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## Research article

### Timing of reproduction underlies fitness tradeoffs for a salmonid fish

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Life history diversity is generated and maintained in part by density-dependent fitness tradeoffs that inhibit a single trait value from reaching fixation. While central to our understanding of evolution, demonstrating density dependence in the strength of fitness tradeoffs is difficult in natural systems. The timing of reproduction is a key life history trait that determines access to breeding habitat and exposure of offspring to competitive interactions and environmental conditions. Understanding the processes underlying diversity in reproductive timing will aid efforts to increase adaptive capacity under global environmental change. Here, we used detailed field studies, genetic parentage assignment, and simulation modeling to evaluate the fitness tradeoffs associated with the timing of reproduction for Yellowstone cutthroat trout *Oncorhynchus clarkii bouvieri* in groundwater-dominated tributaries to the upper Snake River, Wyoming, USA. We conducted our study across two years to understand how the strength of tradeoffs changes with population density. We found that early breeders experienced reduced reproductive success relative to later breeders due to the negative impact of nest superimposition (where later breeders construct nests overlapping those constructed previously) on embryo survival. However, as the risk of superimposition declined in the low-density year and early breeders experienced fewer losses, reproductive success became more similar among individuals breeding at different times. Further, in the spring following the critical period for growth and survival, offspring of early breeders had experienced longer growing seasons, attained larger body sizes, and were equally abundant relative to those of later breeders, suggesting that fitness losses due to superimposition may be offset by size-dependent competitive ability and overwinter survival. Our results illustrate a mechanism underlying diversity in the timing of reproduction for salmonids. This type of life history diversity will help to ensure the resilience and stability of salmonid populations attempting to adapt to changing local stressors associated with global climate change.

Keywords: breeding time, density dependence, growth, life history diversity, redd superimposition, selection



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## Introduction

How life history diversity is generated and maintained is a fundamental question in ecology and evolutionary biology (Stearns 1992). Additionally, life history diversity underlies the diversity of responses to environmental change (Braun et al. 2016), which can increase the resilience, resistance, and stability of ecological systems and ecosystem services (Elmqvist et al. 2003, Schindler et al. 2010). Furthermore, life history diversity may provide populations and species with the adaptive capacity needed to keep pace with global environmental change (Moore and Schindler 2022). Understanding the processes driving life history diversification will aid the design of effective conservation strategies and help avoid inadvertently undermining key evolutionary processes.

Fitness tradeoffs associated with different life history strategies generate and maintain trait diversity by inhibiting a single trait value from reaching fixation (Stearns 1989). For example, it is well appreciated that diversity in maturation age is maintained by the tradeoff between current reproduction and future survival (Stearns 1989). However, adaptive landscapes are often non-stationary, as selective pressures shift among years with population demographics (Siepielski et al. 2009). For example, Calsbeek and Smith (2007) showed that stabilizing selection on brown anole lizard *Anolis sagrei* body size under low density conditions shifted to strong directional selection at high densities as increased competition favored larger body sizes. Therefore, the strength of fitness tradeoffs may be density dependent (Mueller et al. 1991, Einum et al. 2008).

The timing of and habitat selected for reproduction influences the physiological state and demographic performance of offspring (Huey 1991). At the population level, the timing of reproduction is under stabilizing selection as reproduction occurs during a short window of optimal conditions and individuals breeding outside of this window experience reduced fitness (Van Noordwijk et al. 1995). However, individual timing relative to the population mean is important as breeding sites are typically occupied in order of habitat quality (Sergio and Newton 2003) and individuals settling later in low-quality habitats experience reduced reproductive success (Fretwell and Lucas 1970, Smith and Moore 2005). This is especially the case when breeding densities are high relative to the availability of suitable habitat, as a greater proportion of breeders are relegated to low-quality sites (Pulliam and Danielson 1991). Population density may therefore mediate selection on reproductive timing via effects on competition for suitable breeding habitat.

The location and timing of reproduction is particularly relevant to salmonid fishes, as females compete for redd (i.e. nest) sites based on the environmental conditions that maximize embryo survival (Clark et al. 2014). As population densities increase and spawning (i.e. breeding) habitat becomes saturated with redds, competition for high-quality habitat is mediated through redd superimposition, where later spawning females construct redds overlapping those

constructed previously (Blanchfield and Ridgway 2005). Superimposition is assumed to reduce reproductive success via the destruction and dislodgement of previously laid embryos (McNeil 1964, Fukushima et al. 1998). Superimposition is therefore one of the primary density-dependent mechanisms regulating salmonid populations, as average reproductive success declines as superimposition becomes more common (Ricker 1954, McNeil 1964). Redds constructed earlier are at greater risk to superimposition relative to those constructed later (McPhee and Quinn 1998). Superimposition exerts directional selection on spawn timing, conferring fitness advantages to later spawners (Hendry et al. 2004, Dickerson et al. 2005). However, as spawner densities decline and superimposition becomes less common, the fitness consequences associated with early spawning likely diminish (Mogensen and Hutchings 2012), although this has not been tested empirically.

While later spawning can minimize the risk of superimposition, selection for earlier spawning is driven by growth and survival advantages conferred to offspring (Elliott 1990, Einum and Fleming 2000). Offspring of early spawners have a competitive advantage over those of later spawners due to earlier access to feeding territories (Cutts et al. 1999). Longer growing seasons may also allow early emerging offspring to attain size thresholds required to utilize larger, more energy-dense prey (Armstrong et al. 2010), critical for overwinter survival. Selection for early reproduction may be reinforced by size-dependent survival overwinter, as juveniles attaining larger body sizes at the end of the growing season experience greater overwinter survival rates (Smith and Griffith 1994). Thus, spawn timing may generate fitness tradeoffs for salmonids (Fleming 1996), the strength of which appears to be density dependent.

