

Research



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Author for correspondence:

Benjamin R. Sonnenberg
 e-mail: benjamin.r.sonnenberg@gmail.com

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Natural variation in developmental condition has limited effect on spatial cognition in a wild food-caching bird

Benjamin R. Sonnenberg¹, Virginia K. Heinen¹, Angela M. Pitera¹, Lauren M. Benedict¹, Carrie L. Branch², Eli S. Bridge³, Jenny Q. Ouyang¹ and Vladimir V. Pravosudov¹

¹Department of Biology and Ecology, Evolution and Conservation Biology Graduate Program, University of Nevada, Reno, NV, USA

²Department of Psychology, University of Western Ontario, London, ON, Canada

³University of Oklahoma, Norman, OK, USA

ID BRS, 0000-0003-4496-4269; VKH, 0000-0003-1804-3589; AMP, 0000-0002-6166-3639; LMB, 0000-0003-1540-6663; CLB, 0000-0003-1769-5040; VVP, 0000-0003-1117-7875

Laboratory studies show that increased physiological burden during development results in cognitive impairment. In the wild, animals experience a wide range of developmental conditions, and it is critical to understand how variation in such conditions affects cognitive abilities later in life, especially in species that strongly depend on such abilities for survival. We tested whether variation in developmental condition is associated with differences in spatial cognitive abilities in wild food-caching mountain chickadees. Using tail feathers grown during development in juvenile birds, we measured feather corticosterone ($Cort_f$) levels and growth rates and tested these birds during their first winter on two spatial learning tasks. In only 1 of the 3 years, higher feather $Cort_f$ was negatively associated with memory acquisition. No significant associations between feather $Cort_f$ and any other measurement of spatial cognition were detected in the other 2 years of the study or between feather growth rate and any measurement of cognition during the entire study. Our results suggest that in the wild, naturally existing variation in developmental condition has only a limited effect on spatial cognitive abilities, at least in a food-caching species. This suggests that there may be compensatory mechanisms to buffer specialized cognitive abilities against developmental perturbations.

1. Introduction

Animals exhibit large variation, both across and within species, in cognitive abilities, yet the mechanisms underlying such variation remain poorly understood [1–3]. While selection can act on heritable traits associated with genetic differences [4,5], it remains uncertain how much individual variation in cognitive abilities observed in non-human animal populations may be produced by other factors, most notably differences in development [1,2,4,6–8]. Most research on animal cognition takes place in laboratory environments, which allows for the precise control of environmental conditions during both cognitive testing and development [3]. Past laboratory-based work has shown that increased exposure to stress-inducing events during early development can have profoundly negative impacts on the future cognition of young animals [2,7,9–11]. Cognitive traits depend on energetically expensive, specialized tissues (i.e. brain regions) to properly function and non-optimal conditions during development diverts energy expenditure towards short-term survival rather than neural investment [3,7,8,10]. The hippocampus, a brain region involved in spatial navigation and cognitive function, is known to be a major target of stress-mediated effects, which appears to be driven by elevation in glucocorticoid hormones [6,9,12].

Glucocorticoids are a well-studied class of steroid hormone that are known to mediate broad metabolic processes [13–16]. Prolonged exposure to elevated levels of these hormones (namely cortisol and corticosterone) has been shown to increase the overall wear and tear on organisms over time [9,13,14]. Although these processes are regarded as normal signs of ageing, when they occur in young animals, they can severely alter developmental trajectories and appear to have a direct, negative impact on cognitive abilities in general [6,8,14,17], and particularly on hippocampus-dependent spatial abilities [7,10].

The ability to navigate through and remember past environments is a ubiquitous trait in animals. However, some species rely on the hippocampus for more specialized spatial cognitive abilities, for example, food-caching species [3,18]. Scatter caching animals store thousands of individual food items throughout their environments and rely on spatial memory for future cache retrieval [3,18]. In some North American chickadee species (*Poecile atricapillus* & *Poecile gambeli*), the dependence on food caches for overwinter survival has been shown to vary across environments that differ in climatic harshness [18–21]. This environmental variation has also been linked with differences in spatial learning and memory ability and associated hippocampal morphology [18,20,22,23]. Moreover, individual variation in spatial cognitive abilities in food-caching species appears to be associated with differences in overwinter survival [21] and has a genetic basis [5]. This suggests that differences in spatial cognitive abilities in food-caching species probably arose via natural selection [21].

Considering that spatial cognitive abilities are critical for survival in food-caching species, it has been suggested that selection should favour the evolution of mechanisms that may protect them and their associated neural tissue from environmental perturbations during development [2]. Yet, laboratory-based studies still show that increased developmental stress associated with impacts from malnutrition and prolonged exposure to elevated glucocorticoid levels, sometimes directly related to food deficits, result in impaired spatial cognitive abilities in some food-caching species [10,11]. However, laboratory conditions provide highly impoverished environments compared to natural settings and may potentially restrict animals' abilities to resist or cope with developmental stress [2]. Such restrictions include limited use of cognition (i.e. decreased opportunities to learn and practice) as well as rather restricted and researcher determined nutrition (i.e. limited food diversity). Currently, little is known about whether developmental stress is strongly associated with impaired spatial cognitive abilities in wild animals living in their natural environment [1].

