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The development and characteristics of feeding behaviour in captive giant pandas

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Abstract. To explore the relationship between the development of feeding behaviour and energy intake for captive giant pandas, food intake, feeding rate, and discrimination time were analysed for 26 pandas grouped by sex and age (cub, sub-adult, adult, and elderly). Feeding rates were significantly different between all age groups, except between elderly and adults. In addition, significant differences were found in discrimination time among the female age groups, and all male age groups except between the adults and sub-adults. Among adults in the same age groups, significant differences between the sexes existed in their feeding rate and discrimination time. Differences in discrimination time existed among elderly, adult and sub-adult females. This study of the dynamic characteristics of the feeding behaviour of captive pandas could provide a theoretical basis for feeding recommendations to improve the success of giant panda breeding programmes.

Key words: *Ailuropoda melanoleuca*, foraging strategy, feeding rate, discrimination time

Introduction

Foraging is necessary for animal survival and reproduction (Swaney et al. 2001) and is an instinctual individual survival behaviour that occurs throughout the entire lifespan for many species (Galef 1995). The type and amount of food appropriate for consumption determine the costs and benefits of different foraging behaviours (Sun 2001). The treatment and choice of food by animals affect their survival strategies (Morrison et al. 2012).

The giant panda (*Ailuropoda melanoleuca*) consumes bamboo, which has low nutritional value and digestibility (Hu et al. 1985). These features of bamboo influence the amount of time giant pandas invest in acquiring and utilizing bamboo (Wei et al. 2000, Nie et al. 2015a). To adapt to the low nutritional content of bamboo, it is thought that the giant panda increases its daily food intake by selecting bamboo of a certain thickness and nutritional quality (Wei et al. 1999, 2004). As observed in other animals, significant differences in food intake and utilization among different age groups have been observed in giant pandas (Hu 2001). In general, the utilization ratio of bamboo in pandas is the highest among sub-adults and lowest among elderly pandas. However, no sex differences have been found (Wang et al. 2014). The main reason for this tendency in younger and older pandas is that cubs and sub-adults have yet to optimize their feeding efficiency, whereas older pandas are subject to decreases in body function (Hu et al. 1985).

Giant pandas target specific types of bamboo. They exhibit preferences for certain species, regions and feeding sites over others (Wei et al. 2015). In general, young giant pandas primarily feed on breast milk into the sub-adult stage (Zhang & Wei 2006). Adult giant pandas show more advanced food selection and consumption (Hu 2001), whereas cubs and sub-adults are less skilled (Zhang & Wei 2006). As a result of tooth wear and reduced body function in old age, foraging rates decline in elderly giant pandas (Hu et al. 1985). This study investigates the differences in foraging behaviour according to sex and age group to discuss the relationship between the development of feeding behaviour and the energy intake of captive giant pandas.

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Material and Methods

Subjects and observational data

This study was conducted using captive individuals housed in the enclosure of the Chengdu Research Base of Giant Panda Breeding, Chengdu, Sichuan Province, China. A total of 135 giant pandas live in the facility. The giant pandas are moved outdoors at 9:00 every morning and return indoors at 17:30. They are fed at 9:00 and 15:30 each day with a diet supplemented with apple, honey, amino acids, vitamins, calcium and other necessary nutrients. A total of 26 giant pandas were included in our study, of which there were 14 females and 12 males. The female pandas that were included were not lactating (Table 1).

