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

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Abstract:

Across animal taxa, females commonly mate with more than one male, even in monogamous mating systems. These extra-pair (EP) copulations and resulting young may increase the fitness of the female via a variety of mechanisms, including genetic benefits. North American chickadees provide an interesting system to study the role of sexual selection via EP paternity, because they are socially monogamous, nonmigratory birds that rely on spatial cognition to recover food stores and variation in spatial cognition is associated with increased survival, longer lifespan, and is heritable. Given spatial cognitive abilities are heritable and associated with direct survival benefits, these abilities may be under sexual selection if males with better spatial abilities sire more offspring and females prefer to mate with such males. We aimed to address these predictions by quantifying extra-pair paternity and comparing spatial abilities of EP males to those of the social male they cuckold in a wild population of mountain chickadees (*Poecile gambeli*). We found that 1. males with better spatial cognitive abilities have more EP 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 suggest that sexual selection is involved in the evolution of spatial cognitive abilities in food-caching chickadees and are consistent with the good genes hypothesis, which posits that females gain indirect genetic benefits via EP young.

Key words: extra-pair mating, spatial cognition, indirect fitness, genetic benefits, sexual selection

Introduction

Understanding the factors that influence mate choice in animals and the consequences that follow from these decisions is a central focus of evolutionary biology (1-5). Numerous hypotheses have been generated to explain patterns of sexual selection, including those associated with the evolution of seemingly arbitrary attractiveness (e.g., runaway selection (6,7)) or sensory exploitation (e.g., sensory drive (8)), and those at the intersection of sexual and natural selection, when sexually selected traits have direct fitness consequences (e.g., good genes (9)). Although it has been recognized for some time that males can be actively involved in mate choice (10,11), considerable work shows that females tend to be the choosier sex, as females often invest more in gamete production and parental care (12-15). Multiple enduring hypotheses argue that females should prefer males of 'high-quality', frequently indicated by secondary sexual signals including ornaments and courtship displays (9,14,16).

In the literature, 'high-quality' refers to everything from sperm competition (17) and parasite load (18), to direct benefits such as parental care, nuptial gifts, or territory quality (19-21), to indirect genetic benefits (e.g., 'good genes') that offspring are likely to inherit (9,16,22,23). Untangling these potential explanations 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 (24). Identifying and quantifying fitness-related traits in the wild that are associated with sexual selection and mate choice can be challenging especially for complex behaviors, like cognition (25).

Cognitive abilities, including associative learning and memory, allow animals to succeed across variable environments, providing predictable variation or a buffer against unpredictable

availability of resources (26,27). 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 (24). Furthermore, when heritable cognitive variation directly confers a fitness advantage, it may be associated with mate preference via secondary sexual signals or by direct observation of mate behavior (28-32). For example, females of several species show preferences for males with better cognition in lab-based, pairwise choice paradigms (30-32), while in the wild, males with better cognition have been shown to produce more young (33,34). However, there is scant evidence from the wild that females prefer males with better cognition (28), and little evidence outside of model organisms that shows heritability of cognitive abilities (35).

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*) over three breeding seasons. Mountain chickadees are nonmigratory, food caching birds that rely on specialized spatial cognition to recover thousands of scattered food stores throughout their territories to survive harsh montane winters (36,37). Following the breeding season, in the temperate autumn, juvenile chickadees are recruited into flocks of unrelated male-female pairs (36). 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 (38, 39). 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 (40, 41) and in

resource abundant years, females lay larger clutches and fledge larger broods when their social male exhibits better spatial learning and memory abilities (42). Furthermore, 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 (43, 44). Finally, we have shown that spatial cognitive abilities remain stable across birds' natural lifespan (e.g., no detectable senescence (45) and does not change with age (40, 41)). 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, specifically (i.e., caches are not used for provisioning young), we predict that spatial cognition should be an important target of sexual selection via extra-pair mating. We have previously shown that social pairs are not formed based on cognitive abilities (46), likely due to the constraints on social mate choice mentioned above. We predicted that males with better spatial cognitive performance will sire more EPY overall compared to their poorer performing counterparts and that females opportunistically obtain EP matings with males that perform better on a spatial cognitive task compared to their social male (9).

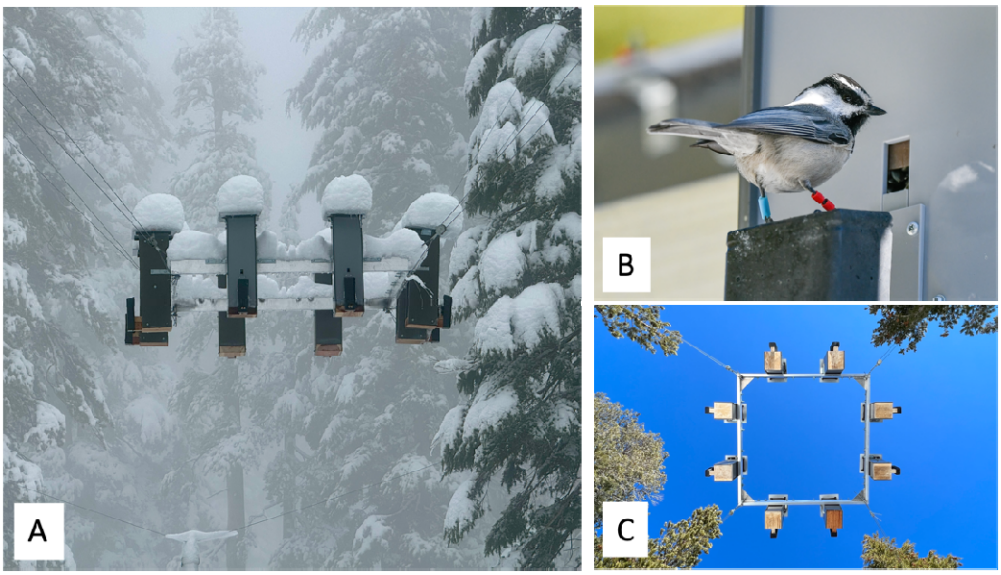

Figure 1. Photographs of spatial cognitive testing apparatus. A. Side-view of one array suspended in the air. B. A mountain chickadee tagged with a passive integrated transponder (PIT) tag visiting the 'smart' feeder array. Motorized door is open. The blue band on the left leg of the bird is the PIT 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 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 2013, we have monitored breeding phenology in uniquely color-banded individuals across two elevations (47,48) and measured the spatial cognitive abilities of hundreds of individuals starting in 2015 (e.g., 40-46, 49, 52-54). 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 (55). 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 m – 2590 m; coordinates: 39.42402, -120.315015 and Low, range: 1965 m – 2070 m; coordinates: 39.443500, -120.243248), following 40-46, 49, 52-54. 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 x 122 cm) aluminum frame suspended ca. 4 m above the ground. Each

feeder is equipped with a small, motorized door. 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, this allowed 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 (54).

