with Dam	# of Minutes Scored
QQ	1984	Multiparous	20	2	87.2
CC	1985	Multiparous	17	2	53.7
YaYa	1990	Multiparous	39	5	123.1

I first examined behavioral categories and compared Initiation behaviors (Bite Move, Paw Move, Re-engage), Contact Maintaining behaviors (Bite, Bite Pull, Paw Swat, Lunge), and Termination behaviors (Break Away, Push, Struggle, and Turn) exhibited by cubs based on partner. Then, to specifically identify where differences in play existed for cubs playing with cubs versus cubs playing with dams, the behaviors from each of the categories were tested separately. Because the hypotheses were nondirectional, I evaluated them with two-tailed tests. I calculated Cohen's *d* indices of effect sizes. Although I used nonparametric statistical tests, I reported means, as these values are more meaningful to the reader than ranks. Table 7 lists the means tested for each of these hypotheses, and corresponding effect sizes.

To examine transitions between behavioral categories, the data were standardized using the Sequential Data Interchange Standard (SDIS) developed by Bakeman & Quera (1995). This created a modified version of the data that was analyzed using the Generalized Sequential Querier (GSEQ) (Bakeman & Quera, 1995). I selected one category of behavior to serve as the "given" event, and another category of behavior to serve as the "target" event. For example, I first examined the transition between Initiation behaviors and Initiation behaviors. Second, I examined the transition between Initiation behaviors and Contact Maintaining behaviors, and so on, until I finally examined the transition between Termination behaviors and Termination behaviors. I only examined "target" events immediately following "given" events (e.g. lag 1). I calculated phi for each of the 18 transitions as a measure of the strength of association between categories (see Bakeman & Gottman, 1997). I then determined the number of subjects for which each transition was positive when playing with dams, and again when

playing with cubs. Using a sign test (Sheskin, 2004), I determined whether the transitions were evidenced by significantly more cubs then expected based on the table on 1142 of Sheskin (2004). I assessed whether the value of phi for these transitions was significantly different by counting the number of subjects for which phi was greater based on partner. The hypotheses were nondirectional and evaluated with two-tailed tests.   Table 8 shows all of the combinations of transitions that I examined and the mean values tested.

Table 7. Mean rates tested for effects of partner in Chapter 3.

Hypothesis	Means for Dam as Partner	Means for Cub as Partner	ES_d
Hypothesis 1a: Initiation	.84	.79	.04
Hypothesis 1b: Initiation behaviors			
Bite Move	2.44	2.13	.20
Paw Move	.05	.13	.68
Re-engage	.02	.1	.97
Hypothesis 2a: Contact Maintaining	.75	1.38	.41
Hypothesis 2b: Contact Maintaining behaviors			
Bite	2.46	4.18	1.46
Bite Pull	.11	.13	.03
Lunge	.02	.05	.59
Paw Swat	.43	1.14	1.71
Hypothesis 3a: Termination	.54	.41	.29
Hypothesis 3b: Termination behaviors			
Break Away	.11	.25	.98
Push	1.10	.74	.60
Struggle	.53	.44	.29
Turn	.42	.22	.92

Table 8. Transitions that were examined for effects of partner in Chapter 2, and tested scores (phi) associated with these transitions.

Given Target	Initiation	Contact Maintaining	Termination
Initiation			
Dam as partner	.06	.00	.11
Cub as partner	.04	.10	.10
Contact Maintaining			
Dam as partner	-.01	.17	-.13
Cub as partner	-.01	.11	-.05
Termination			
Dam as partner	.01	-.10	.06
Cub as partner	.02	-.14	.14
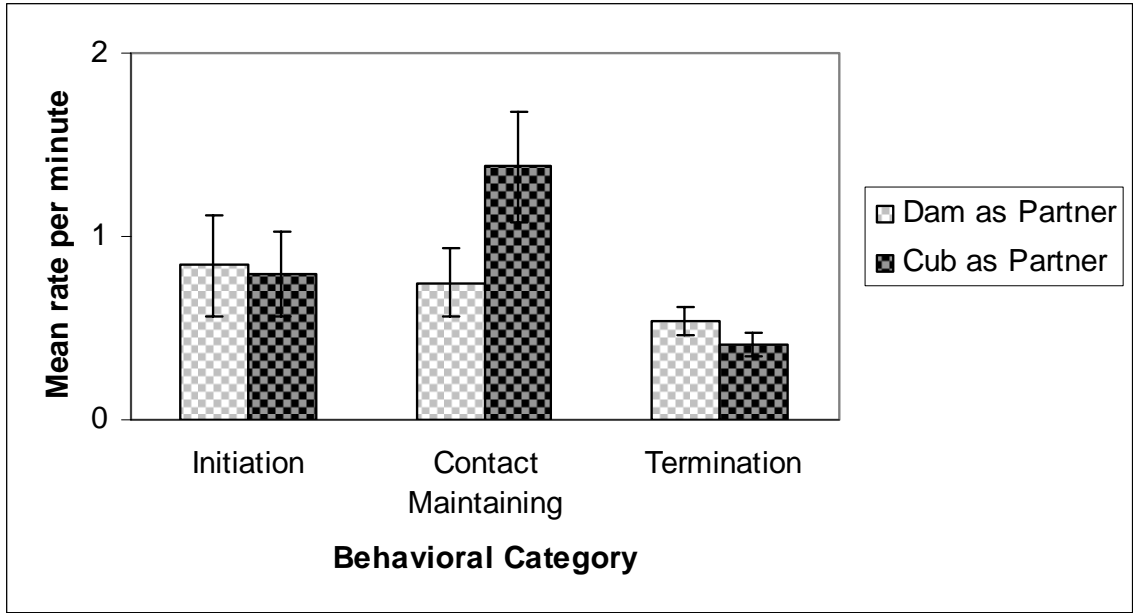
Figure 6. Effects of partner (mean $\pm$ SEM; n=9) on categories of behaviors in cubs.
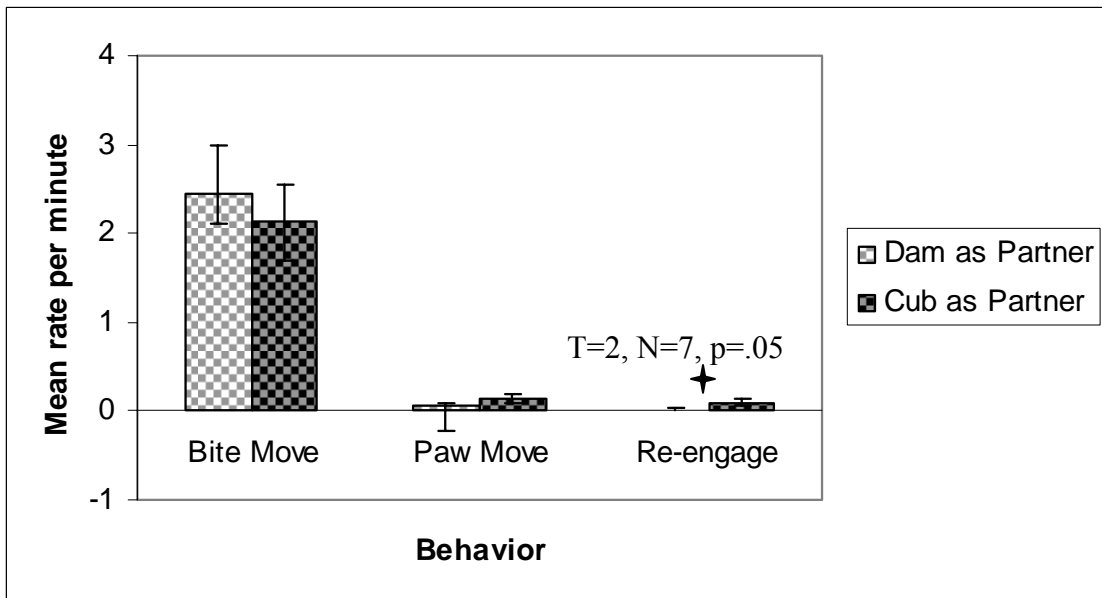
Figure 7. Effects of partner (mean $\pm$ SEM; n=9) on Initiation behaviors in cubs.
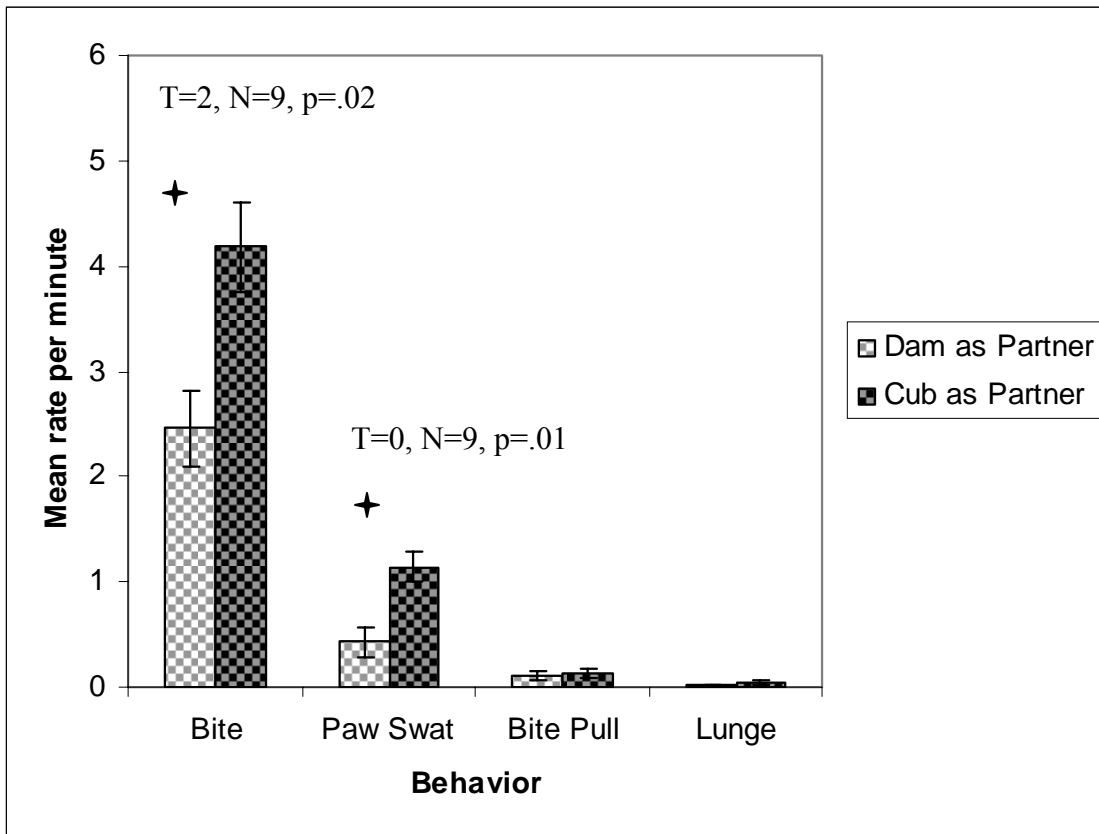
Figure 8. Effects of partner (mean ± SEM; n=9) on Contact Maintaining behaviors in cubs.