The 26 giant pandas were divided into four age groups: cub (0-1.5 year-old), sub-adult (1.5-4.5 year-old), adult (4.5-16 year-old) and elderly (above 16 year-old) (Zhou et al. 2013). The main observations were collected during the first feeding of the day between March 15 and October 20, 2014. The food mainly consisted of mature bamboo or bamboo shoots. If the initial amount was not sufficient (i.e. all of the food was consumed), additional bamboo or bamboo shoots was provided until the pandas no longer eat any more. The pandas were observed from 9:00 until consumption was complete, representing the time from when the food was offered until the time at which the pandas began to go to sleep. The food, which was rinsed in tap water and shaken dry, was weighed prior to feeding and any remaining food after feeding was also weighed to determine the intake of each animal. The eating process was recorded using a Sony camera (HDR-PJ30E) to help to collect and analyse the feed intake, feeding rate, and discrimination time data. Following Suárez et al. (2014), feed intake, and feeding rate were defined as follows:

Feed intake (kg) = Food eaten (kg) = Total food offered (kg) – Food remaining (kg)

$$\text{Feeding rate} = \frac{\text{Food eaten (g)}}{\text{Food time (min)}}$$

Discrimination time was defined as the food selection time, i.e. the time interval between the completion of consumption of one bamboo piece/shoot and the initiation of consumption of the next, which was taken as the time when the panda began to sniff one piece of bamboo (or shoot) or started to eat one selected piece of bamboo (or bamboo shoot). When measuring these behaviours, any action interrupting the continuous selecting behaviour, such as the animal putting down the bamboo, walking to get water, stopping, sniffing and picking out the food, and so on, we stopped recording the timing. We used only the data for continuous feeding when obtaining and analysing the discrimination time.

All the behaviour observation data were collected for 26-28 days each month following the methods of Zhang & Wei (2006) for a total of 210 hours of data during a 7-month period.

Statistical analysis

Statistical analyses were performed using the SPSS software version 19 (SPSS Inc. 2010). A one-way ANOVA was used to test for differences among age groups. The Bonferroni method was used to test for homogeneity of variance, and the Games-Howell method was used for multiple comparisons. The independent samples t-test was used to test for differences between males and females at sample sizes less than 30 (n < 30), and the Mann-Whitney U-test was used for nonparametric tests. Mean values and standard deviations are provided as descriptive statistics.

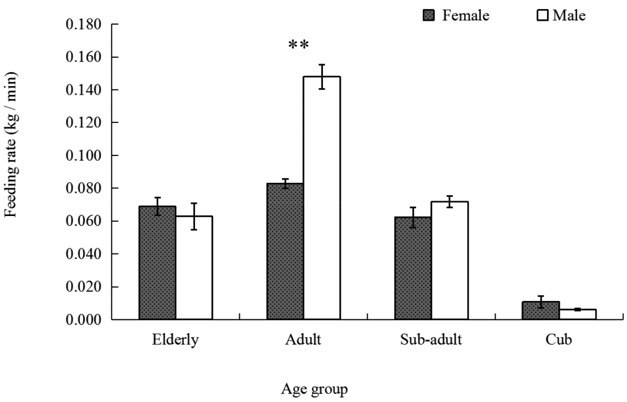

Fig. 1. The feeding rates of giant pandas of different age groups during the consumption of bamboo shoots.

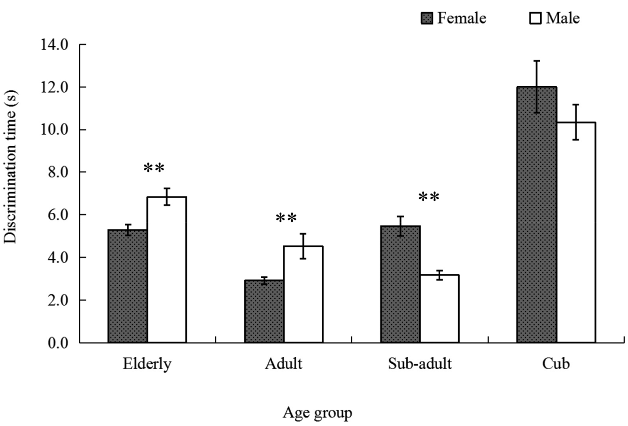

Fig. 2. The discrimination times of giant pandas of different age groups during the consumption of bamboo shoots. Bars with double asterisks indicate that the behaviour was significantly different between females and males at $p < 0.01$.