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 (40-46, 49, 52-54). 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 (40). 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 (40-46, 49, 52-54). We have previously documented that variation in both metrics is associated with significant differences in survival (40), longevity (41), in female reproductive decisions (42), in foraging decisions (53), and in cognitive flexibility (54). 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 (40, 52). 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 one 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 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 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 kits. 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 (56) 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 one 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 1.5x volume of homemade solid-phase reversible immobilization (SPRI) beads, made with Sera-Mag SpeedBead Carboxylate-Modified Magnetic Particles (Cytiva) (57). These pooled samples (index groups) were sent to Cornell University Biotechnology Resource Center (BRC; RRID:SCR_021727) for size selection between 450 – 600 bp using BluePippin (Sage Science). Following size selection, adapter ligated DNA was enriched by 11 cycles of polymerase chain reaction (PCR) 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 0.7x 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 a ~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 were 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 (43) 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 5 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) (58,59). Variant call format (VCF) files were converted to GENEPOP format using the 'radiator' package in R (60).

Before assigning paternity, we imported the yearly GENEPOP files into CERVUS (61), 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 S8). 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 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' (62). 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.

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 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., 63). 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 (40, 41, 52). For each of the models described, 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 (64). 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 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 (65)), 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 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 in a male's nest was affected by whether the male sired any extra-pair offspring. Elevation, clutch size, and year (3 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 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.

We tested whether the spatial cognitive abilities of extra-pair males differed from 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 score was the 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 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 (40-46, 49, 52-54). Here, we tested whether extra-pair males were significantly older than the social males they cuckolded using a chi-square test.

The cognitive abilities of either the male or female could affect the likelihood of a nest containing extra-pair young, so we tested whether cuckoldry was associated with the spatial cognitive abilities of either parent at the 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 cognition score, elevation, and year as fixed effects. Male and female identity were included as random effects. 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 identity 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.

We also tested whether male spatial cognitive ability differed between nests that had extra-pair young compared to those that did not. 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 total trials 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.

We tested whether the mean number of location errors per trial on the first 20 trials correlated with the mean number of location errors per trial over the entire task for males using a linear model. Mean location errors over the entire task was 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. All statistical analyses were performed in R version 4.1.1 (66) and the residual fit of all models was checked using DHARMa (67). Statistical significance was calculated using Wald Chi-square tests.

Results

Extra-pair paternity and spatial cognition

Extra-pair paternity rates

Across three years of data collection (2018, 2020, and 2021), 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 (EPY). We found no significant differences in the number of extra-pair young sired at 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 confirmed previous research showing that female chickadees seek 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 flocks (36, 39, 68, 69). In addition, breeding male territories do not appear to cluster based on cognitive performance (Figure S4).

Male spatial cognitive abilities and extra-pair paternity

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: χ^2_1=6.28, P=0.012 (Figure 2, dashed line); Mean location errors per trial over the entire task: 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: χ^2_1=5.96, P=0.015 (Figure 2, solid line); Mean location errors per trial over the entire task: χ^2_1=7.68, P=0.006, N=41 (34 individual males; Figure S5). This model suggests that of the males that sired at least one EPY, those with the best cognitive performance may sire between 6 and 7 EPY each year, whereas 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 (41) and lack reproductive senescence within their natural life span (70), therefore, males with better cognition are expected to produce significantly more offspring over their lifetime. Importantly, we show that male age was not associated with the number of EPY sired (see Supplemental Results).

Do males that sire EPY lose reproductive benefits in their own nests?

Three years of EP paternity data suggest that EP males do not lose fitness in their own nests compared to males that did not sire any EP 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 EPY and males that did not sire any EPY. 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).

Social parents' spatial cognitive abilities and reproductive success

In addition to testing how cognitive abilities were related to number of EPY, 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 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).

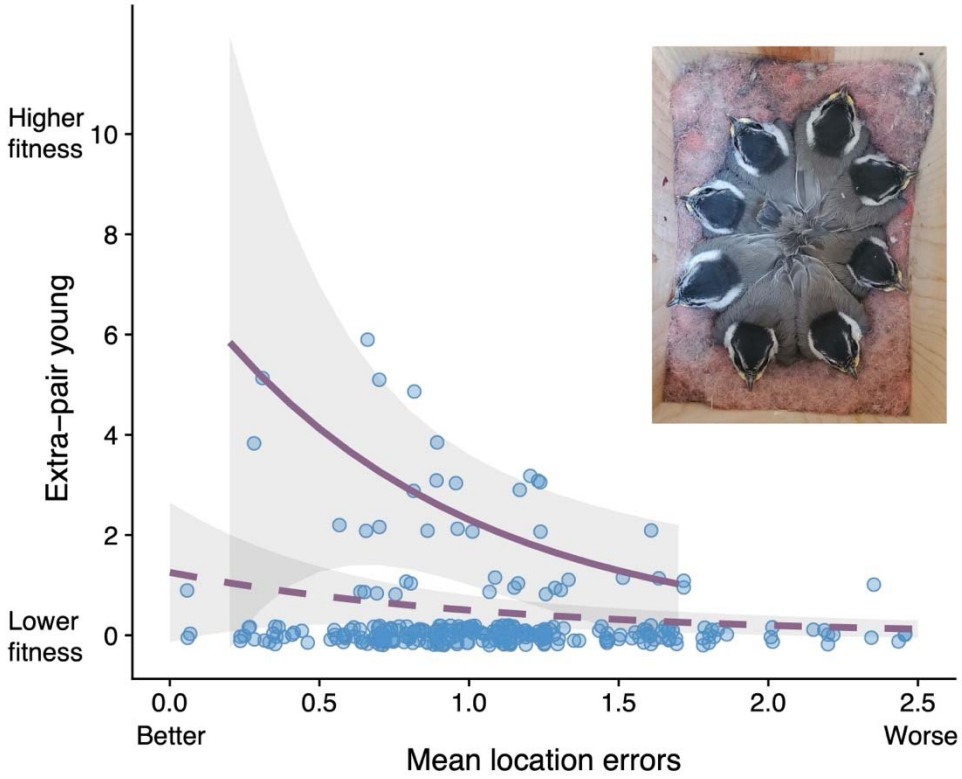

Figure 2. Model predictions of the number of extra-pair young a male sired in a year by the mean number of location errors per trial over the first 20 trials. The dashed line represents a zero-inflated model for all males, including those with no extra-pair young (N=280; 137 individual males), and the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

