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Inbreeding avoidance and cost in a small, isolated trout population

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The persistence of small populations is influenced by the degree and cost of inbreeding, with the degree of inbreeding depending on whether close-kin mating is passively or actively avoided. Few studies have simultaneously studied these factors. We examined inbreeding in a small, isolated population of westslope cutthroat trout using extensive genetic and demographic data. Passive inbreeding avoidance was low, with predicted lifetime dispersal of approximately 36 and 74 m for females and males, respectively. Additionally, we found limited evidence for active inbreeding avoidance during reproduction. Relatives remained spatially clustered into adulthood, and observed relatedness among mate pairs was greater than expected under random mating by 0.09, suggesting that inbreeding is a concern in this population. Further, we examined sex-specific inbreeding depression throughout the life cycle and provide evidence for inbreeding depression in some fitness components, including family size, juvenile survival and reproductive success. Our results suggest that, in an at-risk trout population, limited passive and active inbreeding avoidance lead to a higher degree of inbreeding than expected under random mating. Observed inbreeding, along with evidence for fitness reduction due to inbreeding depression, could put the population at a heightened risk of decline or extirpation.

1. Introduction

Countless populations are threatened by habitat loss and fragmentation [1,2]. A major concern is that small, isolated populations are at increased risk due to inbreeding, which can interact with stochastic demographic and environmental processes to drive extirpation [3]. Inbreeding depression—the reduction in fitness of offspring with related compared with unrelated parents—appears to be a significant threat in wild populations [4]. For example, it has been found to decrease population growth in Alpine ibex (*Capra ibex ibex*) [5] and increase extirpation risk in the Glanville fritillary butterfly (*Melitaea cinxia*) [6]. Concerns over inbreeding depression have led to recent calls for increased genetic management of small, at-risk populations [7].

The population-level consequences of inbreeding can vary substantially depending on the individual fitness cost (i.e. inbreeding depression) and degree (i.e. mean inbreeding coefficient) of inbreeding. The degree of inbreeding is generally elevated in small populations due to the inevitable increase in relatedness among parents compared with large populations [8,9]. The degree of inbreeding is also influenced by whether individuals in a population exhibit inbreeding avoidance, which can occur through both passive and active mechanisms. Passive inbreeding avoidance occurs through processes that lead to spatial separation of opposite-sex kin, such as natal or mating dispersal [10], which decreases the likelihood of mating between close-kin. Active inbreeding avoidance involves behavioural mechanisms that allow individuals to recognize and discriminate among kin and non-kin during mate choice [10]. Despite the possibility for both mechanisms to decrease the degree of inbreeding in a population, few studies have jointly examined active and passive inbreeding avoidance.

Inbreeding avoidance is not necessarily expected in wild populations [11,12]. Selection for inbreeding avoidance requires that additive genetic variation is present in the population and depends on the net fitness costs and fitness benefits that parents experience. The costs of inbreeding avoidance may sometimes be high, e.g. through lost mating opportunities [13,14]. Further, the realized benefits of avoiding reproduction with close-kin may be limited when individuals are unlikely to encounter relatives during mating or inbreeding depression is weak (i.e. low cost of inbreeding) [15]. An often neglected consideration is that close-kin mating can provide an inclusive fitness benefit that under certain conditions favours inbreeding preference, even when inbreeding depression is strong [12]. Theory and recent meta-analytic evidence suggest that inbreeding avoidance may be less common than often thought [12,16]. This finding is particularly important for small, isolated populations because a lack of inbreeding avoidance would increase the threat of extirpation by increasing mean inbreeding coefficients and, as a result, lead to greater population-level consequences of inbreeding [17,18].

Studies that jointly examine inbreeding depression and factors that influence the degree of inbreeding offer important insights into the dynamics of inbreeding. From a basic perspective, accounting for the cost and likelihood of inbreeding may help to explain why studies report variable degrees of inbreeding avoidance and even inbreeding preference [15]. From a conservation standpoint, comprehensive analyses of inbreeding could improve our understanding of how genetic factors influence extinction risk. However, few studies have examined inbreeding avoidance in at-risk populations, and joint analyses of the degree and cost of inbreeding remain rare in any context [15,16].

Westslope cutthroat trout (WCT; *Oncorhynchus lewisi*) in the Missouri River drainage of Montana offer an excellent study system for jointly examining the details and conservation implications of inbreeding. WCT are threatened by invasive trout species [19–21], and now persist exclusively in small, isolated habitat fragments in this region. Many remaining populations have undergone severe bottlenecks, suggesting threats from inbreeding depression could be high [22]. Trout can exhibit long-distance and sex-biased dispersal [23,24], and there is some evidence that they may be able to recognize kin through olfaction [25], providing plausible pathways for both passive and active inbreeding avoidance to occur. Further, the specific population examined here has been isolated in a small patch of stream for approximately 150 years, or roughly 25 generations, a time period over which deleterious mutations may still be segregating in the population (i.e. not purged or fixed) and able to cause inbreeding depression.

Here, we conducted a comprehensive analysis of inbreeding dynamics—including the avoidance, degree and cost—in a small, isolated population of WCT using an extensive genetic and demographic dataset. We address three questions: (1) does inbreeding avoidance occur passively via dispersal or actively during mating? (2) Does spatial genetic structure remain after natal dispersal and does this result in a greater degree of inbreeding than expected under random mating? (3) Does inbreeding depression occur (i.e. does inbreeding have a cost)? Overall, we present one of the most extensive analyses of inbreeding in a wild, at-risk population to date.