Table 1. Characteristics of the captive giant pandas studied in this research in 2014.

Age Group	Females			Males		
	Pedigree number	Birth date	Weight (kg)	Pedigree number	Birth date	Weight (kg)
Elderly	314	1986.8.6	87	342	1987.9	89.3
	387	1992.9.3	90	386	1992.7.28	123.5
Adult	491	1999.9.4	104.5	520	2000.9.1	105
	522	2000.9.11	113.9	630	2006.8.7	109.5
	765	2006	106.5	584	2004.8.26	120
	555	2002.8.28	93	726	2008.8.5	110.5
Sub-adult	848	2012.8.19	74	857	2012.9.12	61.5
	853	2012.8.25	58	858	2012.9.12	63
	855	2012.9.4	56	851	2012.8.19	73
	823	2011.8.13	81	839	2012.7.28	67
	821	2011.8.12	69	-	-	
	818	2011.8.9	71	-	-	
Cub	881	2013.8.6	23.1	876	2013.7.23	24.1
	882	2013.8.6	23.9	899	2013.8.23	21.82
Total	14			12		

Table 2. Measurements of feeding behaviour in giant pandas of different age groups when eating bamboo shoots. [a, b, c, d] identify significant differences in a parameter among age groups. The same letter indicates no significant difference ($p > 0.05$), whereas different letters indicate significant differences ($p < 0.05$).

	Female		Male	
Age groups	Feeding rate (g/min)	Discrimination time (s)	Feeding rate (g/min)	Discrimination time (s)
Elderly	66.69 ± 7.22[ab]	6.406 ± 0.230[a]	55.17 ± 2.68[a]	6.844 ± 0.389[a]
Adult	82.80 ± 2.78[a]	3.094 ± 0.121[b]	151.54 ± 7.95[b]	4.528 ± 0.586[b]
Sub-adult	62.20 ± 6.16[b]	4.302 ± 0.276[c]	71.74 ± 3.54[c]	3.167 ± 0.216[b]
Cub	10.73 ± 3.68[c]	12.00 ± 1.213[d]	6.22 ± 0.69[d]	10.342 ± 0.825[c]

Table 3. Measurements of feeding behaviour in giant pandas of different age groups when eating mature bamboo. [a, b, c, d] identify significant differences in a parameter among age groups. The same letter indicates no significant difference ($p > 0.05$), whereas different letters indicate significant differences ($p < 0.05$).

	Female		Male	
Age groups	Feeding rate (g/min)	Discrimination time (s)	Feeding rate (g/min)	Discrimination time (s)
Elderly	43.13 ± 8.54[a]	9.848 ± 0.472[a]	33.19 ± 9.45[ab]	8.562 ± 0.425[a]
Adult	26.02 ± 2.35[ab]	6.628 ± 0.354[b]	45.13 ± 4.25[a]	6.857 ± 0.377[b]
Sub-adult	19.19 ± 3.03[b]	8.17 ± 0.439[c]	13.04 ± 2.10[b]	8.269 ± 0.911[ab]

Results

Bamboo shoots feeding behaviour in different age groups

Among female giant pandas, the one-way ANOVA showed that the feeding rate in the cub group was significantly different from the other groups. The cubs were the slowest (10.73 g/min), and the adults were the fastest (82.8 g/min). In addition, the feeding rate differed significantly between adults (82.8 g/min) and sub-adults (62.2 g/min) ($p < 0.01$). The discrimination time differed significantly among all four age groups ($p < 0.01$). The longest discrimination time was observed in cubs (12 s) and the shortest was observed in adults (3.1 s, Table 2).