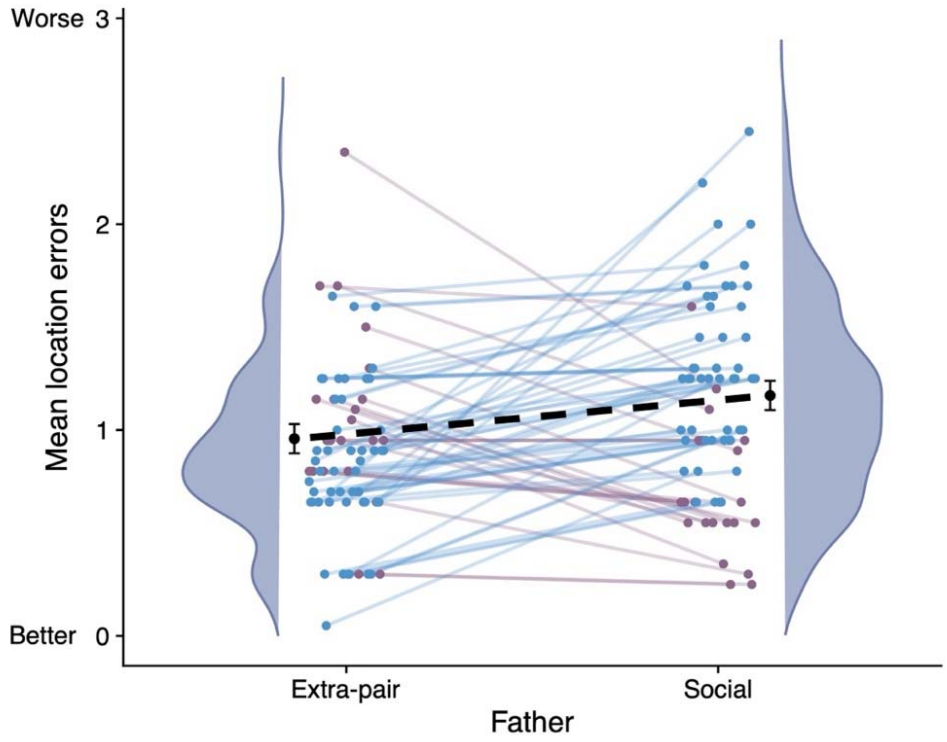

Figure 3. Comparing spatial cognitive performance (mean number of location errors per trial over the first 20 trials) of extra-pair (mean ± SE = 0.96 ± 0.07) and social fathers (mean ± SE = 1.17 ± 0.07, 71 comparisons). Lines connect males by offspring: blue lines show comparisons where the extra-pair 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 father 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 S6.

Does spatial cognition of the social male or female predict presence of EPY?

The finding that extra-pair males have better spatial cognition than the social male of the nest (on average) could suggest that when females obtain EP copulations (EPC), they may do so preferentially with males that have better cognition than their social male. But it is also possible that female cognitive abilities influence their own decisions to seek EPC (i.e., a female may seek EPC to compensate for her own poor cognition). Therefore, we assessed whether the likelihood of having EPY in the nest was related to the spatial cognitive abilities of the social male or the female. The likelihood of being cuckolded was not significantly related to the cognitive abilities of the social males (Offspring level: Mean location errors per trial over first 20: 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 offspring for 42 males; Nest level: Mean location errors per trial over first 20: χ^2_1=0.05, P=0.808; Mean location errors per trial over the entire task: χ^2_1=0.22, P=0.642, N=59 nests for 42 males). In addition, male age did not significantly affect the likelihood of a male being cuckolded (see Supplemental Results). However, females who performed worse on the first 20 trials of the 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 may not engage in EPC

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 (though we are speculating here, as we did not assess all EPC attempts in the system, only those that resulted in young). Nevertheless, males with better spatial cognitive abilities have higher fitness; they produce more EPY overall and we found no evidence of a trade-off for producing more EPY, as cuckoldry rates and reproductive output (brood size and fledgling mass) were similar among males with better and worse spatial cognitive performance.

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, 65) in their social nests, (b) males with better spatial learning and memory abilities sire more EPY than their poorer performing counterparts and, (c) EP 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 EPY in the nest, rather that the differences in cognition between the EP 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 EPP in our mountain chickadee system and do not have data on all EPC 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 EPP may be driven by females for several reasons; 1. Female parids (chickadees and tits) are

known to pursue EPCs with neighboring males (68, 69, 71-74), 2. Parids have never been reported or observed engaging in forced copulation (e.g., 36, 74, 75), 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 EPC (1, 9, 14). In other words, males would benefit from siring EPY 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 (76, 77) and cognitive performance is not associated with social dominance (78). Females, on the other hand, would benefit from obtaining EPCs with males that have better spatial cognition than their social male, as this trait is heritable (43, 44) and would increase the likelihood of producing offspring with better spatial cognition, leading to higher overwinter survival (40) and longer lifespan (41). Indeed, females that performed worse on the spatial cognitive task had more EPY in their nests, while social male cognitive performance did not predict EPY in the nest. This suggests that females may compensate for their poor cognitive abilities via EPY. Considering that alleles associated with better spatial cognitive abilities are not sex linked (43), producing EPY 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 (79).

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 (1, 9, 28, 80). Recent work in closely related black-capped chickadees shows that male cognitive performance is associated with variation in plumage patch brightness and contrast (80). 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 (30, 38), as chickadees are nonmigratory, sedentary birds that aggregate in flocks of unrelated male-female pairs throughout the nonbreeding season and break apart once breeding commences (38, 39). Data from this study confirm previous research showing that female chickadees seek EPCs with neighboring males (68, 69, 74), which would likely be males from their winter flock (38, 39). 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 (40, 41).

An alternative hypothesis for our findings is that females seek EPCs with other males as insurance against the social male's infertility (81), 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 life span (45, 70). In fact, chickadees with better spatial cognition live longer allowing them to produce more offspring over their lifetime compared to chickadees with worse cognition (41).

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 (42). Together with the present findings, we suggest that female mating decisions, including EPCs and reproductive investment, may vary opportunistically. When resources are abundant, females lay larger clutches if their social male has better cognitive abilities (42), and when males with better spatial cognition than her social mate are available for EPCs, they pursue those opportunities. Indeed, we found that females with poorer spatial cognition had more EPY 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 likely benefit disproportionately by mating with the highest quality male they can find, which in the case of food-caching birds, means those with better spatial cognitive abilities (40, 41).

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 (82). Then, because females have extra-pair copulations with neighboring males (68, 69, 74), those neighbors would happen to be males with better spatial cognition. However, in our study system, males do not appear to cluster based on cognitive performance (Figure S4),

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 (83), we see no association with dominance status and spatial cognitive abilities in our system (78) or closely related black-capped chickadees (80). 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., 32), previous data from our system do not support these additional alternative hypotheses. Chickadees with enhanced spatial cognitive abilities are not more aggressive (76) nor do they show higher rates of exploratory behavior (e.g., higher space use) (77).

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 (84), considerable variation persists within species (49). 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 (43, 44, 85). 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 (47, 48). Finally, we have documented elevation-related differences in spatial cognition and the hippocampus of mountain chickadees (49, 50), but there is gene flow among elevations (51) 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 EPY and fledging heavier chicks, which are more likely to survive and be recruited into the breeding population (65). We also show that when there are EPY 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 EPC 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 (40, 41).

Acknowledgements

Thank you to Qwahn Kent, Danielle Schaening-Lopez, Alyssa Nowicki, and Beck Kerdman for assistance with DNA extractions and the Cornell University BRC Bioinformatics Core Facility (RRID:SCR_021757) for providing computing power for all bioinformatics. 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).

Funding

Kessel Fellowship from American Ornithological Society (CLB)

Edward Rose Fellowship from Cornell Lab of Ornithology (CLB)

National Science Foundation Graduate Research Fellowship Program, 2019287870 (BRS)

National Science Foundation Graduate Research Fellowship Program, 2020305313 (LMB)

National Science Foundation IOS1856181 (VVP)

National Science Foundation IOS2119824 (VVP)

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Competing interests: Authors declare that they have no competing interests.

Data Availability: All data, code, and materials used in the analysis are available at https://figshare.com/s/ef7f40371b487b9dabca.

