Sex differences in spatial ability: a test of the range size hypothesis in the order Carnivora

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Sex differences in spatial cognition have been reported for many species ranging from voles to humans. The range size hypothesis predicts that sex differences in spatial ability will only occur in species in which the mating system selects for differential range size. Consistent with this prediction, we observed sex differences in spatial ability in giant pandas, a promiscuous species in which males inhabit larger ranges than females, but did not observe sex differences in Asian small-clawed otters, a related monogamous species in which males and females share home ranges. These results provide the first evidence of sex differences in spatial ability in the order Carnivora, and are consistent with the range size hypothesis.

Keywords: giant panda; otter; sex differences; spatial memory; range size hypothesis

1. INTRODUCTION

Males and females differ in many aspects of physiology, behaviour and cognition [1]. In many species, including humans and non-humans, males outperform females on spatial tasks such as maze navigation [2]. This phenomenon has been investigated from proximate and ultimate perspectives, with hormones representing the most likely proximate mechanism for the difference [3–5]. The current research focused on evolutionary hypotheses regarding sex differences in spatial ability [2,6,7].

The range size hypothesis [8–10] predicts that sex differences will occur in species in which one sex has a larger range than the other, a pattern that results from the mating system. For example, in polygynous or promiscuous mating systems, males can improve reproductive success by expanding their ranges during breeding season and remembering the locations of multiple females. Conversely, in species in which the mating system does not select for differential range size (e.g. monogamy), there should be no obvious reproductive benefit to superior male spatial ability and no sex differences would be expected. As predicted, promiscuous meadow voles exhibit sex differences in spatial ability, but monogamous prairie and pine voles do not [8,9]. Alternatively, the fertility and parental care hypothesis proposes that sex differences do not necessarily occur because of a male advantage, but because of a female disadvantage during certain periods of the reproductive cycle [6,7].

Both of these evolutionary mechanisms may contribute to observed sex differences; however, providing support for the range size hypothesis that is not confounded by other factors is challenging. One way to provide unambiguous support for this hypothesis is to demonstrate the presence of a relationship between sex differences and range size outside the breeding season [2]. However, the period of male range expansion and female oestrus overlaps for many species; thus, a rigorous test of the hypothesis would require the use of a species in which these processes are temporally distinct.

Most of the existing research in sex differences has been conducted in rodents and humans. Though valuable insights have been gained from this work, further advances in evolutionary theory can be achieved by testing additional species. Giant pandas have a promiscuous mating system and male ranges overlap the smaller, more concentrated core areas of females [11]. Beginning in November, males start to roam persistently and testosterone levels are elevated at least three months prior to oestrus [11,12]. Males monitor the location of other males, females and communal scent-marking locations during this period. In contrast, female hormonal and behavioural changes are limited to a brief oestrous period in early spring [11,13]. By testing for sex differences in spatial ability during the period of male range expansion, but prior to female oestrus, we can provide support for the range size hypothesis while controlling for the potential effect of decreased female spatial ability during oestrus. A thorough test of this hypothesis would also require a test of a closely related monogamous species. Within the order Carnivora, giant pandas and Asian small-clawed otters are both on the arctoidea branch (‘bear-like carnivores’) of the sub-order Caniformia [14]. These otters have a monogamous mating system in which males and females share home ranges [15,16]. Females undergo multiple aseasonal oestrous periods each year [17].

We predicted that promiscuous male giant pandas would make fewer errors than females on a spatial memory task, but there would be no sex differences in the performance of monogamous Asian small-clawed otters.

2. MATERIAL AND METHODS

We tested eight male (\(x_{\text{age}} = 11.1\)) and nine female (\(x_{\text{age}} = 8.8\)) giant pandas housed at the Chengdu Research Base and the Chengdu Zoo in Sichuan Province, China. Subjects were tested from November 2009 to February 2010, a period that corresponds to male range expansion and testosterone elevation [11,12], but no behavioural or physiological indicators of oestrus in females were observed. We also tested four male (\(x_{\text{age}} = 7.7\)) and four female (\(x_{\text{age}} = 6.3\)) Asian small-clawed otters housed at Zoo Atlanta from May to June 2010. All subjects were born and reared in captivity at the Chengdu Research Base and the Chengdu Zoo outside Sichuan Province, China.

We used an adaptation of the radial arm maze [18–20]. Eight feeders were arranged in a circular pattern (figure 1). Depleted feeders were not visually apparent or distinct from other feeders [20]. Each feeder was rubbed with the scent of the food item (apple for giant pandas, fish for otters) before each session so that the baited feeders...
could not be identified by olfactory cues. Feeders were cleaned between sessions.

For each session, the same four feeders were baited with the food item, and the other four were left empty. Subjects were allowed to freely explore the feeders, and any contact with a feeder was recorded as a visit. The day after the test sessions, a ‘probe trial’ was conducted in which all feeders were rubbed with the scent of the food item, but none were baited with food. The probe trial further tested the possibility that subjects were using extraneous cues (e.g. scent) rather than spatial cues to find food in the previous task. If performance remained above chance on the probe trial, then spatial location was the relevant information used to solve the task.

