RESEARCH ARTICLE

Male chickadees with better spatial cognition sire more extra-pair young

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This **fundamental** study examines the benefits of spatial cognition in a wild population of mountain chickadees. Using robust genetic analyses and experimental design, the authors show with **compelling** evidence that females seeking out extra-pair copulations prefer males with strong spatial cognition, and that these males have a reproductive advantage over other males. This work will be of broad interest to evolutionary and behavioural biologists.

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Abstract Across animal taxa, females commonly mate with more than one male, even in monogamous mating systems. These extra-pair copulations and resulting young may increase the fitness of the female via a variety of 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, because extra-pair males do not provide parental care. 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 role of sexual selection on spatial cognitive abilities. In the current study, we found that (1) males with better spatial cognitive abilities sired more extra-pair young and produced heavier offspring in their own nests compared to their poorer-performing counterparts, and (2) extra-pair males had significantly better spatial cognition than the social males they cuckolded. These results suggest that sexual selection shapes the evolution of spatial cognition in food-caching chickadees and are consistent with the good genes hypothesis, which posits that females gain indirect genetic benefits via extra-pair young.

Introduction

The role of sexual selection and the consequences that follow from mating decisions are central focuses of evolutionary biology (***Andersson and Simmons, 2006***; ***Rosenthal, 2017***; ***Davies et al., 2020***; ***Henshaw et al., 2022***; ***DuVal et al., 2023***). Numerous hypotheses have been generated to explain patterns of mate choice, including those associated with the evolution of seemingly arbitrary attractiveness (e.g. runaway selection; ***Fisher, 1930***; ***Prokop et al., 2012***) or sensory exploitation (e.g. sensory drive; ***Endler, 1992***), and those at the intersection of sexual and natural selection, when sexually selected traits have direct fitness consequences (e.g. good genes; ***Andersson, 1994***). Although

it has been recognized for some time that males can be actively involved in mate choice (***Bonduriansky, 2001***; ***Gowaty et al., 2003***), considerable work shows that females tend to be the choosier sex, as females often invest more in gamete production and parental care (***Verner and Willson, 1969***; ***Schärer et al., 2012***; ***Rubenstein, 2023***; ***Gowaty, 1996***). Multiple enduring hypotheses argue that females should prefer males of 'high quality', frequently indicated by secondary sexual signals, including ornaments and courtship displays (***Andersson, 1994***; ***Rubenstein, 2023***; ***Zahavi, 1975***).

Throughout the literature, male quality refers to everything from sperm quality (***Birkhead and Møller, 1992***) and parasite load (***Hamilton and Zuk, 1982***), to quality of parental care, nuptial gifts, and territories (e.g. direct benefits; ***Östlund and Ahnesjö, 1998***; ***Hill, 1991***; ***Lewis and Cratsley, 2008***), to 'good genes' that offspring are likely to inherit (e.g. indirect benefits; ***Andersson, 1994***; ***Zahavi, 1975***; ***Patricelli et al., 2003***; ***Kodric-Brown and Brown, 1984***). Untangling these potential targets of sexual selection requires an understanding of the fitness-related traits of interest, including the direction and type of fitness consequences (e.g. survival or reproduction), as well as whether variation in the trait is genetically heritable, so that the 'high quality' of a parent can be inherited by the offspring (***Endler, 1986***). Identifying and quantifying fitness-related traits in the wild that are associated with sexual selection and mate choice is challenging especially for complex behaviors, like cognition (***Morand-Ferron et al., 2016***).

Cognitive abilities, including associative learning and memory, allow animals to succeed across variable environments, providing a buffer against unpredictable availability of resources (***Shettleworth, 2010***; ***Johnston, 1982***). If variation in cognitive abilities is associated with differential fitness outcomes (survival, reproduction, or both), and this variation is heritable, natural selection can shape cognitive variation (***Endler, 1986***). Furthermore, when heritable cognitive variation directly confers a fitness advantage, it may be associated with mate preference via secondary sexual signals or by direct

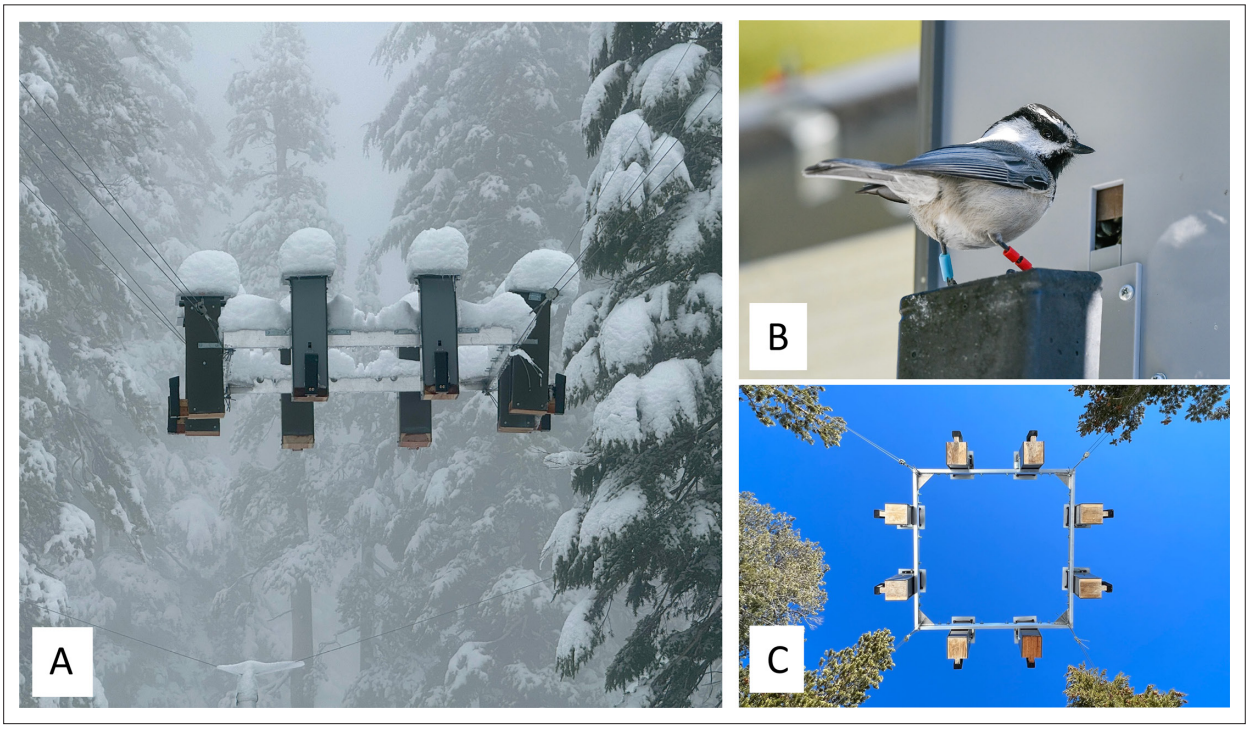

Figure 1. Photographs of spatial cognitive testing apparatus. (**A**) Side view of one array suspended in the air. (**B**) A mountain chickadee tagged with a passive integrated transponder (PIT) tag visiting the 'smart' feeder array. Motorized door is open. The blue band on the left leg of the bird is 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.

The online version of this article includes the following figure supplement(s) for figure 1:

Figure supplement 1. Realtionship between cognitive performance measures and learning curve.

Figure supplement 2. Comparisons of trio LOD scores for first- and second-ranked potential fathers for each offspring by elevation and year (**A**, 2018; **B**, 2020; **C**, 2021).

observation of mate behavior (**Boogert et al., 2011**; **Snowberg and Benkman, 2009**; **Chen et al., 2019**; **Shohet and Watt, 2009**; **Spritzer et al., 2005**). For example, females of several species show preferences for males with better cognition in lab-based, pairwise choice paradigms (**Chen et al., 2019**; **Shohet and Watt, 2009**; **Spritzer et al., 2005**), while in the wild, males with better cognition have been shown to produce more young (**Shaw et al., 2019**; **Keagy et al., 2009**). However, there is scant evidence from the wild that females prefer males with better cognition (**Boogert et al., 2011**), and little evidence outside of model organisms that shows heritability of cognitive abilities (**Croston et al., 2015**).

In the current study, we investigated the potential role of sexual selection on the evolution of spatial cognitive abilities by examining extra-pair paternity in a wild population of socially monogamous mountain chickadees (*Poecile gambeli*). Mountain chickadees are nonmigratory, food caching birds that rely on specialized spatial cognition to recover thousands of scattered food stores throughout their territories, enabling them to survive harsh montane winters (**McCallum et al., 2020**; **Pravosudov and Roth II, 2013**). Following the breeding season, in the temperate autumn, juvenile chickadees are recruited into flocks of unrelated male-female pairs (**McCallum et al., 2020**). Breeding pairs from the recent breeding season typically stay together, providing little opportunity for social mate choice at this time; however, being paired within the flock is critical because it increases overwinter survival, particularly for females (**Lemmon et al., 1997**; **Ekman, 1989**).