Among male giant pandas, significant differences in feeding rate were also observed among the four age groups ($p < 0.01$). The cubs were the slowest (6.22 g/min), and the adults were the fastest (151.54 g/min). There was no significant difference in discrimination time between the adult and sub-adult groups (p =

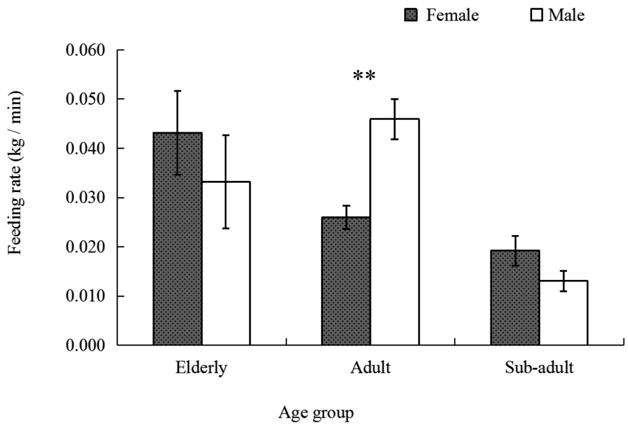

Fig. 3. The feeding rates of giant pandas of different age groups during the consumption of bamboo.

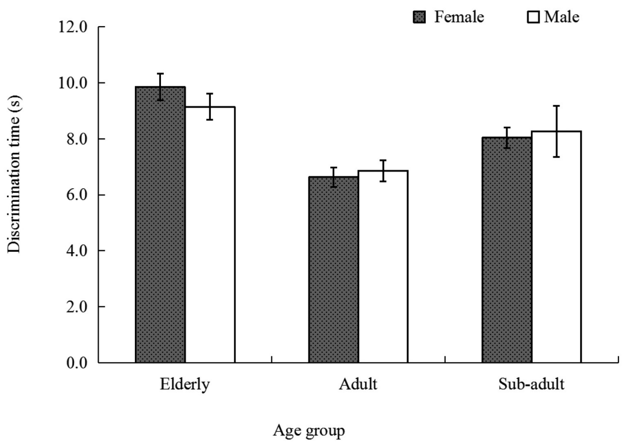

Fig. 4. The discrimination times of giant pandas of different age groups during the consumption of bamboo.

0.145), whereas significant differences were observed in the other groups ($p < 0.01$). The cubs had the longest discrimination time (10.34 s) and the shortest discrimination time occurred in sub-adults (3.17 s, Table 2).

Bamboo shoots feeding behaviour in different sex groups

There were significant differences in the discrimination times between males and females in the elderly, adult and sub-adult groups ($p < 0.01$ t-test) and no differences between males and females in the cubs ($p > 0.05$ t-test, Fig. 1 and 2).

Mature bamboo feeding behaviour in different age groups

Following the one-way ANOVA, a multiple comparison tests revealed a significant difference in the feeding rate between elderly and sub-adult females ($p = 0.046$) but not between adult and elderly females or between adult and sub-adult females ($p = 0.167$ and $p = 0.200$, respectively). There were differences among the elderly, adult and sub-adult females in the discrimination time ($p < 0.05$). In particular, there was a significant difference in the discrimination time between adult and elderly females ($p < 0.01$, Table 3).

Mature bamboo feeding behaviour in different sex groups

There was a significant difference in feeding rate between males and females in the adult group (Mann-Whitney U-test: z = –4.064, $p < 0.01$, Fig. 3 and 4), that males eaten faster than females.

Differences in the feeding rate of mature bamboo and bamboo shoots

There were differences between selection of mature bamboo and bamboo shoots among the elderly, adults and sub-adults in feeding rate ($p < 0.05$ t-test), but no difference between in male elderly in feeding rate ($p > 0.05$, Fig. 5). The females and males all ate faster when they ate bamboo shoots than when they ate mature bamboo.

