Title: Seeking smarts: Male chickadees with better spatial cognition sire more extra-pair young

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Abstract

Across the animal kingdom, females commonly mate with more than one male even when they are monogamous. Extra-pair males rarely contribute resources outside of sperm, therefore, many hypotheses surrounding the fitness benefits of extra-pair (EP) paternity involve genetic mechanisms. The 'good genes' hypothesis suggests that socially monogamous females mate outside their pair bond to increase the fitness of their offspring via indirect genetic benefits. We tested this hypothesis by quantifying extra-pair paternity in nonmigratory, food-caching mountain chickadees (*Poecile gambeli*). Chickadees rely on spatial cognition to recover scattered food caches and variation in spatial cognition is associated with increased survival, longer lifespan, and is heritable, however, less is known about the relationship between reproductive success and spatial cognition. In the current study, we had two main objectives; to assess the relationship between spatial cognition and reproductive output via extra-pair young and to compare the spatial cognition of EP males to the within pair males they cuckolded. We found that 1. males with better spatial cognitive abilities have more extra-pair young and produce heavier offspring in their own nests compared to their poorer performing counterparts, and 2. EP males have significantly better spatial cognition than the social males they cuckolded. These results show that males with better spatial cognitive abilities exhibit higher reproductive success and are consistent with the good genes hypothesis if females gain genetic benefits associated with better cognitive abilities via EP young.

Key words: extra-pair mating, spatial cognition, indirect fitness, good genes, reproduction

Introduction

Understanding the factors that influence mating decisions in animals and the consequences that follow from these decisions is a central focus of evolutionary biology (1-8). Socially monogamous species provide an interesting case as they form seasonal to long-term pair bonds but produce extra-pair young (EPY) outside the pair bond (9-11). While EPY are common and significantly contribute to lifetime reproductive success, rates of extra-pair paternity (EPP) vary widely within and between species (9, 12). Given that extra-pair males rarely contribute to parental care or provide access to resources outside of sperm (13-15), many hypotheses surrounding the fitness benefits of EPP involve genetic mechanisms, including 'good' or 'compatible' genes, genetic diversity, and insurance against male infertility (13, 15-22). Despite potential fitness benefits, the opportunity to pursue EP matings, particularly for females, may be constrained by mate guarding or breeding density (9,14, 21, 23) resulting in the highly variable EPP rates reported in the literature (9).

What constitutes 'good genes' in a particular system or population can often be esoteric, but we can generally assume that genes passed from one generation to the next that enhance fitness will be passed on via selection, regardless of the mechanism. For example, scatter food-caching species in temperate regions do not migrate seasonally, but instead store food in various locations throughout their home ranges when food is abundant, to use later when food is scare (24, 25). The spatial cognitive abilities of food-caching birds have been well studied, and research shows that these birds rely on spatial learning and memory to store and relocate their food items (25, 26). More recently, research in the wild using 'smart' feeders (Figure 1) showed that selection acts on the spatial cognitive abilities of food-caching mountain chickadees, such that individuals that perform better on a spatial learning and memory task in the wild are more

70 likely to survive winter and live longer lives compared to those that perform poorly (27, 28).
71 Furthermore, using genome-wide association and gene network approaches, research shows that
72 individual variation in spatial cognitive abilities is associated with genetic differences, including
73 differences in genes involved in the development and function of the hippocampus, a brain
74 region involved in spatial cognitive function (29, 30). Interestingly, these spatial cognitive
75 abilities remain stable across birds' natural lifespan (e.g., no detectable senescence (31) and
76 spatial cognitive abilities do not change with age (27, 28, 32).

77 While individual variation in spatial learning and memory abilities is associated with
78 genetic differences and better spatial abilities have been shown to increase overwinter survival
79 and life span, we know less about how they influence reproductive success. In several systems,
80 males with better cognition have been shown to produce more young (33-37), however, much of
81 this work focuses on problem-solving which may not be attributed to cognitive mechanisms
82 (e.g., 38), leaving scant evidence for a positive relationship between cognition abilities and
83 reproductive output (37). Previous work in our long-term mountain chickadee system has
84 provided some evidence for a relationship between the cognitive abilities of the social male and
85 reproductive success (39). However, like most Passerine birds, mountain chickadees are socially
86 monogamous; they raise their brood via biparental care (40), while engaging in extra-pair
87 matings outside the pair that commonly result in EPY (11). In the current study, we quantify and
88 compare rates of extra-pair paternity across 3 years of breeding and assess the relationship
89 between male spatial cognitive performance and individual rates of EPP. We predicted that males
90 with better spatial cognitive abilities, and associated 'good genes', would produce more EPY
91 than their poorer performing counterparts.

If males with better spatial abilities sire more EPY, several alternative mechanisms could explain this outcome. For instance, males with better cognitive abilities may be better at soliciting EPCs, they may be more active and move more widely increasing the likelihood of encountering females, or they may hold better quality territories frequented by multiple females (41-44). Alternatively, females may copulate with extra-pair males that have better cognition compared to that of their social mates, as would be predicted by the good genes hypothesis (1,8). While the good genes hypothesis has been commonly proposed to explain female EP mating behavior, there is rather limited support for this hypothesis (18, 21, 23).

Spatial cognition is a fitness-related trait in food-caching chickadees (25, 27), which provides the opportunity to test whether females produce EPY with males that exhibit better spatial cognition than the social males they cuckhold. Producing EPY with higher quality males is expected to benefit females indirectly because EPY should inherit the genes associated with better cognition. Indeed, females of several species show preferences for males with better cognition in lab-based, pairwise choice paradigms (45-49). And previous work from our field system showed that females can discriminate among males based on their cognitive abilities (whether directly or indirectly via secondary sexual traits is unknown) and adjust their reproductive investment (39). Considerable research in Passerine birds shows that females are the primary drivers of extra-pair matings (41, 50, 51), with females often foraying into neighboring male territories to solicit copulations (specifically in chickadees, tits, and titmice: 15, 52-56). Furthermore, forced copulations are uncommon in most Passerines, and when they do occur, may be less likely to result in fertilization (57-59). Specifically, extensive work on breeding behavior in chickadees and their relatives has never reported forced copulations (e.g., 42, 52, 53, 60-63).