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Supplemental Materials for: Male chickadees with better spatial cognition sire more extra-pair young

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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 (40).
2. Life span of chickadees depends on their spatial cognitive abilities - birds with better spatial cognitive abilities live longer (41).
3. Spatial cognitive performance does not change with age (40, 52).
4. Spatial cognitive abilities do not show age-related senescence (45).
5. Spatial cognitive abilities are not associated with social dominance status (78) or with naturally occurring developmental perturbations (86).
6. Individual variation in spatial cognitive abilities is highly heritable and is associated with differences in genes related to cognition and brain development (43, 44).
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 (43, 44), 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 (70).
9. Female cognition is not associated with the number of fledglings (42) 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 (42).
10. Chickadees are socially monogamous species and form long-term social pairs - divorces are rare (87). In addition, it is well established that females leave their territories and visit neighboring male territories for EPCs, which we confirm here, and forced copulation does not occur in chickadees.
11. Social pairing is not associated with spatial learning and memory (46), likely because chickadees form social pairs in Fall and new recruits do not have the choice of any mate - many males are already paired (46, 87), as such the primary way to increase indirect fitness is via EPC.
12. There are no differences in spatial cognitive abilities between males and females (79), 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 (88).

2. SUPPLEMENTAL RESULTS

Across 3 years of data collection on EPCs and reproductive output, we see that on average, there are 1.7 EPY per nest, however, if we constrain this analysis to only nests with at least one EPY,

the mean is 2.5 EPY per nest. Nests ranged from 0% EPY to 100% EPY, 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 S1; see Table S1 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 spatial cognition differ between nests that had and did not have extra-pair young?

Within nests that had spatial cognitive data for the social male, 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 EPY in their nests did not differ from males that had no EPY in their nests (Mean location errors per trial over first 20 trials: mean 1.08 errors vs.

1.01 errors; χ^2_1=0.42, P=0.516, Mean location errors per trial over the entire task: mean 0.38 errors vs. 0.34 errors; χ^2_1=2.07, P=0.150, N=101 nests).

Does male age affect extra-pair paternity?

Male age was not associated with the number of EPY 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 EPY (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=41nests; 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 EPY, social male age did not predict the number of EPY in the nest (χ^2_1=0.23, P=0.635, N=41 nests; 35 individual males).

3. SUPPLEMENTAL FIGURES

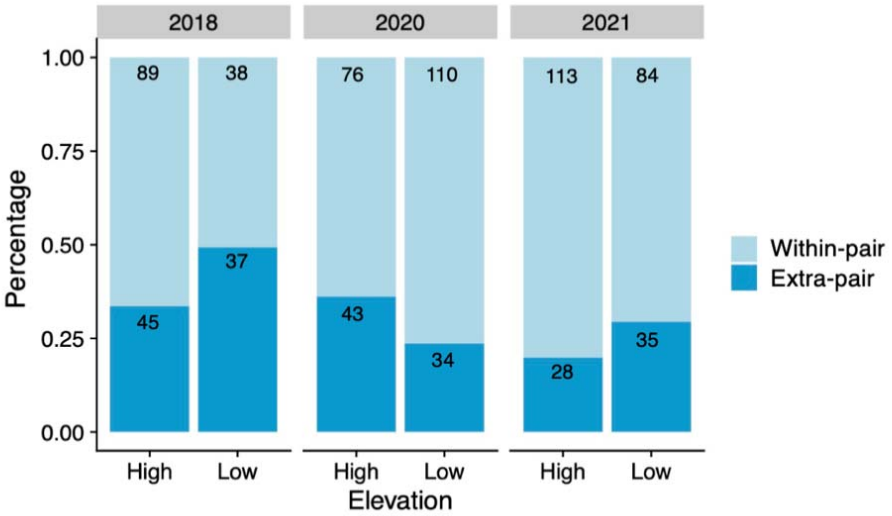


Figure S1. Extra-pair (EPY) and within-pair (WPY) paternity rates across 3 years of data collection and two elevation sites. Number insets represent the number of EPY and WPY for each year and elevation. EPY rates did not differ significantly by year or elevation.

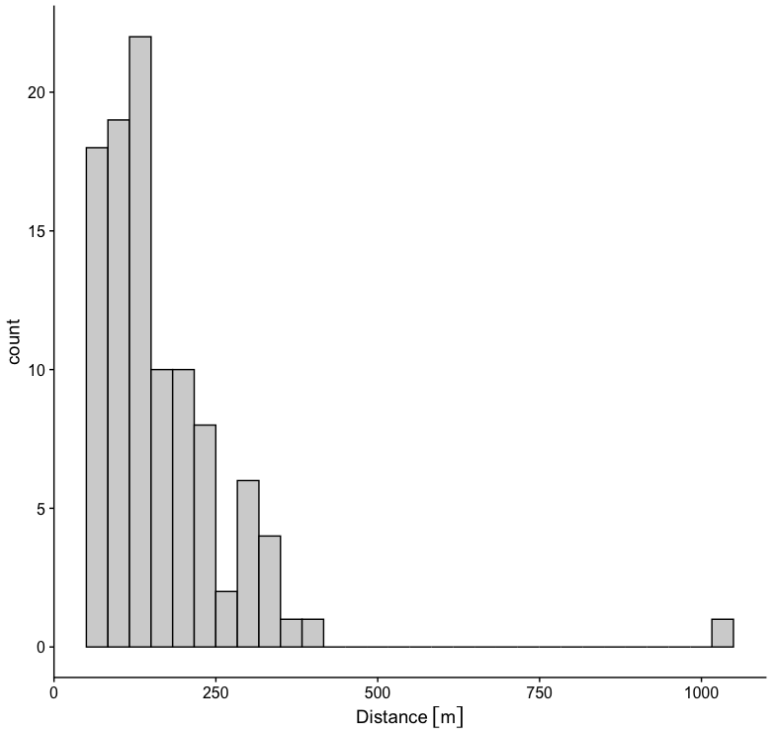


Figure S2. Histogram plotting the distance of extra-pair male nests from the females' nest. Mean = 167 meters and Median = 136 meters. Range is 56 to 1022 meters between nestboxes.