Here, we evaluate the fitness tradeoffs associated with the timing of reproduction for Yellowstone cutthroat trout (YCT) *Oncorhynchus clarkii bouvieri* spawning within spring-fed tributaries (those in which streamflow is sourced from groundwater) to the upper Snake River, Wyoming, USA. We assessed tradeoffs by comparing two metrics with direct ties to fitness: reproductive success (i.e. the number of offspring surviving to emergence; Hendry et al. 2004) and offspring body size. Our first objective was to explore how superimposition mediates the relationship between spawn timing and reproductive success. To address this objective, we first quantified the effect of spawn timing on superimposition risk and the effect of superimposition risk on reproductive success. We then used simulations derived from model outputs to understand how population density affects the strength of fitness tradeoffs. We hypothesized that early spawners at high risk of superimposition would experience reduced reproductive success relative to later spawners, but that reproductive success would be more similar at low densities when overall superimposition risk was low. Our second objective was to quantify the effect of spawn timing on growing season length, offspring body size, and family size (number of offspring sharing a maternal parent) following the critical period for growth and survival. We hypothesized

that offspring of early spawners with access to longer growing seasons would attain larger body sizes than those of later spawners. Our results provide insight into the mechanisms that generate and maintain life history diversity.

## Material and methods

### Study system and species

Yellowstone cutthroat trout (YCT) are an integral component of aquatic and terrestrial food webs (Koel et al. 2019) and support an economically and culturally valuable recreational fishery in the Snake River and its tributaries. Spring-fed streams are considered critical YCT spawning habitat given high spawning densities and disproportionately large contributions to the main-stem Snake River (Kiefling 1997, Homel et al. 2015). Spawning typically occurs over a 10-week period between May and July (Baldock et al. 2023a). Young-of-year (YOY, i.e. offspring less than one year of age) emerge from redds in August and September, typically remain resident in streams until the following summer, emigrate to the Snake River as sub-adults, and return to spawn between ages 3 and 5, commonly superimposing on other redds (Kiefling 1997). We evaluated the fitness tradeoffs associated with spawn timing and redd superimposition in two spring-fed streams during the 2019–2021 spawning and YOY rearing periods (Fig. 1a). Lower Bar BC (LBBC) is a tributary of

the Gros Ventre River, its mouth ~0.5 km upstream of the confluence with the main-stem Snake River. Upper Bar BC (UBBC) drains directly into the Snake River ~17 river km NNE of LBBC within Grand Teton National Park. Both streams are fed by high-volume, cold-water spring seeps, resulting in marked stability in stream temperature and flow regimes (Supporting information).

### Field data collection

In 2019 and 2021, we monitored the spatial and temporal distribution of redd construction to evaluate how spawn timing is associated with risk of superimposition. We conducted redd surveys twice weekly beginning in early May prior to the onset of spawning and ceased surveying when spawning activity was not observed for one week (typically late July). We identified redds by the distinctive pot and tail-spill morphology (Gallagher et al. 2007). We took note of whether redds had been superimposed and visually estimated the proportion of the redd surface area disturbed by superimposition (Fig. 1b). We used redd counts and superimposition data from the final survey in each stream and year as the best estimate of total redd abundance and maximal rates of superimposition.

In 2019, 2020, and 2021 on LBBC and 2019 and 2021 on UBBC, we operated picket weirs (May–July) to describe the timing of the spawning migration and collect tissue samples for subsequent genetic analysis (Zale et al. 2012). Adult

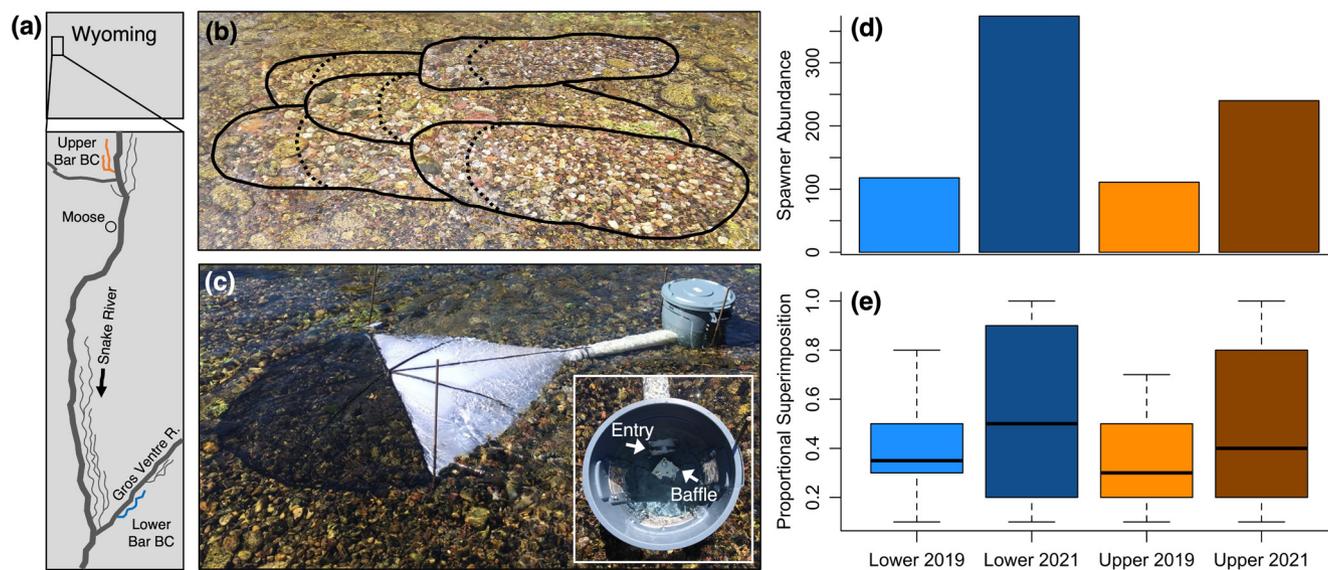


Figure 1. (a) Map of Upper Bar BC (orange lines) and Lower Bar BC (blue line) spring-fed streams within the upper Snake River watershed near Moose, Wyoming, USA. Arrow specifies direction of streamflow. Thick grey lines represent main-stem rivers whereas thin grey lines represent other spring-fed streams. (b) A redd cluster with five superimposed redds (outlined). Dashed lines denote the distinction between the redd pot (area of excavation) and tailspill (location of incubating embryos). Proportional superimposition scores of 0.9, 0.7, 0.4, 0.0, and 0.0 were assigned to redds within this cluster (arranged from most to least affected by superimposition). (c) Custom young-of-year emergence trap based on the designs of Porter (1973) and Field-Dodgson (1983). Inset photo shows detail of the live-well with the entry point and flow baffle noted. Direction of streamflow in (b) and (c) is from left to right. (d) Abundance of migratory, pre-spawn Yellowstone cutthroat trout (YCT) caught in weirs between May and August. (e) Distribution of the proportion of redd surface areas disturbed due to superimposition by a later spawning female (does not include redds unaffected by superimposed, i.e. proportional superimposition = 0).