RESULTS

Rates of Behaviors

<u>Initiation Behaviors</u>

I did not find significant differences in the rates that cubs engaged in Initiation behaviors when playing with cubs compared to when playing with dams (Wilcoxon signed-ranks test: T=22, N=9, two-tailed p>.10). Cubs engaged in higher rates of Initiation behaviors when playing with dams, but this difference was not statistically significant (Figure 6).

Cubs exhibited significantly higher rates of Re-engage (Wilcoxon signed-ranks test: T=2, N=7, two-tailed p=.05) when playing with cubs. I did not find significant differences in the rates that cubs engaged in Bite Move (Wilcoxon signed-ranks test: T=21, N=9, two-tailed p>.10), Paw Move (Wilcoxon signed-ranks test: T=6, N=7, two-tailed p>.10), or when playing with cubs compared to cubs playing with dams. Cubs exhibited slightly higher rates of Paw Move during play bouts with cubs, but this difference was not statistically significant. Cubs exhibited higher rates of Bite Move with dams, but this difference was not statistically significant (Figure 7).

<u>Contact Maintaining Behaviors</u>

I did not find significant differences in the rates that cubs engaged in Contact Maintaining behaviors when playing with cubs compared to playing with dams (Wilcoxon signed-ranks test: T=8, N=9, two-tailed p>.10). Cubs engaged in higher rates of Contact Maintaining behaviors when playing with cubs, but this difference was not statistically significant (Figure 6).

Cubs exhibited significantly higher rates of Bite (Wilcoxon signed-ranks test: T=2, N=9, two-tailed p=.02) and Paw Swat (Wilcoxon signed-ranks test: T=0, N=9, two-tailed p=.01) during play bouts with cubs. Cubs exhibited higher rates of Bite Pull (Wilcoxon signed-ranks test: T=15, N=8, two-tailed p>.10) and Lunge (T=0, N=3, two-tailed p>.10) during bouts with cubs, but these differences were not statistically significant (Figure 8).
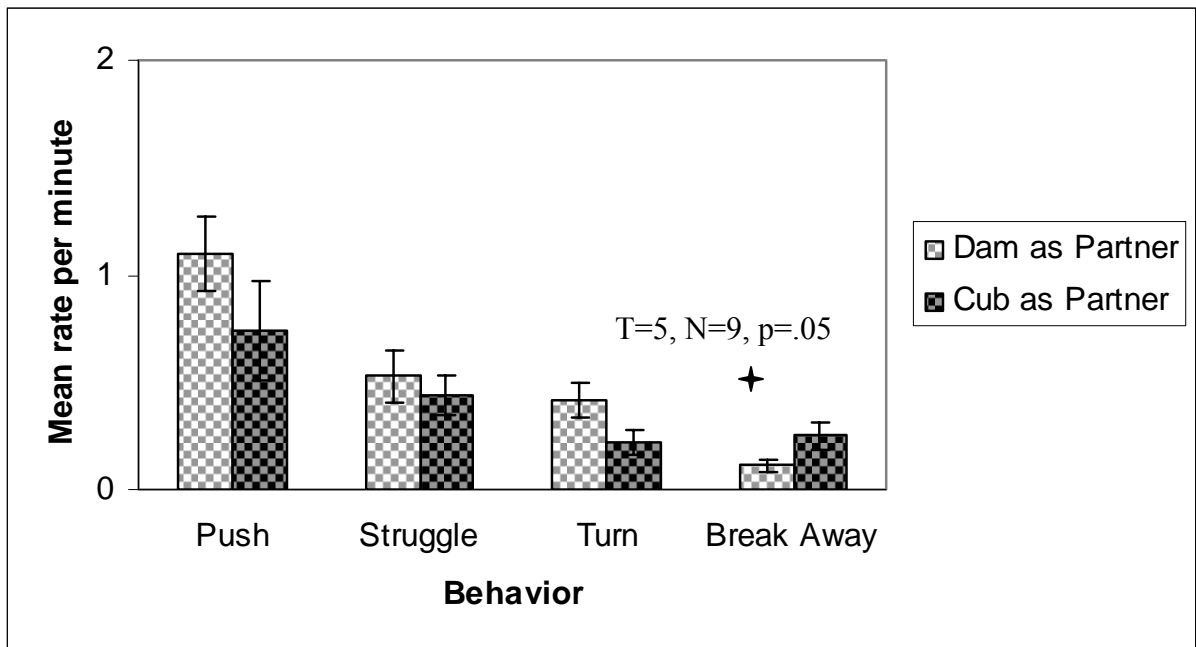
Figure 9. Effects of partner (mean ± SEM; n=9) on Termination behaviors in cubs.

Termination Behaviors

I did not find significant differences in the rates that cubs engaged in Termination behaviors when playing with cubs when compared to play bouts with dams (Wilcoxon

signed-ranks test: T=8, N=9, two-tailed p>.10). Cubs engaged in higher rates of

Termination behaviors when playing with dams, but this difference was not statistically

significant (Figure 6).

Cubs exhibited significantly higher rates of Break Away (Wilcoxon signed-ranks

test: T=5, N=9, two-tailed p=.05) when playing with cubs. I did not find significant

differences in the rates that cubs engaged in Push (Wilcoxon signed-ranks test: T=7, N=9,

two-tailed p>.05), Struggle (Wilcoxon signed-ranks test: T=18, N=9, two-tailed p>.10),

and Turn (Wilcoxon signed-ranks test: T=10, N=9, two-tailed p>.10) when playing with

cubs compared to cubs playing with dams. Cubs exhibited higher rates of Push, Struggle,

and Turn when playing with dams, but these differences were not statistically significant

(Figure 9).

Transitions between Categories

Descriptive Information

For all of the transitions, there were weak relationships between the measured

variables. Of the 18 transitions analyzed, 6 of the transitions were characterized by weak,

indirect relationships, and 12 of the transitions were characterized by weak, direct

relationships.

Initiation Behaviors

I found that the transition between Initiation behaviors and Initiation behaviors

occurred significantly more than expected with cubs, because the number of positive

phi's was 8 (one-tailed p<.05). When I examined this transition based on partner, I did

not find a significant difference in the strength of the association based on partner.

Because the value of phi found for this transition was closer to zero with cubs, however, it showed a less consistent pattern with cubs as play partners.

I did not find significant differences in transitions between Initiation behaviors and Contact Maintaining behaviors or Initiation behaviors and Termination behaviors when I examined transitions by partner.