We have shown that social pairs are not formed based on cognitive abilities (64), likely due to constraints on social pairing. Juvenile chickadees are recruited into flocks following the breeding season (65, 66), and male-female pairs from the previous breeding season typically stay together (67, 68), therefore, social mate choice for the newly recruited juveniles is constrained by the availability of unpaired individuals. Therefore, we predict that females may seek EPCs opportunistically with males that exhibit better spatial cognitive performance than their social male, thus increasing their indirect fitness via 'good genes' (1, 8, 14, 19). We could not directly assess female EPCs, but we used an indirect approach commonly used to address this question: comparing the phenotype of the extra-pair male to that of the social male (e.g., 14, 42, 52, 53, 69). The good genes hypothesis predicts that females should seek EPCs when their social mate is of lower quality and with a male that is of better quality than their social male (1, 8, 14, 19). We tested this hypothesis by comparing the spatial cognition of males siring EPY in a nest to the social male they cuckolded. If females obtain genetic benefits via EPY, we expect EP males to have significantly better spatial cognition compared to the within pair males they cuckold.

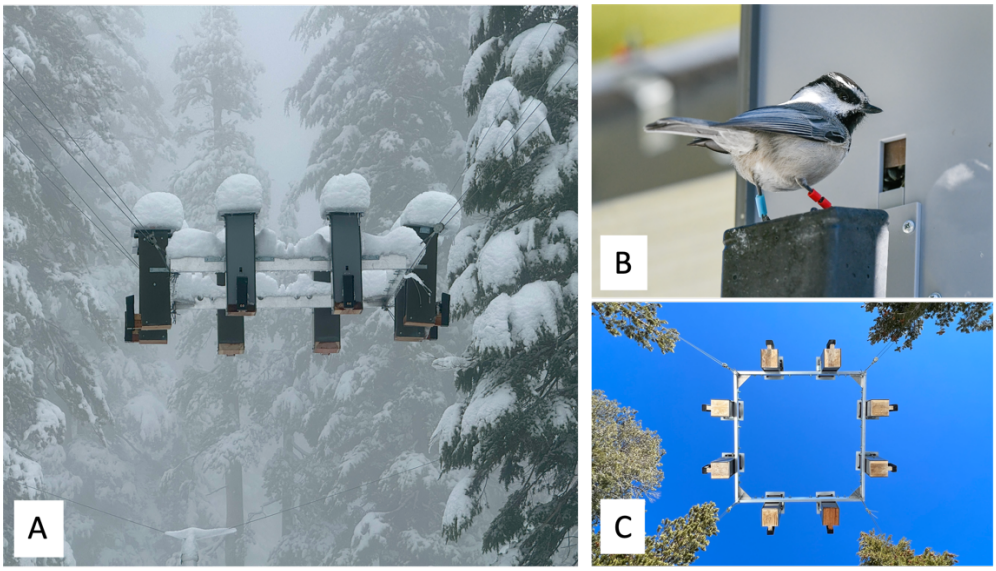


Figure 1. Photographs of spatial cognitive testing apparatus. A. Side-view of one array suspended in the air. B. A mountain chickadee tagged with a passive integrated transponder (PIT) tag visiting the 'smart' feeder array. Motorized door is open. The blue band on the left leg of the bird is the PIT tag. C. View of the testing apparatus from below, depicting equidistant placement of eight 'smart' feeders. Data presented come from four independent feeder arrays.

Methods

Experimental Design

We studied spatial learning and memory abilities and extra-pair paternity (EPP) rates in mountain chickadees (*Poecile gambeli*) at our long-term field site in the northern Sierra Nevada mountains of North America (Sagehen Experimental Forest in northern California, USA, Sagehen Creek Field Station, University of California Berkeley). Since 2015, we have monitored breeding phenology in uniquely color-banded individuals across two elevations (63, 70) and since 2016 we have measured the spatial cognitive abilities of hundreds of individuals (e.g., 27-32, 39, 64, 71-74). Data for the paternity analyses were available for the 2018, 2020, and 2021 breeding seasons, while analyses on overall patterns of reproductive output are from the entire database (2015 – 2023). Cognitive data from individuals spanning 2016 – 2023 was used in conjunction with the 3 breeding seasons used for paternity analyses. Birds participate in our cognitive tasks opportunistically, therefore, if a bird was not tested in one of the 3 years we had paternity data for, we were still able to include their cognitive data, as performance does not change over time (27, 28, 32).

The breeding season begins in April and continues through July, while the non-breeding season spans from August to March of the following year. Mountain chickadees are secondary

154 cavity nesting birds that readily use nest boxes at our field site. Every year in late April we begin
155 monitoring 350 nest boxes throughout our field site for evidence of nest building. Once nesting
156 material is detected we monitor all stages of breeding through fledging of each nest, recording
157 information about the date the first egg is laid, start of incubation, and hatching, and record the
158 clutch size (number of eggs), and the brood size (number of chicks at post-hatch day 16) of each
159 nest. We process all chicks in the nest box at post-hatch day 16, which includes banding them
160 with an aluminum United States Geological Survey (USGS) band, weighing them, and obtaining
161 a small blood sample for genetic and paternity analyses. We trap adult and first-year birds using
162 mist nets at established feeders during annual autumn trapping and by hand at nest boxes during
163 the breeding season. Upon capture, birds are fitted with color-bands and a unique Passive
164 Integrated Transponder (PIT) tag, wing length is measured, and age is estimated using multiple
165 plumage features (75). When nestlings banded with USGS bands are recruited into our
166 population from nest boxes, we band them with an additional color band and PIT tag for
167 identification.
168
169 **Testing spatial cognition in the wild**
170 Spatial learning and memory testing was conducted using two feeder arrays at each of our
171 elevation sites (High, elevation range: 2380 m – 2590 m; coordinates: 39.42402, -120.315015
172 and Low, elevation range: 1965 m – 2070 m; coordinates: 39.443500, -120.243248), following
173 (27, 31, 32, 71). Within an elevation, the feeder arrays were established ca. 1.5 km apart with
174 mostly non-overlapping birds visiting each array. Each array consisted of eight equidistant
175 RFID-based feeders on a square (122 x 122 cm) aluminum frame suspended ca. 4 m above the
176 ground. Each feeder is equipped with a small, motorized door (Figure 1). Prior to testing, we