YCT were measured (total length, mm) and a tissue sample (i.e. fin clip) was collected for genetic analysis. Following weir installation in May, we conducted multi-pass depletion backpack electrofishing (Zale et al. 2012) upstream of weirs to ensure that all potential spawners were represented in our genetic dataset.

During spawning ground surveys, we identified a subset of redd clusters (multiple overlapping and superimposed redds) to monitor for YOY emergence and evaluate the effect of superimposition on YCT reproductive success. We define reproductive success as the number of offspring surviving to emergence from redds, after accounting for the effects of superimposition (Hendry et al. 2004). We selected redd clusters to capture the complete range of proportional superimposition while avoiding areas of high streamflow that would render traps nonfunctional. Following the cessation of spawning activity, we installed teardrop-shaped traps consisting of fisheries grade mesh stretched over a rigid metal frame, where flow through the trap carries emerging YOY into a downstream holding chamber (Fig. 1c; Porter 1973, Field-Dodgson 1983). We deployed four traps in LBBC in both 2019 and 2021, and five and three traps in UBBC in 2019 and 2021, respectively. Two traps failed to catch fish and three were substantially damaged by wildlife; data from these traps were excluded from analysis. The remaining 11 traps covered areas of superimposition ranging from two to five redds (proportional superimposition 0–0.9). We checked emergence traps daily until no YOY were captured for seven consecutive days following the expected date of peak emergence predicted from stream temperature records and 515 Celsius degree days until peak emergence (Kelly 1993). For each trap on each day, we counted all captured YOY and randomly selected approximately 10% to euthanize (overdose of MS-222) for genetic parentage analysis. We chose a minimum daily sample size of five individuals to ensure low catches did not bias parentage results and a maximum daily sample size of 20 individuals to avoid excess mortality. Over the course of the study, this resulted in 27% of captured YOY being euthanized as daily catches were typically low (< 50).

In the spring (May), following the 2019 and 2020 summer spawning periods, we used a single backpack electrofishing unit to sample resident YOY (< 180 mm total length) to understand how offspring body and family size was related to parent spawn timing. Captured fish were measured (total length, mm) and a tissue sample was taken for genetic analysis. A maximum of 100 resident YOY were sampled from each stream in each year. All fish were released within 50 m of their point of capture.

### Genetic parentage analysis

We used genetic parentage assignment to evaluate the effect of redd superimposition on maternal reproductive success and to understand the relationship between spawn timing and resident offspring body size and family size (number of individuals sharing a maternal parent, Hargrove et al. 2021).

This approach allowed us to assign individual offspring (captured in emergence traps or via electrofishing in the spring) to adult parents (captured at weirs) and trace families to specific redds with known levels of superimposition. We extracted genomic DNA from fin clips and screened samples with a single nucleotide polymorphic (SNP) loci panel optimized for parentage studies involving YCT (Hargrove et al. 2021). Genotyping of this panel was performed following the genotyping-in-thousands protocol described by Campbell et al. (2015). Only genotypes  $\geq 75\%$  complete were retained for analyses. See the Supporting information for an in-depth description of genetic analyses.

### Data treatment

To account for differences in average spawn timing among adult cohorts, we converted spawning and migration dates into relative measures by subtracting cohort-specific medians from the date of redd construction and date of weir passage for each redd and adult YCT, respectively (sensu Hulthén et al. 2022). To link our two objectives with a single measure of spawn timing, we considered dates of redd construction and weir passage to be synonymous measures of spawn timing as their relationship approximated a 1:1 relationship for parents successfully assigned to redds monitored with emergence traps (median lag between weir passage and redd construction = 3.5 days, Supporting information).

We assumed YOY captured in emergence traps but not screened for genetics had the same family composition as those that were genetically screened and sampled from the same trap on the same day. For example, if 75% of YOY assigned to parent A and 25% to parent B, the remaining YOY were attributed to those parents at equivalent rates. We calculated maternal reproductive success by summing daily catch of YOY that were assigned to a specific maternal parent across all sampling days. We then matched parents and offspring to a specific redd within the focal redd cluster (with known proportional superimposition) if observed peak emergence corresponded with expected peak emergence from the redd in question, as predicted above. As redds within focal clusters were typically constructed 11 days apart (median, range = 0–40), we were confident parents and offspring would not be erroneously assigned to a redd they did not construct or from which they did not hatch.

### Statistical analysis

We paired a hierarchical Bayesian generalized linear modeling framework with simulations derived from model outputs to explore how superimposition mediates the relationship between spawn timing and reproductive success (objective 1) and quantify the effect of spawn timing on growing season length, offspring body size, and family size (objective 2). Bayesian models included intercept and slope offset terms (i.e. crossed random effects) to understand how modeled relationships varied among streams and years that differed in population density. For each set of offset terms,

we examined distributions of within-sample credible differences (i.e. difference between parameter estimates for each Markov chain Monte Carlo, MCMC, sample) and calculated the probability of direction (the proportion of the distribution that is of the median's sign) to determine the probability that a difference (e.g. between years) is strictly positive or negative (Gelman and Hill 2007, Kruschke 2014).

To address our first objective, we used logistic regression to understand the effect of spawn timing on probability of superimposition (Mogensen and Hutchings 2012):

$$\text{Sup}_{ijk} \sim \text{Bernoulli}(p_{ijk}) \quad (1)$$

$$p_{ijk} = 1 / (1 + e^{-z_{ijk}}) \quad (2)$$

$$z_{ijk} = \alpha_1 + \alpha'_{1,j} + \alpha''_{1,k} + \beta_1 D_{ijk} + \beta'_{1,j} D_{ijk} + \beta''_{1,k} D_{ijk} \quad (3)$$