Contact Maintaining Behaviors

I found that the transition between Contact Maintaining behaviors and Contact Maintaining behaviors occurred significantly more than expected with dams, because the number of positive phi's was 8 (one-tailed $p<.05$). When I examined this transition based on partner, I did not find a significant difference in the strength of the association based on partner. Because the value of phi found for this transition was closer to zero with cubs, however, it shows a less consistent pattern with cubs as play partners.

I did not find significant differences in transitions between Contact Maintaining behaviors and Initiation behaviors or Contact Maintaining behaviors and Termination behaviors when I examined transitions by partner.

Termination Behaviors

I did not find significant differences in transitions between Termination behaviors and all other categories of behaviors.

DISCUSSION

Opportunities Provided by Different Partners

The purpose of this portion of the study was to assess the effects that partners have on play fighting in giant panda cubs. Cubs exhibited significantly higher rates of Re-engage (Hypothesis 1b), Bite (Hypothesis 2b), Paw Swat (Hypothesis 2b), and Break Away (Hypothesis 3b) during bouts with cubs. Animals tend to play with partners that are similar to themselves, including those that are the same age and size (reviewed by Power, 2000), which might explain the previously mentioned significant findings. In this study, during cub-cub play fighting bouts, the cubs were either playing with a twin sibling, or with a peer that was roughly the same age. Dams, on the other hand, were much larger than cubs. Because of this, maintaining contact, through biting and paw swatting was probably much easier when playing with another cub. Similarly, cubs could probably break away from a cub and re-engage with another cub with greater ease than they could with a dam.

Although this might be the case, the findings suggest, however, that dams and cubs might provide different opportunities as play partners. Because cubs engaged in significantly higher rates of a number of behaviors when playing with cubs, it can be concluded that they might get more practice displaying certain play fighting behaviors when their partners are cubs. This additional practice might translate into cubs that are better prepared for adult interactions that include aggressive and reproductive behaviors. Bite, Break Away, Paw Swat, and Re-engage are probably important behaviors for giant panda adults, particularly during aggressive encounters. Although scent plays a key role in mediating social interactions between pandas (Schaller et al., 1985), the potential for

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aggression between adults exists if olfactory cues are not perceived. It is possible that giant panda cubs gain more from playing with other cubs, and that play with peers is important for their development.

Significant differences were not seen in rates of Initiation behaviors and Termination behaviors with dams, but both of these categories of behaviors occurred at higher rates during play bouts with dams. Although not significant, I identified several interesting trends in individual termination behaviors. Specifically, cubs exhibited higher rates of most of these behaviors with dams, and this information provides a more complete picture of the behaviors of giant panda cubs during play fighting bouts. It appears that cubs attempt to break contact with dams by pushing, struggling, and turning at higher rates than they do with cubs. It follows, then, that dams might engage in high rates of Contact Maintaining behaviors when playing with cubs. Zucker, Dennon, Puleo, and Maple (1986) found that adult orangutans attempt to maintain contact more often than younger individuals during play fighting bouts. Additionally, giant panda dams exhibit significantly higher rates of biting behavior during play bouts than do cubs (Snyder, unpublished data). Although this study did not specifically test hypotheses related to play fighting behavior of giant panda dams, these data provide some support to existing studies that indicate that adults and young of the same species play differently. Most importantly, it appears that cubs have more opportunity to engage in Initiation behaviors Termination behaviors, as defined in this study, with dams. I propose that cubs that have access to both an adult female and at least one peer is the ideal combination to prepare cubs for later interactions with other adult giant pandas.

Although I did find significant differences in four behaviors, the fact that I did not obtain additional significant results might be explained by several factors. First, when I tested for effects of partner, I combined all cubs into one category, regardless of sex. Sex differences have been observed in the play fighting behavior of giant panda cubs (see Chapter 2 of this document). Unfortunately, the relatively small sample size studied in this thesis prevented me from me from examining the effects of this variable in detail. Second, the category of "dam as partner" included only three adult female giant pandas. These dams were observed over the course of several years with a number of different cubs. Individual differences among the dams might also have contributed to the results I obtained when I examined play fighting behavior of cubs based on partner.

Play Partners and Self-Handicapping

Significant differences were not found in a number of the behaviors, but this finding is also interesting and relevant to current issues in play fighting. Animals tend to play with well-matched partners (Byers, 1980; Jamieson & Armitage, 1987; Pfeifer, 1985; Watson, 1993), which could provide optimal conditions for motor training. Little work has been done to examine in detail play fighting between parents and offspring, but larger or stronger animals tend to inhibit their behavior when playing with weaker partners (Spinka et al., 2001). This tendency, generally referred to as "self-handicapping", has been identified most commonly in the play behavior of primate adults and offspring (Baldwin & Baldwin, 1978; Biben, 1989; Biben & Suomi, 1993; Hoff et al., 1981). According to Fagen (1981), self-handicapping implies that one animal reduces the likelihood that it will "win" the play fight, thus prolonging the interaction. In this study, one would expect all behaviors to occur at lower rates with dams because of the

differences in size and strength between dams and cubs. The categories of Initiation and Termination behaviors, and Bite Move, Push, Struggle, and Turn, all occurred at higher rates during play bouts with dams. Because of this, dams must modify their behavior to a certain extent when play fighting with cubs. I observed that dams would often lie down or partially recline when playing with cubs as well. Finding that giant panda dams engage in self-handicapping when playing with their cubs would provide additional evidence for the motor training hypothesis (see Chapter 1), because the result of self-handicapping by dams would be prolonged play bouts, which would provide cubs with increased opportunities to practice behaviors related to aggressive and reproductive behaviors required later in life.

Although an interesting explanation for the lack of observed differences, the previously mentioned results lead one to ask why adult female giant pandas would engage in self-handicapping in play fighting bouts with cubs other than their own. In rhesus monkeys, adult females play most often with infants or juveniles that are closely related to them (Symmons, 1978a, cited in Fagen), which likely aids the persistence of their own genes (see Fagen, 1981). What benefit, then, does an adult female giant panda incur from play fighting with a cub(s) with which she is not genetically related? Fagen (1981) has proposed several benefits that adults might incur from playing with young in general. First, an adult can gain status when it holds or interacts with an infant. Second, play fighting may send a "message of long-term goodwill" (p. 445) that indicates that future interactions will be similarly affiliative. Because giant pandas are largely solitary, an adult female will probably not gain status if she plays with a cub that is not genetically related. Further, it is unlikely that giant pandas need to convey that future interactions

might not be competitive for this same reason. It is probable that giant panda dams engage in self-handicapping behavior with cubs that are not biologically related to them, because dams do not differentiate their own cubs from another dam's cubs. Giant panda dams have been observed nursing cubs that are not their own (R. Snyder, pers. comm..), and thus is not surprising that they would engage in self-handicapping with non-related cubs, as this practice is much less energetically costly. The captive environment, in which the needs of the animals are routinely met, probably encouraged self-handicapping behavior in the dams studied in this chapter.

CHAPTER 4

EFFECTS OF EARLY REARING CONDITIONS ON GIANT
PANDA PLAY FIGHTING BEHAVIOR

Social play in young animals is negatively affected when dams do not naturally rear their young (Paquett, 1994; Fox, 1971). Hand-reared gorillas, for example, engage in less social play than gorillas that are reared by their dams (Meder, 1987), and peer-reared giant panda cubs are generally less active than those that are dam-reared (Snyder et al., 2003). It has also been demonstrated, however, that allowing young animals access to peers instead of their mothers reduces these negative behavioral effects. For example, rats that are reared in isolation do not show effects of early social deprivation if they are allowed the opportunity to engage in play fighting with peers for short periods of time each day (Einon, Morgan, & Kibbler, 1978; Potegal & Einon, 1989).

Ewer (1973) hypothesized that play is important in species with relatively lengthy periods of development, during which periods the offspring remain dependent on their parents. Giant panda cubs are nutritionally dependent upon their dams for 12- 18 months (Lu et al., 1994; Snyder et al., 2003), and are not socially independent from their dams until at least 18 months of age (Lu et al., 1994; Schaller et al., 1985). Further, in captivity, giant panda cubs are frequently removed from their dams at a younger age than the two would separate in the wild, and these cubs are often given access to other cubs of the same age (e.g. "peer-reared"). Because giant panda cubs remain nutritionally and socially dependent on their dams for a long period of time, it seems likely that interactions with their dams is vitally important to proper development of giant panda cubs.

I scored video taped play bouts on 15 giant panda cubs, 8 peer reared cubs and 7 dam reared cubs. All data were collected from play bouts between peers, aged 5- 35 months. To assess whether differences existed between cubs reared in these two conditions (dam-reared and peer-reared), behaviors that served to initiate a play fighting bout, maintain contact during a play fighting bout, and terminate a play fighting bout were compared. To specifically identify behaviors that differed based on early rearing conditions, behaviors were examined individually, in addition to categorically. I tested the following hypotheses about the effects of early rearing conditions and partner on giant panda play fighting:

Hypothesis 1a: The rate of Initiation behaviors exhibited by dam-reared cubs during peer play bouts will differ significantly from the rate of Initiation behaviors exhibited by peer-reared cubs during peer play bouts.