Work in our long-term study system using 'smart' feeder arrays (**Figure 1**) shows that individual variation in spatial learning and memory abilities confers a fitness advantage in wild chickadees: individuals with better spatial cognitive abilities are more likely to survive the winter and live longer compared to those with worse abilities (**Sonnenberg et al., 2019**; **Welklin et al., 2024**), and in resource abundant years, females lay larger clutches and fledge larger broods when their social male exhibits better spatial learning and memory abilities (**Branch et al., 2019**). That said, social pairs are not formed assortatively based on cognitive abilities (**Branch et al., 2023**), potentially due to the constraints on social mate choice mentioned above. Previous research in chickadees shows that females often produce extra-pair young with socially dominant males (e.g. **Otter et al., 1994**; **Mennill et al., 2004**); however, in our study system, we have not observed a relationship between social dominance and spatial cognitive abilities (**Heinen et al., 2021a**). One potential explanation for this is that social dominance changes over an individual's lifetime and with age, while spatial cognition is repeatable and consistent over time (**Morand-Ferron et al., 2016**; **Johnston, 1982**; **Boogert et al., 2011**; **Snowberg and Benkman, 2009**; **Chen et al., 2019**; **Shohet and Watt, 2009**; **Spritzer et al., 2005**).

Using genome-wide association and gene network approaches, we have shown that individual variation in spatial cognitive abilities is associated with genetic differences, including genes involved in the development and function of the hippocampus, a brain region involved in spatial cognitive function (**Branch et al., 2022**; **Semenov et al., 2024**). Finally, we have shown that spatial cognitive abilities remain stable across birds' natural lifespan (e.g. no detectable senescence [**Heinen et al., 2021b**] and does not change with age [**Sonnenberg et al., 2019**; **Welklin et al., 2024**]). Due to their life history and reliance on specialized spatial cognition, chickadees provide a great system for studying the role of sexual selection on a cognitive trait in the wild.

Given that individual variation in spatial cognitive abilities in chickadees is genetically heritable and better cognitive abilities lead to increased overwinter survival and longevity, we predicted that spatial cognition should be an important target of sexual selection via extra-pair mating. The good genes hypothesis predicts that females should seek extra-pair copulations when their social mate is of lower quality and with a male that is of better quality than their social male (**Andersson and Simmons, 2006**; **Andersson, 1994**; **Herdtle et al., 2025**; **Neff and Pitcher, 2005**). We tested this hypothesis using three primary approaches: (1) assessing the relationship between male spatial cognition and the number of extra-pair young sired, (2) assessing whether extra-pair young occurred more often in nests of males with poor spatial cognition, and (3) comparing the spatial cognition of males siring extra-pair young in a nest to the social male they cuckolded (e.g. **Otter et al., 1994**; **Mennill et al., 2004**; **Herdtle et al., 2025**; **Bonderud et al., 2018**; **Hsu et al., 2015**). If females obtain genetic benefits via extra-pair young, we expect extra-pair males to have significantly better spatial cognition compared to the within-pair males they cuckold. In addition to testing these primary predictions, we were able to assess potential alternative factors that might explain differences in rates and directional patterns of extra-pair paternity, including effects of (a) elevation, (b) age, (c) reproductive output, (d)

male parental investment, and (e) female's cognitive abilities. Finally, we mapped the location of nests based on paternity status (extra-pair vs. social) and spatial cognition to account for potential bias in male spatial distribution.

Methods

Experimental design

We studied spatial learning and memory abilities and extra-pair paternity rates in mountain chickadees (*P. 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 2013, we have monitored breeding phenology in uniquely color-banded individuals across two elevations (***Kozlovsky et al., 2018***; ***Whitenack et al., 2023***) and measured the spatial cognitive abilities of hundreds of individuals starting in 2015 (e.g.***Sonnenberg et al., 2019***; ***Welklin et al., 2024***; ***Branch et al., 2019***; ***Branch et al., 2023***; ***Heinen et al., 2021a***; ***Branch et al., 2022***; ***Semenov et al., 2024***; ***Heinen et al., 2021b***; ***Croston et al., 2016***; ***Tello-Ramos et al., 2018***; ***Benedict et al., 2021***; ***Benedict et al., 2023***). 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 cavity nesting birds that readily use nest boxes at our field site. Every year in late April, we begin monitoring 350 nest boxes throughout our field site for evidence of nest building. Once nesting material is detected, we monitor all stages of breeding through fledging of each nest, recording information about the date the first egg is laid, start of incubation, and hatching, and record the clutch size (number of eggs) and the brood size (number of chicks at post-hatch day 16) of each nest. We process all chicks in the nest box at post-hatch day 16, which includes banding them with an aluminum United States Geological Survey (USGS) band, weighing them, and obtaining a small blood sample for genetic and paternity analyses. We trap adult and first-year birds using mist nets at established feeders during annual autumn trapping and by hand at nest boxes during the breeding season. Upon capture, birds are fitted with color bands and a unique passive integrated transponder (PIT) tag, wing length is measured, and age is estimated using multiple plumage features (***Pyle, 2022***). When nestlings banded with USGS bands are recruited into our population from nest boxes, we band them with an additional color band and PIT tag for identification.

Testing spatial cognition in the wild

Spatial learning and memory testing was conducted using two feeder arrays at each of our elevation sites (high, range: 2380–2590 m; coordinates: 39.42402, –120.315015; and low, range: 1965–2070 m; coordinates: 39.443500, –120.243248). Within an elevation, the feeder arrays were established ca. 1.5 km apart with mostly non-overlapping birds visiting each array. Each array consisted of eight equidistant RFID-based feeders on a square (122 cm×122 cm) aluminum frame suspended ca. 4 m above the ground (***Figure 1***). Each feeder is equipped with a small, motorized door. Prior to testing, we kept the feeder doors of the arrays open for approximately 1 month. Next, the feeder doors were closed and programmed to open for any bird with a PIT tag; this allowed birds to habituate to the motorized feeder doors for 1 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 eight-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, maximum 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 (***Benedict et al., 2021***).

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 (***Sonnenberg et al., 2019***; ***Welklin et al., 2024***; ***Branch et al., 2019***; ***Branch et al., 2023***; ***Heinen et al., 2021a***; ***Branch et al., 2022***; ***Semenov et al., 2024***; ***Heinen et al., 2021b***; ***Croston et al., 2016***; ***Tello-Ramos et al., 2018***; ***Benedict et al., 2021***; ***Benedict et al., 2023***). These measurements capture learning curves in a single metric (***Figure 1—figure supplement 1***); 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. While these metrics are correlated (***Figure 1—figure supplement 1***), the relationship is not 1 to 1. Performance on the first 20 trials of the task reflects learning acquisition, while performance on the entire task reflects memory retention (***Sonnenberg et al., 2019***). 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 (***Sonnenberg et al., 2019***; ***Welklin et al., 2024***; ***Branch et al., 2019***; ***Branch et al., 2023***; ***Heinen et al., 2021a***; ***Branch et al., 2022***; ***Semenov et al., 2024***; ***Heinen et al., 2021b***; ***Croston et al., 2016***; ***Tello-Ramos et al., 2018***; ***Benedict et al., 2021***; ***Benedict et al., 2023***). We have previously documented that variation in both metrics is associated with significant differences in survival (***Sonnenberg et al., 2019***), longevity (***Welklin et al., 2024***), in female reproductive decisions (***Branch et al., 2019***), in foraging decisions (***Benedict et al., 2021***), and in cognitive flexibility (***Benedict et al., 2023***). For analyses of spatial cognitive abilities and extra-pair paternity, we used cognitive performance measured in the first year each individual completed the task, as cognitive performance on the spatial learning and memory task does not change with age (***Sonnenberg et al., 2019***; ***Tello-Ramos et al., 2018***). In addition, birds were included in analyses if they performed at least 20 trials and made fewer than mean 3 errors across the 4-day testing period. Males that bred in more than 1 year were included in the analyses (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 4 consecutive years (2018–2021). Each year, we prioritized sequencing nests of males and potential extra-pair sires that performed in our cognitive task. Samples from each year were sequenced at the end of each breeding season. 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 Kit. The DNA concentration of each sample was quantified using Qubit Fluorometer 2.0 (Life Technologies) prior to library preparation and sequencing. We used a double digest restriction-site associated DNA (ddRAD) sequencing approach from ***Thrasher et al., 2018***, to obtain single-nucleotide polymorphisms (SNPs) for our paternity analyses. Sequencing was completed in batches following field sampling of each year; therefore, individuals from each breeding year were run together, but separately from the other years. For each individual, 100–500 ng of extracted DNA was digested with restriction enzymes SbfI-HF (NEB) and MspI (NEB) and ligated with 1 of 20 unique P1 adapters and a P2 adapter (P2-MspI). Next, samples were pooled by groups of 20, maintaining individual identity via unique P1 adapters. Samples were then purified using 1.5× volume of homemade solid-phase reversible immobilization (SPRI) beads, made with Sera-Mag SpeedBead Carboxylate-Modified Magnetic Particles (Cytiva) (***Rohland and Reich, 2012***). These pooled samples (index groups) were sent to Cornell University Biotechnology Resource Center (BRC; RRID:SCR_021727) for size selection between 450 and 600 bp using BluePippin (Sage Science). Following size selection, adapter-ligated DNA was enriched by 11 cycles of polymerase chain reaction with a universal i5 primer and a unique indexed i7 primer for each index group using Phusion DNA polymerase (NEB). Reactions were again cleaned using 0.7× volume of homemade SPRI beads (as above), and the index groups pooled in equimolar ratios to create a single sequencing library run on one lane of Ilumnia NextSeq500 (150 bp single end, performed at BRC). Sequencing was performed with an ~20% PhiX spike-in to introduce diversity into the library.