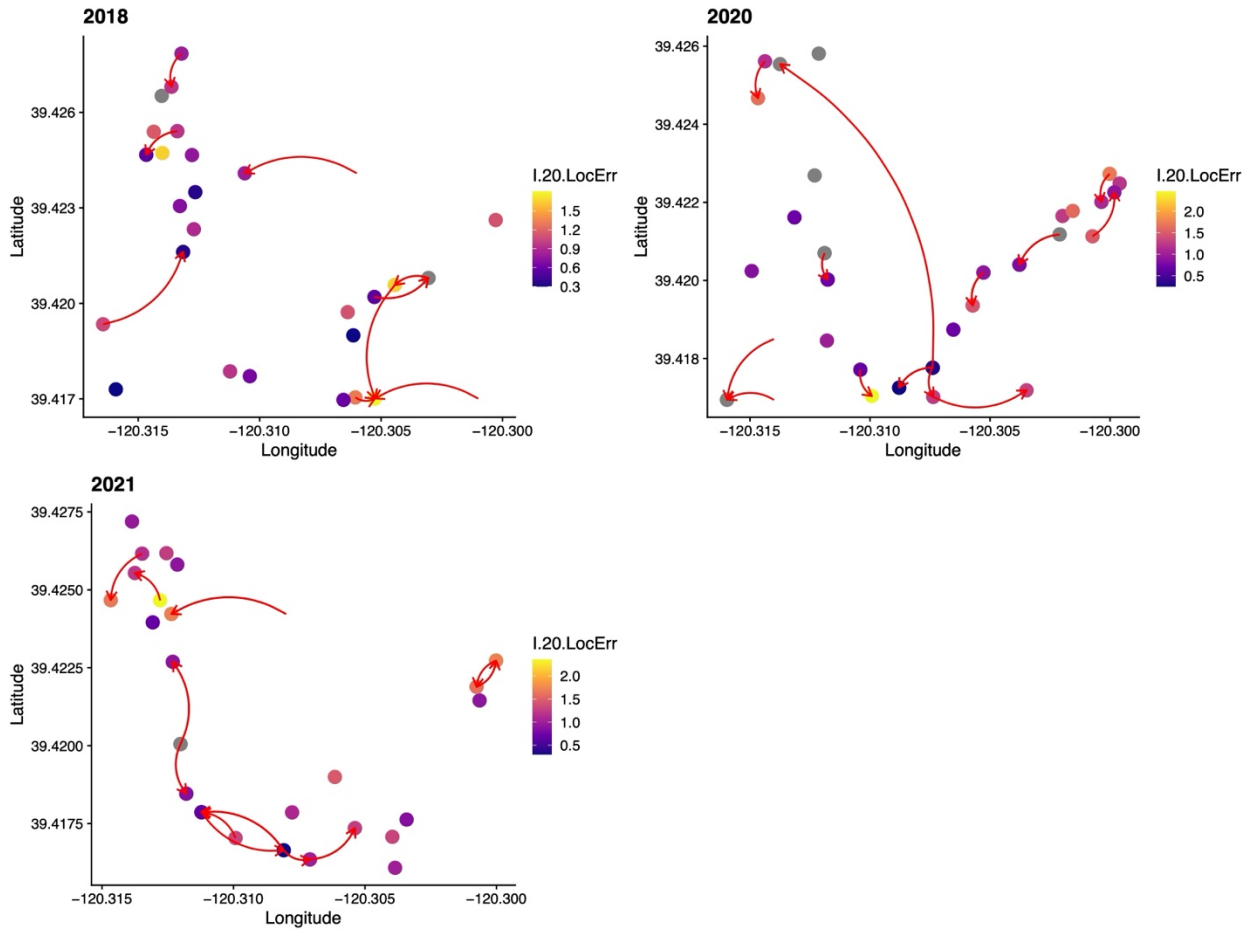


Figure S3a. High elevation extra-pair paternity relationships and cognition scores. Maps show nests with genotyped offspring and the nests of males that sired extra-pair offspring. Red arrows show extra-pair paternity relationships. The direction of the arrow indicates a social male's nest at the blunt end connected to the nest he sired extra-pair young in at the sharp end. Arrows that originate in open space show males that sired extra-pair young but did not breed in our nest boxes in that year (they likely bred in a natural cavity). Point colors represent the cognition scores of the social male at each nest. Gray circles represent males without cognition data. Only nests that included EPY are included on this map, which is a sample of the active nests in each year (Figure S4).

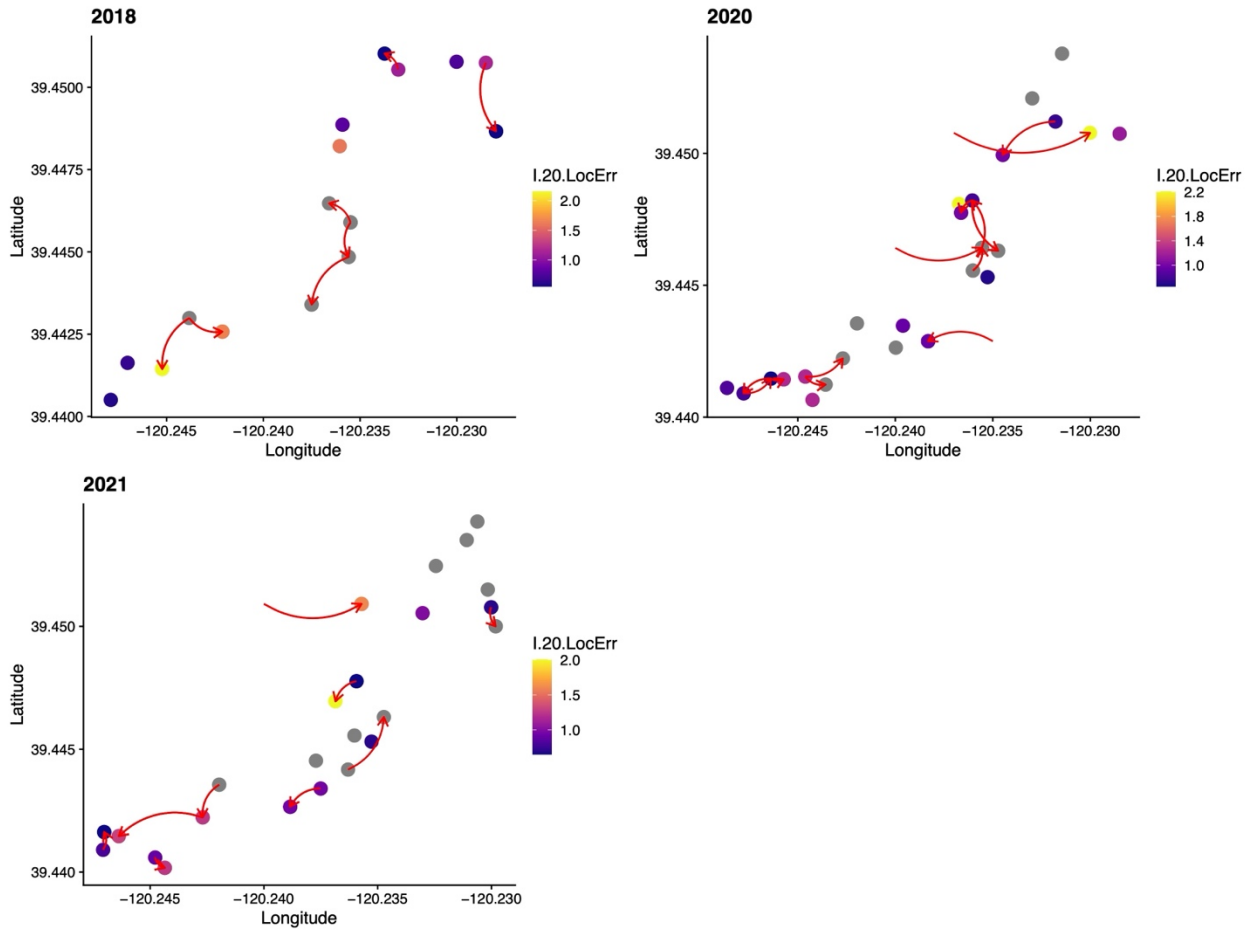


Figure S3b. Low elevation extra-pair paternity relationships and cognition scores. Maps show nests with genotyped offspring and the nests of males that sired extra-pair offspring. Red arrows show extra-pair paternity relationships. The direction of the arrow indicates a social male's nest at the blunt end connected to the nest he sired extra-pair young in at the sharp end. Arrows that originate in open space show males that sired extra-pair young but did not breed in our nest boxes in that year (they likely bred in a natural cavity). Point colors represent the cognition scores of the social male at each nest. Gray circles represent males without cognition data. Only nests that included EPY are included on this map, which is a sample of the active nests in each year (Figure S4).