Hypothesis 1b: Cubs will exhibit significantly different rates of the following behaviors when compared by early rearing conditions: Bite Move, Paw Move, and Re-engage. This hypothesis tests differences of individual Initiation behaviors.

Hypothesis 2a: The rate of Contact Maintaining behaviors exhibited by dam-reared cubs during peer play bouts will differ significantly from the rate of Contact Maintaining behaviors, and behaviors exhibited by peer-reared cubs during peer play bouts.

Hypothesis 2b: Cubs will exhibit significantly different rates of the following behaviors when examined by early rearing conditions: Bite Pull, Bite, Lunge, and Paw Swat. This hypothesis tests differences of individual Contact Maintaining behaviors.

Hypothesis 3a: The rate of Termination behaviors exhibited by dam-reared cubs during peer play bouts will differ significantly from the rate of Termination behaviors exhibited by peer-reared cubs during peer play bouts.

Hypothesis 3b: Cubs will exhibit significantly different rates of the following behaviors when examined by early rearing conditions: Break Away, Push, Struggle, and Turn. This hypothesis tests differences of individual Termination behaviors.

In addition to the aforementioned hypotheses on rates of behaviors, I also examined transitions between the three categories of behaviors to determine whether certain transitions are more characteristic of peer-reared or dam-reared cubs. I tested the following hypothesis about the effects of early rearing conditions on behavioral transitions in giant panda play fighting:

Hypothesis 4a: Cubs will exhibit significantly different transitions between Initiation behaviors and all other categories of behaviors (Initiation, Contact Maintaining, and Termination) when examined by early rearing condition.

Hypothesis 4b: Cubs will exhibit significantly different transitions between Contact Maintaining behaviors and all other categories of behaviors (Initiation, Contact Maintaining, and Termination) when examined by early rearing condition.

Hypothesis 4c: Cubs will exhibit significantly different transitions between Termination behaviors and all other categories of behaviors (Initiation, Contact Maintaining, and Termination) when examined by early rearing condition.
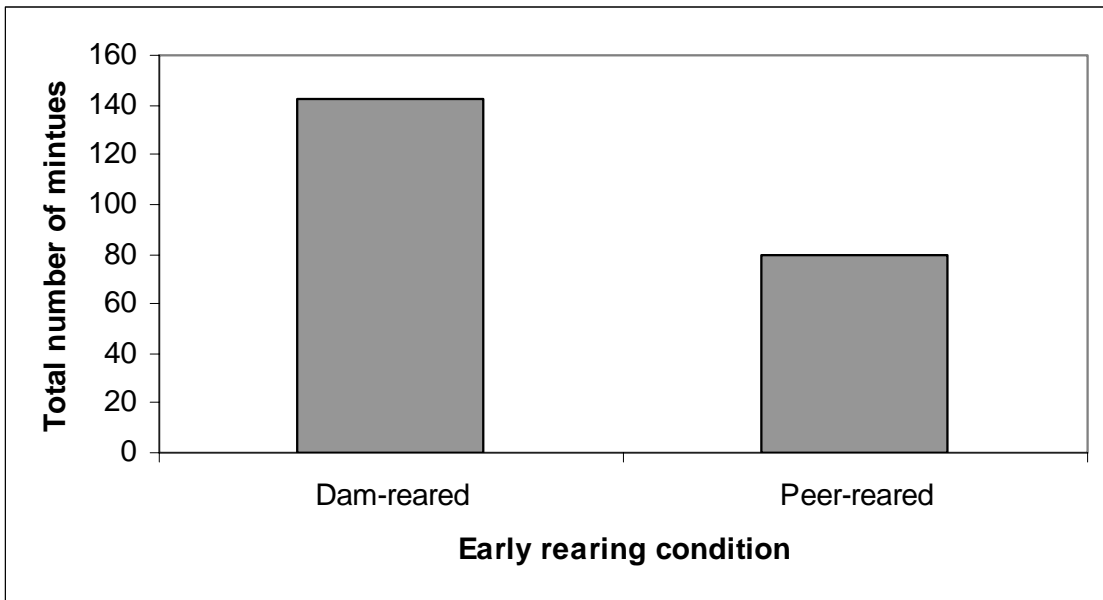
Figure 10. Total minutes of observation on dam-reared and peer-reared cubs.

METHODS

Subjects and Data Collection

I scored video on 15 giant panda cubs, 8 peer-reared cubs and 7 dam-reared cubs,

aged 5- 35 months (Figure 10). Table 9 lists the cubs included in this study. I scored 57

bouts on dam-reared cubs and 43 bouts on peer-reared cubs for a total of 100 scored

bouts. Details about the data collection methodology can be found in Chapter 1 of this

document. Subjects categorized as "dam-reared" cubs were animals that had access to an

adult female (and in some cases a sibling), until 12-13 months of age. In some cases, the

cubs were placed with other adult females (treated as dams for this study), which served

as surrogate dams, for these 12- 13 months instead of their biological dams. After these

12- 13 months, the subjects were then housed with 1- 4 peers (i.e. similarly aged pandas).

Subjects categorized as "peer-reared" cubs were animals that had access to an adult

female until approximately four- five months of age. These subjects were then housed

with 1-4 peers. Four of these cubs (CG, CJ, JW, and QZ) were sometimes given access

to adult females other than their dams after six months of age for a portion of each day.

Statistical Analyses

I used Statistica 6.0 to calculate descriptive statistics for all categories of

behaviors and individual behaviors. Due to the small sample size included in this study,

and because the data appeared skewed upon visual inspection, I tested all hypotheses with

Mann-Whitney U tests (Sheskin, 2004).

Table 9. Giant panda cubs studied in Chapter 4.

Cub ID	DOB	Sex	Predominant Early Rearing Condition	Dam ID	# of Bouts Scored	# of Minutes Scored
YG	2001	Male	Peer	YaYa	3	4.6
YX	2001	Male	Peer	YaYa	3	5.1
LL	2000	Male	Peer	QQ	7	12.8
BX	2000	Male	Dam (CC) + Peer	BB	2	4.5
CG	2000	Female	Peer	CC	4	8.7
CJ	2000	Female	Peer	CC	3	6.4
JW	1999	Female	Peer	MM	9	12.7
QZ	1999	Female	Peer	MM	9	14.8
LJ	1999	Female	Dam (YaYa) + Peer	YaYa	4	8.1
WJ	1999	Female	Dam (YaYa) + Peer	YaYa	4	6.4
SS	1998	Male	Dam (CC)	CC	10	15.1
LunLun	1997	Female	Peer	BB	5	12.3
DS	1997	Female	Dam (QQ) + Peer	QQ	13	43.1
XS	1997	Male	Dam (QQ) + Peer	QQ	17	49.0
YY	1997	Male	Dam (YaYa)	YaYa	7	17.6

After arranging all the scores in order of magnitude, I assigned each of the scores a rank. I computed the sum of the ranks for each group (dam-reared and peer-reared) and determined the U values for each group using the following equations:

$$U_1 = n_1 n_2 + \frac{n_1(n_1+1)}{2} - \sum R_1$$

$$U_2 = n_1 n_2 + \frac{n_2(n_2+1)}{2} - \sum R_2$$

I used the smaller of the two values as my Mann-Whitney U test statistic, and interpreted the U value based on a table of critical values on page 1151 in Sheskin (2004). All of these hypotheses were nondirectional, so I tested them using two-tailed tests. I calculated Cohen's *d* indices of effect sizes. Although I used nonparametric statistical tests, I reported means, as these values are more meaningful to the reader than ranks. Table 10 lists the means tested for each of these hypotheses, and corresponding effect sizes.

To examine transitions between behavioral categories, the data were standardized using the Sequential Data Interchange Standard (SDIS) developed by Bakeman & Quera (1995). Details about the treatment of the data can be found in Chapter 2 of this document. I calculated phi for each transition as a measure of strength of association between categories (see Bakeman & Gottman, 1997). Means were analyzed using Mann-Whitney U tests (Sheskin, 2004) for transitions between categories that had a positive value of phi. The hypotheses about transitions were nondirectional, and were evaluated with two-tailed tests. Table 11 shows all of the combinations of transitions that I examined and the values tested.

Table 10. Mean rates tested for effects of early rearing conditions in Chapter 4 (means include cubs that had access to adult females after 6 months of age)

Hypothesis	Means for Dam-Reared Cubs	Means for Peer-Reared Cubs	ES$_d$
Hypothesis 1a: Initiation	.75	.78	.03
Hypothesis 1b: Initiation behaviors			
Bite Move	2.01	2.18	.14
Paw Move	.15	.05	.08
Re-engage	.10	.08	.17
Hypothesis 2a: Contact Maintaining	1.32	1.41	.05
Hypothesis 2b: Contact Maintaining behaviors			
Bite	4.10	4.25	.09
Bite Pull	.12	.12	.00
Lunge	.05	.04	.16
Paw Swat	1.01	1.01	.00
Hypothesis 3a: Termination	.47	.40	.15
Hypothesis 3b: Termination behaviors			
Break Away	.25	.18	.32
Push	.90	.57	.54
Struggle	.54	.59	.12
Turn	.35	.25	.28

Table 11. Transitions that were examined for effects of early rearing conditions in Chapter 4 and tested scores (phi) associated with these transitions (scores include cubs that had access to adult females after 6 months of age).