SNP analysis and paternity assignment

Quality filtering, demultiplexing, and genome alignment

The following were run the same, but separately for each year of samples. First, the quality of all reads was assessed using FASTQC version 0.11.9 (https://www.bioinformatics.babraham.ac.uk/projects/fastqc/). All sequences were trimmed using *fastx_trimmer* (FASTX-Toolkit) to a length of 147 bp on the 3' end to exclude low-quality SNP calls. Next, reads containing a single base with a Phred quality score less than 10 were removed, and any sequences that had more than 5% of the bases with a Phred quality score lower than 20 were also removed. We then used *process_radtags* from STACKS version 2.65 to demultiplex the sequence reads and obtain files with specific sequences for each individual. Next, we aligned sequences to the chromosome-scale reference genome of mountain chickadees (***Semenov et al., 2024***) using Bowtie2 version 2.5.1. The resulting .sam files were converted to .bam files and sorted using the *view* and *sort* functions in Samtools version 1.18. These aligned reads were used as the input for the *ref_map.pl* program in Stacks 2.65.

SNP filtering and assigning paternity

SNPs were exported using *populations* in Stacks 2 version 2.65, and each year's samples were run separately to maximize the number of SNPs and individuals included for downstream paternity analyses. All male individuals alive during the year of interest were included as potential sires. Individuals with more than 50% missing SNP data were removed from the dataset; only five individuals from the 2021 dataset did not meet this criterion. Loci were exported if they were present in 85% of that year's sample population (*–r*). If a RAD locus had more than one SNP, data were restricted to the first SNP (*–write_single_snp*) to minimize those in high linkage disequilibrium. We required a minor allele frequency of 0.05 to process a nucleotide (*–min_maf*), then filtered for loci in Hardy-Weinberg equilibrium ($p<0.05$) using VCFtools (*--hwe* option) (***Wigginton et al., 2005***; ***Danecek et al., 2011***). Variant call format (VCF) files were converted to GENEPOP format using the 'radiator' package in R (***Gosselin, 2020***).

Before assigning paternity, we imported the yearly GENEPOP files into CERVUS (***Kalinowski et al., 2007***), then ran maternity tests separately for each elevation in each year to confirm mother-offspring relationships identified during field observations. We assessed the quality of these assignments by plotting the distributions of the first- and second-ranked mother's scores for each offspring. First- and second-ranked mother pair LOD scores formed bimodal distributions, with nearly all first-ranked mother scores above zero and nearly all second-ranked mother scores below zero. In rare cases when second-ranked mother scores were positive, these were almost always known sisters or daughters of the mother identified during field observations. Therefore, first-ranked mother-offspring pairs with positive log likelihood (LOD) scores were considered correct assignments, but pairs with negative assignments were not included in paternity analyses because we were not confident in the mother assignment. Offspring resulting from a female laying an egg in a nest that was not her own (i.e. egg dumps) were uncommon and not included in further statistical analyses.

Paternity analyses were conducted in CERVUS separately for each elevation in each year by calculating trio LOD scores for each potential father-offspring pair. Trio LOD scores account for known maternal genotypes when identifying potential fathers. As we did for mother-offspring pairs, we plotted the distribution of the first- and second-ranked male scores and again found a bimodal distribution centered around zero (***Figure 1—figure supplement 2***). Based on these plots, we set cut-off scores to assign paternity by: all first-ranked male scores at an elevation in a year that were positive and greater than the top second-ranked male score at that elevation in that year were 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 the mean number of location errors per trial across the first 20 trials correlated with the mean number of location errors per trial over the entire 4-day task for males using a linear model. Mean location errors per trial over the entire task were used as the response variable while mean location errors over the first 20 trials and the total number of trials completed were included as

fixed effects. Numbers and letters of subheadings correspond to predictions in the last paragraph of the Introduction and carry throughout the Results.

1. Testing effect of male spatial cognition on the number of extra-pair young sired

We employed two methods to test whether spatial cognitive ability was associated with the number of extra-pair young a male sired in a year. Both models included the number of extra-pair young 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 [first 20] and (2) the mean number of location errors per trial over the 4-day task [entire 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), using the R package 'glmmTMB' (***Brooks et al., 2017***) to account for observations of males with zero extra-pair young, whereas the second method restricted the dataset to males that sired at least one extra-pair offspring.

a. *Effect of elevation on number of extra-pair young sired*. Much of the work in our mountain chickadee system has focused on elevation-related differences in spatial learning and memory performance; therefore, we tested whether extra-pair paternity 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' (***Brooks et al., 2017***). Our response variable was whether each offspring was sired by an extra-pair 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 extra-pair paternity rates separately for each year.
b. *Effect of male age on number of extra-pair young sired*. It is possible that a relationship between extra-pair paternity 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. ***Double and Cockburn, 2000***). 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 (***Sonnenberg et al., 2019***; ***Welklin et al., 2024***; ***Tello-Ramos et al., 2018***). 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.
c. *Effects of spatial cognition on brood size and nestling mass*. 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 (***Joe and Zhu, 2005***). 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 enough levels (2015–2023). Male and female identities 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; ***Whitenack et al., 2025***), 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 identities as random effects. Again, year (2015–2023) and male and female identities were included as random effects to control for yearly variation and repeated measures of individual males and females.
d. *Effect of paternity status on male investment*. Siring extra-pair offspring may reduce a male's investment in his own nest, so we tested whether siring extra-pair young 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 3 years of data on extra-pair paternity). Elevation, clutch size, and year (3 years of extra-pair paternity data) were included as fixed effects, and male and female identities 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.

2. Testing effect of male spatial cognition on likelihood of being cuckolded

We also tested whether males with worse spatial cognitive abilities were more likely to be cuckolded than those that performed better on the task. Male spatial cognition was included as the response variable and elevation, and whether the nest had any extra-pair young were included as fixed effects. When modeling the mean number of location errors per trial on the entire task, we used the Gamma distribution and included the total number of trials completed as a fixed effect. Including male identity as a random effect in both models led to convergence errors, so male identity was not included in the models.

e. Effect of female cognition on number of extra-pair young. Both male and female cognitive abilities could affect the likelihood of a nest containing extra-pair young, so we tested whether cuckoldry was associated with the spatial cognitive abilities of both parents at a nest using multiple methods. First, we modeled the relationship between male and female spatial cognitive ability and cuckoldry at the nest and offspring level. At the nest level, we tested whether male or female spatial cognitive ability predicted whether any offspring in a nest were sired by extra-pair males. At the offspring level, we tested whether male or female spatial cognitive ability predicted whether each offspring was sired by an extra-pair male or not. For both tests, we used generalized linear mixed models with binomial distributions that included male and female spatial cognitive performance, elevation, and year as fixed effects. Male and female identities were included as random effects to control for repeated measures of individual males and females.

Second, for nests that had at least one extra-pair young, we tested if the number of extra-pair young in a nest was associated with male or female spatial cognitive ability using a generalized linear mixed model with a truncated Poisson distribution. The number of extra-pair young in the nest was included as the response variable, while male and female performance on the first 20 trials, year, and elevation were included as fixed effects. Male and female identities were included as random effects to control for repeated measures of individual males and females. The effect of male age on cuckoldry rates was tested by adding male age as a fixed effect to each model and comparing models with and without male age using likelihood ratio tests.

3. Comparing spatial cognition of extra-pair males and the social males they cuckold

If males initiate extra-pair copulations, we expect them to be randomly distributed across different nests, since the fitness benefit of extra-pair young is increased for the male regardless of the cognitive abilities of the females' social mate. On the other hand, if females initiate extra-pair copulations, 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 (***Johnston, 1982***; ***Boogert et al., 2011***). 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 (extra-pair 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 vs. 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 the total location errors, we log-transformed the response variable to

improve residual fit and included a quadratic term of total trials completed during the 4-day cognitive testing period, since the number of trials completed influences performance (***Croston et al., 2015***; ***Sonnenberg et al., 2019***; ***Welklin et al., 2024***; ***Tello-Ramos et al., 2018***).

b. Comparing age of social and extra-pair males. Finally, we tested whether extra-pair males were significantly older than the social males they cuckolded using a chi-square test and paired t-test.

All statistical analyses were performed in R version 4.1.1 (***R Development Core Team, 2021***), and the residual fit of all models was checked using DHARMa (***Hartig, 2018***). Statistical significance was calculated using Wald chi-square tests.

Results

There was a strong positive correlation between the number of location errors on the entire 4-day task (entire task) and on the first 20 trials (first 20) for males completing the task in our study (Coef = 0.27, F=121.72, p<0.001; ***Figure 1—figure supplement 1***).

Extra-pair paternity and spatial cognition

Across 3 years of data collection (2018, 2020, and 2021), we were able to genotype and assign paternity to 86% of offspring in the study (630 of 732). We found that 30.3% of the total offspring sampled (222 of 732) were sired by extra-pair males and that 70.1% of nests (89 of 127) had at least one extra-pair young (extra-pair young). Numbers and letters of subheadings correspond to predictions in the last paragraph of the Introduction and Statistical analysis section.