kept the feeder doors of the arrays open for approximately one month. Next, the feeder doors were closed and programmed to open for any bird with a PIT tag, allowing birds to habituate to the motorized feeder doors for one week. Finally, we measured the spatial learning and memory abilities of mountain chickadees using a 4-day task. The spatial learning and memory task involved pseudo-randomly assigning each bird to a single feeder in the 8-feeder array that was not its most-visited feeder during the previous two habituation stages. During this task, each bird can only obtain a food reward (black oil sunflower seed) from its single assigned feeder, but all eight feeders recorded the date, time, and identity of every visit by all PIT tagged individuals. We measured cognitive performance by estimating the number of location errors (e.g., non-rewarding feeders visited prior to visiting the correct rewarding feeder, max 7) per trial, over multiple trials. A trial began when a bird visited any feeder in the array and ended with a visit to the rewarding feeder. If the bird landed on its rewarding feeder first, it was considered to have made zero location errors. Chickadees collect a single sunflower seed during each trial and fly away from the array to nearby trees to either eat or cache the seed before returning to the array and each trial takes just a few seconds (73).

We used the mean number of location errors per trial over the first 20 trials and the mean number of location errors per trial over the entire 4-day task as the two metrics of cognitive performance, following our previous work (27, 31, 32, 71). These measurements capture learning curves in a single metric (Figure S7); as birds learn the rewarding feeder location, they make fewer and fewer errors on each consecutive trial. Using the mean number of location errors over multiple trials captures this improvement – the mean number of location errors per trial over multiple trials is smaller for individuals that improved faster and larger for individuals that improved slower (27). Since birds completed different numbers of trials over the entire task, we

used the total number of trials as a covariate in models involving performance on the entire 4-day task (27, 31, 32, 71). We have previously documented that variation in both metrics is associated with significant differences in survival (27), longevity (28), in female reproductive decisions (39), in foraging decisions (73), and in cognitive flexibility (74). For analyses involving spatial cognitive abilities, we used cognitive performance measured in the first year each individual completed the task (between 2016 and 2023), as cognitive performance on the spatial learning and memory task does not change with age (27, 32). All birds in this study completed a minimum of 20 trials and showed evidence of learning by performing at better than chance (< 3 errors per trial, 27, 28). Males that bred in more than one year were included in the analyses (repeated measures, controlled for using male ID as a random effect); as such when reporting results, we report the sample size for unique nests and 'male-years'.

Assessing extra-pair paternity

DNA extraction and ddRAD sequencing

For this study, we aimed to sequence and genotype parents with cognition data and their nestlings over four consecutive years (2018-2021). Each year, we prioritized sequencing nests of males and potential EP sires that performed in our cognitive task. Samples from each year were sequenced independently, and unfortunately, genotypes from 2019 were of low quality and paternity assignments could not be completed with confidence, therefore we present data from 2018, 2020, and 2021.

Blood samples from adults and nestlings were stored at room temperature in Queens Lysis buffer until DNA was extracted using Qiagen DNeasy Blood & Tissue kits. The DNA concentration of each sample was quantified using Qubit Fluorometer 2.0 (Life Technologies)

223 prior to library preparation and sequencing. We used a double digest restriction-site associated
224 DNA (ddRAD) sequencing approach from (76) to obtain single nucleotide polymorphisms
225 (SNPs) for our paternity analyses. Sequencing was completed in batches following field
226 sampling of each year, therefore, individuals from each breeding year were run together, but
227 separately from the other years. For each individual, 100-500 ng of extracted DNA was digested
228 with restriction enzymes SbfI-HF (NEB) and MspI (NEB), and ligated with one of 20 unique P1
229 adapters and a P2 adapter (P2-MspI). Next, samples were pooled by groups of 20, maintaining
230 individual identity via unique P1 adapters. Samples were then purified using 1.5x volume of
231 homemade solid-phase reversible immobilization (SPRI) beads, made with Sera-Mag SpeedBead
232 Carboxylate-Modified Magnetic Particles (Cytiva) (77). These pooled samples (index groups)
233 were sent to Cornell University Biotechnology Resource Center (BRC) for size selection
234 between 450 – 600 bp using BluePippin (Sage Science). Following size selection, adapter ligated
235 DNA was enriched by 11 cycles of polymerase chain reaction (PCR) with a universal i5 primer
236 and a unique indexed i7 primer for each index group using Phusion DNA polymerase (NEB).
237 Reactions were again cleaned using 0.7x volume of homemade SPRI beads (as above) and the
238 index groups pooled in equimolar ratios to create a single sequencing library run on one lane of
239 Ilumnia NextSeq500 (150 bp single end, performed at BRC). Sequencing was performed with a
240 ~20% PhiX spike-in to introduce diversity into the library.
241
242 ***SNP Analysis and Paternity assignment***
243 **Quality filtering, demultiplexing, and genome alignment**
244 The following were run the same, but separately for each year of samples. First, the quality of all
245 reads were assessed using FASTQC version 0.11.9

246 (https://www.bioinformatics.babraham.ac.uk/projects/fastqc/). All sequences were trimmed using
247 *fastx_trimmer* (FASTX-Toolkit) to a length of 147 bp on the 3' end to exclude low-quality SNP
248 calls. Next, reads containing a single base with a Phred quality score less than 10 were removed
249 and any sequences that had more than 5% of the bases with a Phred quality score lower than 20
250 were also removed. We then used *process_radtags* from STACKS version 2.65 to demultiplex
251 the sequence reads and obtain files with specific sequences for each individual. Next, we aligned
252 sequences to the chromosome scale reference genome of mountain chickadees (29, 30) using
253 Bowtie2 version 2.5.1. The resulting .sam files were converted to .bam files and sorted using the
254 *view* and *sort* functions in Samtools version 1.18. These aligned reads were used as the input for
255 the *ref_map.pl* program in Stacks 2.65.
256