In this study, we investigated whether natural variation in developmental conditions in juvenile birds was associated with differences in their spatial cognitive abilities. This study took place across three years using three separate cohorts of first-year wild mountain chickadees (*P. gambeli*). Mountain chickadees are small, highly sedentary songbirds that rely on specialized spatial cognition associated with food-caching to survive the montane winter environments in temperate western North America [5,18,21,24]. Birds residing at higher elevations that experience longer harsher winters compared to lower elevations appear to generally have better spatial learning and memory abilities [22,25] associated with a larger hippocampus and more hippocampal neurons [22]. Additionally, strong directional selection

favouring first-year birds with better spatial learning and memory performance was detected in an ongoing long-term study [21].

The condition of individual birds during post-hatching development was evaluated via differences in glucocorticoid hormone levels (corticosterone or $Cort_f$) [26,27] and growth rates [28] measured in tail feathers. Malnutrition is known to result in slower feather growth rates and elevated corticosterone levels (e.g. [10,11,28]). Chickadees grow their first plumage while in the nest environment and before becoming nutritionally independent [24]. The quality of each feather, which is indicative of overall developmental conditions, is reflective of both the local environment and parental investment [24,26–31]. Unlike measurements using blood samples, feather $Cort_f$ represents conditions during the entire early developmental period including time in the nest and the early post-fledging period, when tail feathers continue to grow [24,26,27,32]. However, this method does come with some limitations including limited temporal understanding of when the hormone deposition took place and it is used here as a relative measure [26,27].

Tail feather daily growth rates were assessed using feather growth bars (horizontal bands along the length of the feather), which accurately reflect caloric intake during a 24 h period [28]. We predicted that patterns of yearly variation in individual developmental conditions would align with patterns of reproductive success in the larger population (i.e. years with smaller broods or lower nestling mass would also show more $Cort_f$). We collected tail feathers from juvenile chickadees throughout the autumn and winter and then tested their cognitive abilities in the same winter using two spatial cognitive tasks: a spatial learning and memory task and a single spatial reversal learning task (flexibility) following our well-established methods [21,25,33–35]. We predicted that chickadees that experienced worse developmental conditions (higher amounts of $Cort_f$ deposited in feathers across development and smaller, slower growing feathers) would perform worse in both cognitive tasks compared to individuals with less $Cort_f$ exposure and larger, faster growing feathers.

2. Methods

(a) Study site

All data for this study were collected during 2018–2021 at the Sagehen Experimental Forest (Sagehen Creek Field Station, University of California, Berkeley) in the Sierra Nevada, USA. We monitor mountain chickadees year-round and collect annual measurements on reproductive success [36] and spatial cognitive performance [19,21,25,33–35]. We focus on two subsets of the population at two montane elevations, a high elevation site (approx. 2400 m) and a low elevation site (approx. 1900 m), which differ greatly in winter environmental conditions [36]. High elevations are associated with harsher winters characterized by lower temperatures, higher and longer lasting snow levels and unpredictable winter storms compared to lower elevations [35]. We track individually marked birds across years via unique combinations of plastic colour bands, a passive integrated transponder (PIT) tag and in some cases an aluminium US Geological Survey band. We capture chickadees via mist net during the autumn and winter (non-breeding), and at nestboxes during spring and summer (breeding), for banding. Nestlings are banded with only an aluminium leg band at day 16 post-hatch and, if recaptured, are then equipped

with a PIT tag and an additional colour band. All birds are classified as juveniles (less than a year of age) or adults (more than a year of age) at time of initial capture based on multiple plumage characteristics [37], but only juveniles were included in this study.

(b) Spatial cognitive testing

Across three years (2018–2021), we tested juvenile chickadees at both elevations using two spatial cognitive tasks—a spatial learning and memory task and a single spatial reversal learning task [25,33,34]. For cognitive testing, we used four feeder arrays, each composed of eight radio frequency identification (RFID)-based feeders positioned equidistant on a square frame (122 × 122 cm) and suspended ca. 4 m above the ground [21,25,33,34]. Two spatial arrays were used at each elevation, positioned approximately 1.5 km apart [25,33]. Each RFID-equipped feeder contained an antenna embedded in a perch that was linked to an RFID-enabled Arduino circuit board with built-in memory and time keeping [38]. This setup allowed us to record all visits by PIT-tagged birds (identification and visitation timing) and operate a motor-controlled door that managed food access [38]. Before cognitive testing, all array feeders were maintained in ‘open’ mode, in which feeder doors were open and food was clearly visible and available to all visiting birds. One week prior to cognitive testing, all feeders were switched to ‘all’ mode in which all doors were closed but would open when any PIT-tagged bird landed on any feeder perch. This stage allows birds to habituate to the moving doors prior to testing. Following ‘all’ mode, we started the spatial learning and memory task by programming all feeders to ‘target’ mode, in which feeders continue to track visits from all birds, but only one feeder on the array opens for each bird with all birds pseudo-randomly assigned to different feeders within an array [25,33,34]. Following our previous work, we used two metrics to measure cognitive performance in each task: the mean number of ‘location errors’ (non-rewarding feeders visited prior to visiting the correct rewarding feeder) per trial over the first 20 trials and over the entire task (5 days) [21,25,33–35]. A trial started when a bird visited any feeder in the array and ended with a visit to the rewarding feeder [25]. Performance during the first 20 trials of the spatial task represents initial memory acquisition and performance over the entire task reflects longer term memory ability [21]. Previously, we have shown that variation in both metrics is associated with fitness consequences (i.e. individuals that make more errors show a fitness reduction) [21,39] and has genetic basis [5].