1. Males with better spatial cognition produced more extra-pair young

Performance on the spatial learning and memory task predicted the number of extra-pair young a male sired each year (***Figure 2*** and ***Appendix 2—table 3***). Males with better spatial learning and memory abilities (e.g. fewer mean location errors per trial) sired more extra-pair young, both according to a zero-inflated model including males that sired no extra-pair young (first 20 trials: χ^2_1=6.28, p=0.012; ***Figure 2***, dashed line); entire task: χ^2_1=8.12, p=0.004, N=280 (137 individual males; ***Figure 2—figure supplement 1***), and to a model only including males that sired at least one extra-pair young (first 20 trials: χ^2_1=5.96, p=0.015; ***Figure 2***, solid line); entire task: χ^2_1=7.68, p=0.006, N=41 (34 individual males; ***Figure 2—figure supplement 1***). This model suggests that of the males that sired at least one extra-pair young, those with the best cognitive performance may sire between 6 and 7 extra-pair young each year, whereas males with the worst cognitive performance will sire only 1–2 extra-pair young each year. We have shown that birds with better spatial cognitive abilities live longer (***Welklin et al., 2024***) and lack reproductive senescence within their natural lifespan (***Welklin et al., 2025***); therefore, males with better cognition are expected to produce significantly more offspring over their lifetime.

a. *Effect of elevation*. We found no significant differences in the number of extra-pair young sired at high vs. low elevation populations regardless of year sampled (Appendix 1, ***Figure 2—figure supplement 2***, ***Appendix 2—Tables 1 and 2***); therefore, we combined high and low elevations for all later analyses. Data from breeding birds in this study confirmed previous research showing that female chickadees seek extra-pair copulations with neighboring males (on average ~100 m from their own nests; ***Figure 2—figure supplements 3 and 4***), which are likely familiar males from their nonbreeding flocks (***McCallum et al., 2020***; ***Ekman, 1989***; ***Otter et al., 1994***; ***Smith, 1988***). In addition, breeding male territories do not appear to cluster based on cognitive performance (***Figure 2—figure supplement 5***).
b. *Effect of age*. Importantly, we show that male age was not associated with the number of extra-pair young sired (Appendix 1).
c. *Effects of reproductive output*. In addition to testing how cognitive abilities were related to the number of extra-pair young, we also tested whether variation in cognitive abilities had direct consequences on breeding performance. Across 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

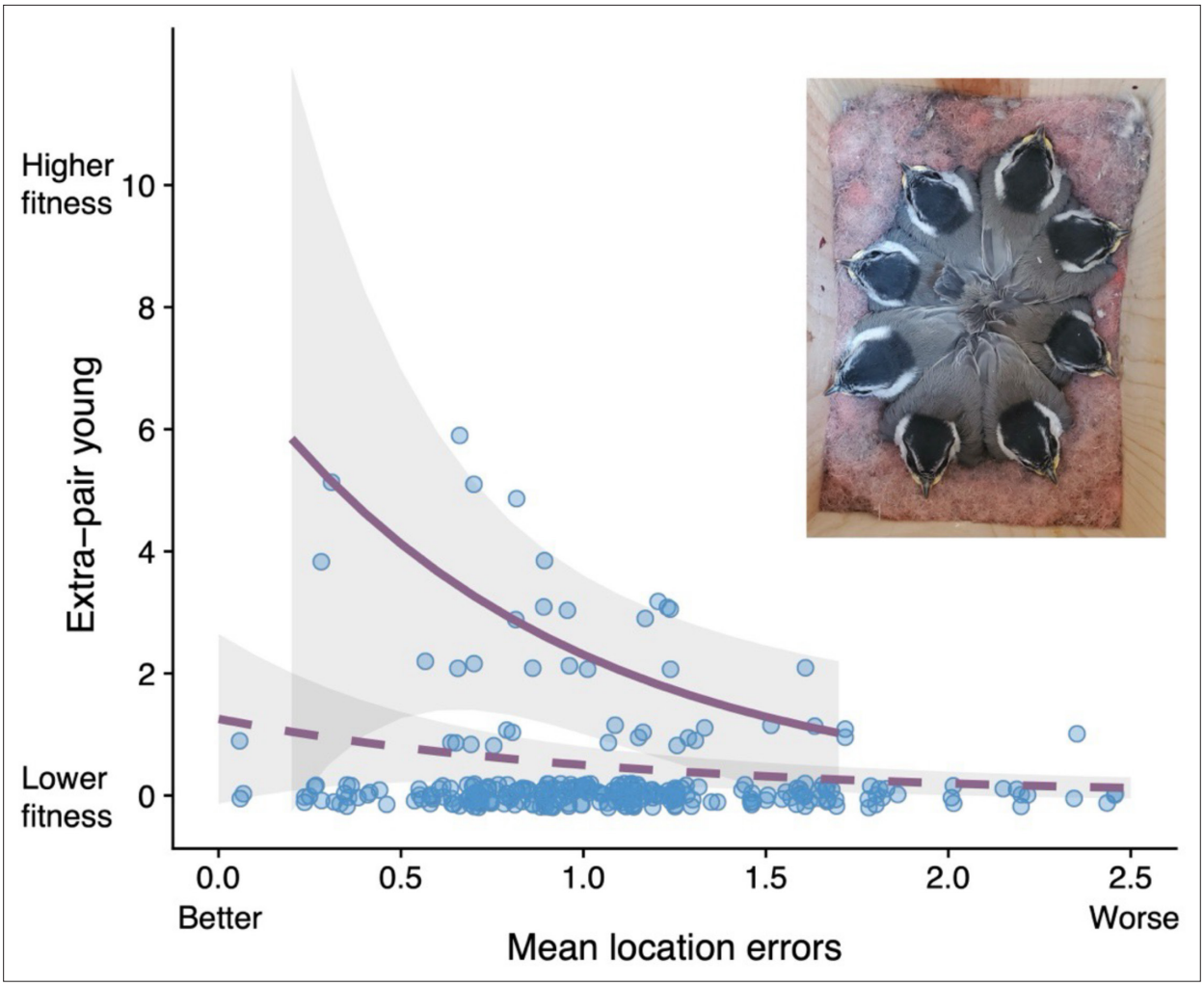

Figure 2. Model predictions of the number of extra-pair young a male sired in a year by the mean number of location errors per trial over the first 20 trials. The dashed line represents a zero-inflated model for all males, including those with no extra-pair young (N=280; 137 individual males), and the 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 2—figure supplement 1***.

The online version of this article includes the following figure supplement(s) for figure 2:

Figure supplement 1. 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 4-day testing period.

Figure supplement 2. Extra-pair (EPY) and within-pair (WPY) paternity rates across 3 years of data collection and two elevation sites.

Figure supplement 3. Histogram plotting the distance of extra-pair male nests from the females' nest.

Figure supplement 4. Distance to extra-pair males.

Figure supplement 5. Heatmaps of male spatial cognitive scores for high and low elevation nest boxes across the 3 years we have extra-pair paternity data from, including those nests that failed before day 16 or were not genotyped.

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 (***Appendix 2—table 4***). However, males with better performance on the first 20 trials raised heavier young (mass at day 16, χ^2_1=4.86, p=0.028, N=202 nests, ***Appendix 2—table 4*** for entire task), while female performance on the first 20 trials showed no significant relationship with offspring mass at day 16 (χ^2_1=0.93, p=0.335, N=202 nests, ***Appendix 2—table 4*** for entire task).

d. *Effect of male investment*. Three years of extra-pair paternity data suggest that extra-pair males do not compromise their own nest investment compared to males that did not sire any extra-pair

offspring, as 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 between males that had extra-pair young and males that did not sire any extra-pair young (***Appendix 2—table 5***). We also 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, ***Appendix 2—table 6***).

2. Does spatial cognition of the social male predict presence of extra-pair young?

Across 3 years of data collection, we had spatial cognition data on the social males of 101 nests; approximately 28% of nests (28/101) had no extra-pair young and 72% of nests had at least one extra-pair young (73/101). The spatial cognitive abilities of males that had extra-pair young in their nests did not differ from males that had no extra-pair young in their nests (first 20 trials: χ^2_1=0.42, p=0.516; entire task: χ^2_1=2.07, p=0.150, N=101 nests, ***Appendix 2—table 8***). Among nests where both the male and female had spatial cognition data, the likelihood of being cuckolded was not significantly related to the cognitive abilities of the social males (offspring level: first 20: χ^2_1=0.25, p=0.620, entire task: χ^2_1=0.43, p=0.513, N=348 offspring for 42 males; nest level: first 20: χ^2_1=0.05, p=0.808; entire task: χ^2_1=0.22, p=0.642, N=59 nests for 42 males, ***Appendix 2—table 8***).

Similarly, for nests that had at least one extra-pair young, the cognitive abilities of the social male did not predict the number of extra-pair young in their nests (first 20: χ^2_1=1.03, p=0.311; entire task: χ^2_1=0.40, p=0.528, N=41 nests for 35 males, ***Appendix 2—table 9***).

b. Effect of age. In addition, male age did not significantly affect the likelihood of a male being cuckolded (see Appendix 1).

e. Effect of female cognition on extra-pair young. A female's cognitive abilities may influence her decision to seek extra-pair copulations (i.e. a female may seek extra-pair copulation to compensate for her own poor cognition). Therefore, we assessed whether the likelihood of having extra-pair young in the nest was related to the spatial cognitive abilities of the female. Females who performed worse on the first 20 trials of the spatial cognitive task were more likely to have extra-pair young in their nests (offspring level: 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 performance across the entire 4-day task (χ^2_1=0.18, p=0.673, N=348 offspring for 42 females), or for either metric at the nest level of analysis (first 20: χ^2_1=0.21, p=0.645, entire task: χ^2_1=0.13, p=0.723, N=59 nests for 42 females, ***Appendix 2—table 8***).