257 **SNP filtering and assigning paternity**

258 SNPs were exported using *populations* in Stacks 2 version 2.65, and each year's samples were
259 run separately to maximize the number of SNPs included for downstream paternity analyses
260 (since every individual does not have data at each SNP locus, using a smaller set of individuals-
261 i.e., individuals from each year- returns more loci for assigning paternity, as we require loci to be
262 present in most individuals; see below). All male individuals alive during the year of interest
263 were included as potential sires. Individuals with more than 50% missing SNP data were
264 removed from the dataset; only 5 individuals from the 2021 dataset did not meet this criterion.
265 Loci were exported if they were present in 85% of that year's sample population (*–r*). If a RAD
266 locus had more than one SNP, data were restricted to the first SNP *(–write_single_snp*) to
267 minimize those in high linkage disequilibrium. We required a minor allele frequency of 0.05 to
268 process a nucleotide *(–min_maf),* then filtered for loci in Hardy-Weinberg equilibrium ($p<0.05$)

269 using VCFtools (--*hwe* option) (78, 79). Variant call format (VCF) files were converted to
270 GENEPOP format using the 'radiator' package in R (80).
271 Before assigning paternity, we imported the yearly GENEPOP files into CERVUS (81),
272 then ran maternity tests separately for each elevation in each year to confirm mother-offspring
273 relationships identified during field observations. We assessed the quality of these assignments
274 by plotting the distributions of the first and second-ranked mother's scores for each offspring.
275 First and second-ranked mother pair log likelihood (LOD) scores formed bimodal distributions,
276 with nearly all first-ranked mother scores above zero and nearly all second-ranked mother scores
277 below zero. In rare cases when second-ranked mother scores were positive, these were almost
278 always known sisters or daughters of the mother identified during field observations. Therefore,
279 first-ranked mother-offspring pairs with positive LOD scores were considered correct
280 assignments, but pairs with negative assignments were not included in paternity analyses because
281 we were not confident in the mother assignment. Offspring resulting from a female laying an egg
282 in a nest that was not her own (i.e., egg dumps) were uncommon and not included in further
283 statistical analyses.
284 Paternity analyses were conducted in CERVUS separately for each elevation in each year
285 by calculating trio LOD scores for each potential father-offspring pair. Trio LOD scores account
286 for known maternal genotypes when identifying potential fathers. As we did for mother-offspring
287 pairs, we plotted the distribution of the first and second-ranked male scores and again found a
288 bimodal distribution centered around zero (Figure S8). Based on these plots, we set cut-off
289 scores to assign paternity by: all first-ranked male scores at an elevation in a year that were
290 positive and greater than the top second-ranked male score at that elevation in that year were
291 assigned as fathers. Offspring sired by the social male at the nest were considered within-pair,

whereas offspring sired by other males were considered extra-pair. Offspring whose social father was genotyped, but we could not assign a father to, were also considered extra-pair.

Statistical analysis

We tested whether EPP rates differed between the high and low elevations using generalized mixed effects models with binomial error distributions and 'logit' links, using the R package 'glmmTMB' (82). Our response variable was whether each offspring was sired by an EP father or not and we only included nests in which more than 50% of the offspring were genotyped and run through the paternity analysis. Elevation was included as a fixed effect and mother identity was included as a random effect in each model. A likelihood ratio test showed statistical support for an interaction between elevation and year ($p<0.05$), so we tested the effect of elevation on EPP rates separately for each year.

We employed two methods to test whether spatial cognitive ability was associated with the number of EPY a male sired in a year. Both models included the number of EPY sired as the response variable, with spatial cognitive performance (refers to separate models run for (1) the mean number of location errors per trial over the first 20 trials and (2) the mean number of location errors per trial over the 4-day task), elevation, and year as fixed effects, and male identity as a random effect to control for repeated measures of males across years. Both models used the Poisson error distribution and a 'log' link, but each model accounted for zeros in the dataset differently. The first method included a zero-inflation parameter (ziformula~1) in 'glmmTMB' to account for observations of males with zero EPY, whereas the second method restricted the dataset to males that sired at least one extra-pair offspring.

It is possible that a relationship between EPP and spatial cognitive ability is driven by age, as older males often sire more extra-pair offspring than younger males in many systems (e.g., 69). While chickadees with better spatial cognition in our study system tend to live longer, cognitive performance does not change with age in the same individuals (27). However, we tested whether including male age as a fixed effect improved each model using likelihood ratio tests that compared models with and without male age.

In addition, cognitive ability could come at a cost to breeding performance, so we tested whether spatial cognitive ability was associated with breeding performance using a generalized linear mixed model with the generalized Poisson distribution (83). Brood size was included as the response variable and male and female spatial performance on the first 20 trials, elevation, and clutch size were included as fixed effects. For these analyses, we used all breeding data available, therefore, year was included as a random effect in this analysis because it had a sufficient number of levels (2015 – 2023). Male and female identity were also included as random effects to control for yearly variation and repeated measures of individual males and females. In a second analysis, we used a linear model that included mean nestling mass at day 16 as the response variable (in our system, mass of nestlings on day 16 is a significant predictor of survival and recruitment (84)), and included male and female performance on the first 20 trials of the spatial cognitive task and elevation as fixed effects, and year (2015 – 2023) and male and female identity as random effects. Again, year (2015-2023) and male and female identity were included as random effects to control for yearly variation and repeated measures of individual males and females.

Siring extra-pair offspring may reduce a male's investment in his own nest, so we tested whether siring EPY was associated with breeding performance. We used a generalized linear

mixed model with the generalized Poisson distribution to test whether brood size in a male's nest was affected by the male siring extra-pair offspring (yes or no), and we used a linear mixed model to test whether the mean mass of the nestlings at day 16 in a male's nest was affected by whether the male sired any extra-pair offspring (using three years of data on EPPs). Elevation, clutch size, and year (three years of EPP data) were included as fixed effects and male and female identity were included as random effects in both models to control for repeated measures of individual males and females. We tested whether the mass of young sired by extra-pair males differed from the mass of young sired by social males using a linear mixed model with nestling mass at day 16 as the response variable and extra-pair status, elevation, and year as fixed effects. Nest identity was included as a random effect to control for nestlings that came from the same nests.