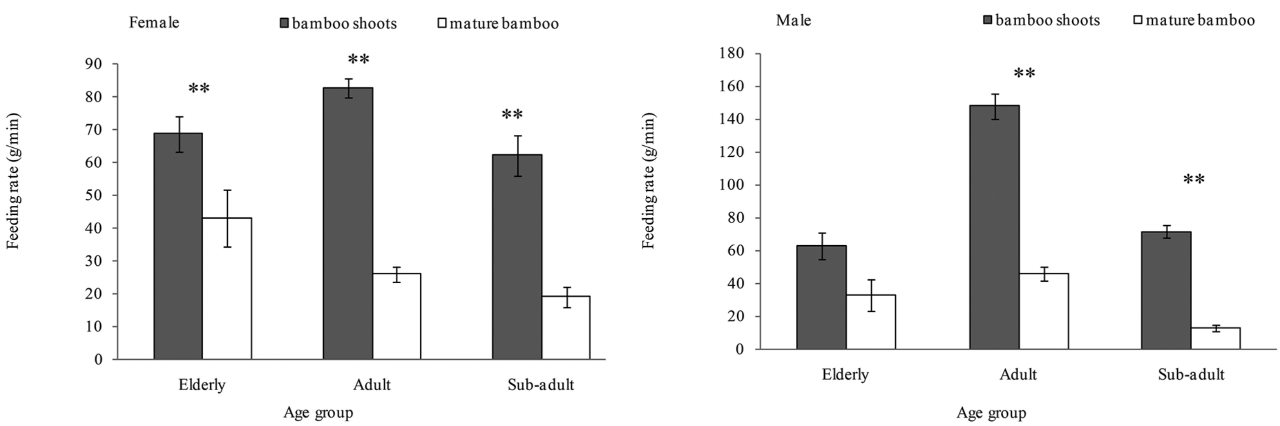

Fig. 5. Differences in feeding rate between mature bamboo and bamboo shoots.

Discussion

As with growth and development in animals, the development of animal behaviour is determined by both genetic and environmental factors (Shang 1998). Animals promote their behavioural development through learning (Galef & Laland 2005). At different developmental stages, animals learn and modify their behaviour according to their environment (Liu et al. 2001). The energy balance of an animal depends on its feeding behaviour. Generally, the longer an animal takes on its discrimination time, the lower their food intake (Sun 2001).

The feeding rate in giant pandas increases gradually from infancy to adulthood, whereas the discrimination time gradually decreases. This pattern is consistent with the optimal foraging strategy (Wei et al. 1999, 2004, Hu & Wei 2004). Giant panda breast milk is the staple food for the first six months of a panda's life, and pandas begin to learn how to eat bamboo shoots or mature bamboo at approximately one year of age (Zhang & Wei 2006). Hong et al. (2016) noted that giant pandas appear to randomly forage bamboo across age groups but feed more on perennial bamboo culms. Because young cubs initially use bamboo shoots or mature bamboo for play, they do not obtain any nutrients from bamboo at this stage (Zhang et al. 2001, Zhou et al. 2013). Accordingly, the food selection time and feeding rate in this study were significantly lower in young cubs than in the other age groups. Young cubs invested more time in identifying food than the other age groups, which affected their overall feeding rate. Generally, foraging efficiency increases with age and development (Shang 1998). However, in the present study, the foraging efficiency was reduced in the elderly individuals, which might be due to the degeneration of function with age. The teeth of giant pandas decay with age, which leads to reduced digestion and absorption efficiencies as well as decreased feeding rates (Zhang & Wei 2006). As Li et al. (2017) said in their study, giant pandas' adaptive foraging strategies are related to subtle seasonal variations in bamboo quality. Wei et al. (2017) noted that temporal variation in diet composition by giant pandas perhaps reflected behaviourally adaptive strategies to changing environmental factors, which helped to maximize their energy intake for successful survival and reproduction. The results of the present study suggest that feeding behaviour in giant pandas follows a developmental pattern throughout the animal's life.