Immediately following the spatial learning and memory task, we carried out a single spatial reversal learning task by re-assigning each bird to a different rewarding feeder in each array. Birds assigned to the same feeder during the spatial learning and memory task were re-assigned to different feeders during the reversal task to prevent social learning [33,34]. As in the previous task, we measured performance using the mean number of location errors per trial over the first 20 trials and over the entire spatial reversal learning task (5 days).

We conducted spatial learning and memory tasks from 8 to 13 April in the 2018–2019 winter (both elevations), from 20 to 24 January at low elevation and from 3 to 7 February at high elevation in 2019–2020, and from 13 to 17 January in 2020–2021 (both elevations). We ran spatial reversal learning tasks at both elevations from 13 to 18 April in 2019, from 24 to 29 January at low elevation and from 7 to 13 February at high elevation in 2020, and at both elevations from 20 to 26 January 2021. Variation in testing dates between years and elevations is due to technical difficulties or environmental perturbations (e.g. winter storms, deep snow) that impeded our ability to access the feeders; however, for each test type the data from five consecutive days was used for analyses.

(c) Feather size and growth rate

We collected a single tail feather from juvenile (first year) birds during the autumn and early winter months in 2018–2020 when birds were captured in mist nets prior to the onset of cognitive testing. We removed the single outermost rectrix (r12) from each bird and placed feathers in labelled coin envelopes that were stored in a cool dry place until processing as previous work has shown that feathers do not degrade overtime [27]. We did not use any damaged or severely worn feathers in the study. Feathers were assessed for overall mass via an electronic scale to the nearest 0.1 mg and length via ruler to the nearest 0.5 mm. This process was repeated before and after the removal of the calamus or the barbless tip of the feather. Calamus removal was required for the glucocorticoid extraction protocol (see below).

We measured feather growth rate using daily growth bar width [28]. Feathers were placed on a white 10.16 × 15.24 cm notecard and exposed to low-angle light to visualize growth bars. The beginning and end of each growth bar were marked on a notecard in light pencil, allowing for clearer visualization and measurement [28]. After marking, each feather card was photographed and ImageJ software (National Institute of Health) was used to measure each growth bar to the nearest 0.1 mm [40]. Mean feather growth bar width was used in all analyses.

(d) Feather corticosterone (Cort_f)

We subjected chickadee tail feathers to a standard corticosterone extraction procedure followed by an enzyme-linked immunosorbent (ELISA) assay using methods established by Bortolotti *et al.* in 2008–2009 and modified following Grant *et al.* in 2020 [26,27,41]. Feathers from all years were extracted in the spring of 2021 and immediately assayed. Individual feathers were cut into multiple pieces (approx. 5 mm in length) and placed (excluding the calamus) into 20 ml scintillation vials with seven mL of HPLC grade 100% methanol. Scintillation vials were sonicated in a room temperature water bath for 30 min and then placed in a shaking 50°C water bath overnight (16 h). The methanol and feather material were separated using vacuum filtration and each vial was washed twice with two ml of methanol each wash. The separated methanol was then dried in a FlexiVap station, which is composed of a heat block that also supplies constant airflow over the surface of the methanol to aid with evaporation rate. We reconstituted dried samples in 500 ml of assay buffer and samples were sealed and frozen until assayed. Reconstitution volume and parallelism were determined by previous assays of serial dilutions of chickadee feathers not used in this experiment. We ran samples diluted by 1 : 300, 1 : 600 and 1 : 900. Parallel curves were generated, and a dilution of 1 : 500 was selected due to this dilution having the highest level of parallelism.

All samples were assayed using a corticosterone ELISA kit supplied by Enzo life sciences (catalog no. ADI-901-097) following the manufacturer's instructions. Feathers from all years were assayed using the same kit to reduce batch bias. We used a serial dilution of known Cort concentration to create a standard curve and used the coefficient of variation (CV) of known standards (20 000 pg ml⁻¹, 4000 pg ml⁻¹, 800 pg ml⁻¹, 160 pg ml⁻¹ and 32 pg ml⁻¹) to calculate inter- (18%) and intra-assay (plate 1: 15%, plate 2: 6%) variation. Inter-plate CV was calculated from duplicated controls made from pooled Cort_f from previous samples and was taken through the entire assay process. Cort values were then standardized by feather length to account for variation in Cort_f deposition during growth [26,27,41]. Samples were randomized across plates.

(e) Reproductive monitoring

We predicted yearly variation in Cort_f and feather growth would match the larger population's reproductive pattern (i.e. years with lower resource availability should lead to both higher Cort_f

and smaller and lower quality broods). To evaluate annual reproductive output of the study population during the 3 years of study, we analysed reproductive parameters used in previous studies as an index of environmental and developmental conditions (e.g. [36,42]). Mountain chickadees rarely produce more than a single brood each year and all juvenile birds produced in a given season are considered a cohort. Only a handful of nestlings reared in provided nestboxes were recaptured for $Cort_f$ analysis and returned to participate in cognitive testing. However, the individuals that were sampled for both $Cort_f$ and cognitive performance were sampled from the same yearly cohorts, allowing for general comparisons between annual trends in measures of developmental condition and reproductive output. Adult chickadees were monitored throughout the spring and summer months for the onset of breeding behaviour, including nest building in provided nestboxes and first egg date [36]. Nests were subsequently monitored on a biweekly basis for onset of incubation, hatching date, brood size and overall success or failure. Nestlings were processed on day 16 post-hatch where we counted brood size, measured individual mass and banded all nestlings with an aluminium USGS band. Larger clutch and brood sizes and higher fledgling mass is typically associated with better environmental conditions during a given year [42]. Within-brood CV in fledgling mass was also estimated. Higher CV of fledgling mass indicates a larger variance in condition of individual fledglings within a nest and may reflect relatively worse developmental conditions (i.e. food availability, parental quality, conditions of the nest).