where  $\text{Sup}_{ijk}$  denotes whether redd  $i$  in stream  $j$  and year  $k$  was disturbed due to superimposition by a later spawning female (0/1),  $p_{ijk}$  is a parameter of the Bernoulli distribution (probability of superimposition),  $z_{ijk}$  is the logistic transformation of  $p_{ijk}$ ,  $\alpha$  is the global intercept,  $\alpha'_j$  is the stream-specific offset to the global intercept,  $\alpha''_k$  is the year-specific offset to the global intercept,  $\beta$  is the global slope,  $\beta'_j$  is the stream-specific offset to the global slope,  $\beta''_k$  is the year-specific offset to the global slope, and  $D_{ijk}$  is the relative spawning date. The numeric component of the  $\alpha$  and  $\beta$  parameter subscripts reflects the applicable model: 1) for probability of superimposition (above), 2) for proportional superimposition, 3) for reproductive success, 4) for body size, and 5) for family size. We then used linear regression to understand the effect of spawn timing on proportional superimposition:

$$\text{logit}(P_{ijk}) \sim \text{Normal}(\mu_{ijk}, \tau) \quad (4)$$

$$\mu_{ijk} = \alpha_2 + \alpha'_{2,j} + \alpha''_{2,k} + \beta_2 D_{ijk} + \beta'_{2,j} D_{ijk} + \beta''_{2,k} D_{ijk} \quad (5)$$

where  $P_{ijk}$  is the proportion of redd disturbed to due to superimposition by a later spawning female (logit-transformed for proportional data),  $\mu_{ijk}$  and  $\tau$  are parameters of the normal distribution, and all other parameters are defined as above. Finally, we modeled reproductive success as a function of proportional superimposition, following a negative binomial distribution to account for overdispersion in count data:

$$R_{ijk} \sim \text{Negative Binomial}(\delta_{ijk}, \text{size}) \quad (6)$$

$$\delta_{ijk} = \text{size} / (\text{size} + \lambda_{ijk}) \quad (7)$$

$$\ln(\lambda_{ijk}) = \alpha_3 + \alpha'_{3,j} + \alpha''_{3,k} + \beta_3 P_{ijk} + \beta'_{3,j} P_{ijk} + \beta''_{3,k} P_{ijk} \quad (8)$$

where  $R_{ijk}$  is the number of offspring produced from a specific redd/maternal parent;  $\delta_{ijk}$ ,  $\text{size}$ , and  $\lambda_{ijk}$  are parameters of the negative binomial distribution;  $P_{ijk}$  is the proportion of redd disturbed to due to superimposition; and all other parameters are defined as above.

We did not include spawn timing in our model of reproductive success as selection of redd clusters to monitor with emergence traps was non-random (i.e. we only selected redd clusters containing two or more superimposed redds such that spawn timing and proportional superimposition were correlated: Pearson's  $r = -0.62$ ). Instead, we used a simulation approach (Gelman and Hill 2007) to understand how superimposition modulates the effect of spawn timing on reproductive success for all redds in our study. For each iteration of our simulation ( $n = 1000$ ), we took random draws from the posterior probability distributions for each parameter of the reproductive success model Eq. 6–8 and simulated YOY production ( $R$ ) given the observed proportional superimposition ( $P$ ) for each redd in our study. In other words, we used Eq. 6–8 to generate 1000 estimates of reproductive success for every redd, accounting for model uncertainty. For each stream and year, we used locally estimated scatterplot smoothing (LOESS) to describe how reproductive success changes as a function of spawn timing and calculated the relative difference in reproductive success between late and early spawners by dividing the fitted value of the LOESS curve at the 95th quantile of spawn timing by that of the 5th quantile.

To address our second objective, we first calculated growing season length as the cumulative growing degree-days (sum of mean daily temperatures above 0) between spawning and juvenile sampling the following spring. Degree-days accounts for temperature-dependent physiological processes driving growth and is a better predictor of body size than time when temperatures are variable (Neuheimer and Taggart 2007). We then used a hierarchical Bayesian linear model to quantify the effect of spawn timing (i.e. relative migration date) on resident YOY body size in the spring following the spawning period:

$$B_{ijk} \sim \text{Normal}(\gamma_{ijk}, \kappa) \quad (9)$$

$$\gamma_{ijk} = \alpha_4 + \alpha'_{4,j} + \alpha''_{4,k} + \beta_4 D_{ijk} + \beta'_{4,j} D_{ijk} + \beta''_{4,k} D_{ijk} \quad (10)$$

where  $B_{ijk}$  is offspring body size (total length, mm),  $\gamma_{ijk}$  and  $\kappa$  are parameters of the normal distribution,  $D_{ijk}$  is the relative spawning date, and all other parameters are defined as above.

Table 1. Yellowstone cutthroat trout (YCT) migration and spawning period characteristics in Lower Bar BC and Upper Bar BC streams. Populations can be parsed into low (2019) and high (2021) density spawning years. The occurrence of superimposition refers to the proportion of redds that were superimposed into redd clusters. The extent of superimposition refers to the proportion of redd surface area disturbed due to superimposition by a later spawning female, excluding redds unaffected by superimposition.

	Lower Bar BC		Upper Bar BC	
	2019	2021	2019	2021
Migration period (days)	9 May–31 Jul (83)	15 May–13 Jul (59)	12 Jun–28 Jul (46)	21 May–6 Jul (46)
Redd construction (days)	9 May–27 Jul(79)	25 May–14 Jul (50)	19 Jun–3 Aug (45)	5 Jun–14 Jul (39)
Spawner abundance	130	362	104	247
Redd abundance	47	168	59	162
Spawner body size, mm (range)	190–470	135–520	315–510	231–485
Occurrence of superimposition	65%	74%	63%	70%
Extent of superimposition (mean $\pm$ SD)	0.38 $\pm$ 0.23	0.55 $\pm$ 0.31	0.34 $\pm$ 0.18	0.49 $\pm$ 0.31

We used a similar model structure to quantify the effect of spawn timing on resident YOY family size, following a negative binomial distribution to account for overdispersion in count data:

$$F_{ijk} \sim \text{Negative Binomial}(v_{ijk}, \zeta) \quad (11)$$

$$v_{ijk} = \zeta / (\zeta + \varphi_{ijk}) \quad (12)$$

$$\ln(\varphi_{ijkl}) = \alpha_5 + \alpha'_{5,j} + \alpha''_{5,k} + \beta_5 D_{ijk} + \beta'_{5,j} D_{ijk} + \beta''_{5,k} D_{ijk} \quad (13)$$

where  $F_{ijk}$  is offspring cohort size (number of siblings),  $v_{ijk}$ ,  $\zeta$ , and  $\varphi_{ijk}$  are parameters of the negative binomial distribution,  $D_{ijk}$  is the relative spawning date, and all other parameters are defined as above.