2. Methods

(a) Overview

We examined the dynamics of inbreeding in a single population using 5 years of individual-based mark-recapture data along with genotype data for all sampled individuals. The study population was closed to immigration and nearly closed to emigration. This, along with high detection probabilities, allowed us to sample a large proportion of fish in the population. For all captured individuals, we inserted and recorded passive integrated transponder (PIT) tags, recorded body length and stream position (40 m sections), and took a fin clip for genetics. We used the genotypic data to: (1) identify recaptured individuals that were not PIT tagged, (2) call individual sex, (3) estimate the effective population size, (4) estimate relatedness between individuals, (5) estimate individual inbreeding coefficients, and (6) construct a pedigree to estimate family relationships and estimate fitness measures, including family size and reproductive success. The mark-recapture data allowed us to estimate fitness-related and ecological traits, including dispersal, growth and survival. The combination of genetic and demographic data allowed us to additionally examine spawning movement, spatial genetic structure, characteristics of mate pairs and inbreeding depression. Overall, our detailed data allowed us to conduct an exhaustive assessment of inbreeding risk in this vulnerable population.

(b) Taxon and study population

WCT are iteroparous and spawn in late spring with young of year emerging in mid- to late-summer. In the Missouri drainage of Montana, WCT males start to mature at age-2 and females at age-3. WCT in the region can live to at least 8 years [26], although greater ages have been documented. WCT exhibit redd (nest) building behaviour with a polygamous and iteroparous mating system.

We focused on an isolated WCT population in Gold Run Creek, Montana, USA. Gold Run Creek (hereafter, Gold Run) contains a WCT population that likely originated from miners who translocated fish from immediately downstream to upstream of a waterfall barrier in the late 1800s. Although this population likely originated through translocation, the population is still of high conservation relevance due to being one of the few remaining populations in the region that is not hybridized with non-native trout. The Gold Run WCT population is confined by an upstream waterfall to 1.44 km of first-order stream with no tributaries, and is thus a nearly closed system. WCT in Gold Run likely have a later age at maturity and maximum age than most populations in the region [27], and no other fish species occur in Gold Run. This population has low genetic variation relative to WCT populations throughout Montana [22].

(c) Sampling procedures

We measured 40 m sections of the stream starting at the downstream isolation barrier and ending at the upstream barrier. This resulted in 36 40 m stream sections, which allowed us to examine spatial genetic structure and movement. We sampled the entire inhabited length of Gold Run using backpack electrofishing for five summers (2017–2021). We additionally returned to Gold Run to perform a within-year recapture sample 1–2 weeks after the first sampling occasion in 2017 and 2018 to estimate abundance. Sampling occurred during summer, between July 23 and September 6.

For all captured fish, we measured individual total length, recorded stream section of capture and clipped a small piece of the caudal fin for genetic analyses. We inserted 12 mm PIT tags into the body cavity of all fish over 70 mm on the first capture, following general recommendations for salmonids [28]. All captured fish were scanned for PIT tags. Fish were first captured at age-1 because age-0 fish emerge shortly after our annual sampling.

(d) General genetic analyses

We genotyped all captured fish using an existing genotyping-in-thousands by sequencing (GTseq) single nucleotide polymorphism (SNP) panel and restriction site-associated DNA capture (RAD-capture) SNP panel (see electronic supplementary material for laboratory, bioinformatic and genotype filtering methods). The GTseq panel included a highly accurate sex identification marker [29]. After quality-control filtering, we retained 213 SNPs across both SNP panels that were variable in the Gold Run population.

We used a genetic-based estimation of effective population size (N_e) based on linkage disequilibrium using the program *LDNe* [30]. We assumed polygamy and only included alleles with a minor allele frequency of 0.02 or higher [31]. We estimated N_e separately for each year of sampling and included adults that were predicted to have a 0.25 or greater probability of being mature (maturity determination is described in *General demographic analyses*). Our estimates of N_e were based on a mixed age sample, which likely results in estimates to be 70–90% of the true N_e estimate [32]. We estimated relatedness (r_W) [33] in the *R* package *related* [34]. We calculated a genetic estimator of inbreeding that is derived from a genomic relationship matrix (F_{GRM}; [35]). We estimated additional relatedness and inbreeding metrics to test the consistency of estimates. These additional metrics were highly correlated with the measures we used for analyses (electronic supplementary material).

The pedigree was constructed using joint sibship and parentage in *Colony2*. We allowed for polygamy in both males and females, and for inbreeding, which relaxes Hardy–Weinberg assumptions about spatial structure [36–38]. We ran *Colony2* separately for all five cohorts due to the different offspring and parent pools. The offspring in cohort *t* included age-1 juveniles caught at year *t+ 1*, and age-2 fish caught at year *t+ 2*. The potential mother and father groups included all sampled fish stream-wide with a probability of 0.25 or greater of being sexually mature in the cohort year. We used a maturity threshold of 0.25 to be inclusive of potential parents while also reducing the chance of including offspring into the potential parent pool. Parents were called based on a 0.95 probability threshold. We tested our power to determine parent–offspring pairs and full-sibling pairs using the *CKMRsim* package in *R* ([39]; see electronic supplementary material).

The pedigree was used to infer familial relationships and derive several parameter estimates used in the main analyses. The relationships include parent–offspring pairs based on dyads and mate pairs based on triads. Full siblings were inferred based on offspring that shared both parents and were in the same cohort. Full sibling family size was calculated as the number of age-1 full siblings in a family. Annual reproductive success was the number of age-1 offspring assigned to an adult in a given cohort year. Mate pairs included male–female pairs that were assigned the same age-1 or age-2 offspring.