Similarly, for nests that had at least one extra-pair young, females that performed worse on the first 20 trials had significantly more extra-pair young in their nests (first 20: χ^2_1=6.79, p=0.009, N=41 nests for 32 females), but there was no significant relationship across the entire 4-day task (entire task: χ^2_1=1.04, p=0.308, N=41 nests for 32 females, ***Appendix 2—table 9***).

3. Extra-pair males have better spatial cognition than the social males they cuckold

When there were extra-pair young in a nest, they were sired by males with better spatial learning and memory abilities (on average) compared to those of the social male they cuckolded (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***); entire task: χ^2_1=6.08, p=0.014, N=71 comparisons (***Figure 3—figure supplement 1*** and ***Appendix 2—table 7***)).

b. Effect of age. Furthermore, 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). A paired-samples t-test of social and extra-pair father ages returned a similar result (χ^2_1=0.27, p=0.662).

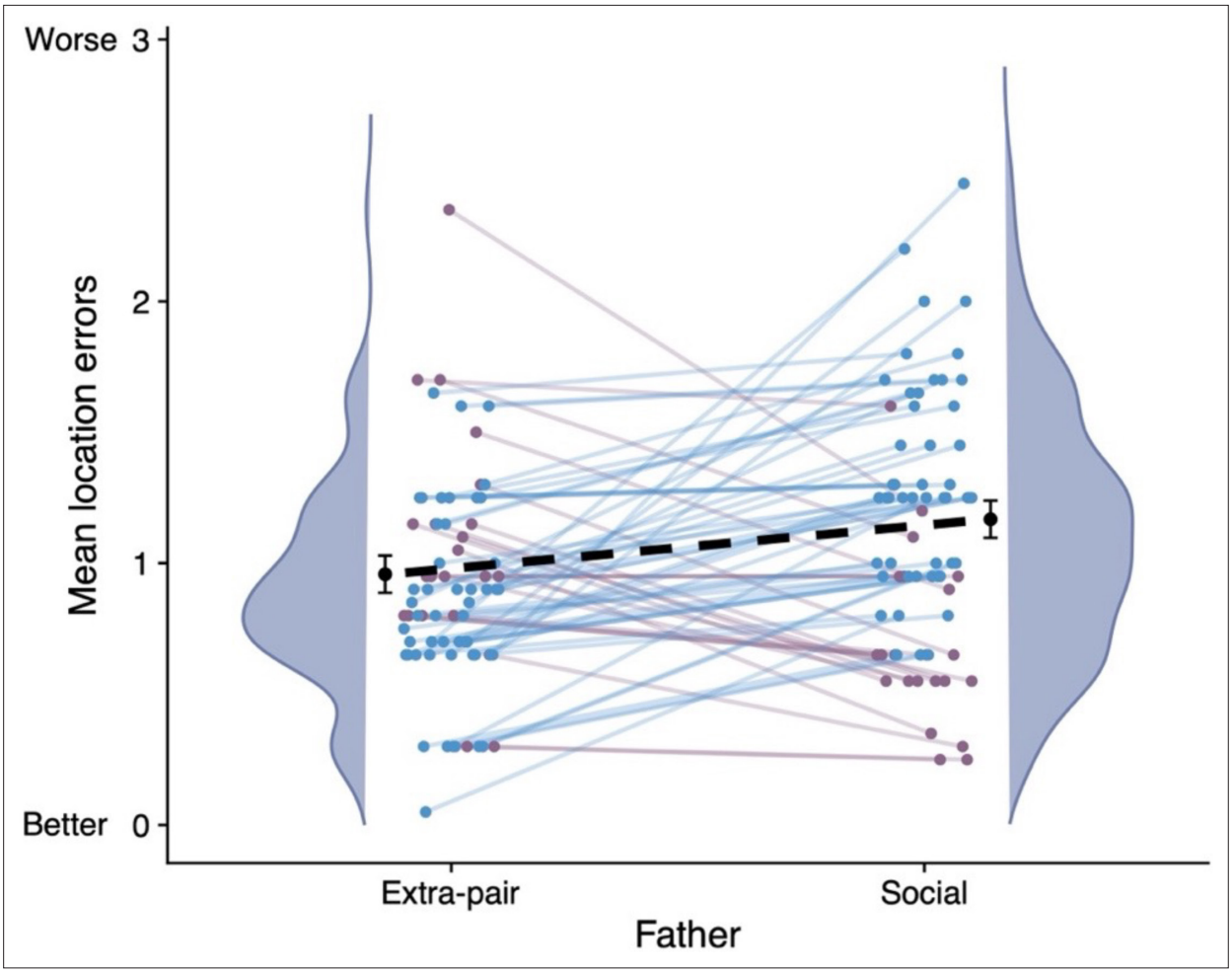

Figure 3. Comparing spatial cognitive performance (mean number of location errors per trial over the first 20 trials) of extra-pair (mean±SE = 0.96±0.07) and social fathers (mean±SE = 1.17±0.07, 71 comparisons). Lines connect males by offspring: blue lines show comparisons where the extra-pair father performed better than the social father (49 of 71 cases or 69%), and purple lines show comparisons where the social father performed better than the extra-pair father (19 of 71 cases, or 26.7%; in 3 cases, the extra-pair and social fathers had the same cognition score). Shaded distributions represent smoothed histograms of cognitive performance for each father type. The same analysis is presented for performance over the 4-day testing period in ***Figure 3—figure supplement 1***.

The online version of this article includes the following figure supplement(s) for figure 3:

Figure supplement 1. Comparing spatial cognitive performance (mean number of location errors per trial over the 4-day task) of extra-pair and social fathers (total of 71 comparisons).

Discussion

Our findings show that sexual selection acts on the spatial cognitive abilities of free-living, food-caching mountain chickadees via extra-pair paternity. We found that (a) males, but not females, with better spatial cognitive abilities produce higher quality offspring (higher mass, 70) in their social nests, (b) males with better spatial learning and memory abilities sire more extra-pair young than their poorer-performing counterparts, and (c) extra-pair males have better spatial cognitive abilities than the social males they cuckold, regardless of age. Importantly, our data show that absolute male cognitive abilities do not predict extra-pair young in the nest, rather that the differences in cognition between the extra-pair male and the social male are relative to each other – a good quality male can lose paternity to an even better-quality male.

We specifically quantified extra-pair paternity in our mountain chickadee system and do not have data on all extra-pair copulation attempts by males or females. However, given the extensive research on chickadee breeding behavior and their closely related Eurasian relatives (tits), we suggest these patterns of extra-pair paternity may be driven by females for several reasons: (1) female parids

(chickadees and tits) are known to pursue extra-pair copulations with neighboring males (**Otter et al., 1994**; **Mennill et al., 2004**; **Smith, 1988**; **Hasselquist and Sherman, 2001**; **Kempenaers et al., 1992**; **Sheldon, 1994**), (2) parids have never been reported or observed engaging in forced copulation (e.g. **Mennill et al., 2004**; **Smith, 1988**; **Sheldon, 1994**), 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, where females seek high-quality males (in this case, those with better spatial cognitive abilities) for extra-pair copulation (**Andersson and Simmons, 2006**; **Andersson, 1994**; **Rubenstein, 2023**). In other words, males would benefit from siring extra-pair young with any female regardless of her social male's cognitive abilities.

That said, active choice need not be implied, as males with poor spatial cognitive abilities could be 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 aggressive (**Branch et al., 2015**; **Kozlovsky et al., 2014**), and cognitive performance is not associated with social dominance (**Heinen et al., 2021a**). Females, on the other hand, would benefit from obtaining extra-pair copulations with males that have better spatial cognition than their social male, as this trait is heritable (**Branch et al., 2022**; **Semenov et al., 2024**) and would increase the likelihood of producing offspring with better spatial cognition, leading to higher overwinter survival (**Sonnenberg et al., 2019**) and longer lifespan (**Welklin et al., 2024**). Indeed, females with poorer spatial memory acquisition (made more errors on the first 20 trials) had more extra-pair young in their nests, while social male cognitive performance did not predict extra-pair young in the nest. This suggests that females may compensate for their poor cognitive abilities via extra-pair young. Considering that alleles associated with better spatial cognitive abilities are not sex linked (**Branch et al., 2022**), producing extra-pair young with better quality males increases selection pressure on spatial cognitive abilities in both males and females, as both sexes rely on spatial cognition for survival (**Branch et al., 2020**).