If males initiate EPCs, we expect them to be randomly distributed across different nests, since the fitness benefit of EPY is increased for the male regardless of the females' social mates' cognitive abilities. On the other hand, if females initiate EPCs, we expect them to select males of better quality than their social mate – in our case, males with better spatial cognition – as this could result in indirect benefits to the female via offspring with better cognition and higher likelihood of survival (27, 28). Therefore, we tested whether the spatial cognitive abilities of extra-pair males differed from those of the males they cuckolded by comparing spatial cognition between father types (EP male vs social male within the same nest) using linear mixed models. Spatial cognitive performance was used as the response variable, then father type (extra-pair mate versus social mate) and elevation were included as fixed effects. Offspring identity was included as a random effect to restrict comparisons to within offspring and mother identity was included as a random effect to control for repeated measures of females. When fitting models to

360 the total location errors, we log-transformed the response variable to improve residual fit and
361 included a quadratic term of total trials completed during the 4-day cognitive testing period,
362 since the number of trials completed influences performance (27, 31, 32, 71). We tested whether
363 extra-pair males were significantly older than the social males they cuckolded using a chi-square
364 test.

365 Both male and female cognitive abilities could affect the likelihood of a nest containing
366 extra-pair young, so we tested whether cuckoldry was associated with the spatial cognitive
367 abilities of both parents at a nest using multiple methods. First, we modeled the relationship
368 between male and female spatial cognitive ability and cuckoldry at the nest and offspring level.
369 At the nest level, we tested whether male or female spatial cognitive ability predicted whether
370 any offspring in a nest were sired by extra-pair males. At the offspring level, we tested whether
371 male or female spatial cognitive ability predicted whether each offspring was sired by an extra-
372 pair male or not. For both tests, we used generalized linear mixed models with binomial
373 distributions that included male and female spatial cognitive performance, elevation, and year as
374 fixed effects. Male and female identity were included as random effects to control for repeated
375 measures of individual males and females. Second, for nests that had at least one extra-pair
376 young, we tested if the number of extra-pair young in a nest was associated with male or female
377 spatial cognitive ability using a generalized linear mixed model with a truncated Poisson
378 distribution. The number of extra-pair young in the nest was included as the response variable,
379 while male and female performance on the first 20 trials, year, and elevation were included as
380 fixed effects. Male and female identity were included as random effects to control for repeated
381 measures of individual males and females. The effect of male age on cuckoldry rates was tested

382 by adding male age as a fixed effect to each model and comparing models with and without male
383 age using likelihood ratio tests.
384 We also tested whether male spatial cognitive ability differed between nests that had EPY
385 compared to those that did not. Male spatial cognition was included as the response variable and
386 elevation and whether the nest had any EPY were included as fixed effects. When modeling the
387 mean number of location errors per trial on the entire task we used the Gamma distribution and
388 included a quadratic term for the total number of trials completed as a fixed effect. Including
389 male identity as a random effect in both models led to convergence errors, so male identity was
390 not included in the models.
391 We tested whether the mean number of location errors per trial across the first 20 trials
392 correlated with the mean number of location errors per trial over the entire 4-day task for males
393 using a linear model. Mean location errors per trial over the entire task was used as the response
394 variable while mean location errors over the first 20 trials and a quadratic term of the total
395 number of trials completed were included as fixed effects. All statistical analyses were performed
396 in R version 4.1.1 (85) and the residual fit of all models was checked using DHARMa (86).
397 Statistical significance was calculated using Wald Chi-square tests.
398

399 **Results**

400 **Extra-pair paternity and spatial cognition**

401 Across three years of data collection on EPP (2018, 2020, and 2021), we found that 30.3% of the
402 total offspring sampled (222 of 732) were sired by extra-pair males and that 70.1% of nests (89
403 of 127) had at least one EPY. We found no significant differences in the number of EPY sired at
404 high versus low elevation populations regardless of year sampled (Supplemental Results, Figure

S1, Table S1), therefore, we combined high and low elevations for all later analyses. Data from breeding birds in this study confirms previous research showing that female chickadees obtain extra-pair copulations with neighboring males (on average ~100 m from their own nests; Figures S2 and S3), which are likely familiar males from their nonbreeding flock (52, 65, 66). In addition, breeding male territories do not appear to cluster based on males' cognitive performance (Figure S4).

Performance on the spatial learning and memory task predicted the number of EPY a male sired each year (Figure 2). Males with better spatial learning and memory abilities (e.g., fewer mean location errors per trial) sired more EPY, both according to a zero-inflated model including males that sired no extra-pair young (Mean location errors per trial over first 20 trials: slope = -0.92, χ^2_1=6.28, P=0.012 (Figure 2, dashed line); Mean location errors per trial over the entire task: slope = -1.86, χ^2_1=8.12, P=0.004, N=280 (137 individual males; Figure S5)), and to a model only including males that sired at least one EPY (Mean location errors per trial over first 20 trials: slope = -1.16, χ^2_1=5.96, P=0.015 (Figure 2, solid line); Mean location errors per trial over the entire task: slope = -2.55, χ^2_1=7.68, P=0.006, N=41 (34 individual males; Figure S5)). Our model suggests that of the males that sired at least one EPY, the males with the best cognitive performance may sire between 6 and 7 EPY each year, whereas the males with the worst cognitive performance will sire only 1 to 2 EPY each year. We have shown that birds with better spatial cognitive abilities live longer (27) and lack reproductive senescence within their natural life span (87), therefore, males with better cognition are expected to produce significantly more offspring over their lifetime. Male age was not associated with the number of EPY sired (see Supplemental Results).

In addition to testing how cognitive abilities were related to number of EPY, we also tested whether variation in cognitive abilities was associated with breeding performance. Using 9 years of breeding data (2015-2023), we detected no relationship between the social males' spatial cognitive abilities and brood size (χ^2_1=2.32, P=0.127, N=205 nests), or the females' spatial cognitive abilities and brood size (χ^2_1=1.75, P=0.186, N=205 nests). Controlling for the effect of clutch size on brood size produced similar results (Table S4). However, males with better spatial cognition raised heavier young (mass at day 16, χ^2_1=4.86, P=0.028, N=202 nests), while female spatial cognition showed no significant relationship with offspring mass at day 16 (χ^2_1=0.93, P=0.335, N=202 nests). Based on these findings, we used the 3 years of EPP data to indirectly assess differences in parental care and overall male condition by comparing the brood size and mean fledgling mass of young from nests of males that sired EPY versus those that did not sire EPY. Neither brood size (brood size: χ^2_1=0.30, P=0.584, N=144 nests) nor mean nestling mass (mean mass: χ^2_1=2.10, P=0.147, N=140 nests) differed significantly among males with and without EPY. Furthermore, we compared the mass of young sired by extra-pair males to those sired by the social males raised in the same nests and found no significant difference (χ^2_1=2.83, P=0.093, N=719 offspring).