(e) General demographic analyses

Individual length was incorporated into most analyses addressing our three primary questions to account for life-history differences, either directly as a covariate or to infer age or sexual maturity of an individual, as age and maturity data were not directly recorded. We used a growth model to estimate the body length of individuals that were not captured in a given sampling year. We calculated annual growth as the difference in the length (mm) of all fish captured in two sequential years. Individual, annual growth was then modelled with a quadratic term for length using a generalized linear model (GLM) with a normal distribution and a log link, which was used to predict missing length values (electronic supplementary material).

Age-1 fish were determined by visual inspection of sex-specific length–frequency histograms, which typically resulted in a clear trough between age-1 and age-2+ fish (electronic supplementary material, figure S1, table S1). We additionally called newly captured age-2 fish using length–frequency histograms, although troughs were often less clear. Due to greater age uncertainty, the age-2 designation was only used to help identify mate pairs, and not in other demographic analyses. Maturity was based on measured or predicted length in the focal year and a sex-specific relationship between length and probability of maturity (p(maturity)) that was estimated in previous research on WCT in the same region [26] (electronic supplementary material). We used different p(maturity) thresholds to designate potentially mature fish depending on whether the analysis warranted being less or more inclusive of classifying individuals as mature.

For fish not captured in a given year, missing stream sections were set equal to the previous stream section for all time points after the first capture and to the subsequent stream section for years prior to the first capture. Preliminary analyses of the full capture history dataset showed that movement was very limited, suggesting that our assumption of no annual movement for filling in missing positional data was justified. We estimated adult abundance corrected for probability of maturity using the 2 years of within-year mark-recapture surveys (electronic supplementary material).

(f) Q1: does passive or active inbreeding avoidance occur via dispersal or mate selection?

We examined dispersal by estimating annual, sex-specific, linear movement for three life stages: juveniles $p(\text{maturity} < 0.5)$, partially mature $p(\text{maturity} > 0.5 \text{ and } < 0.95)$ and fully mature $p(\text{maturity} > 0.95)$. We included the classification of fully mature to capture fish most likely to have completed natal dispersal. This provided a test of sex-specific passive inbreeding avoidance via natal dispersal. Movement was quantified as the number of 40 m sections separating the locations of capture of a marked fish in consecutive years. Note that we use the phrase ‘annual movement’ to mean the net movement between annual sampling events. Small annual movements could compound to large movements throughout the lifespan of a fish, and inference based on these short time scales could bias estimates of lifetime movement downward [40]. To examine whether annual movements compounded over time, we also quantified the movement of fish age-1 and older over different time spans between samples, ranging from 1 to 4 years.

Annual (net) movements ignore the possibility of seasonal movements, such as during spawning. Spawning movement was calculated as the distance between the section in which the parent was captured during the cohort year and mean section of their age-1 offspring (based on parent–offspring dyads from the pedigree). Note that this incorporates both spawning movement and age-0 movement. Thus, although sampling occurred annually, these analyses together capture the key aspects of movement with regard to inbreeding risk, including natal and spawning dispersal. Mean movements for each of the above categories (e.g. life stage, time span, sex) were estimated using the number of 40 m sections moved as the response variable in a GLM with a Poisson distribution and a log link, which accounted for the discrete, non-negative response. The estimated number of 40 m sections moved was multiplied by 40 m to obtain an approximate distanced moved.

We next examined whether relatedness influenced mate pairing as a test for active inbreeding avoidance. We used a model analogous to a step selection function commonly applied in resource selection studies [41], but instead of selecting for habitat units based on environmental characteristics, here, fish select for potential mates based on mate pair characteristics. Specifically, we examined mate selection intensity using a Poisson generalized linear mixed model (GLMM), which is the likelihood equivalent of a conditional logistic regression commonly applied in step selection functions [41,42]. This framework accounts for the different set of potential mates available to each female during each time period. The dependent variable y_{ftj} was a binary variable indicating whether a mate pair was observed (1) or available but unobserved (0) based on pedigree triads. Given f females with j potential mates in year t, we estimated the relative intensity of mate selection y_{ftj} using:

$$\lambda_{ftj} = \exp\left(\alpha_{ft} + \boldsymbol{\beta}^T \boldsymbol{x}_{ftj}\right),$$

$$\alpha_{ft} \sim Normal\left(0,\ \sigma_\alpha^2\right),$$

$$y_{ftj} \sim Poisson\left(\lambda_{ftj}\right),$$

where α_{ft} is the stratum-specific random intercept (where strata are females within a cohort year), $\boldsymbol{\beta}^T$ is the transpose of the vector $\boldsymbol{\beta}$ of mate selection coefficients, $\boldsymbol{x}_{ftj}$ is the covariate vector and σ_α^2 is the variance for the random intercept. We used a large constant variance for the random intercept ($\sigma_\alpha^2 = 100$) to reduce shrinkage while allowing for more efficient model convergence [42]. Note that this produces similar results as a logistic regression (electronic supplementary material), but provides more robust standard error estimates.

The main covariate of interest was r_W for each potential or observed mate pair. To control for other factors influencing mate selection, we additionally included the stream distance between the mate pair and male length (to account for possible size-based competition and size-assortative mating) during the year of reproduction as covariates. Relatedness and distance between mate pairs were minimally correlated (Pearson’s $r = -0.163$) relative to common thresholds for including multiple covariates (e.g. Pearson’s $r = 0.7$ [43]). One assumption of our model is that the probability of detecting a mate pair was not influenced by inbreeding. Matings between relatives could be harder to detect due to the lower survival of juveniles, which could bias our estimates towards greater inbreeding avoidance.