(f) Statistical analyses

All analyses and associated figures for this study were generated using R v. 4.1.2 [43,44]. We used linear and generalized linear models to investigate the relationship between $Cort_f$ and feather morphometrics and individual variation in spatial cognitive performance (mean number of location errors per trial during the first 20 trials and during the entire task) of first-year chickadees. We tested each model for its residual fit using the R package 'DHARMA' [45].

We quantified the presence of corticosterone in each feather in picograms per mm and used these values for the majority of analyses. The only exceptions were analyses that included feather length or mass as a response variable; in these cases, we used the total picogram values per sample. We fit models to test for variation across time and location using year and elevation as fixed effects and $Cort_f$ (controlling for feather mass), feather length (mm), feather mass (g) and mean feather growth rate (mm per 24 h) as response variables. Each response variable was investigated in an independent model. We ran an additional model with capture time (Julian date) as a fixed effect and $Cort_f$ as the response to test whether earlier sampled individuals had higher $Cort_f$ compared to individuals sampled later in the season. The importance of each fixed effect was tested using a type III Wald chi-square test. When year or elevation was significant, we conducted *post hoc* Tukey analyses to determine significant differences across levels using the 'emmeans' R package [46].

We fit models testing for $Cort_f$'s relationship with spatial cognitive metrics using $Cort_f$, elevation and year as fixed effects and mean location errors per trial made during the first 20 trials as well as during the entire task (both spatial learning and memory or single spatial reversal learning) as the response variables. For models using mean location errors over the entire trial, we included the total number of trials completed during the task as a control predictor to account for differences in the total number of trials across individuals [25,34]. The mean number of errors per trial over the entire task was log-transformed for both the spatial and reversal learning tasks to fit the assumptions of the model. We only used birds that completed a minimum of 20 trials in both tasks for the analyses [25,34]. We fit similar

models using mean daily feather growth, feather length and feather mass as fixed effects. All initial models were first tested for an interaction between the focal predictor ($Cort_f$, growth, length and mass) and year as well as an interaction between year and elevation. If there was a significant interaction found in the interaction model, each year was subsequently analysed separately to investigate the nature of the interaction; otherwise, the interactions were removed. Sample sizes broken down by elevation and year are included in a summary table within the supplementary information.

Lastly, to investigate overall differences among the 3 years of breeding conditions, we fit general linear mixed-effects models using the package 'glmmTMB' [47] to compare reproductive parameters of the nestbox population. We used all available data from each study year despite the vast majority of individuals from the nestbox population not being recaptured for feather analysis or returned to participate in the cognitive tasks. We used elevation and year as fixed effects and breeding pair identification as a random effect to test for differences in clutch size, brood size, mean nestling mass and the CV of nestling mass. Clutch size and brood size models used a generalized Poisson distribution to adjust for count data containing a lack of zero values [48]. Each of these four response variables was run separately but clutch size was also used as a fixed predictor in the brood size model. This allows for the examination of how many nestlings fledged relative to eggs laid.

3. Results

(a) Variation in feather $Cort_f$, mass, length and growth rate across years and elevations

There were no significant differences in $Cort_f$ between elevations, but $Cort_f$ varied significantly among years (electronic supplementary material, table S1, figure S1A). In 2018, $Cort_f$ was significantly higher compared to 2019 ($p = 0.04$) and 2020 ($p < 0.001$) and in 2020, $Cort_f$ was significantly lower than in 2019 ($p = 0.015$). Neither variation in feather mass, length, nor 24 h growth rate were significantly associated with differences in $Cort_f$ (electronic supplementary material, table S2); larger, longer and faster growing feathers did not have significantly higher or lower $Cort_f$. Additionally, capture time (Julian date) did not significantly predict $Cort_f$ after controlling for elevation and year showing that feathers collected earlier in the season did not contain more or less $Cort_f$ compared to individuals sampled later (electronic supplementary material, table S2). Capture dates varied from early autumn (20 August) to late winter (29 March), and these results suggest that we were not capturing individuals with more or less $Cort_f$ earlier or later in a given season.

Feather mass did not vary significantly across elevations but there were significant differences across years (electronic supplementary material, table S1, figure S1B). Feather mass was significantly higher in 2019 compared to both 2018 ($p < 0.001$) and 2020 ($p < 0.001$). At the same time, there were no significant differences in feather mass between 2018 and 2020 ($p = 0.44$, electronic supplementary material, figure S1B). Similarly, feathers were significantly longer in 2019 compared to both 2018 ($p = 0.01$) and 2020 ($p = 0.012$), with no significant differences in feather length between 2018 and 2020 ($p = 0.92$) and no differences associated with elevation (electronic supplementary material, table S1). This year-to-year variation was also evident in feather growth rates (i.e. mean feather bar width), which were significantly higher in 2019 compared to 2020 ($p < 0.001$)

Table 1. Mean location errors per trial over two spatial tasks and Cort_f.