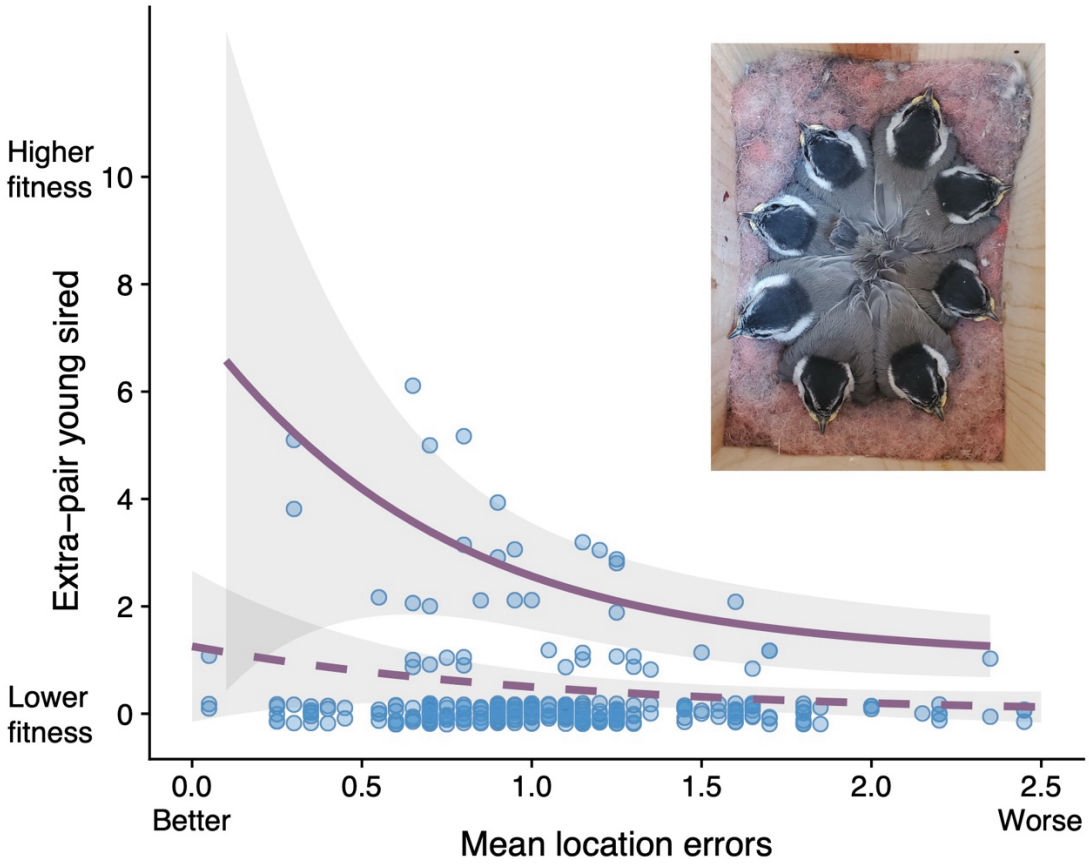
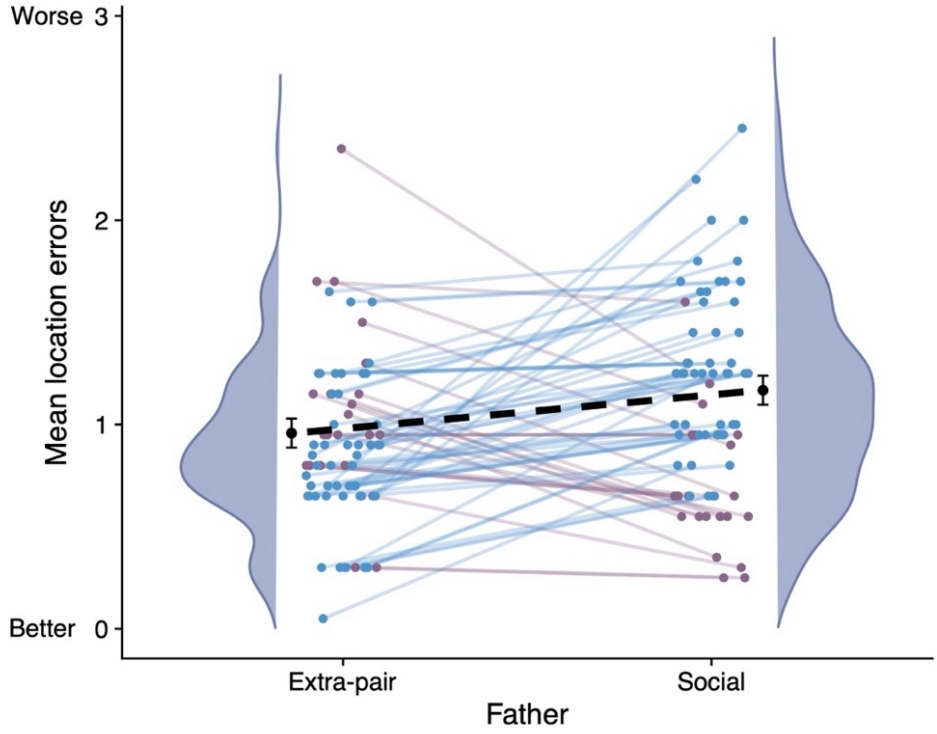


Figure 2. Model predictions of the number of extra-pair young a male sired in a year by the mean number of location errors per trial over the first 20 trials. The dashed line represents a zero-inflated model for all males, including those with no extra-pair young (N=280; 137 individual males), and the solid line represents the model prediction for males that sired at least one extra-pair young (N=41; 34 individual males). Points are slightly *jittered* on the y-axis to improve readability. Shading represents bootstrapped 95% confidence intervals. Inset depicts 8 nestlings at 16 days post-hatching. See model predictions for the number of extra-pair young a male sired in a year by total 4-day testing performance in Figure S5.