We specified the available mate pool for each female within each year that she successfully reproduced based on several criteria. The potential mate pool was limited to males who were captured during or after the cohort year to ensure they were alive during mate selection. Second, we only included males with a $p(\text{maturity}) > 0.25$. This maturity threshold was chosen to be more inclusive of the pool of potential mates. For each female in each year, only those males within 280 m of the female were considered potential mates, which was the maximum distance between an observed mate pair (based on pedigree results). Finally, for each female during each year, we randomly sampled 20 males from the remaining mate pool. We subsampled the available mates to a constant number to reduce the computational time while improving model convergence [41,42].

(g) Q2: does spatial clustering of relatives remain after natal dispersal and increase the degree of inbreeding?

We examined the degree to which related males and females were spatially clustered within the stream as both age-1 juveniles and mature adults as an indication of how natal dispersal influenced inbreeding risk. Specifically, we assessed how pairwise relatedness (r_W) changed as a function of stream distance (number of 40 m sections) between pairs of males and females using a linear mixed model with random effects for both male ID and female ID to control for repeated comparisons. Additionally, we calculated the proportion of male and female pairs that were close-kin ($r_W > 0.25$) separated by different numbers of stream sections using a GLMM with a binomial distribution. These relationships were estimated separately for juveniles (i.e. age-1 fish) and fish with a $p(\text{maturity}) > 0.75$ in a given cohort year. We chose a higher maturity threshold for this analysis to focus on the fish that were more likely to be mature and have completed any spawning dispersal. Inference for this question was based on comparison of the relationships between stream distance and relatedness for juveniles versus adults.

To estimate the increase of inbreeding in the population compared with random mating expectations, we performed a *t*-test of relatedness among identified mate pairs (based on triads from pedigree results) and relatedness among all possible mate pairs. Mean relatedness among all possible mate pairs in this population provides a population-specific estimate of random mating, which is preferable to assuming a value of zero. Potential mate pairs were included that had a $p(\text{maturity}) > 0.75$, which was selected because very few observed mates were a length corresponding to a $p(\text{maturity})$ less than this value.

(h) Q3: does inbreeding depression occur?

We examined whether fitness components throughout the life cycle were influenced by inbreeding. For all fitness components, we estimated both the sex-specific inbreeding effects and the combined inbreeding effect. First, age-1 full sibling family size was modelled as a function of parental relatedness (r_W). We used parental r_W instead of the mean family inbreeding coefficient because we did not sample families until age-1, and juvenile mortality of individuals with the highest inbreeding coefficients could have biased F_{GRM} downward. We included maternal length as a covariate to control for length-based differences in fecundity and included year as a fixed effect. Although other factors can influence family size, the remaining difference in age-1 family size should be, in part, based on survival from embryo to age-1, and the effect of r_W can be considered a proxy for influence of inbreeding on embryo to age-1 survival. Family size was modelled using a GLM with a log link and a zero-truncated Poisson distribution. The zero-truncation was used because we could only identify families in which at least one offspring was captured.

We estimated the effect of F_{GRM} on all other fitness components. We also repeated all inbreeding depression analyses using F_H [44] (electronic supplementary material). We modelled age-1 length using linear regression and included year as a fixed effect. We modelled individual, annual growth using a GLM with a normal distribution and a log link. We included individual length as a quadratic term for each sex and year as a fixed effect. We estimated survival using a Cormack–Jolly–Seber model [45]. We included fixed effects for year on both detection and survival probability, and constrained the final 2 years to be the same value to allow for parameter identifiability. For both the growth and survival model, we estimated the effect of F_{GRM} separately for juveniles and likely adults based on a $p(\text{maturity})$ cut-off of 0.5, which was chosen as an intermediate cut-off.

We modelled annual reproductive success as a two part 'hurdle' model [46], which includes the probability of reproduction and, given successful reproduction, the number of offspring produced. Length and year were included as fixed effects in both components for the model. We modelled the probability of successful annual reproduction as a function of F_{GRM} using a GLM with a Bernoulli distribution and a logit link. An individual was designated to be reproductively successful for a given cohort if an age-1 fish was assigned as their offspring at time $t+1$, and was designated to not be successful if it was not assigned an offspring but was in the mate pool for that cohort. The mate pool included fish with a $p(\text{maturity}) > 0.25$ in the focal year to be inclusive of potential mates, and with a final capture occasion of time $t-1$ or later to help control for mortality of unobserved fish. Finally, we modelled the number of age-1 offspring assigned to an individual in a cohort, given successful reproduction, using a GLM with a zero-truncated Poisson distribution with a log link [46].

(i) Bayesian parameter estimation

All models were analysed using Bayesian inference from JAGS [47] in the R program jagsUI [48]. All continuous covariates (e.g. F_{GRM} and length) were standardized to improve model convergence and interpretation. Models were run with a minimum burn-in of 5000 iterations and a minimum of 5000 addition iterations using five chains. Additional iterations were used when model convergence was not reached. Successful convergence was reached in all models based on $\widehat{R}$ values less than 1.1 and visual inspection of Markov chain Monte Carlo (MCMC) chains. We report 95% credible intervals (CRIs) and probabilities of direction (*pd*; the proportion of estimates in the more common direction). All parameter estimates from JAGS are provided in the electronic supplementary material.