Although it remains unknown whether chickadees can evaluate cognitive abilities directly or indirectly via some correlated trait(s), the life history and breeding ecology of mountain chickadees provide several possibilities. For example, female chickadees may use secondary sexual signals, such as song and plumage variation associated with spatial cognitive abilities, to identify high-performing males (**Andersson and Simmons, 2006**; **Andersson, 1994**; **Boogert et al., 2011**; **Robayo Noguera et al., 2025**). Recently, we have shown that males that perform better on our spatial learning and memory task sing more throughout the day (**Haley et al., 2026**) and exhibit brighter black eyelines (**Lane, 2026**) compared to their poorer-performing counterparts. However, this variation is correlative, and we have not shown that females use this information in discriminations. Alternatively, it is possible that females can directly assess a male's ability to successfully recover food stores over winter and base mating decisions on this information in the spring (**Chen et al., 2019**; **Lemmon et al., 1997**; **Ekman, 1989**). Chickadees are nonmigratory, sedentary birds that aggregate in flocks of unrelated male-female pairs throughout the nonbreeding season and break apart once breeding commences (**McCallum et al., 2020**; **Ekman, 1989**). Data from this study confirm previous research showing that female chickadees seek extra-pair copulations with neighboring males (**Otter et al., 1994**; **Smith, 1988**; **Lifjeld et al., 2025**), which would likely be males from their winter flock (**McCallum et al., 2020**; **Ekman, 1989**). Regardless of if and how females evaluate male cognition, mating with males with better cognitive performance should increase female fitness by increasing the likelihood of offspring inheriting the specific alleles associated with better cognition, which would be expected to lead to higher offspring survival and longer lifespan (**Sonnenberg et al., 2019**; **Welklin et al., 2024**).

An alternative hypothesis for our findings is that females seek extra-pair copulations with other males as insurance against the social male's infertility (**Lifjeld et al., 2025**), again gaining indirect genetic benefits. This hypothesis does not explain the direction of our findings because male cognitive abilities did not predict the number of offspring a male produced in his own nest (i.e. cuckolded social males still fathered chicks in their nests), suggesting that males with poorer cognition do not suffer from infertility. That said, we do not have data on the sperm quality of these birds and therefore cannot exclude differences in fertility or sperm competition between males with better and worse spatial cognition. Related, we have not detected fitness trade-offs or negative effects associated with better cognitive abilities in our system; we do not see cognitive or reproductive senescence within

birds' naturally occurring lifespan (**Heinen et al., 2021b**; **Welklin et al., 2025**). In fact, chickadees with better spatial cognition live longer, allowing them to produce more offspring over their lifetime compared to chickadees with worse cognition (**Welklin et al., 2024**).

Interestingly, a previous study in our system showed that females mated to social males with better spatial abilities lay larger clutches and fledge larger broods in years of resource abundance (**Branch et al., 2019**). Together with the present findings, we suggest that female mating decisions, including extra-pair copulations and reproductive investment, may vary opportunistically. When resources are abundant, females lay larger clutches if their social male has better cognitive abilities (**Branch et al., 2019**), and when males with better spatial cognition than her social mate are available for extra-pair copulations, they pursue those opportunities. Indeed, we found that females with poorer spatial cognition had more extra-pair young in their nests, suggesting female mating decisions could be based on some physiological signal associated with poorer cognition that serves as a compensatory mechanism. At the ultimate level, females with poorer cognition may benefit disproportionately by mating with the highest quality male they can find, which in the case of food-caching birds, likely means those with better spatial cognitive abilities (**Sonnenberg et al., 2019**; **Welklin et al., 2024**).

An additional alternative explanation for our findings is that birds with better spatial cognitive abilities have access to better territories and therefore are clustered based on cognitive abilities (**Canal et al., 2012**). Then, because females have extra-pair copulations with neighboring males (**Otter et al., 1994**; **Smith, 1988**; **Lifjeld et al., 2025**), those neighbors would be males with better spatial cognition. However, in our study system, males do not appear to cluster based on cognitive performance (**Figure 2—figure supplement 5**), suggesting that females are not finding males with better cognitive abilities than their social males by chance. Furthermore, while higher social dominance status is associated with access to better territories in chickadees (**Ratcliffe et al., 2007**), we see no association with dominance status and spatial cognitive abilities in our system (**Heinen et al., 2021a**) or closely related black-capped chickadees (**Robayo Noguera et al., 2025**). While it is possible that our results reflect some unmeasured trait(s) linked to spatial cognitive ability, such as boldness, aggression, or increased exploratory behavior (e.g. **Spritzer et al., 2005**), previous data from our system do not support these additional alternative hypotheses. Chickadees with enhanced spatial cognitive abilities are not more aggressive (**Branch et al., 2015**), nor do they show higher rates of exploratory behavior (e.g. higher space use) (**Kozlovsky et al., 2014**).

Given the fitness advantages of superior spatial cognitive abilities for food-caching chickadees, how variation is maintained and why enhanced spatial cognitive abilities have not evolved to fixation may seem puzzling. While food-caching birds exhibit superior spatial cognitive abilities compared to their non-caching counterparts (**Brodbeck and Shettleworth, 1995**), considerable variation persists within species (**Croston et al., 2016**). Research from our system demonstrates the highly polygenic nature of the spatial cognitive phenotype, meaning there are multiple genetic pathways that may produce the same cognitive phenotype (**Branch et al., 2022**; **Semenov et al., 2024**; **Pritchard et al., 2010**). In addition, selection strength varies with annual variation in winter climate, which in milder years may allow individuals to survive and reproduce despite comparatively poor spatial cognitive abilities (**Sonnenberg et al., 2019**; **Kozlovsky et al., 2018**; **Whitenack et al., 2023**; **Croston et al., 2016**). Finally, we have documented elevation-related differences in spatial cognition and the hippocampus of mountain chickadees (**Freas et al., 2012**), but there is gene flow among elevations (**Branch et al., 2017**) which moves allelic variation associated with poorer cognition within the population.

Overall, our study provides novel results showing that sexual selection contributes to the evolution of spatial cognitive abilities in a food-caching species, which rely on such spatial cognition for survival. We show that males with better spatial cognition exhibit higher reproductive output, via siring more extra-pair young and fledging heavier chicks, which are more likely to survive and be recruited into the breeding population (**Whitenack et al., 2025**). We also show that when there are extra-pair young in the nest, they are sired by males with better spatial cognition than the social male (on average), which suggests that females may be selectively obtaining extra-pair copulation with higher quality males; though we do not have direct experimental evidence of female choice. Whether these patterns are driven by females or males, males with better spatial cognitive abilities exhibit higher fitness by producing more offspring, adding to the evidence for selection on spatial cognitive abilities, including differential survival and longevity in food-caching birds (**Sonnenberg et al., 2019**; **Welklin et al., 2024**).

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Author contributions

Carrie L Branch, Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Writing – original draft, Writing – review and editing; Benjamin R Sonnenberg, Data curation, Investigation, Writing – review and editing; Joseph F Welklin, Data curation, Formal analysis, Writing – review and editing; Bronwyn G Butcher, Eli Bridge, Resources, Methodology, Writing – review and editing; Virginia K Heinen, Angela M Pitera, Lauren Benedict, Data curation, Writing – review and editing; Irby Lovette, Michael S Webster, Resources, Supervision, Writing – review and editing; Vladimir Pravosudov, Conceptualization, Resources, Funding acquisition, Methodology, Writing – review and editing

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Ethics

All procedures were in accordance with University of Nevada Reno IACUC (protocols 20-11-1103-1, 20-06-1014, 20-08-1062) and California State Fish and Wildlife Scientific Collecting Permit (S-193630001-20007-001).

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Supplementary files
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Appendix 1

Summary of previous work on Sierra Nevada mountain chickadee study system

The hypothesis presented in the current paper is based on established results in this system, all collected over multiple years and including different groupings of birds:

1. Survival of juveniles in their first year of life is dependent on their spatial cognitive abilities, representing directional selection (***Sonnenberg et al., 2019***).
2. Lifespan of chickadees depends on their spatial cognitive abilities – birds with better spatial cognitive abilities live longer (***Welklin et al., 2024***).
3. Spatial cognitive performance does not change with age (***Sonnenberg et al., 2019***; ***Tello-Ramos et al., 2018***).
4. Spatial cognitive abilities do not show age-related senescence (***Heinen et al., 2021b***).
5. Spatial cognitive abilities are not associated with social dominance status (***Heinen et al., 2021a***) or with naturally occurring developmental perturbations (***Sonnenberg et al., 2022***).
6. Individual variation in spatial cognitive abilities is highly heritable and is associated with differences in genes related to cognition and brain development (***Branch et al., 2022***; ***Semenov et al., 2024***).
7. Genotypes of birds with the worst cognition disappear from populations before winter (e.g. homozygous recessive birds), likely due to mortality, yet these genotypes must have been present at fledging (***Branch et al., 2022***; ***Semenov et al., 2024***), which shows that birds with worse cognition die early on in their first winter.
8. There is no detectable senescence in reproduction within the naturally occurring lifespan of chickadees, and females increase their reproductive success with age (***Welklin et al., 2025***).
9. Female cognition is not associated with the number of fledglings (***Branch et al., 2019***) or fledgling mass (current study); however, in a high resource year, male cognition is associated with larger clutch and brood size in their social nest – a finding driven by female behavior (***Branch et al., 2019***).
10. Chickadees are socially monogamous species and form long-term social pairs – divorces are rare (***Pitera et al., 2021***). In addition, it is well established that females leave their territories and visit neighboring male territories for extra-pair copulations, which we confirm here, and forced copulation does not occur in chickadees.
11. Social pairing is not associated with spatial learning and memory (***Branch et al., 2023***), likely because chickadees form social pairs in Fall and new recruits do not have the choice of any mate – many males are already paired (***Branch et al., 2023***; ***Pitera et al., 2021***), as such the primary way to increase indirect fitness is via extra-pair copulation.
12. There are no differences in spatial cognitive abilities between males and females (***Branch et al., 2020***), as both rely on spatial cognition to survive the winter.
13. We have shown that supplementary food does not affect reproductive success in our system (***Sonnenberg, 2022***).

