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Author for correspondence:
Carrie L. Branch
e-mail: clb345@cornell.edu

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Testing the greater male variability phenomenon: male mountain chickadees exhibit larger variation in reversal learning performance compared with females

Carrie L. Branch[1], Benjamin R. Sonnenberg[2], Angela M. Pitera[2], Lauren M. Benedict[2], Dovid Y. Kozlovsky[3], Eli S. Bridge[4] and Vladimir V. Pravosudov[2]

[1]Cornell Lab of Ornithology, Cornell University, Ithaca, NY 14850, USA
[2]Ecology, Evolution, and Conservation Biology Graduate Program, University of Nevada Reno, Reno, NV 89557, USA
[3]Department of Biology, Villanova University, Villanova, PA 19085, USA
[4]Ecology and Evolutionary Biology, University of Oklahoma, Norman, OK 73019, USA

CLB, 0000-0003-1769-5040; AMP, 0000-0002-6166-3639

The greater male variability phenomenon predicts that males exhibit larger ranges of variation in cognitive performance compared with females; however, support for this pattern has come exclusively from studies of humans and lacks mechanistic explanation. Furthermore, the vast majority of the literature assessing sex differences in cognition is based on studies of humans and a few other mammals. In order to elucidate the underpinnings of cognitive variation and the potential for fitness consequences, we must investigate sex differences in cognition in non-mammalian systems as well. Here, we assess the performance of male and female food-caching birds on a spatial learning and memory task and a reversal spatial task to address whether there are sex differences in mean cognitive performance or in the range of variation in performance. For both tasks, male and female mean performance was similar across four years of testing; however, males did exhibit a wider range of variation in performance on the reversal spatial task compared with females. The implications for mate choice and sexual selection of cognitive abilities are discussed and future directions are suggested to aid in the understanding of sex-related cognitive variation.

1. Introduction

Across the fields of comparative cognition and cognitive ecology, it is widely accepted that cognitive abilities vary among and within taxa [1,2]. What remains to be understood is when and why such variation exists. One possible source of variation may be differences in male and female cognitive abilities. However, the overall findings of sex differences in cognitive abilities are largely equivocal [3,4]; some research suggests males outperform females on cognitive tasks (see meta-analysis in [5]), some show that females outperform males [6,7] and some show no sex-based differences [3,8,9].

One cognitive ability that does appear to differ consistently between males and females is spatial cognition, with males typically outperforming females [3,10–12]. However, most of this work has been conducted in humans or rodents in the laboratory and is potentially confounded by differential sex responses to stress and external factors [3,8,13–16]. Several hypotheses have been proposed to explain sex differences in spatial cognition, including the 'range size hypothesis' [10,11,17] and the 'dispersal hypothesis' [18]. However,

both of these hypotheses are limited in scope because they only pertain to differences in *mean* cognitive performance among species where sexes use space differentially.

Unlike mammals, the majority of bird species are socially monogamous, and males establish territories to attract females, who then take on the territory with no known differences in spatial use [19]. Furthermore, in avian caching species, specialized spatial cognitive abilities are required to locate and recover food stores in order to survive winter [20], with males and females equally reliant on food caches for overwinter survival. As such, sex-based differences in spatial cognition would not be predicted. Given that natural selection is expected to decrease variation in traits, such as the spatial cognitive abilities of caching species, it is somewhat of a paradox that substantial variation in spatial cognitive performance still persists [21].

For over 100 years, psychologists have investigated the greater male variability phenomenon in which males exhibit larger variation in their cognitive abilities compared with females, resulting in similar mean performance, but a larger variance in males (termed the 'greater male variability hypothesis' [9,16,22]). Much of this work has investigated sex-based differences in human intelligence, with large-scale meta-analyses showing that males exhibit larger variation in performance on quantitative and spatial tasks compared with females [23,24]. While it has been suggested that these differences in cognitive performance are innate [22,25], this remains controversial, as a lack of cross-cultural consistency [24] and decreases in the magnitude of sex-based cognitive differences over time suggest the importance of environmental factors [26].