Table 1. Sample sizes of captured fish and background information on the population size. The number of sampled fish in Gold Run Creek by year, categorized as either new captures or recaptures, is shown. The effective population size was estimated for mixed age adults (p(maturity) > 0.25) using a linkage disequilibrium-based method and adult population size was estimated using within-year mark-recapture. Parentheses for effective population size and adult population size are the 95% CIs and CRIs, respectively.

year	recaptures	new captures	total captures	mixed age effective size (N_e)	adult population size (N_c)
2017	0	408	408	48.6 (42.5, 55.5)	371.6 (326.3, 429.8)
2018	243	312	555	46.7 (41.8, 51.9)	467.4 (410.6, 541.3)
2019	292	229	521	47.1 (41.6, 53.0)	445.1 (390.7, 516.6)
2020	284	101	385	43.5 (37.5, 50.5)	391.7 (343.9, 457.8)
2021	327	210	537	40.7 (35.1, 47.0)	501.9 (438.2, 592.2)
total	1146	1260	2406		

3. Results

(a) Genetic analysis summary

Parent assignment from our pedigree was high, with 98.7% of offspring assigned to at least one parent, and 73.7% assigned to both (electronic supplementary material, table S2). Power analyses showed high power to distinguish both parent–offspring pairs and full-sibling pairs from unrelated individuals (electronic supplementary material, figure S23). The mixed-age effective population size (N_e) estimates ranged from 40.7 to 48.6 across the 5 years of the study (table 1; electronic supplementary material, table S3).

(b) Demographic analysis summary

Adult population size (accounting for probability of maturity) ranged from 371.6 to 501.9 from 2017 to 2021 (table 1; electronic supplementary material, table S4). After accounting for genetic identification of individuals with shed PIT tags, we captured a total 1260 unique, successfully genotyped fish. We had 2406 capture events, resulting in 1146 recapture events (electronic supplementary material, table S5). The detection probability was high for adults (e.g. 0.66 for 180 mm fish; electronic supplementary material, figure S4, table S6). For instance, of the captured fish that were greater than 180 mm in the final study year, only 3 were new and 110 were recaptures. This indicates that the majority of the adult population was sampled by the final year of the study.

(c) Q1: passive and active inbreeding avoidance

Annual movements were restricted to short distances throughout the lifespan of both males and females (figure 1*a*; electronic supplementary material, table S7, figure S5). Five of six sex-specific life stages had mean annual movements under one 40 m section ($pd > 0.999$ for all five estimates). The lone exception was for large adult males (p(maturity > 0.95)), which moved an average of 1.18 sections annually (95% CRI = 1.01–1.38). Movement was also limited over longer time spans between recaptures—up to 4 years. Although movements of fish captured 4 years apart were greater than annual movements, movements 3 years apart did not significantly differ from those 4 years apart for either males ($pd = 0.77$) or females ($pd = 0.60$). This suggests that 4 year movements approximated lifetime dispersal. As such, the approximate number of 40 m sections moved throughout the lifetime was, on average, 0.89 for females (95% CRI = 0.68–1.14) and 1.84 for males (95% CRI = 1.44–2.31; figure 1*b*; electronic supplementary material, table S8). Approximated lifetime movements were over two times greater for males than females ($pd > 0.999$; figure 2*b*). Spawning movements were larger than net, annual movements but still small, with a mean of 1.97 sections (95% CRI = 1.71–2.26) and 2.14 sections (95% CRI = 1.85–2.47) for females and males, respectively (electronic supplementary material, table S9). Overall, sex-biased dispersal occurred in mature adults, with greater dispersal in males, and spawning movements were larger than annual net movements, but dispersal distances for both sexes were small on average in comparison to the 1.44 km stream.

After controlling for male length and distance between potential mates, individuals showed neither avoidance nor preference for close-kin matings. We found that r_W had no association with the probability of mate pairing ($pd = 0.83$; figure 2; electronic supplementary material, table S10). Larger males were more likely to mate (positive effect of male length; $pd > 0.999$; figure 2), and stream distance between mates reduced mate selection probability, even over short distances ($pd > 0.999$; figure 2).

(d) Q2: spatial genetic structure and the degree of inbreeding

We compared relatedness by distance between juveniles and mature fish to determine whether genetic structure decreased over the lifespan. Relatedness (r_W) decreased by 0.03 (95% CRI = −0.031 to −0.028) with every 100 m of stream distance between pairs of male and female age-1 juveniles (figure 3*a*; electronic supplementary material, table S11). As an example of the decline of relatedness with distance, the proportion of close-kin for juveniles was 0.513 (95% CRI = 0.443–0.583) for fish in the