Previous studies have shown that primates increase their feeding time to obtain adequate nutrients from low-quality food during periods of food shortage (Dunbar & Dunbar 1988). For example, when fruit is scarce, gibbons increase the time invested in chewing leaves to increase their energy intake (Raemaekers 1978). Similarly, captive giant pandas prefer to consume bamboo shoots (Nie et al. 2015b). Giant pandas have lower utilization rates and a lower feeding rate when consuming mature bamboo than when consuming bamboo shoots. This observation is similar to observations in primates in which individuals increase their feeding time to obtain sufficient nutrients. The preferred feeding strategy is consistent with the optimum selection principle of feeding efficiency, i.e. each species will choose the most effective and favourite type of food resources for obtaining nutrients (Sun 2001). The effects of sex and age on behaviour are widespread in birds (Kim & Zuk 2000), ungulates (Ruckstuhl 1998, Côté & Festa-Bianchet 2001), carnivorous animals (Golla et al. 1999) and primates (Alberts 1994). Sexual dimorphism in body size leads to different nutritional requirements (Hu et al. 1985, Qi et al. 2011), and the different nutritional requirements of the sexes in ungulates cause sex differences in their behaviour patterns and time allocation (Ruckstuhl 1998). In the present study, behavioural characteristics differed between male and female giant pandas in the adult age group. However, no significant differences in feeding rate or discrimination time were observed between the sexes in any of the other age groups, i.e. cubs, sub-adults, and elderly individuals. This dimorphism is consistent with the findings of Hu et al. (1985). These differences may be due to the well-developed body functions of adults and the gradual development of sex differences. It is also possible that the sex differences are related to energy efficiency because the different sizes and reproductive roles of males and females require that the sexes adopt different energy strategies (Qi et al. 2011). In addition to the energy requirements needed for basic survival, adult individuals need to consider the requirements for breeding investment and territorial behaviour. These additional energy expenditures lead to sex differences in the rates of food selection, feeding, and discrimination. The cubs included in the present study were all at approximately the same stage of development and had thus not developed large differences in their sizes and body functions. Therefore, there were no significant differences in feeding behaviour between male and female cubs.

Panda cubs undergo learning, imitation, and maturation (Li et al. 2005). The captive giant pandas used in the present study showed a dynamic learning and development process in feeding rate and discrimination cost. Differences were observed between adult males and females, and feeding behaviour became less efficient in elderly individuals due to the degradation of body function with age. This finding is consistent with the study by Zhou et al. (2013), which determined that the critical period of behavioural development occurs from birth to adulthood, that behavioural patterns become fixed after sexual maturity, and that some behavioural patterns begin to disintegrate in old age. Furthermore, studies have shown that breeding techniques, food sources and habitats can all affect animal feeding rates and can also affect animal health (Suárez et al. 2014). In the 1990s, among captive giant pandas, only 1/3 of females and 1/10 of males underwent normal development (Hu et al. 1990). This finding is related to nutrition received during the sub-adult stage and breeding management (Zhang & Wei 2006). Qing et al. (2016) suggested that the giant panda is an area-sensitive species. For captive giant pandas, to help improve this population viability, it is necessary to take effective breeding measures. For sub-adult individuals, we can increase the supply of fresh bamboo or bamboo shoots supply, and reduce the proportion of concentrated food (such as apples, cakes, and honey). This would increase the chances of the animals learning the correct feeding skills. By contrast, we suggest that the concentrated food supplies should be increased to meet the nutritional requirements of elderly pandas.

Conclusion

The development of feeding behaviours and energy intake in this study showed variations within captive giant pandas. The feeding rates were significantly different not only between sexes but also among different age groups, except between elderly and adults pandas, as well as a significant difference between elderly and sub-adult females. Significant differences were found in the discrimination times among all the female age groups and male age groups; there were significant differences among elderly, adult and sub-adult females, but not between the adults and sub-adults. In addition, among adults in the same age groups, there were significant differences between the sexes in their feeding rates and discrimination times. Other than for elderly males, there were differences between consuming mature bamboo and bamboo shoots among the elderly, adults and sub-adults in terms of the feeding rate.

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