Extra-pair males have better spatial cognitive abilities than the social males they cuckold

When there were EPY in a nest, they were sired by males with better spatial learning and memory abilities (on average) compared to the social male of the female (Mean location errors per trial over first 20 trials: χ^2_1=14.81, P<0.001, N=71 comparisons of a social male and the extra-pair male sire (Figure 3); Mean location errors per trial over the total task: χ^2_1=6.08, P=0.014, N=71 comparisons (Figure S6)). Extra-pair males did not differ significantly in age from the males they cuckolded (28 offspring were sired by an extra-pair male that was older than the social male, 19 offspring were sired by an extra-pair male that was the same age as the social male, and 24 offspring were sired by an extra-pair male that was younger than the social male; Chi-square test: χ^2_2= 1.72, P=0.424).



467 Figure 3. Comparing spatial cognitive performance (mean number of location errors per trial
468 over the first 20 trials) of extra-pair (mean ± SE = 0.96 ± 0.07) and social fathers (mean ± SE =
469 1.17 ± 0.07, 71 comparisons). Lines connect males by offspring: blue lines show comparisons
470 where the extra-pair father performed better than the social father (49 of 71 cases or 69%), and
471 purple lines show comparisons where the social father performed better than the extra-pair father
472 (19 of 71 cases, or 26.7%; in 3 cases the extra-pair and social father had the same cognition
473 score). Shaded distributions represent smoothed histograms of cognitive performance for each
474 father type. The same analysis is presented for performance over the 4-day testing period in
475 Figure S6.
476
477 The finding that extra-pair males have better spatial cognition than the social male of the
478 nest (on average) could be explained by the cognitive abilities of the social male or female, as
479 either sex may have cognitive deficiencies (i.e., females seek EPC to compensate for her or her
480 social male's poor cognition) or be better at obtaining EPC. Therefore, we assessed whether the
481 likelihood of EPY in the nest was related to the spatial cognitive abilities of the social male or
482 the female. The likelihood of being cuckolded was not significantly related to the cognitive
483 abilities of the social males (Offspring level: Mean location errors per trial over first 20:
484 χ^2_1=0.25, P=0.620, Mean location errors per trial over the entire task: χ^2_1=0.43, P=0.513, N=348
485 offspring for 42 males; Nest level: Mean location errors per trial over first 20: χ^2_1=0.05, P=0.808;
486 Mean location errors per trial over the entire task: χ^2_1=0.22, P=0.642, N=59 nests for 42 males).
487 In addition, male age did not significantly affect the likelihood of a male being cuckolded (see
488 Supplemental Results). However, females who performed worse on the first 20 trials of the
489 spatial cognitive task were more likely to have EPY in their nests (Offspring level: Mean

location errors per trial over first 20: χ^2_1=6.21, P=0.013, N=348 offspring for 42 females); though this relationship was not significant when we analyzed cognitive performance across the entire 4-day task (χ^2_1=0.18, P=0.673, N=348 offspring for 42 females), or at the nest level of analysis (Mean location errors per trial over first 20: χ^2_1=0.21, P=0.645, Mean location errors per trial over the entire task: χ^2_1=0.13, P=0.723, N=59 nests for 42 females).

Similarly, for nests that had at least one EPY, the cognitive abilities of the social male did not predict the number of EPY in their nests (χ^2_1=1.03, P=0.311, N=41 nests for 35 males), however, females that performed worse on the task had significantly more EPY in their nests (χ^2_1=6.79, P=0.009, N=41 nests for 32 females). In other words, females would not have sought EPCs solely in response to their social mate's poor cognition. Instead, the data suggest that females may engage in EPCs based on their own cognitive deficiencies, and when doing so, may seek males with better spatial cognitive abilities than their social mate. As a result, males with better spatial cognitive abilities exhibit higher fitness; they did not lose paternity in their own nests (i.e., male spatial cognition does not predict if a male will be cuckolded or how many EPY are in the nest), they produced similar quality of offspring compared to males with worse cognitive abilities (e.g., similar brood size and fledgling mass), and gained more EPY overall.

Discussion

Our findings show that spatial cognitive abilities influence extra-pair paternity in free-living, food-caching mountain chickadees. Males with better spatial learning and memory abilities sire more EPY than their poorer performing counterparts and, more importantly, EP males have better spatial cognitive abilities than the social males they cuckold, regardless of age. While we are unable to rule out effects of sperm competition, the direction of our findings suggest EPP may be

driven by females foraying into male territories, as opposed to male intruders, for several reasons; 1. Female chickadees (and Passerines more broadly) are known to pursue EPCs with neighboring males (41, 50, 51, 52, 53, 88, 89), 2. Chickadees have never been reported or observed engaging in forced copulation (42, 52, 53), and 3. Resident males are highly territorial and do not tolerate male conspecifics in their territories. In addition, the directional relationship between the cognitive phenotype of the social and extra-pair male would not be predicted by male choice but is consistent with good genes hypotheses (1, 8, 14).

If EPCs were driven by male forays, we would expect EPY to be present in nests regardless of the cognitive abilities of the social male, as there is no clear biological reason for a male seeking EPCs to selectively target females mated to males with worse cognitive abilities. That said, it is possible that males with poor spatial cognitive abilities are worse at defending their territories from other males, which may allow those males with better cognitive abilities to intrude and copulate with the resident female. We think this explanation is unlikely as males with worse cognitive abilities tend to be more proactively aggressive (90) and cognitive performance is not associated with social dominance (91). However, females, would benefit from obtaining EPCs with males that have better spatial cognition than their social male, as this trait is heritable (29, 30) and would increase the likelihood of producing offspring with better spatial cognition, leading to higher overwinter survival (27) and longer lifespan (28). Finally, our finding that the EP males have better spatial cognitive abilities compared to the social males they cuckhold is consistent with the good genes hypothesis, that females engage in EPCs with higher quality males to obtain indirect benefits for their offspring (1, 8, 14). Comparing phenotypic quality of the EP male to that of the social male they cuckhold has been one of the main methods to test for the good gene hypothesis. Considering that alleles associated with better spatial cognitive

536 abilities are not associated with sex (30), producing EPY with better quality males increases
537 selection pressure on spatial cognitive abilities in both males and females, as both sexes rely on
538 spatial cognition for survival (92).