The number of reference memory errors (i.e. visit to a location that is never baited with food) and working memory errors (i.e. re-visit to a location that has already been visited in that session) were recorded [19]. For this analysis, the first nine test trials were summarized into three-session intervals. For each interval, the number of errors made by males and females was compared using a Mann–Whitney U-test (one-tailed). We also calculated unbiased Hedges’ g-values to determine the effect size. Performance on the probe trial was compared with chance performance using a one-sample r-test. We also recorded the duration of time spent moving, an indirect measure of range expansion, and compared male and female giant pandas using a Mann–Whitney U-test (one-tailed) and otters using a χ²-test.

3. RESULTS

On the probe trial, giant pandas (t = 4.197, d.f. = 16, p < 0.05) and otters (t = 2.39, d.f. = 7, p < 0.05) were significantly more likely than chance to visit correct locations (i.e. baited on previous trials) in the first four visits, even though no food was present. Male giant pandas made significantly fewer reference memory errors (i.e. visits to never-baited locations) than females in interval 2 (U = 18.5, p = 0.047; g = 0.835) and interval 3 (U = 17.5, p = 0.037; g = 0.860), and significantly fewer working memory errors (i.e. re-visits to locations) in interval 1 (U = 13.5, p = 0.014; g = 0.945), interval

2 (U = 9.5, p = 0.004; g = 1.752) and interval 3 (U = 9.0, p = 0.004; g = 1.501) (figure 2). There were no significant sex differences in otter performance (p > 0.50 in all intervals; figure 2). Although the otter sample size is small, statistical analysis and visual inspection of the data reveal absolutely no trend towards sex differences in performance. Male giant pandas spent more time locomoting than females (U = 16, p = 0.03; g = 0.67), but locomotion was evenly distributed between male and female otters (χ² = 1.14, p > 0.05).

4. DISCUSSION

We found that male giant pandas outperformed females on a spatial memory task, but no sex differences were observed in Asian small-clawed otter performance. These data provide the first support for the range size hypothesis in the order Carnivora. Males and females of both species learned the task, as evidenced by the performance on the probe trial. Thus, the differences we observed in giant pandas were not because one sex failed to acquire the task. Additionally, we controlled for visual and olfactory cues, further supporting that performance differences were based on sex differences in spatial ability.

The sex difference in giant panda working memory errors was evident from the onset of testing. Previous research [21,22] suggests that the magnitude of the male advantage in spatial ability may be greatest for working memory tasks, and testosterone is most probably responsible for this effect [23]. The range size hypothesis provides an evolutionary basis for understanding the greater advantage on working memory. If the sex difference relates to improved male reproductive success, as predicted by this hypothesis, there would be no obvious advantage for superior male spatial memory for unchanging characteristics of the environment (i.e. reference memory), such as the location of water sources. Instead, remembering flexible, changing information (i.e. working memory) such as the location of females or communal scent-marking locations would be relevant for males. Thus, the advantage on working memory tasks can be interpreted from an evolutionary perspective.

Sex differences in the giant pandas’ performance were observed during the period of male range expansion and outside the female reproductive period. Thus, the potentially confounding influence of decreased female spatial ability during reproductive periods [6] was avoided in the current study. The range size hypothesis further predicts that no sex differences will be observed in a monogamous species with equal range sizes. Despite the close phylogenetic relationship to the giant panda within the order Carnivora, no sex differences were observed in Asian small-clawed otter performance, which is consistent with findings from other monogamous species [8,9,24]. This finding supports the hypothesis that different mating systems and ranging patterns are predictive of sex differences in spatial ability.

Finally, this study illustrates the usefulness of testing animals in captivity in order to broaden our understanding of the evolution of cognition. All subjects were raised in captivity, and males and females occupied enclosures with equivalent spatial parameters.

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Despite male giant pandas having never actually inhabited a larger range than females, sex differences were still observed. We also found a sex difference in giant panda locomotion, which is an indirect indicator of range expansion, but no differences were observed in otters. Testing in a captive environment controls for experiential factors and emphasizes the importance of biological factors, such as testosterone, in determining the sex difference. By investigating and integrating across ultimate and proximate levels of explanation, we can better understand the cause of sex differences in cognition.

This work was supported by the Elizabeth Smithgall Watts endowment at the Georgia Institute of Technology and Charles T. Bailey fellowship at Zoo Atlanta. We would like to thank all of the animal keepers, Kenn Harwood, Yuan Bo, Zhang Liang and Drs Jin Ping Yu, Hou Rong, Tara Stoinski, Joseph Mendelson, Ben Charlton, Brian McMahon, Anderson Smith and Paul Corballis.

Figure 2. Sex differences in memory errors. (a) Giant panda reference memory, (b) giant panda working memory, (c) otter reference memory, and (d) otter working memory. Filled triangles, female; crosses, male.