predictor	spatial learning task		single reversal learning task	
	location errors per trial in the first 20 trials <i>n</i> = 101 ^a	location errors per trial in the entire task	location errors per trial in the first 20 trials <i>n</i> = 87 ^b	location errors per trial in the entire task
elevation	$\chi^2_1 = 1.18, p = 0.277$	$\chi^2_1 = 0.13, p = 0.714$	$\chi^2_1 = 0.02, p = 0.874$	$\chi^2_1 = 0.10, p = 0.756$
year	$\chi^2_2 = 2.79, p = 0.248$	$\chi^2_2 = 6.84, p = \mathbf{0.033}$	$\chi^2_2 = 5.82, p = 0.05$	$\chi^2_2 = 4.73, p = 0.094$
Cort _f (pg mm ⁻¹)	$\chi^2_1 = 0.46, p = 0.499$	$\chi^2_1 = 3.77, p = 0.052$	$\chi^2_1 = 0.15, p = 0.702$	$\chi^2_1 = 1.39, p = 0.238$
total trial number	NA	$\chi^2_1 = 81.25, p < \mathbf{0.001}$	NA	$\chi^2_1 = 35.23, p < \mathbf{0.001}$
year $\times$ Cort _f	$\chi^2_2 = 8.12, p = \mathbf{0.017}$	$\chi^2_2 = 7.94, p = \mathbf{0.019}$	NA	NA
adjusted <i>R</i> ²	0.06	0.47	0.07	0.38

^aSample sizes by elevation and year for the spatial learning task: 2018 (low: 2; high: 26); 2019 (low: 6; high: 22); 2020 (low: 26; high: 19).

^bSample sizes by elevation and year for the single reversal learning task: 2018 (low: 1; high: 20); 2019 (low: 6; high: 21); 2020 (low: 22; high: 17).

but not significantly different from growth rate in 2018 ($p = 0.05$). There were no significant differences in feather growth rate between 2018 and 2020 ($p = 0.23$, electronic supplementary material, table S1, figure S1c), and again there were no significant differences between elevations.

(b) Spatial learning and memory

There was no significant association between performance in the first 20 trials of the learning and memory task (mean number of errors per trial) and Cort_f, elevation or year (table 1). However, there was a significant interaction between Cort_f and year (table 1). When analysed separately within each year, higher levels of Cort_f were associated with worse performance across the first 20 trials (larger mean number of errors per trial) but only in 2018 and only at high elevation (as no data from low elevation were included in this model due to low sample size; table 2; figure 1a). There were no significant associations between performance on the first 20 trials of the task and Cort_f in either 2019 or 2020 (table 2; figure 1b,c).

There were no significant associations between performance in the entire spatial learning and memory task and Cort_f, but there was a significant year effect and significant Cort_f by year interaction (table 1). *Post hoc* analyses showed no statistically significant differences in performance across the entire task between any years (2018|2019: $p = 0.89$; 2018|2020: $p = 0.92$; 2019|2020: $p = 0.99$). There were also no statistically significant associations between the number of location errors per trial over the entire task and Cort_f within each of the 3 years when run in separate independent models (table 1; figure 1d–f).

There were no significant associations between performance either in the first 20 trials of the spatial learning and memory task or during the entire task and mean feather bar width (electronic supplementary material, table S3). Variation in feather length and mass similarly was not associated with differences in cognitive performance (electronic supplementary material, table S3).

(c) Spatial reversal learning

There were no significant associations between Cort_f and performance (mean number of errors per trial) on a single

reversal task performance in the first 20 trials (table 1; figure 2a–c) or during the entire task (table 1, figure 2d–f).

There was no significant association between performance in the first 20 trials of the single reversal learning task and mean feather growth bar width, but there was a significant elevation by year interaction (electronic supplementary material, table S3). *Post hoc* analyses revealed no significant differences between elevations ($p = 0.81$) or between years (2018|2019: $p = 0.18$; 2018|2020: $p = 0.58$; 2019|2020: $p = 0.20$) despite the overall results of the model.

There was no significant association between mean feather bar width and performance over the entire spatial reversal learning task (electronic supplementary material, table S3). Variation in feather mass and length was similarly not associated with differences in performance in a spatial reversal learning task (electronic supplementary material, tables S3 and S4).

(d) Population-level year differences in fledgling condition

Mean fledgling mass was not significantly different between elevations but varied significantly across years and the interaction between elevation and year was statistically significant (electronic supplementary material, table S5). *Post hoc* analyses confirmed that there were no significant differences between elevations ($p = 0.82$) but there was a significant difference across years with 2020 associated with significantly lower mass compared to 2018 ($p < 0.001$) and 2019 ($p < 0.001$). There were no significant differences in mass between 2018 and 2019 ($p = 0.14$).

The variation of nestling mass within nests (CV) also varied significantly across years but not elevations (electronic supplementary material, table S5). *Post hoc* analyses showed that the CV of fledgling mass was higher in 2020 compared to both 2018 ($p = 0.005$) and 2019 ($p = 0.012$) but there were no significant differences between 2018 and 2019 ($p = 0.96$).