539 Although it remains unknown whether chickadees can evaluate cognitive abilities directly
540 or indirectly via some correlated trait(s), the life history and breeding ecology of mountain
541 chickadees provide several possibilities. For example, female chickadees may use secondary
542 sexual signals, such as song and plumage variation associated with spatial cognitive abilities, to
543 identify high-performing males (1, 48, 93). Recent work in closely related black-capped
544 chickadees shows that male cognitive performance is associated with variation in plumage patch
545 brightness and contrast (93). Alternatively, it is possible that females can directly assess a male's
546 ability to successfully recover food stores over winter and base mating decisions on this
547 information in the spring (49, 94). Chickadees are nonmigratory, sedentary birds that aggregate
548 in flocks of unrelated male-female pairs throughout the nonbreeding season and break apart once
549 breeding commences (65, 94). Data from this study confirm previous research showing that
550 female chickadees seek EPCs with neighboring males (15, 52, 53), which would be familiar
551 males from their winter flock (65, 94). Regardless of how females evaluate male cognition,
552 mating with males with better cognitive performance should increase female fitness by
553 increasing the likelihood of offspring inheriting the specific alleles associated with better
554 cognition, which would be expected to lead to higher offspring survival and longer lifespan (27,
555 28).

556 An alternative hypothesis for our findings is that females seek EPCs with other males as
557 insurance against the social male's infertility (15, 22), again gaining genetic benefits. However,
558 this hypothesis does not explain the direction of our findings, because male cognitive ability did

559 not predict the number of offspring a male produced in his own nest (i.e., most cuckolded social
560 males still fathered chicks in their own nests), suggesting that males with poorer cognition do not
561 suffer from infertility. That said, we do not have data on the sperm quality of these birds and
562 therefore cannot directly exclude differences in fertility or sperm competition between males
563 with better and worse spatial cognition. Related, we have not detected fitness trade-offs or
564 negative effects associated with better cognitive abilities in our system. We do not see cognitive
565 or reproductive senescence within birds' naturally occurring life span (31, 87). In fact,
566 chickadees with better spatial cognition live longer allowing them to produce more offspring
567 over their lifetime compared to chickadees with worse cognition (28).

568 Based on our research to date, male chickadees with better spatial cognitive abilities have
569 higher reproductive success than their poorer performing counterparts: these males produce more
570 EPY (without losing paternity in their own nests) and raise heavier young, which are more likely
571 to survive and be recruited into the population (84). Females can potentially gain indirect and
572 direct benefits from reproducing with males exhibiting better spatial cognition. Producing EPY
573 with males that have better cognition increases the likelihood that their young inherit good genes
574 and if their social male has better cognition, they benefit directly by raising heavier chicks. These
575 fitness benefits would be expected to increase selection on any mechanism allowing
576 discrimination based on cognition.

577 Interestingly, a previous study in our system showed that females mated to social males
578 with better spatial abilities lay larger clutches and fledge larger broods in years of high resource
579 abundance (39). Together with the present findings, we suggest that female mating decisions,
580 including EPCs, and reproductive investment may vary opportunistically. When resources are
581 abundant, females lay larger clutches if their social male has better cognitive abilities (39), and

582 when males with better spatial cognition than her social mate are available for EPCs, they pursue
583 those opportunities. Furthermore, we found that females with poorer spatial cognition had more
584 EPY in their nests, suggesting females' mating decisions could be based on some physiological
585 signal associated with poorer cognition. At the ultimate level, females with poorer cognition
586 likely benefit disproportionately by mating with the highest quality male they can find, which in
587 the case of food-caching birds, means those with better spatial cognitive abilities (27, 28).

588 An additional alternative explanation for our findings is that birds with better spatial
589 cognitive abilities have access to better territories and therefore are clustered based on cognitive
590 abilities. Then, because females have extra-pair copulations with neighboring males (15, 52, 53),
591 those neighbors would happen to be males with better spatial cognition. However, in our study
592 system, males do not appear to cluster based on cognitive performance (Figure S4), suggesting
593 that females are not finding males with better cognitive abilities than their social males by
594 chance. Furthermore, higher social dominance status is associated with access to better territories
595 in chickadees (95), but we see no association with dominance status and spatial cognitive
596 abilities in our system (91) or closely related black-capped chickadees (93). While it is possible
597 that our results reflect some unmeasured trait(s) linked to spatial cognitive ability, such as
598 boldness, aggression, or increased exploratory behavior (e.g., 46), previous data from our system
599 do not support these additional alternative hypotheses. Chickadees with enhanced spatial
600 cognitive abilities are not more proactively aggressive (90) nor do they show higher rates of
601 exploratory behavior (e.g., higher space use) (96).

602 Given the fitness advantages of superior spatial cognitive abilities for food-caching
603 chickadees, how variation is maintained and why enhanced spatial cognitive abilities have not
604 evolved to fixation may seem puzzling. While food-caching birds exhibit superior spatial

605 cognitive abilities compared to their non-caching counterparts (87), considerable variation
606 persists within species (71). Research from our system demonstrates the highly polygenic nature
607 of the spatial cognitive phenotype, meaning there are multiple genetic pathways that may
608 produce the same cognitive phenotype (29, 30, 98). In addition, selection strength varies with
609 annual variation in winter climate, which in milder years, may allow individuals to survive and
610 reproduce despite comparatively poor spatial cognitive abilities (27, 63, 70, 71). Finally, we have
611 documented elevation-related differences in spatial cognition and the hippocampus of mountain
612 chickadees (71, 72), but there is gene flow among elevations (99) which moves allelic variation
613 associated with poorer cognition within the population.

614 The results presented here are an exciting contribution to the field because: 1. We show
615 that males with better spatial cognition exhibit higher reproductive output, via siring more EPY
616 and fledging heavier chicks which are more likely to survive and be recruited into the breeding
617 population, and 2. We show that when there are EPY in the nest, they are sired by males with
618 better spatial cognition than the social male (on average), suggesting these mating decisions may
619 be driven by females. However, we cannot completely rule out alternative explanations related to
620 sperm competition. Regardless of whether these patterns are driven by females or males, males
621 with better spatial cognitive abilities exhibit higher fitness by producing more offspring, adding
622 to the evidence for selection on spatial cognitive abilities, including differential survival and
623 longevity in food-caching birds (27, 28).

624

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