All models were analyzed in the Just Another Gibbs Sampler (JAGS) MCMC sampling environment (Plummer 2003), implemented through R ([www.r-project.org](http://www.r-project.org)), using the 'HDInterval', 'lubridate', 'MCMCvis', 'R2jags', 'scales', and 'tidyverse' packages (Supporting information). We assessed model convergence based on large effective sample sizes, low Gelman–Rubin scale reduction factors ( $\hat{R} < 1.001$ ), and visual inspection of MCMC trace plots (Gelman and Hill 2007). JAGS models were run with broad parameter prior probability distributions (Supporting information).

## Results

### Field sampling and genetic analysis

Among all adult cohorts, the YCT spawning migration and redd construction periods occurred between early May and early August (Table 1). Cohorts can be parsed into low (2019) and high (2021) density years, as spawner and redd abundances were 2.4–3.6 times greater in 2021 compared to 2019 (Table 1, Fig. 1d). Superimposition was common throughout our study; however, both the occurrence and extent of superimposition were greater in the high-density

year (2021) relative to the low-density year (2019; Table 1). Of the redds that were disturbed due to superimposition, proportional superimposition was significantly greater in 2021 than in 2019, but did not differ among streams (Tukey HSD,  $p > 0.05$ ; Fig. 1e). All (100%) adult YCT genotyped successfully ( $\geq 75\%$  completeness).

In total, we captured 4053 emerging YOY, 1102 of which were sacrificed for genetic analyses. Of the sampled YOY, 98.1% genotyped successfully and 91.9% assigned to maternal parents sampled as pre-spawn adults at weirs. In the spring following the primary spawning period, we captured 93 and 78 resident YOY in LBBC (spawning years 2019 and 2020, respectively) and 49 resident YOY in UBBC (2019). All (100%) resident YOY genotyped successfully and 77.3% assigned to maternal parents sampled as pre-spawn adults at weirs. The majority of emerging and resident YOY samples that failed to assign to parents were collected from LBBC in spawning year 2019, suggesting our sampling of the spawn population was incomplete in that year.

### Superimposition mediates the effect of spawn timing on reproductive success

The risk of redds to superimposition was strongly related to spawn timing (relative date of redd construction) but varied among years with spawning density. The probability of a redd being superimposed declined for redds that were constructed later; this relationship was slightly weaker in the low-density year when superimposition was less common (probability of direction = 100%; Fig. 2a). Similarly, proportional superimposition declined for redds that were constructed later, but this relationship was considerably weaker in the low-density year when the extent of superimposition was lower (probability of direction = 100%; Fig. 2b). The difference among streams was smaller and less certain (probability of direction = 87 and 64%, respectively) than the difference among years. We also found that as proportional superimposition increased, reproductive success of maternal parents (i.e. YOY production from individual redds) decreased (Fig. 3). For every 10% increase in proportional superimposition, reproductive success declined by 29.9% (−49.1 to −8.5%; mean and 95% credible interval).

Our simulation analysis revealed that redd superimposition mediated the effect of spawn timing on reproductive

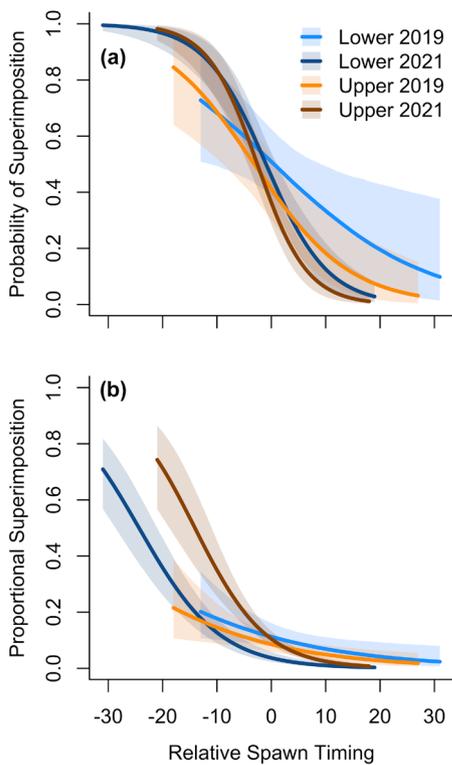


Figure 2. Effect of relative spawn timing on the (a) probability of superimposition and (b) proportional superimposition for different cohorts (color). Lines and shaded polygons represent the mean effects and 95% credible intervals, respectively.

success. Later spawners typically experienced greater reproductive success than early spawners, as early spawners suffered greater losses due to superimposition (Fig. 4). However, as the risk of superimposition declined in the low-density year and early spawners experienced relatively fewer losses, reproductive success became more similar among individuals spawning at different times. Specifically, in 2021 when spawning densities and the risk of superimposition were both high, reproductive success of later spawners was 11.4 and 5.9 (median across all iterations) times greater than early spawners in LBBC and UBBC, respectively. In contrast, in 2019 when spawning densities and the risk of superimposition were both low, later spawners were just 1.5 and 1.8 times more successful than early spawners, respectively.

### Spawn timing has variable effects on resident offspring

In the spring following the spawning period, offspring of early spawners had experienced longer growing seasons (more degree-days) and attained larger body sizes than those of later spawners (Fig. 5a–b). For example, for the LBBC 2019 cohort, offspring of early spawners experienced 26% more degree-days and were on average 33% larger than offspring of later spawners. While spawn timing effects on body size were less apparent for other cohorts (i.e. 95% credible intervals overlapped 0), there was an 83 and 85% probability that