Supplemental results

Across 3 years of data collection on extra-pair copulations and reproductive output, we see that, on average, there are 1.7 extra-pair young per nest; however, if we constrain this analysis to only nests with at least one extra-pair young, the mean is 2.5 extra-pair young per nest. Nests ranged from 0% extra-pair young to 100% extra-pair young, with the most being 6/6 nestlings sired by extra-pair fathers.

Elevation by year comparisons

Elevation by year comparison of extra-pair rates using binomial generalized mixed-effects modeling revealed a significant interaction between elevation and year, suggesting the direction of the differences in extra-pair paternity rate between the high and low elevation sites differed across years (***Figure 2—figure supplement 2*** and ***Appendix 2—table 1*** for sample sizes by year and elevation). Therefore, we ran a separate model for each year. In 2018, the extra-pair paternity rate was higher

at the low elevation site, but this difference was not significant (elevation term: χ^2_1=2.24, p=0.134, N=209 offspring [134 at high, 75 at low]). In 2020, the extra-pair paternity rate was higher at the high elevation site, but this difference was not statistically significant (elevation term: χ^2_1=2.45, p=0.118, N=263 offspring [119 at high, 144 at low]). In 2021, the extra-pair paternity rate was higher at the low elevation site, but this difference was not statistically significant (elevation term: χ^2_1=1.72, p=0.190, N=260 offspring [141 at high, 119 at low]).

Does male age affect extra-pair paternity?

Male age was not associated with the number of extra-pair young a male sired, both according to a zero-inflated model including males that sired no extra-pair young (age as fixed effect in the first 20 trials model: χ^2_1=0.83, p=0.362; age as fixed effect in the entire task model: χ^2_1=2.41, p=0.121, N=280 [137 individual males]), and using a model only including males that sired at least one extra-pair young (age as fixed effect in the first 20 trials model: χ^2_1=1.29, p=0.255; age as fixed effect in the entire task model: χ^2_1=0.16, p=0.687, N=41 nests; 34 individual males).

Male age did not affect the likelihood of a male being cuckolded (offspring level: age as fixed effect in the first 20 trials model: χ^2_1=0.08, p=0.783, age as fixed effect in the entire task model: χ^2_1=0.18, p=0.676, N=348 offspring for 42 males; nest level: age as fixed effect in the first 20 trials model: χ^2_1=0.09, p=0.768; age as fixed effect in the entire task model: χ^2_1=2.02, p=0.570, N=59 nests for 42 males). Within nests that had at least one extra-pair young, social male age did not predict the number of extra-pair young in the nest (χ^2_1=0.23, p=0.635, N=41 nests; 35 individual males).

Appendix 2

Appendix 2—table 1. Sample sizes for extra-pair paternity broken down by year and elevation for both the nest and offspring level.

	Year	Elevation	No EPY	≥1 EPY	Rate
Nest level					
	2018	High	8	17	68.00%
		Low	1	13	92.90%
	2020	High	6	18	75.00%
		Low	8	14	63.60%
	2021	High	9	13	59.10%
		Low	6	14	70.00%
	Total	High	23	48	67.60%
		Low	15	41	73.20%
Offspring level	Year	Elevation	WPY	EPY	Rate
	2018	High	89	45	33.60%
		Low	38	37	49.30%
	2020	High	76	43	36.10%
		Low	110	34	23.60%
	2021	High	113	28	19.90%
		Low	84	35	29.40%
	Total	High	278	116	29.40%
		Low	232	106	31.40%

Appendix 2—table 2. Differences in extra-pair paternity rates between high and low elevations. A likelihood ratio test indicated that an interaction between elevation and year improved the model, so years were run separately.

2018			
	Estimate	Standard error	Z value
Intercept	–0.85	0.35	–2.42
Elevation (low)	0.84	0.56	1.50
Random effects	Variance	Std deviation	
Mother ID	1.66	1.29	
N=209 offspring, 39 mothers			
2020			
	Estimate	Standard error	Z value
Intercept	–0.72	0.39	–1.86
Elevation (low)	–0.88	0.56	–1.57
Random effects	Variance	Std deviation	
Mother ID	2.15	1.47	
N=263 offspring, 46 mothers			

Appendix 2—table 2 Continued on next page

Appendix 2—table 2 Continued

2021			
	Estimate	Standard error	Z value
Intercept	–1.79	0.40	–4.53
Elevation (low)	0.69	0.53	1.31
Random effects	Variance	Std deviation	
Mother ID	1.56	1.25	
N=260 offspring, 42 mothers			

Appendix 2—table 3. Relationship between spatial cognitive ability and extra-pair young sired.
Two models are presented for each spatial cognitive measure, a model that included a zero-inflation parameter for all observations and a model that only included male-years where the male sired at least one offspring.

3 A. First 20 trials mean location error with zero-inflation parameter

Conditional model	Estimate	Standard error	Z value
Intercept	0.4	0.54	0.75
First 20 trials mean location error	–0.92	0.37	–2.51
Elevation (low)	0.61	0.31	1.99
Year 2020	0.67	0.43	1.54
Year 2021	0.74	0.43	1.7
Zero-inflation model	Estimate	Standard error	Z value
Intercept	1.28	0.23	5.55
Random effects	Variance	Std deviation	
Male ID	0.08	0.29	
N=280 male-years (137 unique males over 3 breeding seasons)			

3B. First 20 trials mean location error with positive-only values

	Estimate	Standard error	Z value
Intercept	0.5	0.63	0.79
First 20 trials mean location error	–1.16	0.48	–2.44
Elevation (low)	0.74	0.34	2.17
Year 2020	0.73	0.55	1.33
Year 2021	0.76	0.55	1.38
Random effects	Variance	Std deviation	
Male ID	0.11	0.33	
N=41 male-years (34 unique males over 3 breeding seasons)			

3 C. Entire task mean location error with zero-inflation parameter

Conditional model	Estimate	Standard error	Z value
Intercept	0.18	0.46	0.4
Entire task mean location error	–1.86	0.65	–2.85
Elevation (low)	0.76	0.29	2.65
Year 2020	0.73	0.42	1.75

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3 C. Entire task mean location error with zero-inflation parameter			
Year 2021	0.79	0.41	1.91
Zero-inflation model	Estimate	Standard error	Z value
Intercept	1.34	0.22	6.07
Random effects	Variance	Std deviation	
Male ID	0.03	0.17	
N=280 male-years (137 unique males over 3 breeding seasons)			

3D. Entire task mean location error with positive-only values			
	Estimate	Standard error	Z value
Intercept	0.24	0.56	0.43
Entire task mean location error	–2.55	0.92	–2.77
Elevation (low)	0.85	0.32	2.65
Year 2020	0.81	0.54	1.5
Year 2021	0.88	0.54	1.64
Random effects	Variance	Std deviation	
Male ID	0.03	0.18	
N=41 male-years (34 unique males over 3 breeding seasons)			

Appendix 2—table 4. Relationship between male and female spatial cognitive ability and breeding performance.

Results calculated using mean location error over the entire task as fixed effects may be less informative than models using the first 20 trials scores as fixed effects. The total number of trials completed over the entire task is a strong predictor of mean location errors over the entire task, but when mean location errors over the entire task are included as a fixed effect, we could not control for the number of total trials completed over the entire task.

4 A. Brood size: first 20 trials			
	Estimate	Standard error	Z value
Intercept	1.75	0.07	26.07
Male First 20 trials mean location error	0.06	0.04	1.52
Female First 20 trials mean location error	–0.05	0.04	–1.32
Elevation (Low)	0.08	0.04	2.1
Random effects	Variance	Std deviation	
Year (2015–2023)	<0.01	0.08	
Male ID	<0.01	0.09	
Female ID	<0.01	0.06	
N=205 nests over 9 years for 108 males and 89 females.			

4B. Brood size: entire task			
	Estimate	Standard error	Z value
Intercept	1.75	0.06	29.78
Male mean location error over entire task	0.04	0.1	0.4
Female mean location error over entire task	–0.04	0.09	–0.48

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4B. Brood size: entire task

Elevation (low)	0.09	0.04	2.32
Random effects	Variance	Std deviation	
Year (2015–2023)	0.01	0.07	
Male ID	0.01	0.1	
Female ID	<0.01	0.05	
N=205 nests over 9 years for 108 males and 89 females.			

4 C. Brood size relative to clutch size: first 20 trials

	Estimate	Standard error	Z value
Intercept	0.72	0.1	7.39
Male First 20 trials mean location error	0.02	0.02	1
Female First 20 trials mean location error	0.02	0.03	0.7
Elevation (Low)	0.02	0.02	0.97
Clutch size	0.14	0.01	12.05
Random effects	Variance	Std deviation	
Year (2015–2023)	<0.01	0.04	
Male ID	<0.01	<0.01	
Female ID	<0.01	<0.01	
N=205 nests over 9 years for 108 males and 89 females.			

4D. Brood size relative to clutch size: entire task

	Estimate	Standard error	Z value
Intercept	0.74	0.09	7.93
Male mean location error over entire task	<0.01	0.06	0.03
Female mean location error over entire task	0.05	0.06	0.88
Elevation (low)	0.02	0.02	1.03
Clutch size	0.15	0.01	12.36
Random effects	Variance	Std deviation	
Year (2015–2023)	<0.01	0.04	
Male ID	<0.01	<0.01	
Female ID	<0.01	<0.01	
N=205 nests over 9 years for 108 males and 89 females.			