While the 'greater male variability hypothesis' or greater male variability phenomenon, as we will refer to it here, has been widely documented in humans, little has been proposed to explain why males may exhibit larger variance in cognitive abilities compared with females. Research investigating sexual selection and variation in secondary sexual characteristics of non-human animals may shed light on the mechanisms maintaining larger variation in male cognitive abilities. Secondary sexual traits reflect the quality or condition of the male, therefore, providing an honest indicator of quality for female choice that will increase her fitness via enhanced offspring viability [27]. Despite strong female preference for particular phenotypes, which often include exaggerated ornaments, males continue to exhibit large variation in secondary sexual traits (e.g. the lek paradox [28]). The paradox of large variation in the face of strong preference or selection pressure has been explained by the 'genic capture hypothesis', which suggests that male 'condition' linked to secondary sexual traits is a complex phenotype dependent on numerous loci across the genome [29,30]. The complex genetic control of condition, variation in the optimal condition phenotype depending on environment, and additive genetic variation all combine to maintain substantial variation in secondary sexual characteristics despite directional sexual selection [30]. Indeed, while natural selection should decrease the amount of variation in the spatial cognitive abilities of food-caching birds, relatively large amounts of variation persist. Similar to male condition, spatial cognitive ability has been shown to predict survival in food-caching birds [20] and male spatial cognitive ability appears to be associated with female reproductive decisions [31]. Furthermore, genes that are responsible for spatial cognitive abilities probably also have complex, polygenic underpinnings, as has been proposed for traits reflecting male quality or condition [30] (Branch *et al*. unpublished).

If females are able to cue in on and choose males with better cognitive abilities, this would enhance their offspring's survival. In fact, recent work has shown that female food-caching birds invest more in reproductive output when mated to males with better spatial cognitive abilities [31]. This work suggests that cognitive abilities may reflect male condition and are important in female choice [32], as such spatial cognitive abilities may exhibit wider variance in males compared with females similar to that seen in secondary sexual traits and explained by genic capture [29,30].

The current study assesses differences in spatial cognition among free-living male and female mountain chickadees (*Poecile gambeli*). By assessing cognition in the wild, we eliminate the issue of differential effects of acute stress from being in captivity on males and females, which have been shown to affect the spatial performance of rodents [14]. Furthermore, unlike many mammal species in which males and females occupy different spatial areas, mountain chickadees are socially monogamous, and males and females share territories. Because individual variation in spatial cognition is associated with survival in mountain chickadees [20], and territories are shared among male and female pairs in the breeding season, we did not predict differences between male and female chickadees in their mean spatial cognitive performance. Similarly, it may also be expected that selection for better spatial cognition should reduce individual variation equally in both males and females. Conversely, there is no direct evidence that reversal learning, a proxy for cognitive flexibility, is under selection in these birds [20,33]; therefore, we expect larger variation in reversal learning among both sexes. Given that our previous work reflects substantial variation in both cognitive tasks, we expect males to show significantly larger variation in both spatial and reversal cognitive tasks compared with females [16,22], which would be indicated by a lack of homogeneity in the variance of male and female performance distributions [34].

2. Methods

(a) Study system

We investigated differences in cognitive performance among free-living male and female food-caching mountain chickadees inhabiting high (approx. 2400 m) and low (approx. 1900 m) elevations at our long-term study site in Sagehen Experimental Forest, northern California, USA [21,33,35]. Males and females were tested on two spatial cognitive tasks across four winter seasons (winter testing across 4 years: 2015/16, 2016/17, 2017/18 and 2018/19 has been simplified throughout the manuscript as 2016, 2017, 2018 and 2019, respectively): (i) a spatial learning and memory task (proxy for spatial cognitive abilities) and (ii) a reversal spatial learning task (proxy for cognitive flexibility). Birds were tested in the wild using 'smart' feeder spatial arrays equipped with radiofrequency identification (RFID) technology [20,21,33,35]. Prior to each year of testing, chickadees were trapped using mistnets at established feeders (nine feeders at low elevation and six feeders at high elevation) and their legs were fitted with unique colour-band and passive integrated transponder (PIT)-tag combinations.

(b) Cognitive testing

Birds were tested on both cognitive tasks using four spatial arrays (two at each elevation), each containing 8 RFID-enabled feeders mounted equidistant on an aluminium square frame (1.2 ×

1.2 m), suspended 4–5 m above the ground (details in [21,33,35]). Within each elevation, the two arrays were positioned roughly 1.5 km apart and each were visited by mostly non-overlapping groups of chickadees. Each feeder has a perch with an embedded RFID antenna that is mounted in front of a motorized door that allows access to a black oil sunflower seed reward. Feeders can function in one of three modes: (i) 'open' mode, where the door remains open with visible food; (ii) 'all' mode, where the door remains closed but opens when any PIT-tagged bird lands on the perch, allowing access to food; and (iii) 'target' mode, where the door opens only for PIT-tag IDs that have been programmed into the RFID board memory. 'Open' and 'all' modes are largely used for training whereas 'target' mode allows us to restrict food access for individual birds to a specific feeder. In all three modes, every feeder records the PIT-tag ID, date and time of all visits. Across all four years, birds were habituated to the moving feeder door (i.e. 'all' mode) for at least two weeks prior to testing. Birds that were consistently visiting the feeder arrays were pseudo-randomly assigned to an individual feeder within the array and used for testing. Birds tested in multiple years were assigned different rewarding feeders for each year.