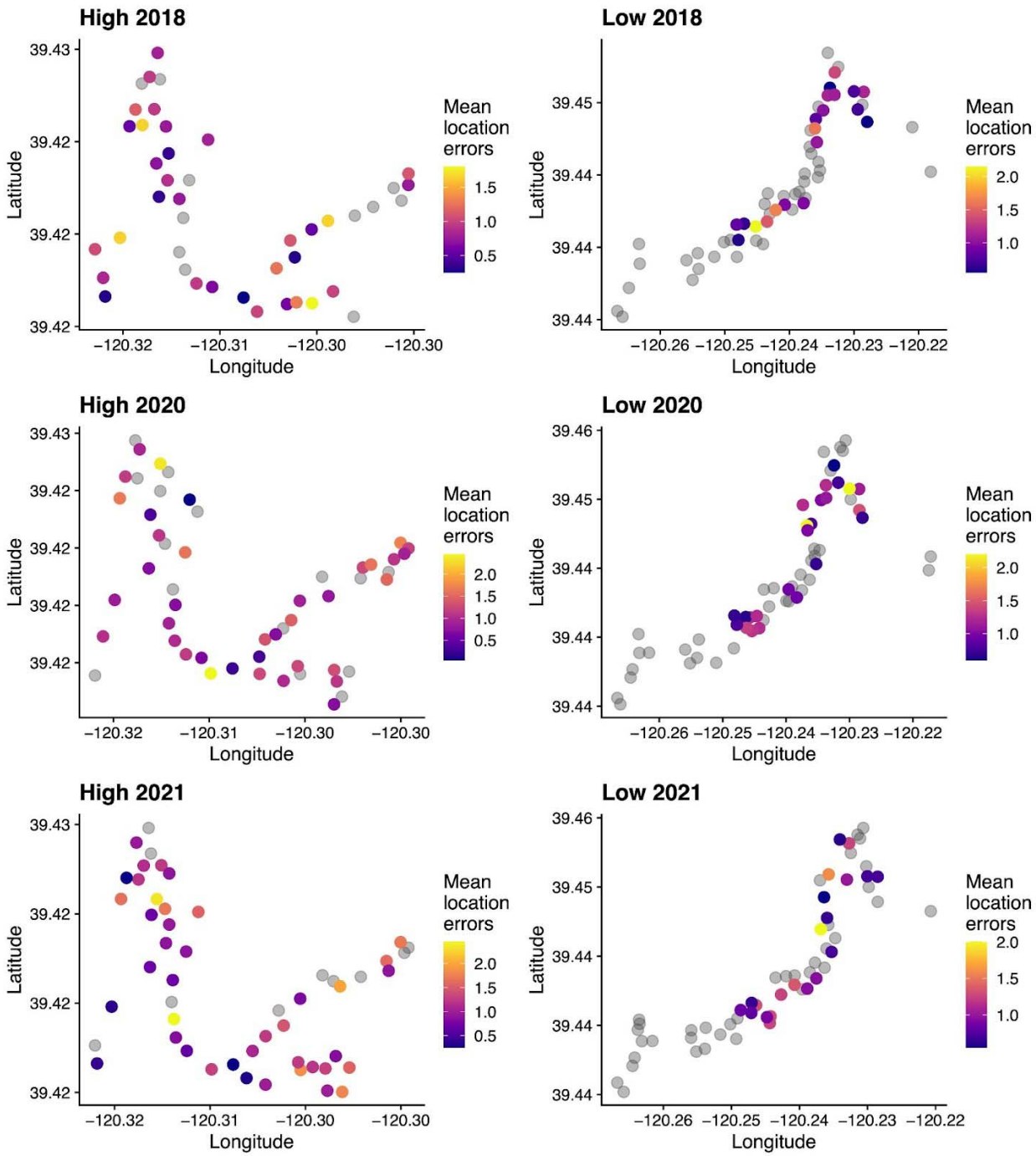


Figure S4. Heat maps of male spatial cognitive scores for high and low elevation nestboxes across the 3 years we have extra-pair paternity data from, including those nests that failed before day 16 or were not genotyped. Each point represents a nestbox. Color gradient represents mean location errors of male on the first 20 trials of the spatial cognitive task. Gray circles indicate nestboxes with no cognitive data for the male. Data shows that nestboxes are not clustered by male cognitive performance. Some of the males on the maps did not participate in cognitive testing until after these breeding seasons, but since spatial cognitive ability does not change with age, we present their scores here as well.