4E. Mean nestling mass: first 20 trials

	Estimate	Standard error	df	t-Value
Intercept	12.47	0.25	67.48	50.35
Male first 20 trials mean location error	–0.28	0.13	94.91	–2.2
Female first 20 trials mean location error	0.15	0.15	46.89	0.97
Elevation (low)	–0.38	0.13	56.62	–2.86
Random effects	Variance	Std deviation		
Year (2015–2023)	0.1	0.31		

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4E. Mean nestling mass: first 20 trials

Male ID	0.04	0.19
Female ID	0.13	0.35
Residual	0.41	0.64
N=202 nests over 9 years for 107 males and 89 females.		

4 F. Mean nestling mass: entire task

	Estimate	Standard error	df	t-Value
Intercept	12.37	0.22	54.65	56.37
Male mean location error over entire task	–0.19	0.33	131.24	–0.57
Female mean location error over entire task	0.11	0.32	70.54	0.33
Elevation (low)	–0.4	0.13	54.32	-3
Random effects	Variance	Std deviation		
Year (2015–2023)	0.1	0.31		
Male ID	0.06	0.25		
Female ID	0.1	0.32		
Residual	0.41	0.64		
N=202 nests over 9 years for 107 males and 89 females.				

Appendix 2—table 5. Test of whether siring extra-pair offspring affected the offspring in a male's own nest.

Whether a male sired extra-pair offspring or not was compared to (A) brood size, (B) brood size controlled for clutch size, and (C) mean nestling mass.

5 A. Brood size

	Estimate	Standard error	Z value
Intercept	1.78	0.04	45.66
Sired EPY (yes)	0.03	0.05	0.55
Elevation (low)	0.04	0.04	0.95
Year 2020	–0.06	0.04	–1.33
Year 2021	0.06	0.04	1.34
Random effects	Variance	Std deviation	
Male ID	0.01	0.12	
Female ID	<0.01	0.04	
N=144 nests for 99 males and 104 females			

5B. Brood size relative to clutch size

	Estimate	Standard error	Z value
Intercept	0.71	0.1	7.09
Sired EPY (yes)	<0.01	0.03	0.03
Elevation (low)	<−0.01	0.03	–0.17
Clutch size	0.15	0.01	11.41
Year 2020	–0.03	0.03	–0.86

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5B. Brood size relative to clutch size

Year 2021	–0.01	0.03	–0.26
Random effects	Variance	Std deviation	
Male ID	<0.01	<0.01	
Female ID	<0.01	<0.01	
N=144 nests for 99 males and 104 females			

5 C. Mean nestling mass

	Estimate	Standard error	df	t-Value
Intercept	12.41	0.14	134.89	87.98
Sired EPY (yes)	0.26	0.18	134.89	1.45
Elevation (low)	–0.32	0.16	85.75	–1.94
Year 2020	–0.68	0.17	115.82	–3.94
Year 2021	–0.14	0.17	115.13	–0.82
Random effects	Variance	Std deviation		
Male ID	0.12	0.35		
Female ID	0	0		
Residual	0.61	0.78		
N=140 nests for 98 males and 101 females				

Appendix 2—table 6. Test of whether offspring sired by extra-pair fathers differed in mass from offspring sired by social males.

	Estimate	Standard error	df	t-Value
Intercept	12.44	0.15	135.23	82.34
Extra-pair (yes)	0.14	0.08	694.45	1.68
Elevation (low)	–0.50	0.15	121.56	–3.25
Year 2020	–0.71	0.19	124.70	–3.80
Year 2021	–0.16	0.19	122.26	–0.83
Random effects	Variance	Std deviation		
Nest ID	0.59	0.77		
Residual	0.72	0.85		
N=719 offspring from 125 nests				

Appendix 2—table 7. Comparison of spatial cognition scores between social males and extra-pair males they were cuckolded by.

Log-transformed values are reported in (B) – entire task mean location error model.

7A. First 20 trials mean location error model

	Estimate	Standard error	df	t-Value
Intercept	1.00	0.09	37.00	11.21
Father type (social)	0.21	0.05	108.11	3.85
Elevation (low)	–0.10	0.13	27.36	–0.73
Random effects	Variance	Std deviation		

Appendix 2—table 7 Continued on next page

Appendix 2—table 7 Continued

7A. First 20 trials mean location error model

Offspring ID	0.00	0.00
Mother ID	0.10	0.32
Residual	0.11	0.32
N=71 social male-extra-pair male comparisons (71 offspring) from 32 mothers		

7B. Entire task mean location error model

	Estimate	Standard error	df	t-Value
Intercept	–1.07	0.06	42.35	–16.78
Father type (social)	0.11	0.05	107.68	2.44
Elevation (low)	–0.17	0.09	27.30	–1.93
Trials completed	–4.80	0.33	136.81	–14.63
Trials completed^2	1.67	0.33	136.51	5.03
Random effects	Variance	Std deviation		
Offspring ID	0.00	0.00		
Mother ID	0.04	0.19		
Residual	0.08	0.28		
N=71 social male-extra-pair male comparisons (71 offspring) from 32 mothers				

Appendix 2—table 8. Test of whether a male's spatial cognition score was associated with whether he was cuckolded or not.

8 A. First 20 trials mean location error offspring model

	Estimate	Standard error	Z value
Intercept	–2.05	0.75	–2.74
Male first 20 trials mean location error	–0.2	0.4	–0.5
Female first 20 trials mean location error	1.23	0.49	2.49
Elevation (low)	0.52	0.41	1.26
Year 2020	–0.83	0.38	–2.15
Year 2021	–0.55	0.39	–1.4
Random effects	Variance	Std deviation	
Male ID	0.23	0.48	
Female ID	0.41	0.64	
N=348 offspring from 42 females and 42 males over 3 breeding seasons			

8B. Entire task mean location error offspring model

	Estimate	Standard error	Z value
Intercept	–0.79	0.61	–1.31
Male entire task mean location error	–0.67	1.02	–0.65
Female entire task mean location error	0.41	0.97	0.42
Elevation (low)	0.16	0.44	0.37
Year 2020	–0.81	0.4	–2.02
Year 2021	–0.53	0.4	–1.32

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8B. Entire task mean location error offspring model

Random effects	Variance	Std deviation
Male ID	0.05	0.22
Female ID	0.86	0.93
N=348 offspring from 42 females and 42 males over 3 breeding seasons		

8 C. First 20 trials mean location error nest model

	Estimate	Standard error	Z value
Intercept	0.35	1.11	0.32
Male first 20 trials mean location error	0.16	0.67	0.24
Female first 20 trials mean location error	0.35	0.76	0.46
Elevation (low)	0.2	0.64	0.3
Year 2020	0.21	0.73	0.29
Year 2021	–0.73	0.72	–1.01
Random effects	Variance	Std deviation	
Male ID	<0.01	<0.01	
Female ID	<0.01	<0.01	
N=59 nests from 42 females and 42 males over 3 breeding seasons			

8D. Entire task mean location error nest model

	Estimate	Standard error	Z value
Intercept	0.82	0.91	0.9
Male entire task mean location error	0.8	1.72	0.47
Female entire task mean location error	–0.52	1.48	–0.35
Elevation (low)	0.07	0.62	0.11
Year 2020	0.32	0.73	0.44
Year 2021	–0.71	0.73	–0.98
Random effects	Variance	Std deviation	
Male ID	<0.01	<0.01	
Female ID	<0.01	<0.01	
N=59 nests from 42 mothers and 42 fathers over 3 breeding seasons			

Appendix 2—table 9. Test of whether the number of extra-pair young in a nest is associated with spatial cognitive ability.

Results calculated using mean location error over the entire task as fixed effects may be less informative than models using the first 20 trials scores as fixed effects. The total number of trials completed over the entire task is a strong predictor of mean location errors over the entire task, but when mean location errors over the entire task is included as a fixed effect, we could not control for the number of total trials completed over the entire task.

9A. First 20 trials model

	Estimate	Standard error	Z value
Intercept	–0.26	0.55	–0.48
Male first 20 trials mean location error	–0.30	0.30	–1.01

Appendix 2—table 9 Continued on next page

Appendix 2—table 9 Continued

9A. First 20 trials model

Female first 20 trials mean location error	0.92	0.35	2.61
Elevation (low)	0.79	0.35	2.23
Year 2020	–0.70	0.34	–2.09
Year 2021	0.09	0.31	0.31
Random effects	Variance	Std deviation	
Father ID	<0.01	<0.01	
Mother ID	<0.01	<0.01	
N=41 nests with extra-pair offspring from 35 males and 32 females			

9B. Entire task model

	Estimate	Standard error	Z value
Intercept	0.54	0.43	1.27
Male mean location error over entire task	–0.42	0.67	–0.63
Female mean location error over entire task	0.74	0.73	1.02
Elevation (low)	0.33	0.28	1.19
Year 2020	–0.69	0.34	–2.02
Year 2021	0.14	0.30	0.45
Random effects	Variance	Std deviation	
Father ID	<0.01	<0.01	
Mother ID	<0.01	<0.01	
N=41 nests with extra-pair offspring from 35 males and 32 females			