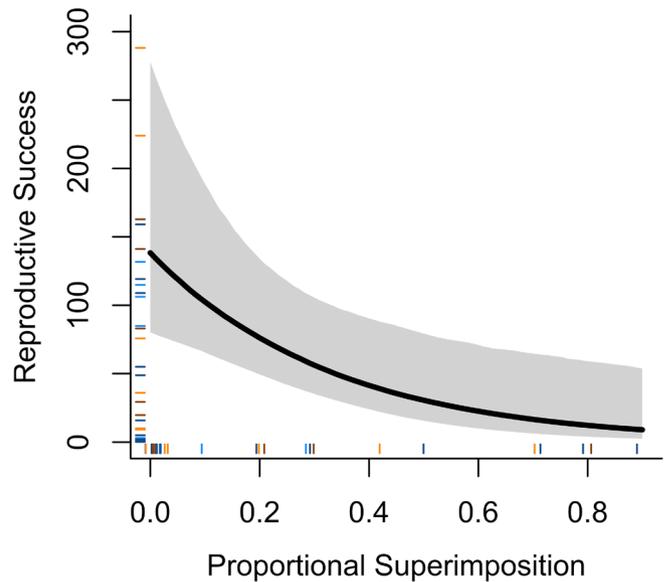


Figure 3. Effect of proportional superimposition on maternal parent reproductive success (i.e. the number of young-of-year (YOY) produced from specific redds). Black line and grey polygon represent the mean effect and 95% credible interval, respectively. Rug marks denote the distribution of the data, with the color scheme matching that of all other figures.

offspring of early spawners were larger for the UBBC 2019 and LBBC 2020 cohorts, respectively. In comparison, we found that spawn timing had no consistent effect on family size of resident offspring (Fig. 5c). The 95% credible interval of the slope from the data-rich spawning year (LBBC 2019) broadly overlapped 0, indicating no relationship, while results from other cohorts were mixed.

## Discussion

Here, we demonstrate that the timing of reproduction, a key life history trait, generates density-dependent fitness tradeoffs for YCT, a stream-dwelling salmonid with substantial ecological and economic value. YCT spawning early experienced reduced reproductive success relative to later spawners (Fig. 4) due to elevated risk of redd superimposition (Fig. 2) and associated negative impacts on offspring survival (Fig. 3). However, as the risk of superimposition declined in the low-density year and early spawners experienced relatively fewer losses, reproductive success became more similar among individuals spawning at different times. Further, in the following spring, offspring of early breeders had experienced longer growing seasons, attained larger body sizes, and were equally abundant relative to those of later breeders (Fig. 5), suggesting the negative effects of superimposition on reproductive success may be offset by size-dependent overwinter survival of offspring. Our results provide a possible mechanism for recent work finding a broad peak in relative reproductive success at intermediate spawning dates (Hargrove et al. 2021). Such a pattern may result from the tradeoff described here,

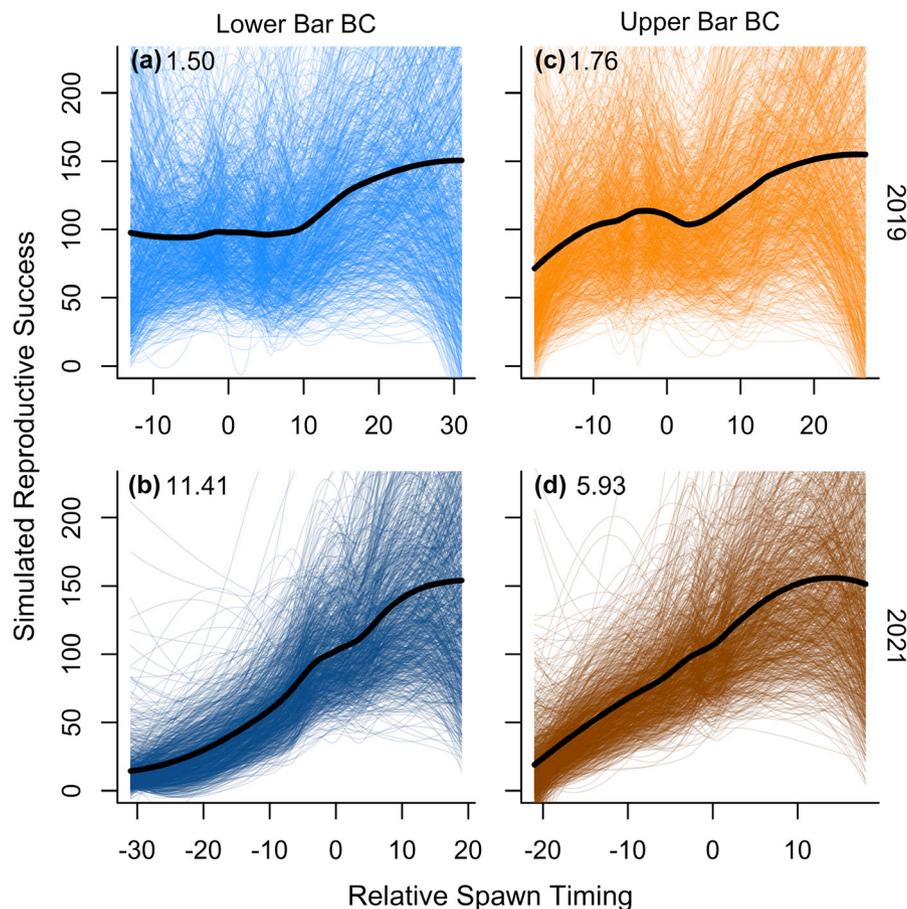


Figure 4. Simulated reproductive success as a function of relative spawn timing for (a,b) Lower bar BC and (c,d) Upper bar BC in (a,c) 2019 and (b,d) 2021. Thin colored lines represent locally estimated scatterplot smoothing (LOESS) fits (span = 0.75) to 1000 individual simulations. Thick black lines represent LOESS fits to the data averaged across all simulations. Number in the upper left-hand corner of each panel is the median relative difference in reproductive success between late and early spawners (median across all simulations).

which benefits different components of fitness over the course of the spawning period. Our results illustrate how diversity in the timing of reproduction may be generated and maintained in salmonids.

### Density-dependent fitness tradeoffs

There are numerous examples of how population density influences the shape and strength of selective pressure (Calsbeek and Smith 2007, Einum et al. 2008). This necessarily implies density-dependence in the strength of fitness tradeoffs, but has been difficult to demonstrate beyond laboratory experiments conducted on model organisms (Mueller et al. 1991). Our study provides a rare example of how density-dependent fitness tradeoffs are associated with life history diversity in the wild for a species of conservation concern. The two years considered in our study represent historically low (2019) and above average (2021) spawner densities (Baldock et al. 2023a). While we cannot necessarily distinguish density dependence from random variation among years, a strong theoretical basis and consistency in our results among streams provide support for our conclusions. Our results are significant in suggesting that

the degree of life history diversity may ultimately depend on the magnitude and frequency of fluctuations in population density that differentially favor alternative life history strategies.