(i) Spatial cognitive task

Spatial cognitive ability was tested by assigning each bird access to a single feeder in the array (1 of 8, with different birds assigned to separate feeders); when a bird landed on the perch of its assigned feeder, the feeder door would open and the bird would obtain one sunflower seed. Performance on the spatial task was measured as the number of location errors an individual made within a trial. A trial began when the bird visited any feeder within the array and ended when they visited their rewarding feeder, at which time the number of location errors was reset to zero and a new trial started. Location errors were defined as the number of unrewarding feeders a bird visited before landing on the correct, rewarding feeder. The mean number of location errors per trial were calculated both within the first 20 trials and across the entire testing period (16 days in 2016 and 5 days in 2017–2019 [21,33]).

(ii) Reversal spatial cognitive task

In order to assess reversal spatial cognitive abilities, immediately following spatial learning and memory testing, all tested birds were assigned to a new feeder location within the array and their previous feeder location no longer provided a food reward. Birds that had been assigned to the same feeder during the spatial learning and memory task were re-assigned to different feeders during the reversal spatial task to avoid social learning.

Again, the number of unrewarding feeders visited before visiting the newly rewarding feeder was used to calculate the mean number of location errors per trial across the first 20 trials and the entire reversal testing session (13 days in 2016 and 5 days in 2017, 2018 and 2019 [20,21,33]). Each visit to the correctly assigned feeder resulted in the feeder door opening to allow access to a sunflower seed.

(c) Analyses

Both spatial cognitive tests were conducted in the wild across 4 years (2016–2019). In 2018, low elevation birds did not visit our feeder arrays and therefore were not tested on either task (see electronic supplementary material, table S1 for sample sizes). Each bird had to complete at least 20 trials to be included in analyses and any individual that made, on average, more than three location errors across the first 20 trials was considered an outlier and removed from the dataset (four removed out of 305 observations (1.31%)). To assess sex differences in mean performance on the spatial and reversal cognitive tasks, general linear mixed models (GLMM) were run using the *lmer()* function in R version 3.6.1 (packages lme4 and lmerTest [36,37]).

For both cognitive tasks, we assessed the mean number of errors per trial over the first 20 trials completed and the mean number of errors per trial across the entire testing period. These same measures have been used in all of our previous studies on spatial cognition in wild mountain chickadees [21,33,35] and appear ecologically relevant as we have previously shown that spatial cognitive ability predicts overwinter survival [20] and that females increase reproductive output when mated to males with better spatial cognition [31]. Performance does improve over the entire testing period compared with the first 20 trials, suggesting that these measures reflect different properties of spatial cognition: initial learning and memory acquisition (first 20 trials) and overall long-term spatial learning and memory (all trials completed).

Two models were run on spatial learning and memory performance and two were run on reversal spatial learning and memory performance. For both tasks, one model was run with performance on the first 20 trials as the response variable and the other was run with performance across all trials as the response variable. Sex (male or female) and elevation (high or low) were run as fixed factors and testing year and individual ID as random factors (as some individuals were tested in multiple years). Elevation was used as a fixed factor in all models because there are significant differences in spatial and reversal spatial cognitive performance of high and low elevation birds [33,35]. Total number of trials was used as a fixed factor in total trials analyses to control for the effect of motivation and differences in the number of trials completed across birds over the fixed testing period.

To assess sex differences in the range of variance in performance on spatial and reversal learning, we tested for homogeneity of variances [34] (or homoscedasticity for GLMM) between males and females on both spatial and reversal spatial cognitive tasks. To do this, we extracted the residuals of each GLMM and used the absolute values of those residuals to perform a linear model by sex (function *lm*() in base R 3.6.1).