4. Discussion

Overall, we found limited support for the hypothesis that the condition during development of wild mountain chickadees

Table 2. Mean location errors per trial over the entire learning and memory task and for the first 20 trials and $Cort_r$ by year.

year	<i>n</i>	predictor	location errors/trial in the first 20 trials	location errors/trial in the entire task
2018	total: 26	elevation	removed due to lack of samples	removed due to lack of samples
	low: 0			
	high: 26	$Cort_r$ (pg mm ⁻¹)	estimate = 0.05 ± 0.02, $t = 2.56$, $p = 0.017$	estimate = 0.03 ± 0.01 , $t = 1.88$, $p = 0.072$
		total trial number	NA	estimate = $-2.7 \times 10^{-3} \pm 5.0 \times 10^{-4}$, $t = -5.45$, $p < 0.001$
		Adj. R^2	0.21	0.59
2019	total: 28	elevation	estimate = 0.36 ± 0.19 , $t = 1.93$, $p = 0.065$	estimate = 0.26 ± 0.17 , $t = 1.54$, $p = 0.137$
	low: 6			
	high: 22	$Cort_r$ (pg mm ⁻¹)	estimate = $-4.3 \times 10^{-3} \pm 0.01$, $t = -0.37$, $p = 0.712$	estimate = $-4.6 \times 10^{-3} \pm 0.01$, $t = -0.46$, $p = 0.653$
		total trial number	NA	estimate = $-1.2 \times 10^{-3} \pm 3.4 \times 10^{-4}$, $t = -3.64$, $p = 0.001$
		Adj. R^2	0.13	0.46
2020	total: 45	elevation	estimate = 0.05 ± 0.12 , $t = 0.37$, $p = 0.708$	estimate = $-3.0 \times 10^{-3} \pm 0.11$, $t = -0.03$, $p = 0.980$
	low: 26			
	high: 19	$Cort_r$ (pg mm ⁻¹)	estimate = $-6.1 \times 10^{-3} \pm 0.01$, $t = -0.48$, $p = 0.635$	estimate = -0.01 ± 0.01 , $t = -0.17$, $p = 0.169$
		total trial number	NA	estimate = $-1.4 \times 10^{-3} \pm 2.4 \times 10^{-4}$, $t = -5.89$, $p < 0.001$
		Adj. R^2	0.01	0.47

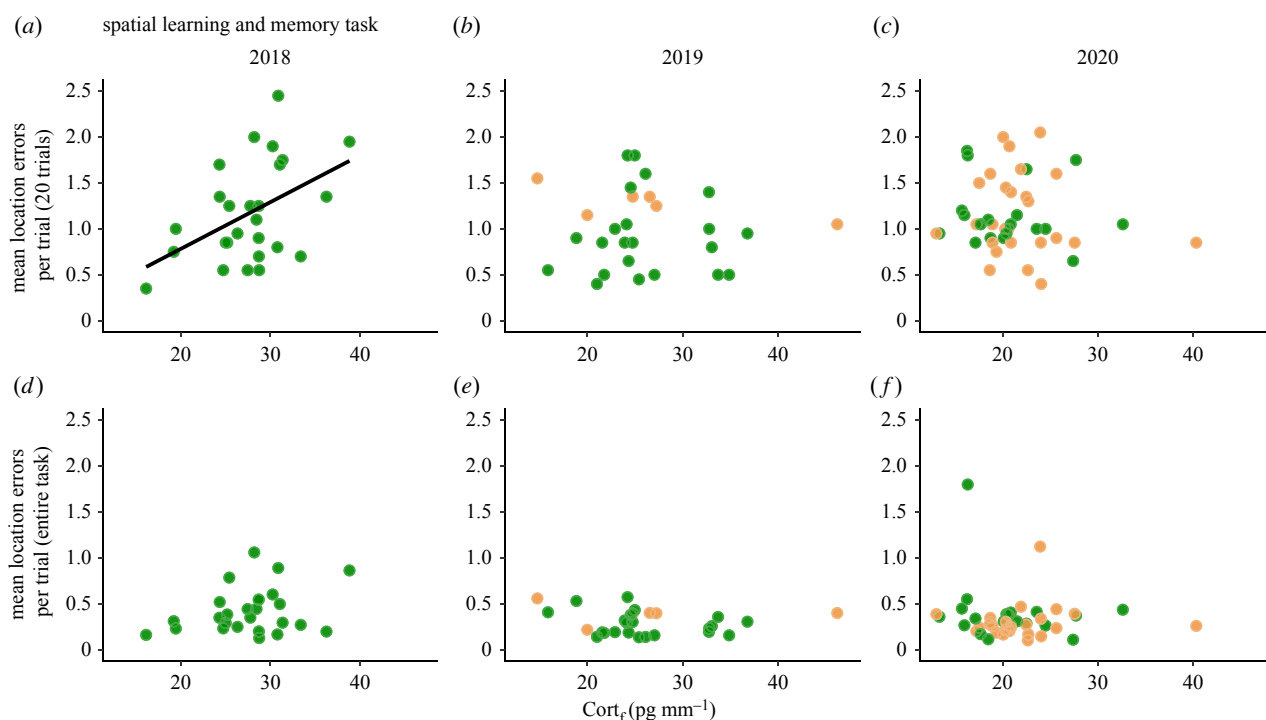


Figure 1. Performance on the spatial learning and memory task, showing mean location errors per trial (*a–c*) during the first 20 trials and (*d–f*) over the entire task in relation to Cort_f across the 3 years of the study, with high elevation marked in green and low elevation marked in orange.

results in impaired spatial cognitive abilities. We only detected a significant negative association between spatial cognitive ability and feather Cort_f in the initial memory acquisition phase (first 20 trials) during 1 year of the 3-year study. At the same time, we did not detect a significant association between developmental Cort_f and spatial cognitive ability in the memory retention phase (performance across entire testing period) during any of the 3 years. As the first 20 trials reflect the memory acquisition phase, while performance over the entire task represents longer term memory ability [21], our results suggest that elevated developmental Cort_f may have limited effects on memory acquisition, but no detectable effects on longer term memory ability. However, as this effect only occurred in a single year this result may be due to chance. We did not detect differences between Cort_f and performance on the single spatial reversal learning task during any year of the study. It is possible that individuals with worse developmental conditions died before our sampling—if this were the case, our results would only be limited to individuals that survived at least a month after fledging and to the age where spatial abilities are relevant to their survival. Although, we did not detect a relationship between Cort_f and sampling date, which argues against the idea that birds with higher Cort_f may die earlier in the post-fledging period. Overall, our results are likely reflective of the relevant naturally existing variation in developmental condition.