Our result that offspring of early spawners were larger and equally numerous relative to those of later spawners suggests that fitness losses due to superimposition may be offset by competitive and survival advantages conferred by longer growing seasons and larger body sizes (Elliott 1990, Smith and Griffith 1994, Einum and Fleming 2000). Based on this logic alone, early spawners appear to have greater overall fitness, consistent with past work (Einum and Fleming 2000). However, YOY body and family size data were only available for low-density spawning years (2019–2020) in which early spawners experienced only slightly reduced reproductive success relative to YCT spawning later. In high-density years, we hypothesize that the effect of spawn timing on reproductive success via superimposition propagates through the winter, such that offspring number would increase for later spawners. Conversely, the effect of spawn timing on body size may also become more negative as the offspring of later spawners are increasingly disadvantaged under more intense competition (Einum and Fleming 2000).

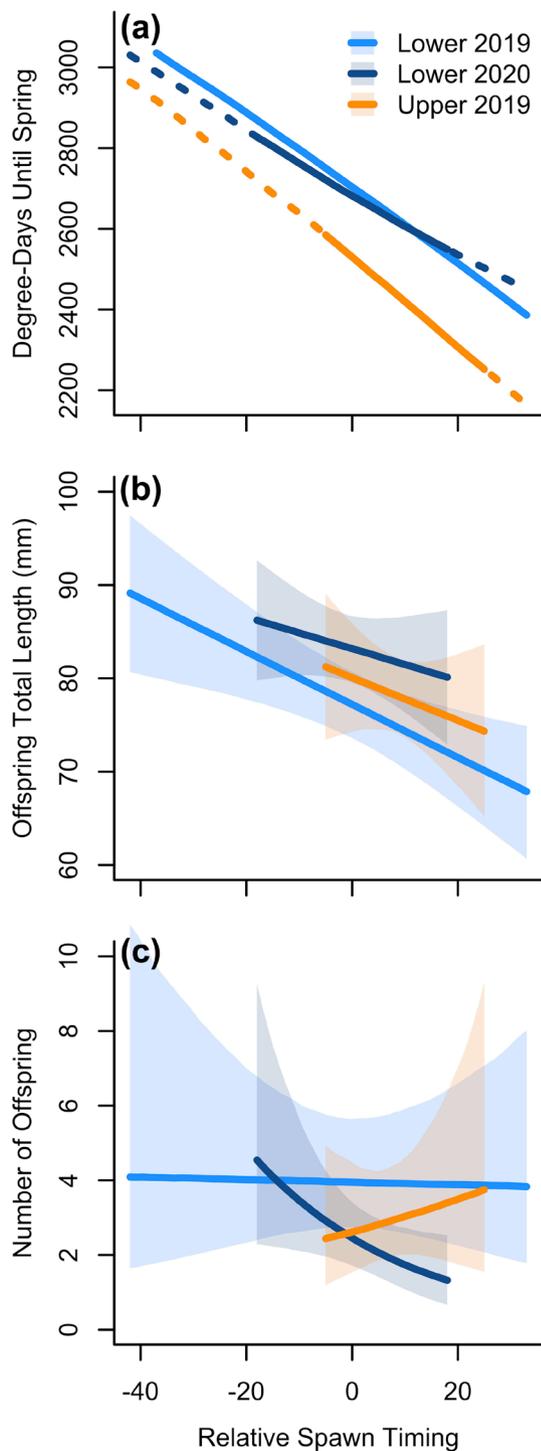


Figure 5. Relationship between relative spawn timing (i.e. parent migration date) and (a) cumulative growing degree-days until spring sampling (i.e. growing season length), (b) total length, and (c) family size of offspring sampled in the spring. Solid lines in (a) denote cumulative degree-days over the spawning period represented by juveniles that were sampled, whereas dashed lines denote degree-days over the entire spawning period, for reference. Lines and shaded polygons in (b) and (c) represent the mean effects and 95% credible intervals, respectively. Color denotes different cohorts.

Importantly, our analysis of the relationship between spawn timing and YOY body and family size is restricted to YOY remaining resident in streams overwinter. Resident YOY likely contribute more to adult fitness than those dispersing to the Snake River as spring-fed streams provide enhanced opportunities for growth and survival (Smith and Griffith 1994). Spring-fed streams are associated with elevated nutrient concentrations and macroinvertebrate densities (Lusardi et al. 2021) and stay ice-free and warm overwinter relative to the Snake River (Supporting information). The configuration of local habitat conditions may be particularly important for YOY, which have limited ability to track physiologically optimal conditions. While YOY emigrating to the Snake River are likely in poor condition relative to residents (Elliott 1990, Kanno et al. 2021), spring-fed streams are small in size and limited in the number of resident fish they can support. Spring-fed streams may therefore provide important larval subsidies to larger neighboring habitats, which offer contrasting and potentially complementary habitat conditions (Tsuboi et al. 2022), suggesting that transitional habitats supporting phenotypic diversity should not be overlooked (Wynne et al. 2023).

### Ecological and evolutionary roles of superimposition

Redd superimposition has important population and ecosystem-level consequences. Our finding that reproductive success declined with increasing superimposition provides empirical support for long-held assumptions regarding the mechanisms of population regulation for salmonids (Ricker 1954, McNeil 1964). Our model of reproductive success can be used to inform superimposition risk (Dudley 2019) and its effects on stock–recruit relationships (Maunder 1997) and spawning habitat capacity (Overstreet et al. 2016). Additionally, superimposition provides energy-dense eggs to stream consumers (Moore et al. 2008), allowing for persistence in watersheds of otherwise low in situ productivity (Armstrong and Bond 2013). Our results could therefore be used to identify population density thresholds under which stream consumers may become food limited, thus altering energy flows in stream food webs.

High rates of superimposition across a wide range of densities (Supporting information) indicate a preference for superimposition, as has been shown for other species (Essington et al. 1998). Re-using previously excavated gravels may reduce the energetic costs associated with redd construction (McVeigh et al. 2007), reduce the time exposed to predators, and increasingly remove fine sediment that limits egg-to-fry survival (Jensen et al. 2009). While redd guarding can protect against superimposition (McPhee and Quinn 1998), guarding is uncommon in trout (Bennett et al. 2014). Iteroparous species such as YCT are posed with the tradeoff between current reproductive success and survival among reproductive events (Stearns 1992), and energetic investment in reproduction – including redd guarding – comes at a cost to post spawning survival (Jonsson et al. 1997). Superimposition may therefore be a strategy to negotiate the

reproductive success–adult survival tradeoff, where existing redds indicate favorable habitat conditions for embryo development (Danchin et al. 1998).