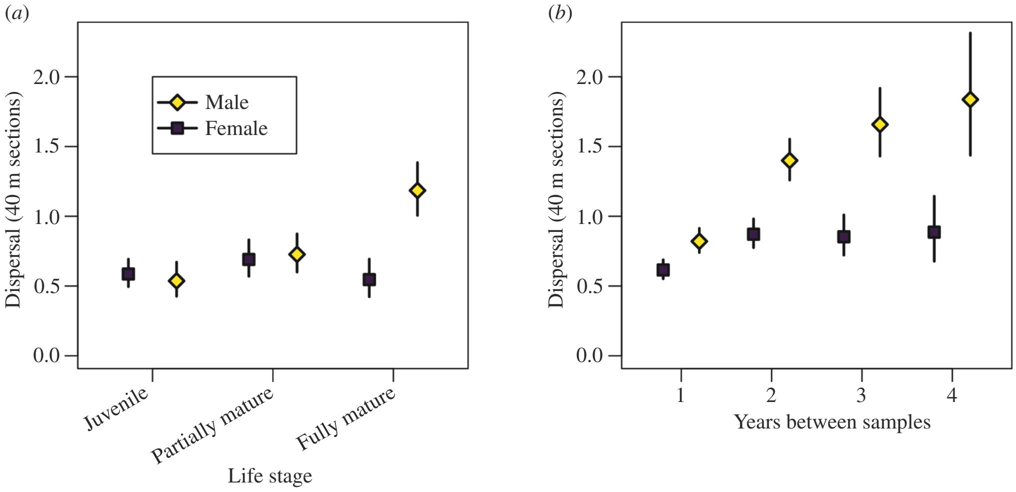

Figure 1. Dispersal is limited to short distances, with males showing greater movement. (*a*) Mean annual number of 40 m sections moved by life stage and sex. (*b*) Mean number of 40 m sections moved by sex based on the number of years between sampling events for fish age-1 and older. Life states in (*a*) include juvenile $p(\text{maturity} < 0.5)$, partially mature $p(\text{maturity} > 0.5 \text{ and } < 0.95)$ and fully mature $p(\text{maturity} > 0.95)$. Estimates are from a Poisson GLM of the number of 40 m sections separating the locations of capture of a marked fish in consecutive years. Error bars indicate 95% CRIs.

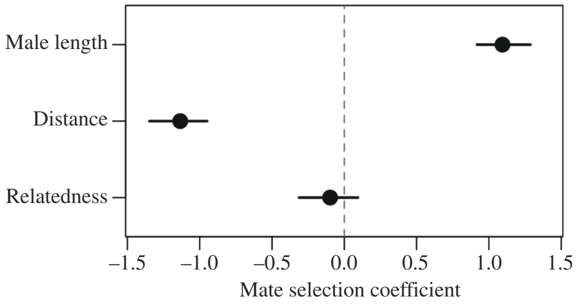

Figure 2. Relatedness has minimal influence on mate pairing. Mate selection coefficients of females derived from a step selection function for male length (mm), stream distance between the male and female (km), and relatedness (r_W) between the potential mate pair. Covariates are standardized, so effect sizes represent the change associated with a 1 s.d. increase in the covariate. Error bars indicate 95% CRIs.

same section compared with 0.064 (95% CRI = 0.035–0.106) for fish 200 m apart (figure 3*c*). Despite small lifetime movement, dispersal reduced the spatial clustering of relatives for reproductively mature adults. The slope of the relationship between r_W and distance between male and female pairs was half as steep for adults compared with juveniles (95% CRI = 50.1%–55.9%; electronic supplementary material, table S12). As an example of the reduction in clustering of relatives, the proportion of adults ($p(\text{maturity}) > 0.75$) in the same section that were close-kin was 0.189 (95% CRI = 0.172–0.208; figure 3*d*) compared with 0.513 in juveniles. Nevertheless, spatial clustering of relatives persisted for pairs of potential mates, based on the observation that both r_W and the proportion of close-kin had negative relationships with stream distance for adults (figure 3*b*,*d*).

We next tested if observed mate pairs were more related than expected under random mating. Mean r_W among observed mates was 0.044 (95% CRI = 0.014–0.075) while mean stream-wide r_W between potential mates was −0.046 (95% CRI = −0.048 to −0.044), an increase in relatedness among observed mates of 0.091 compared with random mating expectations ($pd > 0.999$; electronic supplementary material, figure S6). Close-kin mating occurred in 11.6% of observed mate pairs versus just 4.6% expected under random mating. Six mate pairs had r_W greater than 0.4, which was in the range of relatedness for known parent–offspring pairs (electronic supplementary material), suggesting these mate pairs could be first-order relatives (e.g. parent–offspring or full-sibling pairs).

(e) Q3: inbreeding depression throughout the life cycle

We found evidence for inbreeding depression in several traits throughout the lifespan of WCT (table 2; electronic supplementary material, tables S13–S18). Inbreeding (r_W or F_{GRM}) had significant negative effects (i.e. $pd > 0.95$) on family size and age-1 length for both sexes combined, and on age-1 length, juvenile survival and the annual number of assigned offspring in males. However, we found no significant effects of inbreeding for females. Some of the significant inbreeding effects were likely biologically significant. For example, a 1 s.d. increase in parental r_W reduced family size by 17.5% and a 1 s.d. increase in F_{GRM} decreased the annual number of offspring a male had by 17.3%. Inbreeding analyses using F_H provided similar results, although the effects were generally weaker (electronic supplementary material, table S19).