Given Target	Initiation	Contact Maintaining	Termination
Initiation			
Dam as partner	.06	.03	.00
Cub as partner	.13	-.03	.00
Contact Maintaining			
Dam as partner	-.02	.19	-.11
Cub as partner	-.10	.19	-.04
Termination			
Dam as partner	.01	-.16	.13
Cub as partner	.01	-.10	.08
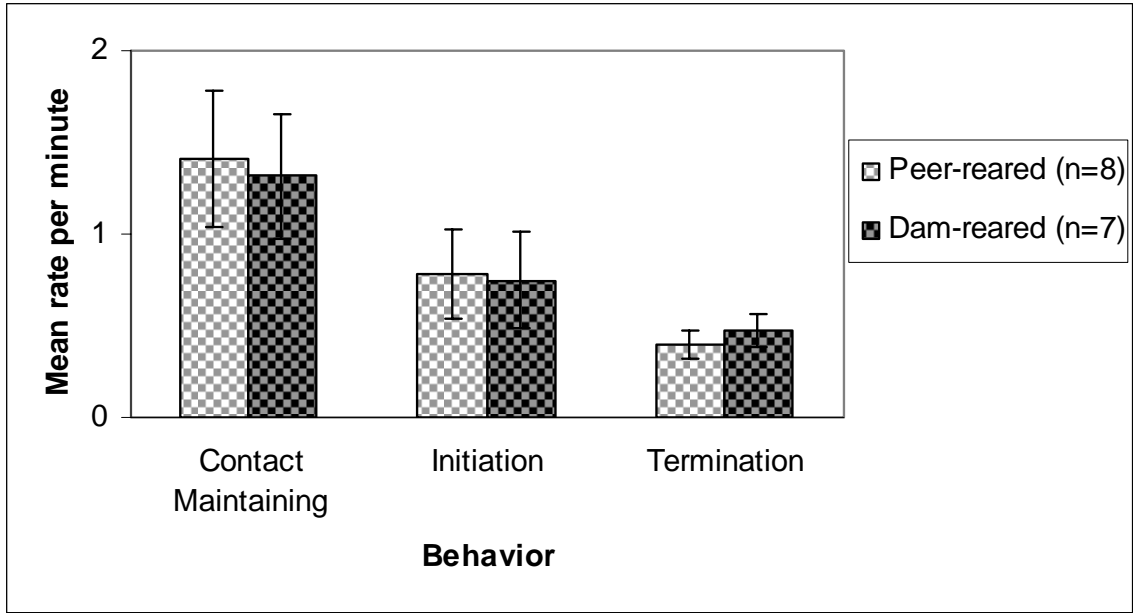
Figure 11. Effects of early rearing conditions (mean± SEM) on categories of behaviors in cubs.
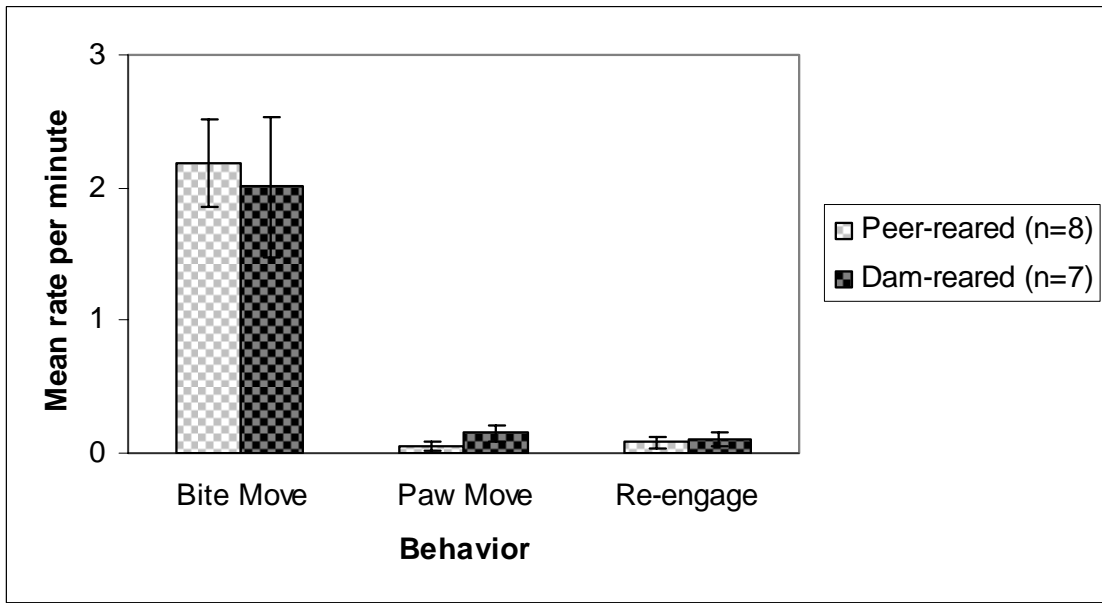
Figure 12. Effects of early rearing conditions (mean± SEM) on Initiation behaviors in cubs.

RESULTS

Rates of Behaviors

Initiation behaviors

I did not find significant differences in rates of Initiation behaviors when examined by early rearing conditions (Mann-Whitney U test: U(7,8)=25, two-tailed p>.05). Peer-reared cubs exhibited higher rates of Initiation behaviors, but this difference was not significantly different (Figure 11).

I did not find significant differences in the rates that cubs engaged in Bite Move (Mann-Whitney U test: U(7,8)=18, two-tailed p>.05), Paw Move (Mann-Whitney U test: U(7,8)=16.5, two-tailed p>.05), or Re-engage (Mann-Whitney U test: U(7,8)=26.5, two-tailed p>.05) when examined by early rearing conditions. Peer-reared cubs exhibited higher rates of Bite Move, but this difference was not statistically significant. Dam-reared cubs exhibited higher rates of Paw Move and Re-engage, but these differences were not statistically significant (Figure 12).

Contact Maintaining behaviors

I did not find significant differences in rates of Contact Maintaining behaviors when examined by early rearing conditions (Mann-Whitney U test: U(7,8)=12, two-tailed p>.05). Peer-reared cubs exhibited higher rates of Contact Maintaining behaviors, but this difference was not statistically significant (Figure 11).

I did not find significant differences in the rates that cubs engaged in Bite (Mann-Whitney U test: U(7,8)=25.5, two-tailed p>.05), Bite Pull (Mann-Whitney U test: U(7,8)=28, two-tailed p>.05), Lunge (Mann-Whitney U test: U(7,8)=25.5, two-tailed p>.05), and Paw Swat (Mann-Whitney U test: U(7,8)=27, two-tailed p>.05) when

examined by early rearing conditions. Peer-reared cubs exhibited higher rates of Bite, but this difference was not statistically significant. Dam-reared cubs exhibited slightly higher rates of Lunge, but this difference was not statistically significant. Peer-reared cubs and dam-reared cubs exhibited relatively equal rates of Bite Pull and Paw Swat (Figure 13).
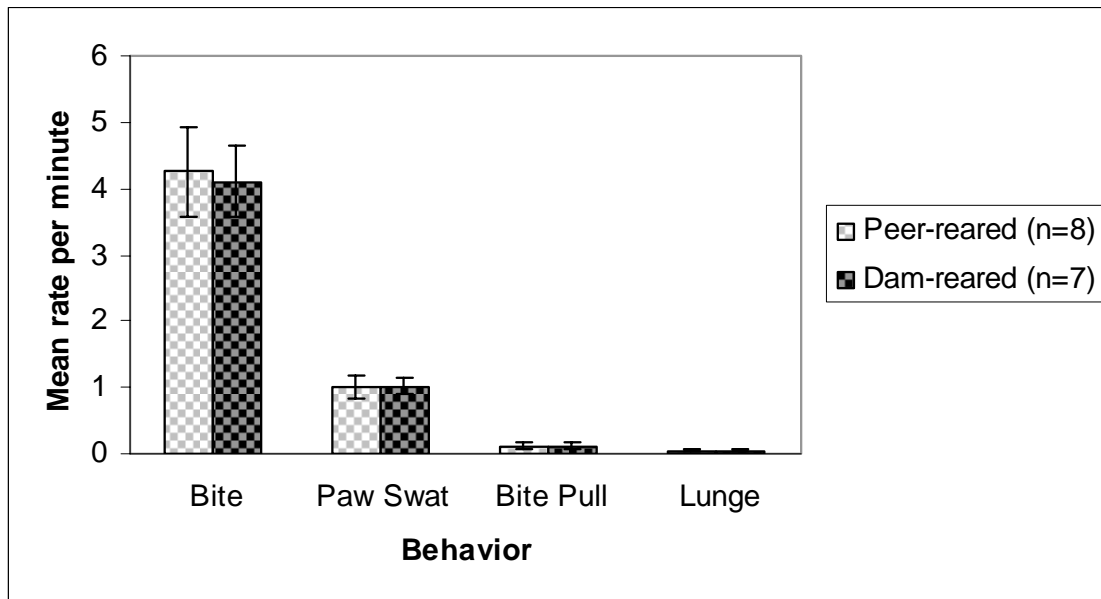
Figure 13. Effects of early rearing conditions (mean± SEM) on Contact Maintaining behaviors in cubs.