Across years, there were significant differences in the total Cort_f: mean Cort_f was highest in the 2018 cohort, followed by the 2019 cohort and finally lowest in the 2020 cohort. Despite the detected mean yearly differences, each year was associated with large individual variation. Feather growth, mass and length also varied across years but only 2019 had significantly larger and faster growing feathers compared to both 2018 and 2020. We detected no significant associations between feather growth rates or feather mass and any measure of spatial cognitive performance.

There were no significant differences in cognitive performance across years on either the spatial learning and memory or the spatial reversal tasks. The only exception was a small difference among years in spatial learning and memory performance, but only in models with feather length and mass (see electronic supplemental materials). This disparity is likely to be due to a slight difference in sample size as not all feathers survived the hormone extraction process. These models showed cognitive performance in 2018 (year with the highest Cort_f) was worse than 2019 but statistically similar to that in 2020 (the year with the lowest Cort_f). Thus, these results corroborate our conclusions that developmental conditions had only a limited effect on spatial cognitive abilities.

There were significant differences in the reproductive parameters among years. Chickadees fledged the lightest massed nestlings in 2020 compared to both 2018 and 2019. The within brood variation in nestling mass was significantly larger in 2020 compared to both 2018 and 2019. All these results suggest that 2020 was associated with lower quality developmental conditions. However, feather Cort_f in 2020 was the lowest among the 3 years of study. These data suggest that there were no broad associations between developmental conditions (as indicated by fledgling body mass and CV of fledgling mass within a nest) and feather Cort_f across years. One explanation for this mismatch is that the pattern seen between years in reproductive output may only be evident at the population level and not the level of the individual. Additionally, there were no striking differences in cognitive performance between years despite large differences in overall developmental conditions.

Despite strong laboratory-based evidence that perturbations during early development can lead to negative impacts on cognitive abilities (e.g. [2,6,7,17]), we did not find strong support for this pattern in wild food-caching mountain chickadees tested in their natural environment. This may partly be driven

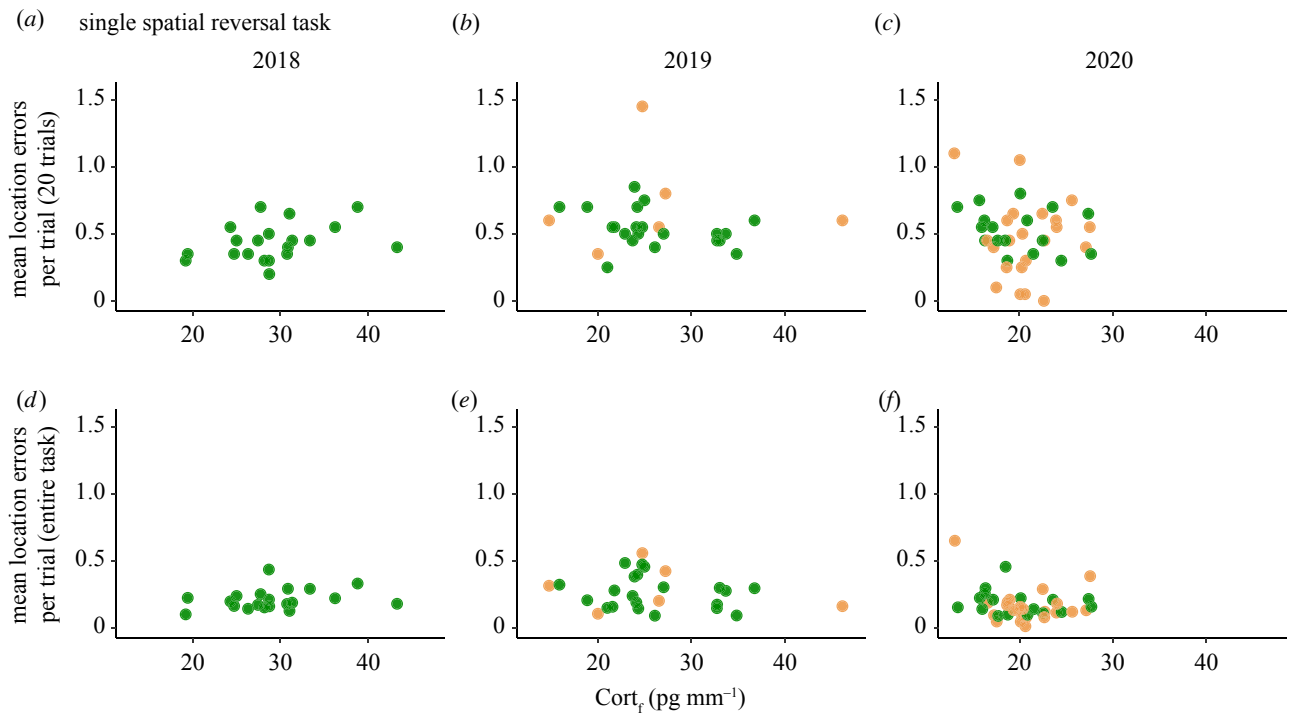


Figure 2. Performance on the single reversal spatial learning and memory task, showing mean location errors per trial (*a–c*) during the first 20 trials and (*d–f*) over the entire task in relation to Cort_f across the 3 years of the study, with high elevation marked in green and low elevation marked in orange.

by the inability of laboratory animals to respond to such effects in the absence of resources from natural environments [2]. The basic needs of captive animals are met in the laboratory but if there are compensatory mechanisms mediated via resources only available in natural settings, this may inhibit animals from mounting a compensatory response [2].