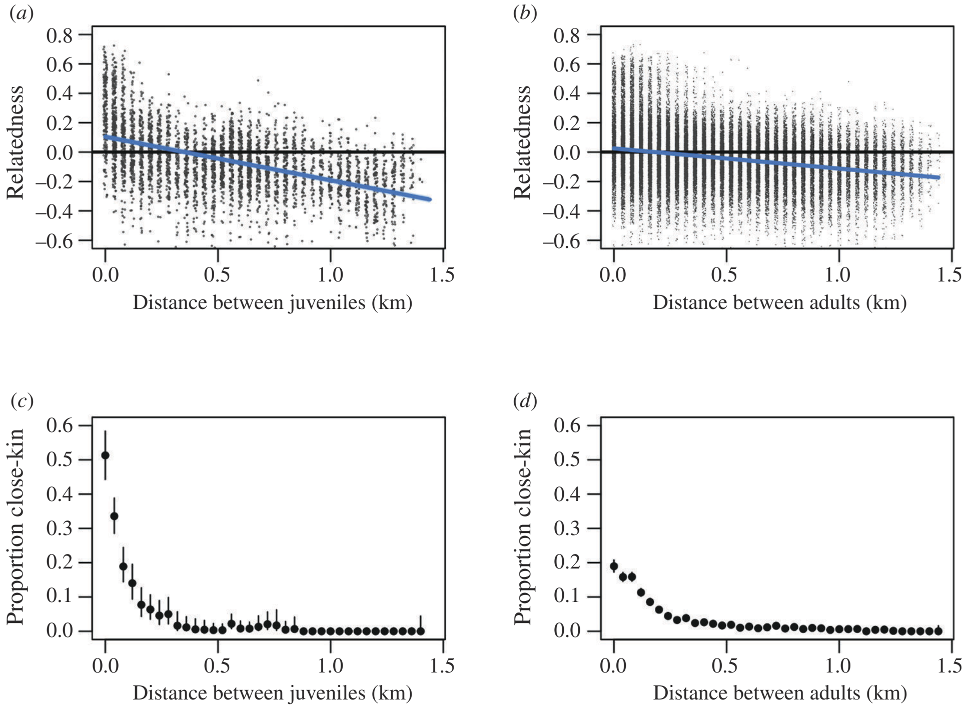

Figure 3. Relatedness (r_W) and the proportion of close-kin decline with increasing stream distance between male and female pairs for juveniles and mature adults. (*a*, *b*) r_W plotted against the distance between male and female pairs (km) for juveniles (*a*) and adults (*b*). (*c*, *d*) The proportion of close-kin (defined here as pairs with $r_W > 0.25$, equivalent to half-siblings) against the distance between male and female pairs (km) for juveniles (*c*) and adults (*d*). Male and female pairs include pairwise comparisons between all age-1 fish within a cohort for juveniles and pairwise comparisons between possible mate pairs in a given cohort for adults. Possible mate pairs include individuals with a probability of maturity ≥ 0.75. The blue trend lines (*a*, *b*) are from linear mixed models that included male and female identity as random effects, and the estimates of close-kin are from a binomial GLMM. Error bars indicate 95% CRIs.

4. Discussion

Our study demonstrates that a small, isolated population of WCT displayed limited passive inbreeding avoidance via dispersal and no active inbreeding avoidance during mate selection. Consequently, clustering of close-kin persisted into adulthood and the observed degree of inbreeding was higher than expected under random mating. Furthermore, we show evidence for inbreeding depression in some fitness components across the life cycle, especially in males. Taken together, our study suggests that inbreeding could threaten the viability of this population.

Dispersal can passively reduce inbreeding by spatially separating close relatives [49]. Despite the ability of salmonids, including WCT, to migrate and disperse vast distances [50,51], lifetime movement is often highly restricted in resident, stream-dwelling salmonids [52]. Consistent with these past results, we found that lifetime dispersal in Gold Run averaged approximately 36 and 74 m for females and males, respectively (based on converting the number of 40 m sections moved to metres moved). In addition to general dispersal, sex-biased dispersal is a common mechanism that reduces close-kin mating [53,54], and it has been documented in a wide variety of vertebrate taxa [55], including salmonids. For example, male brook trout (*Salvelinus fontinalis*) were found to disperse 2.5 times as far as females [24], which is similar to our finding that males disperse more than 2 times further than females throughout their lives. Although dispersal increased the spatial separation of relatives, we show that close-kin remained clustered during mating due to the short absolute dispersal distances. Limited spatial and temporal extent of movement analyses can bias movement estimates downward [23,40], which has led some to suggest that fish movement may be greater than many studies indicate [23]. However, as we sampled the entirety of our study population and tested for movement distances spanning multiple years and during spawning, biases are likely minimal in our study. Despite potential biases in past movement studies in this taxon, the common pattern of minimal movement suggests that clustering of close-kin may be high in many populations of related species.

When the likelihood of mating with close-kin remains high for adults, active avoidance of inbreeding may occur during mating. Active inbreeding avoidance has been documented in several taxa [54], including fishes (e.g. [56]), and can occur through multiple mechanisms. Salmonids can recognize kin based on olfactory cues from shared Major Histocompatibility Complex (MHC) alleles [25,57], providing a plausible mechanism for active inbreeding avoidance during reproduction. However, we found no evidence of active inbreeding avoidance in this isolated trout population. A recent meta-analysis examining laboratory studies found that evidence for active inbreeding avoidance is inconsistent [16], and several studies have documented inbreeding preference despite inbreeding depression (e.g. [58]). Other aspects of salmonid evolutionary ecology may also increase the likelihood of inbreeding that we could not account for, preventing us from conclusively demonstrating that kin were avoided or preferred during mating. For example, timing of reproduction often has a high heritability in salmonid fishes [59], which may further predispose individuals toward mating with close-kin. Nevertheless, the data presented here suggest inbreeding avoidance, either passive or active, was limited in this study population, resulting in a greater degree of observed inbreeding than expected under random mating.