3. Results

Across four years of testing, 201 individuals (109 males and 92 females) were tested on the spatial learning and memory task; out of these, 145 individuals (81 males and 64 females) were then also tested on the reversal spatial learning and memory task. Analyses were run on measurements across the four years of testing, as such the number of observations is larger than the individual sample sizes (spatial learning and memory task: 301 total measurements; 169 male and 132 female; reversal spatial learning task: 210 total measurements; 121 male and 89 female; see breakdown of sample sizes by year and elevation in electronic supplementary material, table S1). Values reported in text are mean and standard deviation (mean ± s.d.).

Due to the differences in methodology and performance, we ran separate analyses on 2016 alone, all 4 years together, and on all 3 comparable years without 2016; however, we only saw an effect when all 4 years were run together and therefore present those results in the main text (see electronic supplementary material, table S2 for additional analysis and performance × year analyses).

(a) Cognitive performance across 4 years

(i) Spatial cognitive task

Across the first 20 trials completed, where learning acquisition was tested, there was no significant difference

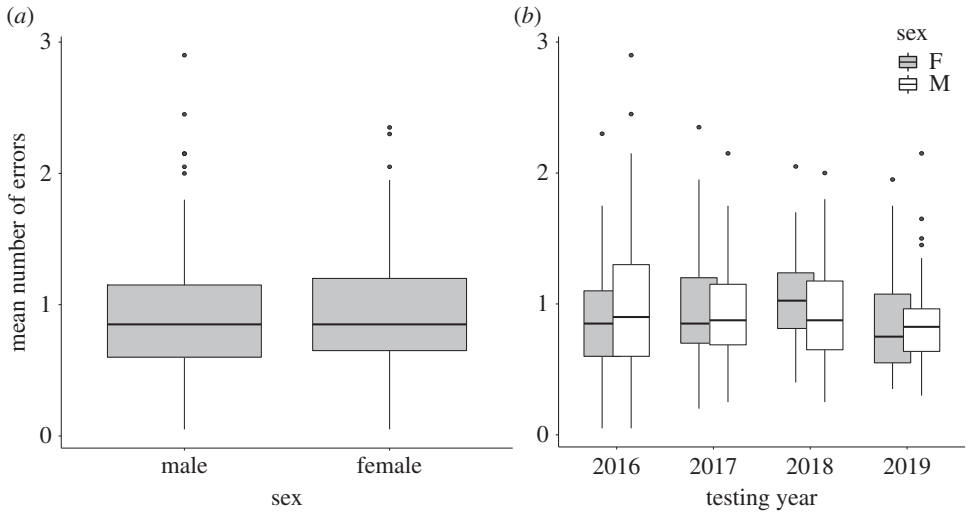

Figure 1. Spatial cognitive task. (*a*) Boxplots comparing male and female performance on the first 20 trials and (*b*) Boxplots showing median number of errors on the first 20 trials by year. Median number of errors are depicted in centre line of the box, while boxes represent interquartile range (25% and 75%, respectively) and whiskers show largest and smallest values 1.5 times the respective interquartile ranges.

between male (mean errors per trial: 0.946 ± 0.47) and female (0.958 ± 0.438) performance on the spatial learning and memory task ($t = -0.054$, $p = 0.957$), nor was there a significant effect of elevation ($t = 0.186$, $p = 0.853$). Using the residuals from this model, variances between males and females were homogeneous ($F_{1,299} = 1.964$, $p = 0.162$), meaning there was no significant difference in the range of variation in performance (figure 1*a*,*b*).

Across all trials completed, where overall cognitive performance was tested, there were also no significant differences between male (mean errors per trial: 0.322 ± 0.20) and female (0.361 ± 0.243) performance ($t = 0.292$, $p = 0.771$), nor was there a significant effect of elevation ($t = -1.199$, $p = 0.232$). However, as noted in the methods, the total number of trials was significantly associated with performance ($t = -7.032$, $p < 0.0001$). Using the residuals from this model, variances between males and females were homogeneous ($F_{1,299} = 3.418$, $p = 0.065$).

(ii) Reversal spatial cognitive task

There was no significant difference between male (mean errors per trial: 0.681 ± 0.488) and female (0.568 ± 0.327) performance on the reversal spatial cognitive task across the first 20 trials ($t = 0.971$, $p = 0.333$). However, birds from high elevation performed significantly worse compared with birds at low elevations ($t = -3.86$, $p = 0.0002$; supporting our previous results in Refs. [33,35]). Using the residuals from this model, variances between males and females were not homogeneous ($F_{1,208} = 4.628$, $p = 0.033$), indicating a significant difference in the range of variation, with males having a larger range of variation in performance (figure 2*a* and *b*).