Our definition of reproductive success (YOY output from individual redds) is non-traditional in that YCT may construct multiple redds (sensu Blanchfield and Ridgway 1997). Constructing multiple redds may buffer against the negative effects of superimposition on spawning success, a form of bet-hedging (Barlaup et al. 1994, Garcia-Gonzalez et al. 2015). We also did not consider female body size, which can mediate the fitness consequences of spawn timing associated with superimposition (Mogensen and Hutchings 2012) as larger females bury eggs deeper in gravel substrate (van den Berghe and Gross 1984). We could not consider body size in our analysis as we did not have female body size data for redds not specifically targeted with emergence traps. In addition, early migrants were only marginally larger than late migrants (< 5 cm on average, Supporting information), and the depth of spawning gravel in our system is shallow (< 7 cm), with redds typically excavated to the point of embeddedness. Thus, we do not believe large females spawning early were able to bury eggs deep enough to protect against superimposition by smaller females spawning later.

### Additional drivers of diversity in reproductive timing

Diversity in the timing of reproduction (within sites) may arise through mechanisms beyond those detailed in this study, such as interannual variability in the timing of optimal juvenile rearing conditions (Lof et al. 2012). Theory and empirical work suggest that spawning occurs at a time that allows for YOY emergence during optimal conditions (Brannon 1987, Webb and McLay 1996). In streams dominated by runoff and snowmelt, temporal variation in water temperature and food production creates distinct but fleeting periods during which growth and survival is maximal (Tattam et al. 2017). As the timing of optimal conditions shifts among years, offspring of adults spawning at different times may experience differential rates of survival, depending on the degree of mismatch (Reed et al. 2013). However, our study was conducted in spring-fed streams in which water temperature, discharge, and secondary production are relatively stable (Supporting information; Lusardi et al. 2021). As a result, the timing of optimal rearing conditions and resulting selection pressure is diffuse compared to seasonal environments, suggesting that variation in spawn timing documented here is more likely maintained by redd superimposition and size-dependent offspring survival. The relative influence of multiple, interacting agents of selection in generating and maintaining life history diversity may therefore be context dependent, with the degree of environmental variability being of particular importance (Robinson et al. 2012).

While our study focused on evolution of reproductive timing via selection on offspring fitness, traits may also evolve via selection on maternal fitness. For example, predator swamping may exert stabilizing selection on spawn timing if per

capita predation on spawners is greatest at the tails of the breeding season (Quinn et al. 2003). Selection on breeding time may also be shaped by energetic investment in reproduction. For populations at high elevations and latitudes, depleted nutritional condition after spawning is associated with high overwinter mortality and low probability of future reproduction (Bordeleau et al. 2019). Females breeding early have more time to regain energy prior to winter, potentially selecting for earlier spawning. Evaluating the relative strength of selection on maternal versus offspring fitness and the impacts on trait evolution would be a productive area of future research.

### Conservation applications under global change

Despite widespread declines and extirpations (Wenger et al. 2011), YCT within our study area – the upper Snake River watershed – display successful natural reproduction, low introgression by non-native species, and stable trends in population abundance (Endicott et al. 2016). As such, populations within our study area are given high priority for conservation and protection efforts (Al-Chokhachy et al. 2018) and are expected to serve as critical strongholds as climate change renders other habitats unsuitable (Haak and Williams 2012). Given that superimposition is often interpreted as a sign of limited habitat availability (Blanchfield and Ridgway 1997), high rates of superimposition in spring-fed tributaries have been used to justify costly spawning habitat restoration projects (Kiefling 1997). Analysis of historical redd count data (1970–2020) reveals no temporal trend in the proportion of redds that are superimposed (Supporting information), suggesting management efforts seeking to reduce rates of superimposition have had and may continue to be met with limited success. On the contrary, considering the present study, such efforts may threaten the evolutionary processes that give rise to diversity in the timing of reproduction.

Preserving diversity in the timing of reproduction may be required for adaptation to global climate change (Tillotson and Quinn 2018). As climate change is expected advance the annual timing of optimal juvenile rearing conditions (Visser and Both 2005), selection for earlier spawn timing may lead to changes in mean trait values over time (Crozier et al. 2008). The adaptive capacity required to track shifts in optimal conditions may therefore hinge on the prevalence of the early spawning phenotype. In addition to phenological shifts, climate change is expected to increase the frequency and magnitude of extreme events (Easterling et al. 2000), such as flooding during spawning and emergence. Such extremes can have detrimental impacts on YOY survival and recruitment (Sweka and Wagner 2022). Diversity in spawn timing thus buffers populations against environmental stochasticity by spreading risk among individuals (Schindler et al. 2015). Maintaining diversity in reproductive phenotypes, added to the suite of conservation actions being developed, would work toward maximizing adaptive capacity in the face of climate change (Snyder et al. 2022).

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## Author contributions

**Jeffrey R. Baldock:** Conceptualization (equal); Data curation (lead); Formal analysis (lead); Funding acquisition (equal); Investigation (lead); Methodology (equal); Project administration (equal); Resources (equal); Supervision (equal); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (lead).

**Robert K. Al-Chokhachy:** Conceptualization (equal); Funding acquisition (equal); Methodology (equal); Supervision (supporting); Validation (equal); Visualization (supporting); Writing – review and editing (supporting).

**Matthew R. Campbell:** Data curation (supporting); Formal analysis (supporting); Investigation (supporting); Methodology (supporting); Resources (supporting); Supervision (supporting); Validation (supporting); Writing – review and editing (supporting). **Annika Walters:** Conceptualization (equal); Formal analysis (supporting); Funding acquisition (equal); Investigation (supporting); Methodology (equal); Project administration (equal); Resources (equal); Supervision (equal); Validation (equal); Visualization (supporting); Writing – review and editing (supporting).

## Data availability statement

Data are available from the Zenodo Digital Repository: <https://doi.org/10.5281/zenodo.7839081> (Baldock et al. 2023b).

## Supporting information

The Supporting information associated with this article is available with the online version.

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