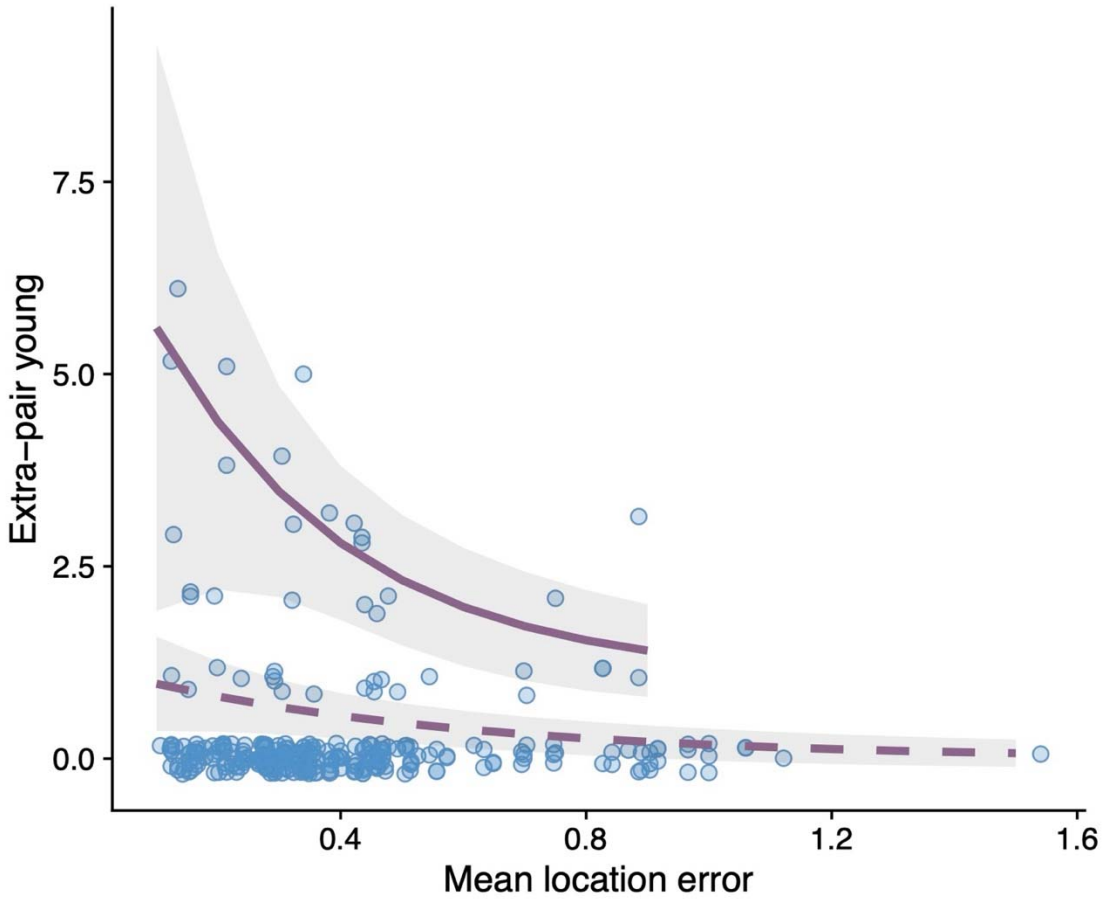


Figure S5. Model predictions of the number of extra-pair young a male sired in a year by the mean number of location errors per trial over the 4-day testing period. The dashed line represents a zero-inflated model for all males, including those with no extra-pair young (N=280; 137 individual males), and the solid line represents the model prediction for males that sired at least one extra-pair young (N=41; 34 individual males). Shading represents bootstrapped 95% confidence intervals. Note: data presented in figure do not account for total trials completed, which was accounted for in statistical analysis.

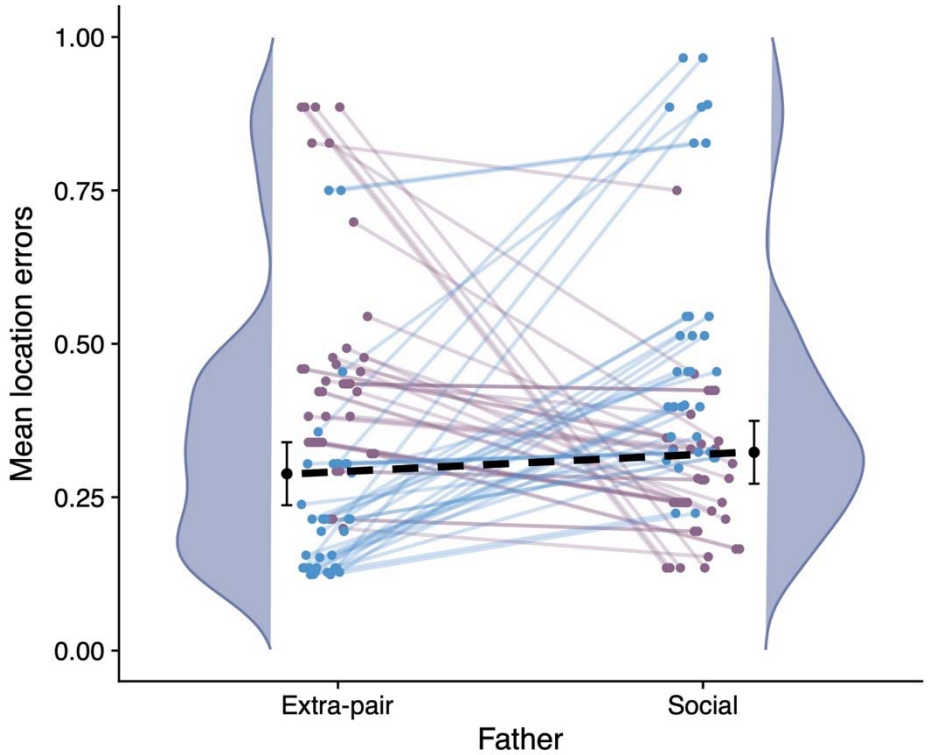


Figure S6. Comparing spatial cognitive performance (mean number of location errors per trial over the 4-day task) of extra-pair and social fathers (total of 71 comparisons). Lines connect males by offspring: blue lines show comparisons where the extra-pair father performed better than the social father (34 of 71 cases or 47.9%), and purple lines show comparisons where the social father performed better than the extra-pair father (37 of 71 cases or 52.1%). Shaded distributions represent smoothed histograms of cognitive performance. Note that the data presented in the figure do not account for the total number of trials completed, which was accounted for in the statistical analysis.

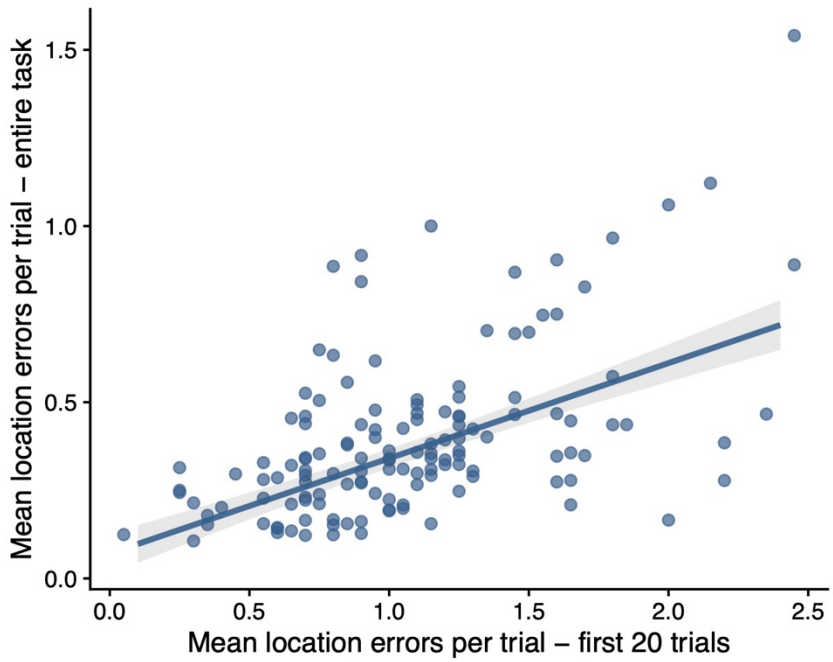


Figure S7a. There is a strong positive correlation between the number of location errors on the entire 4-day task and on the first 20 trials for males completing the task (Coef=0.27, F=121.72, P<0.001).