Termination behaviors

I did not find significant differences in rates of Termination behaviors when examined by early rearing conditions (Mann-Whitney U test: U(7,8)=22, two-tailed p>.05). Dam-reared cubs exhibited higher rates of Termination behaviors, but this difference was not statistically significant (Figure 11).

I did not find significant differences in the rates that cubs engaged in Break Away (Mann-Whitney U test: U(7,8)=18, two-tailed p>.05), Push (Mann-Whitney U test: U(7,8)=23, two-tailed p>.05), Struggle (Mann-Whitney U test: U(7,8)=28, two-tailed p>.05), and Turn (Mann-Whitney U test: U(7,8)=22, two-tailed p>.05) when examined by early rearing conditions. Peer-reared cubs exhibited higher rates of Struggle, but these differences were not statistically significant. Dam-reared cubs exhibited higher rates of Break Away, Push and Turn, but these differences were not statistically significant (Figure 14).
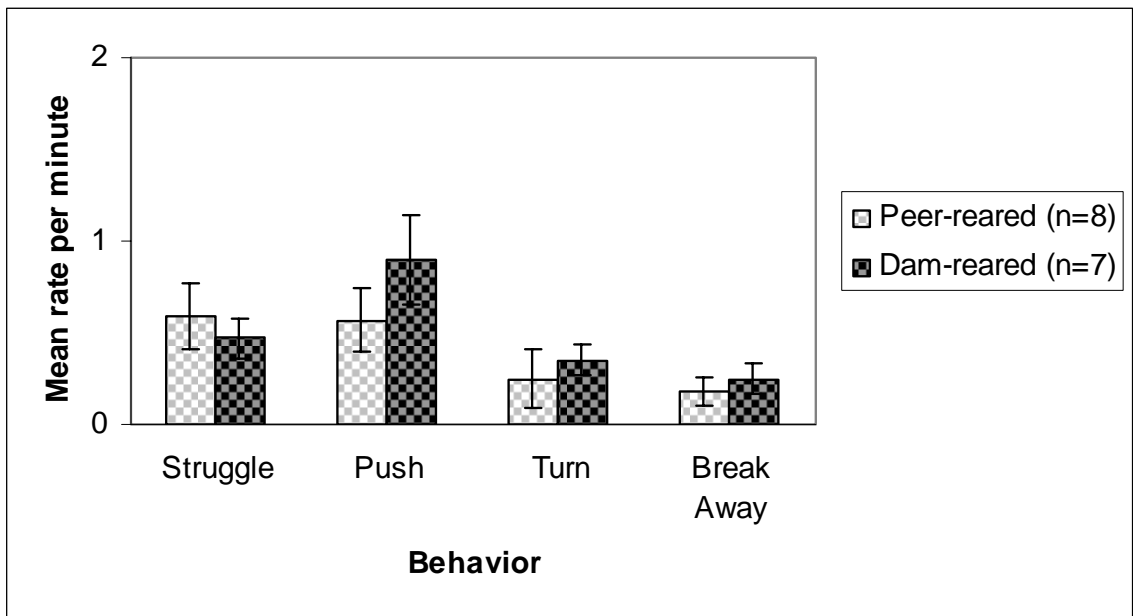
Figure 14. Effects of early rearing conditions (mean+ SEM) on Termination behaviors in cubs.

Transitions between Categories

<u>Descriptive Information</u>

For all of the transitions, there were weak relationships between the measured variables. Of the 18 transitions analyzed, 6 of the transitions were characterized by weak, indirect relationships, 12 of the transitions were characterized by weak, direct relationships.

<u>Initiation Behaviors</u>

I did not find significant differences in the transitions between Initiation behaviors and Initiation behaviors (Mann-Whitney U test: U(7,8)=7, two-tailed p>.10) or Initiation behaviors and Termination behaviors (Mann-Whitney U test: U(7,8)=9, two-tailed p>.10). The transition between Initiation behaviors and Contact Maintaining behaviors was excluded from the analysis because the phi was negative for peer-reared cubs.

<u>Contact Maintaining Behaviors</u>

I did not find significant differences in the transitions between Contact Maintaining behaviors and Contact Maintaining behaviors (Mann-Whitney U test: (7,8)=9.5, two-tailed p>.10). The transitions between Contact Maintaining behaviors and Initiation behaviors and Contact Maintaining behaviors and Termination behaviors were excluded because phis were negative for both dam-reared and peer-reared cubs.

<u>Termination Behaviors</u>

I did not find significant differences in the transitions between Termination behaviors and Initiation behaviors (Mann-Whitney U test: U(7,8)=13.5, two-tailed p>.05) or Termination behaviors and Termination behaviors (Mann-Whitney U test: U(7,8)=12, p>.10). The transition between Termination behaviors and Contact Maintaining

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behaviors was excluded because the phis were negative for both dam-reared and peer-reared cubs.

Table 12. Mean rates tested for effects of early rearing conditions in Chapter 4 (means do not include cubs that had access to adult females after 6 months of age)

Hypothesis	Means for Dam-Reared Cubs	Means for Peer-Reared Cubs	ES_d
Hypothesis 1a: Initiation	.75	.72	.03
Hypothesis 1b: Initiation behaviors			
Bite Move	2.01	2.05	.03
Paw Move	.15	.05	.75
Re-engage	.10	.08	.14
Hypothesis 2a: Contact Maintaining	1.32	1.54	.10
Hypothesis 2b: Contact Maintaining behaviors			
Bite	4.10	5.18	.62
Bite Pull	.12	.16	.25
Lunge	.05	.02	.53
Paw Swat	1.01	.80	.76
Hypothesis 3a: Termination	.47	.25	.55
Hypothesis 3b: Terminations behaviors			
Break Away	.25	.06	1.27
Push	.90	.49	.67
Struggle	.47	.35	.45
Turn	.35	.12	1.02

Additional tests: Rates of behaviors

Because I did not find significant differences in categories of behaviors, or individual behaviors, I eliminated from the analyses those cubs that had access to adult females after six months of age to further limit my definition of "peer-rearing". For these analyses, I used Mann-Whitney U tests (Sheskin, 2004) to test the hypotheses listed above on four peer-reared cubs (LL, LunLun, YG, and YX) and seven dam-reared cubs (BX, DS, LJ, SS, WJ, XS, and YY). Table 12 lists the means tested for these hypotheses, and corresponding effect sizes.

<u>Initiation behaviors</u>

I did not find significant differences in the rates of Initiation behaviors when examined by early rearing conditions (U(4,7)=12, two-tailed p>.05). Dam-reared cubs exhibited higher rates of Initiation behaviors, but this difference was not statistically significant.

 I did not find significant differences in the rates that cubs engaged in Bite Move (U(4,7)=12.5, two-tailed p>.05), Paw Move (U(4,7)=8, N=11, p>.05), or Re-engage (U(4,7)=10.5, two-tailed p>.05). Peer-reared cubs exhibited higher rates of Bite Move, but this difference was not statistically significant. Dam-reared cubs exhibited higher rates of Paw Move and Re-engage, but these differences were not statistically significant.

<u>Contact Maintaining behaviors</u>

I did not find significant differences in rates of Contact Maintaining behaviors when examined by early rearing conditions (U(4,7)=9, two-tailed p>.05). Peer-reared cubs exhibited higher rates of Contact Maintaining behaviors, but this difference was not statistically significant.

I did not find significant differences in the rates that cubs engaged in Bite (U(4,7)=7, two-tailed p>.05), Bite Pull (U(4,7)=13.0, two-tailed p>.05), Lunge (U(4,7)=10.5, two-tailed p>.05), and Paw Swat (U(4,7)=6.0, two-tailed p>.05). Dam-reared cubs exhibited higher rates of Lunge and Paw Swat, but these differences were not statistically significant. Peer-reared cubs exhibited higher rates of Bite and Bite Pull, but these differences were not statistically significant.

Termination behaviors

I did not find significant differences in the rates of Termination behaviors when examined by early rearing conditions (U(4,7)=8, two-tailed p>.05). Dam-reared cubs exhibited higher rates of Termination behaviors, but this difference was not statistically significant.