Table 2. Inbreeding depression estimates across the lifespan of WCT shown both separately for each sex and combined. The slope of the relationship between inbreeding coefficients (parental r_W for family size and F_{GRM} for all other models) and eight components of fitness, including family size (an indicator of age-0 survival), age-1 length, juvenile survival, juvenile growth, adult survival, adult growth, probability of successful annual reproduction and annual number of offspring produced given successful reproduction. Survival estimates are from a Cormack-Jolly-Seber model and all other estimates are from GLMs. Juveniles and adults are designated based on a *p*(maturity) of 0.25. Estimates are on the regular scale for age-1 length, the logit scale for survival and probability of reproduction, and the log scale for survival, growth and number of offspring. Inbreeding coefficients are standardized, so effect sizes represent the change associated with a 1 s.d. increase in inbreeding coefficients. Estimates show the posterior mean and posterior s.d. *pd* is the probability of direction and significant effects (where $pd > 0.95$) are highlighted in bold.

parameter	sex	estimate	*pd*
family size	female	−0.24 (0.18)	0.905
	male	−0.31 (0.21)	0.933
	combined	−0.19 (0.11)	**0.957**
age-1 length	female	−0.52 (0.5)	0.849
	male	−1.47 (0.62)	**0.993**
	combined	−0.9 (0.39)	**0.986**
juvenile survival	female	0.22 (0.16)	0.926
	male	−0.37 (0.16)	**0.985**
	combined	0.01 (0.11)	0.501
juvenile growth	female	−0.01 (0.01)	0.779
	male	−0.01 (0.02)	0.76
	combined	−0.01 (0.01)	0.851
adult survival	female	0.09 (0.21)	0.657
	male	0.25 (0.17)	0.94
	combined	0.17 (0.13)	0.912
adult growth	female	0.02 (0.07)	0.631
	male	−0.04 (0.03)	0.898
	combined	−0.03 (0.03)	0.846
reproduction	female	0.15 (0.12)	0.899
	male	−0.06 (0.13)	0.653
	combined	0.06 (0.09)	0.744
number of offspring	female	0.05 (0.11)	0.681
	male	−0.19 (0.11)	**0.958**
	combined	−0.07 (0.08)	0.812

The lack of evidence for inbreeding avoidance observed here could be due to several factors. First, historic selection pressure might have been low under conditions with connectivity, and recently isolated populations, even if facing stronger selection, might not have had enough time to evolve inbreeding avoidance. WCT in Gold Run are thought to have come from a larger downstream source population and to have been isolated for approximately 25 generations, which may not be enough time for evolution by natural section to occur. Second, genetic drift may prevent or overwhelm selection for inbreeding avoidance in small populations [60], such as this one. Our estimates of N_e, even after accounting for the fact that they might be biased downward by approximately 10–30%, suggest that genetic drift could overwhelm natural selection in this population. WCT in Gold Run Creek also have low genetic variation compared with other populations in Montana [22], further suggesting relatively strong genetic drift. Third, additive genetic variation for inbreeding avoidance must be present for evolution by selection to occur [61], and trait variation is generally lower in small populations [8]. These last two points highlight why inbreeding avoidance might not evolve in small, isolated populations that may need it the most. Fourth, passive inbreeding avoidance via dispersal might be less likely to evolve in this population because it is confined to a 1.44 km stream with impassable waterfalls at each end, and fish that move over the downstream waterfall are eliminated from the population. Thus, dispersal could be under asymmetric stabilizing selection with strong selection against large movements. Fifth, iteroparity and polygamy, both of which occur in this species, reduce the cost of incestuous mating as lifetime reproductive success is not solely dependent on one breeding event. Finally, inbreeding can provide an inclusive fitness benefit, which can lead to tolerance or even preference for inbreeding despite inbreeding depression [12], a possibility that is almost universally ignored, especially in conservation contexts where the focus is generally on population fitness (growth rate) rather than individual fitness.

We used detailed fitness and genetic data to examine inbreeding depression throughout the life cycle, which remains rare in studies of wild populations [62]. We found some evidence of inbreeding depression for fitness traits, particularly during early life stages and in males. Despite these findings, inbreeding depression was likely underestimated in this study. Spatial structuring of inbreeding coefficients made it more challenging to separate potential environmental effects from inbreeding on fitness components (electronic supplementary material, figure S7). Additionally, a challenge of our study was that the low genetic diversity in this population limited the number of SNPs (n = 213), which can result in low precision in inbreeding coefficients and can bias estimates of inbreeding depression downward [63]. Despite this limitation, our study included detailed fitness data spanning the entire life cycle, which is rare and equally important for obtaining lifetime estimates of inbreeding depression. Although inbreeding depression may not always translate into population declines [64], the inbreeding depression documented here, along with the high degree of inbreeding, likely places this population at increased risk of decline and extirpation.

Genetic rescue is a conservation action that could improve population viability in small populations suffering from inbreeding depression [65,66]. Genetic rescue is often not performed without a demonstrated risk of inbreeding because of concerns about disease transfer and loss of local adaptations [1]. Our work suggests that isolated trout populations may be at greater risk of inbreeding than often recognized due to a lack of inbreeding avoidance and observed inbreeding depression. Genetic rescue may therefore be warranted in populations such as these because it has the potential to improve population viability.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. Data and code are available at Dryad [67].

Supplementary material is available online [68].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. D.A.B.: conceptualization, data curation, formal analysis, investigation, methodology, visualization, writing—original draft, writing—review and editing; R.P.K.: conceptualization, funding acquisition, investigation, methodology, supervision, writing—review and editing; A.R.W.: conceptualization, funding acquisition, investigation, methodology, project administration, supervision, writing—review and editing.

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

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

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