There was no significant difference between male (mean errors per trial: 0.298 ± 0.384) and female (0.26 ± 0.237) performance across all trials ($t = 1.200$, $p = 0.232$); however, there was a significant effect of elevation ($t = -5.070$, $p < 0.0001$). Again, as noted in the methods, the total number of trials was significantly associated with performance ($t = -7.728$, $p < 0.0001$). Using the residuals from this model, variances between males and females were homogeneous ($F_{1,208} = 1.350$, $p = 0.247$), meaning there was no significant difference in the range of variation in performance.

4. Discussion

Using four years of data from wild-tested birds, we found no significant differences between male and female mean performance on the spatial cognitive task or the reversal cognitive task. However, we did find partial support for the greater male variability phenomenon, as males exhibited greater variability in initial learning acquisition on the reversal task compared with females. While it is difficult to interpret null findings, we predicted that mean spatial cognitive performance would be similar between males and females, as spatial memory is critical for overwinter survival in both sexes [20] and territory sizes are not known to differ by sex. In addition, the fact that we saw no significant association between sex and mean performance across four years with a rather large sample size bolsters our confidence in this result.

Differences in variability during the first 20 trials appeared to have been driven mainly by the 2016 testing year, when birds were tested on the spatial learning and memory task for 16 days compared with 5 days in the other testing years. Work on reversal learning and cognitive flexibility suggests that the longer an animal receives reinforcement for a particular response, the harder it is for them to extinguish that behaviour and shift to a new one [35,38]. As such, the birds' memory of where it first obtained food during the 2016 season would be stronger than that in the other testing years. The 2016 reversal task was thus probably more difficult, which may explain why performance in 2016 differed significantly from the other 3 years of testing (electronic supplementary material). However, when 2016 data were run separately or when analyses were run without 2016, the variance of male and female performance was statistically homogeneous (electronic supplementary material). As such, our support for the greater male variability phenomenon only stands when all four years of data are run together, suggesting the larger sample size and not differences in methodology, may be responsible for our ability to detect greater variance in male performance. Interestingly, we did not detect a significant difference in spatial learning and memory performance between high and low elevation birds when these 4 years of testing were combined, which we have previously shown in 2 of these years [21,33]. That said,

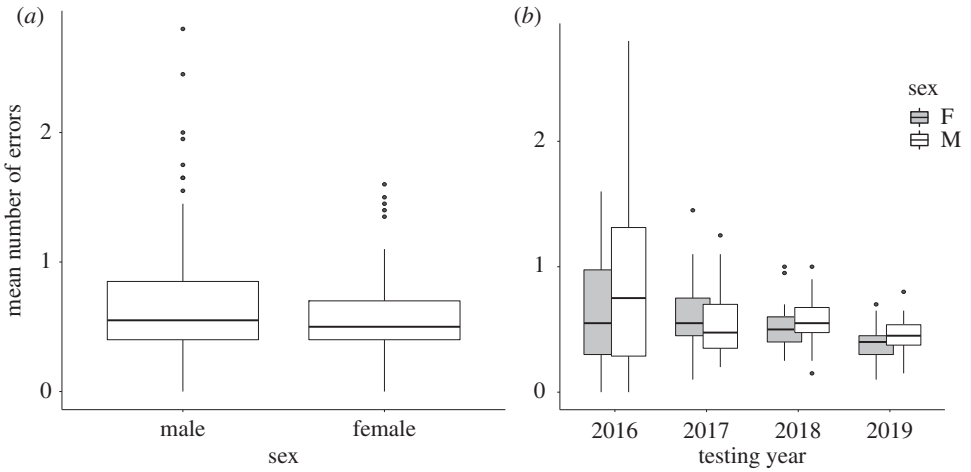

Figure 2. Reversal spatial cognitive task. (*a*) Boxplots comparing male and female performance on the first 20 trials and (*b*) Boxplots showing median number of errors on the first 20 trials by year. Median number of errors are depicted in centre line of the box, while boxes represent interquartile range (25% and 75%, respectively) and whiskers show largest and smallest values 1.5 times the respective interquartile ranges.

we have previously published non-significant differences between high and low elevation birds [35], and it is important to note that the data used in this study were a subset of the entire dataset, as only individuals of known sex were included (reducing the sample size by 173 observations).