For example, it has been shown that the amino sulfonic acid, taurine can rescue neural tissue and related cognitive functions from the negative effects of environmental stressors [49–52]. Taurine is found ubiquitously in nature and while most organisms can synthesize their own source, some avian species may lack this ability during early development and can only gain taurine by consuming certain food sources. For example, spiders contain 40–100 times more taurine than other common arthropod food resources and are a common component of chickadee diets [53]. Past work has shown that chickadees and close relatives seek out spiders to consume and feed to developing nestlings [54,55] and that experimental supplementation of taurine results in rescued and in some cases better spatial cognitive abilities [49,50,54]. Thus, adult chickadees may seek out spider prey to buffer against the negative impacts of developmental stress on structures like the hippocampus, preserving future spatial cognitive function. As a result, additional taurine in the diet may counteract the negative effects of lower daily nutrition due to lower food availability [51,52]. Laboratory environments restrict parental behaviors such as selective feeding, as they lack diverse resources, which may explain the consistent negative effects of increased developmental stress on cognitive function [2,3].

Animals in the laboratory are also severely limited in their opportunities to use cognition. This is especially true for spatial cognition—captive environments are well known to result in reduced hippocampal volume [56,57]. It is possible that wild animals in their natural environment may be able

to counter negative effects of developmental stress on spatial cognitive abilities through extensive use of such abilities later in life [3]. Food-caching birds cache tens of thousands of individual food caches every autumn and use spatial memory to recover these caches [18]. It is possible that this considerable daily use of spatial cognition will compensate or rescue cognitive function from some developmental perturbations [2].

The use of Cort_f to evaluate nestling condition was established by Bortolotti and colleagues [26,27]. Although, the use of this method for examining short-term stressors has been discouraged [58], our use of Cort_f as an index of nesting conditions aligns with several other studies that focus on tradeoffs during early development [30–32]. However, this method does not allow for a temporal understanding of Cort deposition into the feather tissue. A bird with higher Cort_f compared to others in its cohort may have initially experienced significant perturbations that then declined throughout the rest of development. Thus, some individuals with higher Cort_f may have had the ability to recover from this exposure. It is also possible that the detected levels of Cort_f were indicative of system-wide Cort concentrations that were below a harmful threshold. Additionally, there have been some studies showing that poor developmental conditions result in lower levels of glucocorticoid hormones [59,60], and that higher levels may be more indicative of a normal function [61]. We did see our predicted relationship between higher levels of hormone and worse memory performance but only in a single year and elevation. This result does not remove the possibility that in natural populations higher Cort may be related to more ideal conditions but in either case, variation in developmental conditions in our study is likely representative of naturally present and rather large variation across multiple years in our population.

As the survival of young songbirds during the post-fledging period is very low [42], and our study only includes

birds that survived at least a few months after fledgling, our sample may be biased towards higher-quality individuals that received lower exposure to developmental harm. On the other hand, laboratory-based studies showed negative effects of rather small differences in developmental stress associated with limited variation in nutrition [10,11]. If young birds with worse developmental condition indeed die earlier, we would expect samples collected earlier in the autumn to contain higher $Cort_4$. Yet we detected no such pattern. This suggests that birds with higher levels were not being selected out of the population more quickly during the post-fledging period compared to those with lower levels. Also, if the individuals with worse developmental conditions die soon after fledging, their mortality could not be associated with worse spatial cognitive abilities as these are impossible to sample that early in development in a wild population. This study was completely dependent on individuals that not only survived to fledging but also survived long enough to participate in the cognitive tasks later in the winter.

Overall, our results show that mountain chickadees in their natural environment do not exhibit strong negative effects associated with large natural variation in developmental condition. This may be due to evolved mechanisms allowing them to protect their cognitive abilities during development [2]. However, the nature of such potential mechanisms remains unclear. While future work should focus on untangling such potential mechanisms, this study shows that wild animals in their natural environment may be largely unaffected by naturally existing variation in developmental condition, which is in direct contrast to a large body of laboratory-based research. Our results suggest that individual cognitive variation in our population is probably not strongly influenced by differences in naturally existing

developmental conditions. This emphasizes the importance of investigating basic biological processes in wild animals in their natural environments, as previous results gathered in captive environments may not accurately reflect inherent abilities of these populations.

Ethics. All work was in accordance with the University of Nevada Reno Institutional Animal Care and Use Committee (Protocol 00818, 00046 and 00603), California Department of Fish, and Wildlife Permit D-0011776516-4.

Data accessibility. The data are provided in electronic supplementary material [62].

Authors' contributions. B.R.S.: conceptualization, data curation, formal analysis, funding acquisition, resources, writing—original draft, writing—review and editing; V.K.H.: data curation, investigation, writing—review and editing; A.M.P.: data curation, investigation, writing—review and editing; L.M.B.: data curation, investigation, writing—review and editing; C.L.B.: data curation, investigation, writing—review and editing; E.S.B.: funding acquisition, methodology, resources, writing—review and editing; J.Q.O.: conceptualization, methodology, resources, writing—review and editing; V.V.P.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, resources, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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