I did not find significant differences in the rates that cubs engaged in Break Away (U(4,7)=4., two-tailed p>.05), Push (U(4,7)=11, two-tailed p>.05), Struggle (U(4,7)=10, two-tailed p>.05), and Turn (U(4,7)=10, two-tailed p>.05). Dam-reared cubs exhibited higher rates of Break Away, Push, Struggle, and Turn, but these differences were not statistically significant.

Additional tests: Transitions between Categories

Because I did not find significant differences the transitions between behavioral categories, I eliminated from the analyses those cubs that had access to adult females after six months of age to further limit my definition of "peer-rearing". Table 13 shows all of the combinations of transitions that I examined and the values tested.

<u>Descriptive Information</u>

For all of the transitions, there were weak relationships between the measured variables. Of the 18 transitions analyzed, 10 of the transitions were characterized by weak, indirect relationships, 8 of the transitions were characterized by weak, direct relationships.

<u>Initiation Behaviors</u>

I did not find significant differences in the transitions between Initiation behaviors and Initiation behaviors (Mann-Whitney U test: U(4,7)=7, two-tailed p>.10) or Initiation behaviors and Termination behaviors (Mann-Whitney U test: U(4,7)=9, two-tailed p>.10). The transition between Initiation behaviors and Termination behaviors and Initiation behaviors and Contact Maintaining behaviors were excluded from the analysis because phis were negative for both dam-reared and peer-reared cubs.

<u>Contact Maintaining Behaviors</u>

I did not find significant differences in the transitions between Contact Maintaining behaviors and Contact Maintaining behaviors (Mann-Whitney U test: (4,7)=9.5, two-tailed p>.10. The transitions between Contact Maintaining behaviors and Initiation behaviors and Contact Maintaining behaviors and Termination behaviors were excluded because phis were negative for both dam-reared and peer-reared cubs.

<u>Termination Behaviors</u>

I did not find significant differences in the transitions between Termination behaviors and Termination beahviors(Mann-Whitney U test: U(7,8)=12, p>.01). The transitions between Termination behaviors were excluded because phis were negative for one or both groups.

Table 13. Transitions that were examined for effects of early rearing conditions in Chapter 4 and tested scores (phi) associated with these transitions (scores do not include cubs that had access to adult females after 6 months of age).

Given Target ↓ →	Initiation	Contact Maintaining	Termination
Initiation			
Dam-reared	.06	.03	-.00
Peer-reared	.19	-.08	-.03
Contact Maintaining			
Dam-reared	-.02	.19	-.11
Peer-reared	-.11	.21	-.05
Termination			
Dam-reared	.01	-.16	.13
Peer-reared	-.03	-.08	.09

DISCUSSION

Early Rearing Conditions and Behavioral Effects

In this portion of the study I examined the rates at which dam-reared and peer-reared cubs engaged in Initiation behaviors, Contact Maintaining behaviors, and Termination behaviors when play fighting with peers, and assessed whether the rates at which cubs engaged in these categories of behaviors differed during play bouts (Hypotheses 1a, 2a, and 3a). I did not find significant differences in the rates of any of these categories when examined by early rearing conditions, even when cubs that had access to adult females after six months of age were excluded from the analyses. Peer-reared cubs engaged in higher rates of Contact Maintaining behaviors, regardless of whether they had access to an adult female after six months of age. This finding is interesting, because peer-reared animals have been found to engage in less play fighting in general than dam-reared cubs (e.g. gorillas, Meder, 1987), which might lead one to hypothesize that peer-reared cubs would exhibit lower rates of Contact Maintaining behaviors. The fact that animals are exposed to consequences of social interactions during play fighting might also explain why peer-reared cubs engaged in higher rates of Contact Maintaining behaviors. This exposure to consequences trains animals to tolerate at least some level of discomfort during these interactions (Potegal & Einon, 1989). Because play between peers generally results in more evenly-matched pairs than play between a dam and a cub, peer-reared cubs might have had greater exposure to physical discomfort during play fighting bouts, and thus develop a greater tolerance for discomfort during play. Therefore, they might be more willing and likely to attempt to maintain contact during these bouts, as I found in this chapter. This would be particularly true if

giant panda mothers do engage in self-handicapping and modify their behavior to allow cubs to remain in a play fighting bout (see Chapter 3 of this document).

Taken as a whole, the results indicate that transitions between behavioral categories (as defined in this study) exhibited by peer-reared and dam-reared cubs are relatively similar, as are rates of behaviors in these two groups of cubs. These results persisted, even when I excluded from the analyses the cubs that had access to adult females after six months of age. These results are particularly important for captive giant panda management, as current practices often dictate that cubs are removed from their dams earlier than would occur in the wild. These data suggest that the practice of peer-rearing giant panda cubs has little effect on individual play fighting behaviors or categories of play fighting behaviors, or on the transitions between behavioral categories during play fighting bouts.

Few studies have examined, in detail, the effects of early rearing conditions on play fighting behaviors or behavioral categories. In a similar study, however, Potegal and Einon (1989) found that one hour of play fighting each day was enough to eliminate the effects of early social deprivation in rats. In this study, I analyzed data from peer-reared cubs that periodically had access to an adult female for at least some period of time during their development. The opportunity to interact with an adult female might have been enough to negate any potentially negative effects caused by peer rearing. Because I did not statistically compare the two groups of "peer-reared" cubs, however, the results presented in this chapter should be interpreted with caution. Play fighting behavior is not the only measure that should be used to assess the potential behavioral differences that result from early rearing conditions. It is also quite likely that play experience is not the

only type of social interaction that influences the development of young animals (Bekoff, 1976).

A number of variables exist that I could not control in the present study, which might have resulted in the lack of significant differences between the two groups of cubs. First, some cubs classified as "peer-reared" had limited access to adult females, while others did not. As such, the early rearing conditions that defined peer rearing in this study varied. Although I attempted to address this issue with additional analyses, I was unable to assess whether there were differences between these two groups of peer-reared cubs. As such, I am unable to conclude to what degree their behaviors, or categories of behaviors, might be affected. Second, peer-reared cubs that had access to adult females spent varying amounts of time with these females. This made it unwise to compare cubs from the two early rearing condition categories. Finally, some of the cubs classified as "dam-reared" were not reared by their own dams, but were instead reared by biologically unrelated adult females. Despite these issues, and the challenges associated with interpreting data from a small sample size, I argue that the aforementioned results point to the fact that play fighting behavior in giant panda cubs might not be significantly affected if cubs are reared with peers during their development.

Transitions, Play Signals, and Rearing

Although it is quite possible the early rearing conditions have little effect on play fighting behavior in giant panda cubs, there might also be reasons related to giant panda behavioral ecology that account for the lack of observed differences. I did not find significant differences in rates of categories of behaviors, individual behaviors, or transitions between behavioral categories. Further, the transitions that I examined

showed weak relationships between variables. This suggests that giant pandas might not

rely only on patterns of behavior to signal play fighting to their partners. It can be

difficult to demonstrate that a particular behavior functions to signal play fighting (Pellis

& Pellis, 1996). Nonetheless, play signals have been identified for a number of species

(see Power, 2000) for review; see pages 3- 4 of this thesis). The fact that giant pandas are

solitary carnivores might also explain why significant differences were not found in

transitions between categories, despite the fact that early rearing conditions varied among

cubs. Play signals employed by a certain species might be related to the degree of

sociality practiced by a species, and clear signals might be necessary for largely solitary

species to ensure that rarely used signals are perceived correctly by the participants

during play fighting bouts. In a study on the sequences of behaviors exhibited by three

species of canids during play fighting, Biben (1983) found that highly social bush dogs

exhibited the most complex sequence of behaviors during play fighting compared to less

social canids. As a solitary species, it seems likely that giant pandas might require a very

simple sequence of behaviors to signal play. In this study, I examined the behavioral

category immediately following the criterion (e.g. lag 1), which is a very simple sequence

of categories of behaviors. Given that this is the most basic sequence that I could have

examined, it provides additional evidence that transitions between categories of behaviors

might not signal play in giant pandas.

The fact that giant pandas are carnivores might also affect the play signals they

employ. Specifically, clear signals might be necessary in carnivores to avoid injury

because they have the potential to inflict serious damage upon their play partners (Power,

2000). American black bears, for example, use two types of signals (ear position and

facial expressions) as a part of their play-signaling system (Henry & Herrero, 1974). In

contrast, giant pandas have little ability to move their ears or facial muscles (Schaller et

al., 1985). As such, these are not likely play signals to be employed by giant pandas.

Taken together with the idea that transitions between categories might not signal play

fighting in giant pandas, one could conclude that giant pandas probably rely to a great

degree on large body movements to signal play to their partners. In this study, however,

significant differences in behaviors were also not found, despite differences in early

rearing conditions. It appears that the behavior of giant pandas might be relatively stable

regardless of early rearing condition based on the fact that they are solitary carnivores.