Spatial cognition for recovering food caches is critical for overwinter survival in food-caching birds [20]; however, cognitive flexibility has been proposed as a mechanism for coping with less predictable environments (e.g. [39]). In the mountain chickadee system, we have previously shown that birds from milder, low elevations perform better on the reversal spatial learning task compared with those from harsher, high elevations [33,35] and suggested that while high elevations are harsher than low elevations, they are predictably harsh [40]. Indeed, the key to surviving in predictably harsh environments is probably accurate spatial learning and memory used for cache recovery, and not necessarily cognitive flexibility [33]. Our findings further suggest that selection on spatial learning and memory abilities is strong and should reduce variation in traits under directional selection [41]. At the same time, there may be weaker selection on cognitive flexibility in this system, allowing cognitive flexibility, assessed via reversal learning performance, to vary more widely. While males would also benefit from mating with females with enhanced spatial cognition via offspring with enhanced spatial cognition, their investment in reproduction is inherently lower than that of females [31,42], and they do not have the option to increase brood size when mated to a female with better cognitive abilities, as we have observed in females [31].

To date, there is little work investigating sex differences in spatial cognitive abilities outside of mammals, and none that has investigated the greater male variability phenomenon in non-human animals [9,16,22]. If cognitive abilities reflect male condition and are under sexual selection via female choice [31,43], males would be expected to exhibit a wider range of variation in cognition compared with females [29,30]. However, this pattern may not be equally predicted among all cognitive abilities, as we have shown here, because natural selection may result in specialized cognitive abilities required for survival. Because fitness is a combination of survival and reproductive output, an individual must survive its first winter in order to have the opportunity to reproduce. Spatial learning and memory are used to recover caches and are critical for overwinter survival in chickadees [20]; therefore, perhaps we should not expect spatial cognitive abilities to vary similarly to secondary sexual traits that reflect male condition (e.g. lek paradox). While female chickadees have been shown to increase their reproductive investment when mated to males with better spatial cognition [31], these enhanced spatial abilities are required for survival, unlike many secondary sexual traits. Perhaps males in excellent condition have excess energy to allocate to additional cognitive abilities and related expensive brain tissues, such as cognitive flexibility.

Interestingly, we found that females' performance on the spatial learning and memory task predicted their performance on the reversal spatial task, but that was not the case for males (see electronic supplementary material for analyses and electronic supplementary material, figure S1). While speculative, we think this suggests that such differences exist not because males have excess energy to devote to other cognitive abilities, but rather because natural selection for enhanced cognitive abilities may be stronger on females. Males and females experience strong selective pressures on their spatial memory abilities during the winter; however, during the breeding season, while male phenotypes may be affected by female choice, variation in female cognitive abilities may be further narrowed by natural selection. Indeed, we know that females, but not males, with better spatial cognitive abilities produce heavier fledglings compared with those with worse spatial cognitive abilities [31], and higher mass at fledging has been associated greater juvenile survival and recruitment [44,45]. Furthermore, females are able to adjust initiation of their clutch and its size, which again are measures related to reproductive success that males cannot regulate [31,42]. Our findings on the relationship between sex, elevation and task performance raise more questions about sex differences in cognitive abilities and highlight the need for further investigation.

To date, the research that has investigated sex differences in cognitive abilities demonstrates the importance of life-history and ecology driving such variation. For example, female brown-headed cowbirds (*Molothrus ater*) have superior spatial abilities compared with males, as females must locate host nests to lay their eggs [6] (although see [46]), while hummingbirds do not exhibit differences in spatial cognitive abilities between males and females as both sexes use spatial memory for successful foraging [47], much like chickadees.

Overall, we show that male and female mountain chickadees exhibit similar mean performance on both the spatial and reversal cognitive tasks and provide some of the first support for the greater male variability phenomenon in a non-human system. We suggest that the fields of comparative cognition and cognitive ecology may benefit from considering sex-based differences as a potential mechanism creating and maintaining variation in cognition.

Ethics. To the best of our knowledge, no birds were harmed by the collection of this data. All procedures were approved by the UNR IACUC ethics committee and in accordance with the UNR IACUC protocol (00046), under California Department of Fish and Wildlife Permit SC-5210 (DocID: D-0019571790-9).

Data accessibility. Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.j6q573nb4 [48].

Authors' contributions. C.L.B. and V.V.P. designed the experiment. E.S.B. and V.V.P. co-designed the 'smart' feeder arrays; E.S.B. designed RFID boards and wrote the software. C.L.B., B.R.S., A.M.P., L.M.B., D.Y.K. and V.V.P. collected data across the four years of cognitive sampling. C.L.B. conducted analyses and wrote the manuscript. All authors provided critical feedback for the manuscript.

Competing interest. We declare we have no competing interests

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