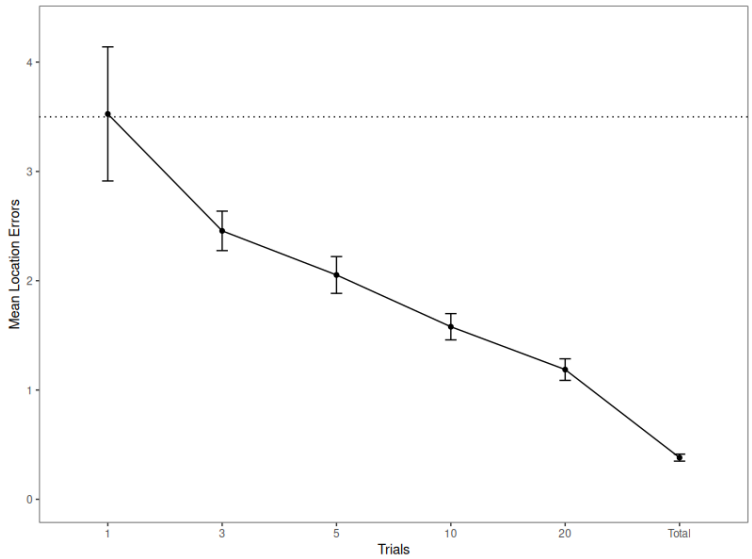
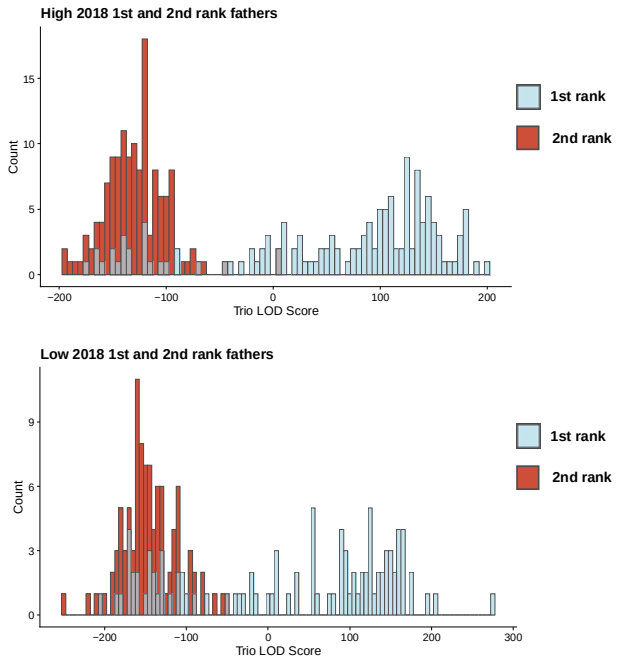
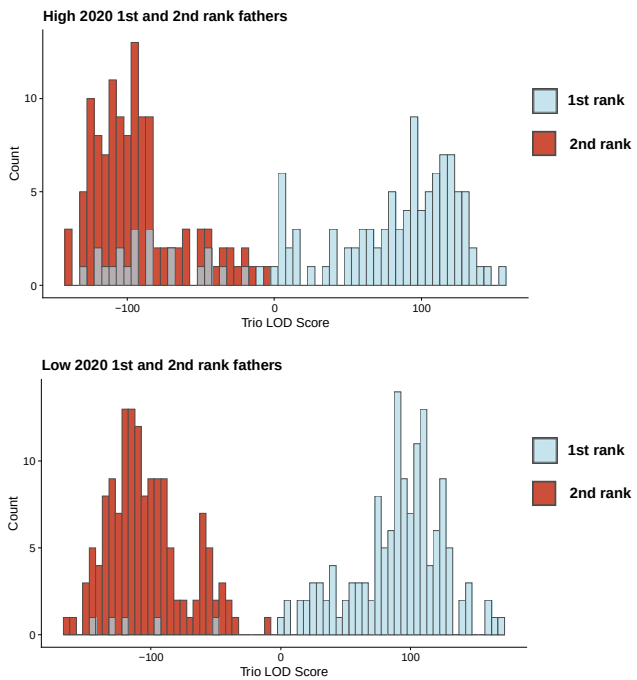


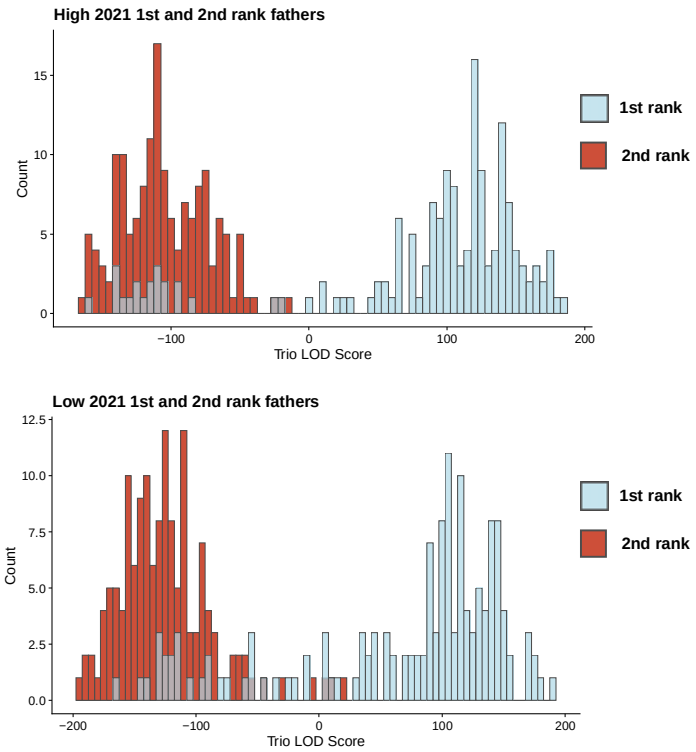
Figure S7b. Representative learning curve of 19 males included in the extra-pair paternity analysis, from the 2021 breeding season. Dotted line represented chance level performance on the task at 3.5 mean location errors. Curve includes performance on trials 1 – 20 and over the entire 4-day task. Errors bars represent standard error of the mean.


High 2018 1st and 2nd rank fathers
Count
Trio LOD Score
1st rank
2nd rank
Low 2018 1st and 2nd rank fathers
Count
Trio LOD Score
1st rank
2nd rank

8A.


High 2020 1st and 2nd rank fathers
Count
Trio LOD Score
1st rank
2nd rank
Low 2020 1st and 2nd rank fathers
Count
Trio LOD Score
1st rank
2nd rank

8B.



8C.

Figure S8. Comparisons of Trio LOD scores for 1st and 2nd ranked potential fathers for each offspring by elevation and year. Note the mostly bimodal distribution in which 1st-ranked males (blue) consistently out-performed 2nd-ranked males (red). Offspring with low 1st-ranked male Trio LOD scores are cases where we did not sample the offspring's genetic father.

4. SUPPLEMENTAL TABLES

Table S1. 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%

Table S2. 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

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

Table S3. 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.

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

Conditional model	Estimate	Standard error	Z value
Intercept	0.40	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	1.70
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	0.50	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)

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

Conditional model	Estimate	Standard error	Z value
Intercept	0.18	0.46	0.40
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
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	1.50
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)

Table S4. Relationship between male and female spatial cognitive ability (mean location errors per trial over the first 20 trials) and breeding performance.

4A. Brood size

	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	2.10
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 relative to clutch size

	Estimate	Standard error	Z value
Intercept	0.72	0.10	7.39
Male First 20 trials mean location error	0.02	0.02	1.00
Female First 20 trials mean location error	0.02	0.03	0.70
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.

4C. Mean nestling mass

	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	-2.20
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)	0.10	0.31		
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.

Table S5. 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.

5A. 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	0.10	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
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

5C. 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	0.00	0.00		
Residual	0.61	0.78		

N=140 nests for 98 males and 101 females

Table S6. 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

Table S7. Comparison of spatial cognition scores between social males and extra-pair males they were cuckolded by. Log-transformed values are reported in Table 4B – 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		
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

Table S8. Test of whether a male's spatial cognition score was associated with whether he was cuckolded or not.

8A. 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	-0.20	0.40	-0.50
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	-1.40
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	0.40	-2.02
Year 2021	-0.53	0.40	-1.32
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

8C. 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)	0.20	0.64	0.30
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	0.90
Male entire task mean location error	0.80	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

Table S9. Test of whether the number of extra-pair young in nests with at least one extra-pair young is associated with spatial cognitive ability (performance on the first 20 trials).

	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
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.