Due to the vocal repertoire of giant pandas (see Schaller et al., 1985), it is possible that

vocalizations play a critical role in mediating play fighting in giant pandas. Due to the

quality of the video tapes I scored, documentation of vocalizations that occurred during

play fighting bouts was not possible.

The lack of significant differences that I identified in this chapter might also have

additional explanations. The small sample size that I examined, particularly after I

excluded cubs that had access to adult females after six months of age, might have

contributed to the lack of significant findings. Second, I only examined transitions

between behavioral categories, and not sequences of specific behaviors. It could be that I

did not categorize the behaviors in a way that allowed me to easily extract this

information, or that individual behaviors are more important in play fighting than

categories of behaviors.

CHAPTER 5

CONCLUSIONS

Thesis Summary

Using data collected by video tape over a three-year period, I investigated the factors that affect giant panda play fighting behavior. In Chapter 2, I found evidence to support existing studies that have found sex differences in play fighting in other species. Specifically, male giant panda cubs engaged in significantly higher rates of biting behavior than females during play fighting bouts, and female engaged in higher rates of paw swatting behavior than males during play fighting bouts. Taken together, these results can be explained by the motor training hypothesis, and suggest that there is a relationship between adult roles and earlier play fighting behavior. Although significant differences were not found in rough and reproductive play behavior when examined by sex, these differences might not emerge until later in life.

In Chapter 3, I examined the effects of partner on play fighting behavior in giant panda cubs. Partner had a significant effect on specific play fighting behaviors of giant panda cubs. Specifically, cubs exhibited significantly higher rates of Bite, Break Away, Paw Swat, and Re-engage when playing with other cubs. Because significant differences were found in some of the behaviors, it appears that characteristics of the play partners affect giant panda play fighting behavior. Conversely, significant differences were not found in the rates of many of the other behaviors, and some of these behaviors occurred at higher rates with dams. Dams might engage in self-handicapping during play bouts with cubs, which resulted in the lack of significant findings.

Finally, in Chapter 4, I documented the effects of early rearing conditions on play fighting behavior in giant panda cubs. Peer-reared cubs exhibited higher rates of all categories of behaviors, but differences were not statistically significant. Additionally, early rearing conditions did not have significant effects on behaviors when I examined them individually. I found similar results when I excluded from the analyses cubs that had access to adult females after six moths of age. Taken together, these results suggest that early rearing conditions have little effect on play fighting behavior in giant panda cubs. Alternative explanations for the lack of significant findings might be related to the behavioral ecology of giant pandas, which results in stable play signals that persist regardless of early rearing conditions. A summary of results from Chapters 2, 3, and 4 can be found in Table 14.

Future Research

A large body of literature on play behavior in animals exists, providing a solid platform from which to examine an endless number of hypotheses about giant panda play fighting behavior. Despite this fact, the functions of specific play fighting behaviors in bears are unclear. Future studies should attempt to identify whether paw swatting behavior in female giant panda cubs is additional evidence that supports the motor training hypothesis, or whether paw swatting behavior acts as a play signal that initiates or continues a play fighting bout. The topic of self-handicapping, which has been identified in a number of species, but not clearly in giant panda dams, is also worth further study. Because captive management sometimes dictates that giant panda cubs are removed from their mothers earlier than the two would separate in the wild, additional studies of a longitudinal nature should be conducted to see if negative behavioral effects

resulting from peer rearing are apparent later in life. Specifically, later reproductive success, and abilities to compete for females and defend cubs should be quantified. Studies that determine the amount of time needed with adult females are also necessary to refine captive management. This was the first attempt to document behavioral sequences and transitions in play fighting behavior in bears. In general, very few studies exist that document the timing and sequencing of behaviors during play fighting in both humans and animals (Power, 2000). As such, there are numerous opportunities for this type of work, including documenting the sequences that occur between play partners. The play fighting literature could also benefit from studies that further examine functional hypotheses about play fighting in bears. Specifically, predictions that support motor training, training for the unexpected, and self-assessment should be tested to better understand self-handicapping, and the effects of play partners and age on play fighting behavior in bears. Additionally, individual differences, vocalizations, and interactions between sex and play partner in bears remains understudied.

Table 14. Summary of results.

Chapter 2: Effects of Sex	
Hypothesis	**Result**
Hypothesis 1: Male giant panda cubs will engage in significantly higher rates of biting behavior during play fighting bouts with their peers than female giant panda cubs.	Supported
Hypothesis 2: Significantly different rates of paw swatting behavior during play fighting bouts with their peers will not be seen when examined by sex.	Supported
Hypothesis 3: Male giant panda cubs will play more roughly during play fighting bouts with their peers than female giant panda cubs.	Not supported
Hypothesis 4: Male giant panda cubs will exhibit significantly higher rates of behaviors related to adult male giant panda reproductive behavior in play fighting bouts than female giant panda cubs.	Not supported
Chapter 3: Effects of Partner	
Hypothesis	**Result**
Hypothesis 1a: The rate of Initiation behaviors exhibited by cubs when playing with dams will differ significantly from the rates of Initiation behaviors exhibit by cubs when playing with cubs.	Not Supported
Hypothesis 1b: Cubs will exhibit significantly different rates of Bite Move, Paw Move, and Re-engage when compared by partner.	Not Supported
Hypothesis 2a: The rate of Contact Maintaining behaviors exhibited by cubs when playing with dams will differ significantly from the rates of Contact Maintaining behaviors exhibited by cubs when playing with cubs.	Not supported
Hypothesis 2b: Cubs will exhibit significantly different rates of Bite, Bite Pull, Lunge, and Paw Swat when compared by partner.	Inconclusive: Cubs exhibited two of the four behaviors at significantly higher rates when playing with cubs
Hypothesis 3a: The rates of Termination behaviors exhibited by cubs when playing with dams will differ significantly from the rates of Termination behaviors exhibited by cubs when playing with cubs.	Not supported

Table 14 (continued).

Hypothesis 3b: Cubs will exhibit significantly different rates of Break Away, Push, Struggle, and Turn when compared by partner.	Inconclusive: Cubs exhibited one of the four behaviors at significantly higher rates when playing with dams
Hypotheses 4a: Cubs will exhibit significantly different transitions between Initiation behaviors and other categories of behaviors (Initiation, Contact Maintaining, and Termination) when examined by partner.	Not supported
Hypotheses 4b: Cubs will exhibit significantly different transitions between Contact Maintaining behaviors and other categories of behaviors (Initiation, Contact Maintaining, and Termination) when examined by partner.	Not supported
Hypotheses 4c: Cubs will exhibit significantly different transitions between Termination behaviors and other categories of behaviors (Initiation, Contact Maintaining, and Termination) when examined by partner.	Not supported
Chapter 4: Effects of Early Rearing Conditions	
Hypothesis	**Result**
Hypothesis 1a: The rate of Initiation behaviors exhibited by peer-reared cubs will differ significantly from the rates of Initiation behaviors exhibit by dam-reared cubs when playing with peers.	Not supported, even with exclusion of cubs that had access to adult females after 6 months of age
Hypothesis 1b: Cubs will exhibit significantly different rates of Bite Move, Paw Move, and Re-engage when compared by early rearing conditions.	Not supported, even with exclusion of cubs that had access to adult females after 6 months of age
Hypothesis 2a: The rate of Contact Maintaining behaviors exhibited by peer-reared cubs will differ significantly from the rates of Contact Maintaining behaviors exhibited by dam-reared cubs when playing with peers.	Not supported, even with exclusion of cubs that had access to adult females after 6 months of age
Hypothesis 2b: Cubs will exhibit significantly different rates of Bite, Bite Pull, Lunge, and Paw Swat when compared by early rearing conditions.	Not supported, even with exclusion of cubs that had access to adult females after 6 months of age

Table 14 (continued).

Hypothesis 3a: The rate of Termination behaviors exhibited by peer-reared cubs will differ significantly from the rates of Termination behaviors exhibit by dam-eared cubs when playing with peers.	Not supported, even with exclusion of cubs that had access to adult females after 6 months of age
Hypothesis 3b: Cubs will exhibit significantly different rates of Break Away, Push, Struggle, and Turn when compared by early rearing conditions.	Not supported, even with exclusion of cubs that had access to adult females after 6 months of age
Hypotheses 4a: The probabilities of transitions between Initiation behaviors and other categories of behaviors exhibited by cubs will differ significantly when examined by early rearing conditions.	Not supported, even with exclusion of cubs that had access to adult females after 6 months of age
Hypotheses 4b: The probabilities of transitions between Contact Maintaining behaviors and other categories of behaviors exhibited by cubs will differ significantly when examined by early rearing conditions.	Not supported, even with exclusion of cubs that had access to adult females after 6 months of age
Hypotheses 4c: The probabilities of transitions between Termination behaviors and other categories of behaviors exhibited by cubs will differ significantly when examined by early rearing conditions.	Not supported, even with exclusion of cubs that had access to adult females after 6 months of age

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