Received: 21 February 2024 | Revised: 22 May 2024 | Accepted: 10 July 2024

DOI: 10.1002/eap.3033

ARTICLE

ECOLOGICAL APPLICATIONS
ECOLOGICAL SOCIETY OF AMERICA

Understanding how restoration reduces competition for habitat by combining theory, observation, and experiment

Carlos M. Polivka[1] | **Margaret A. Malone**[2,3] | **Spencer A. Carran**[4] | **Greg Dwyer**[4]

[1]Pacific Northwest Research Station, USDA Forest Service, Wenatchee, Washington, USA

[2]Cascadia Conservation District, Wenatchee, Washington, USA

[3]Institute of Environment Department of Biological Sciences, Florida International University, North Miami, Florida, USA

[4]Department of Ecology and Evolution, University of Chicago, Chicago, Illinois, USA

Correspondence
Carlos M. Polivka
Email: carlos.polivka@usda.gov

Funding information
United States Bureau of Reclamation; Bonneville Power Administration (Integrated Status and Effectiveness Monitoring Program); Pacific Northwest Research Station (USDA Forest Service)

Handling Editor: Colin J. Torney

Abstract

Habitat selection theory enables inferences about species habitat choice across a range of observed population densities. However, it is relatively uncommon to use habitat selection theory in studies of habitat restoration efficacy to understand the effect of restoration on habitat competition. We combined observational density data and resource selection functions to analyze habitat correlations with both habitat selection theory and a mark–recapture experiment to show how habitat restoration can mitigate competition between species with similar habitat preferences. To restore degraded and channelized riverine habitat for juvenile Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead trout (*Oncorhynchus mykiss*) engineered log jams (ELJs) have been installed to create pools to enhance growth and rearing. Application of habitat selection theory first showed that both species share a preference for ELJ-treated habitat over unrestored habitat. Linear models showed that steelhead are generalists with respect to depth in unrestored habitat, whereas both species' abundance varies along a depth gradient in ELJ-treated habitat. Selective versus opportunistic use of deep and shallow ELJ pools was density-dependent. We found a range of densities at which a "ghost of competition" exists, where Chinook are selective on deep ELJ-treated pools and steelhead are selective on shallow pools. A mark–recapture experiment confirmed that steelhead limit Chinook movement into unrestored habitat, but this competitive effect vanished in ELJ-treated habitat where selection occurred with respect to pool depth. The experiment, combined with theory, enabled (1) the identification of a mechanism allowing for shared preference of restored habitat and (2) the description of how restoration can mitigate competition.

KEYWORDS
habitat restoration, habitat selection theory, isodars, isolegs, resource selection functions, salmonids

INTRODUCTION

Competition between species is often mitigated by habitat selection, which can allow competitors to coexist in similar environments (Pimm et al., 1985; Pimm & Rosenzweig, 1981). Strong selection on density-dependent behavior can lead species to become generalists or specialists in available habitat types. Habitat selection therefore

provides mechanisms by which species can coexist in a heterogenous landscape (Brown, 1996; Morris, 1999a; Rosenzweig, 1974; Schmidt et al., 2000). Mathematical models for understanding data on habitat selection have been developed to relate fitness-optimizing dispersal to observations of habitat selection behavior (Morris, 1988; Rosenzweig, 1987). Demonstrating that habitat selection patterns facilitate coexistence in nature, however, is often difficult, partly because it is difficult to infer mechanisms from distributional data. In some cases, however, a range of densities can be identified that shows habitat partitioning, that is, selective use of separate habitats indicative of a "ghost of competition" (Morris, 1999a; Rosenzweig, 1987). The habitat separation reveals the ghost at densities of the two species at which stable coexistence occurs. Experimental evidence can confirm that competition would occur at these densities and that the observed selection of separate habitats reveals ("busts") the ghost by demonstrating its existence under those conditions (Abramsky et al., 1986; Rosenzweig, 1991; Schmidt et al., 2000). High habitat quality can therefore allow for the possibility of partitioning, implying that manipulations of habitat quality in a conservation context might affect the outcome of competition and the existence of a ghost (Morris, 2003a).

Habitat selection can be described by the "isodar" and "isoleg" theories, which are based on fitness optimizing patterns resulting in an equilibrium described by the Ideal Free Distribution (IFD; Fretwell & Lucas, 1970). The IFD predicts that the difference in density between habitats reflects the difference in productivity between habitats, on the assumption that dispersal is not limiting. Isodars then plot the combinations of density in each habitat type that result in equal fitness (iso = equal, dar = Darwinian fitness) thereby quantifying habitat preference (Morris, 1988, 2003b). Isodars both quantify habitat selection across a range of population sizes (Figure 1A) and can identify shared preferences among species for a given habitat type, enabling estimation of the competition coefficient. Shared habitat preferences among species are indicated when the isodars of each species have overlapping slopes (also depending upon the intercepts of the isodars) Such shared habitat preferences highlight the potential for interspecific competition to shape habitat selection patterns (e.g., Tarjuelo et al., 2017).

Isoleg theory (iso = same, legos = choice) enables inferences about habitat selection due to competition among species at a population level (Morris, 1989, 1999a; Rosenzweig, 1981). Isolegs are lines in a plot of population densities along which species behavior shifts among

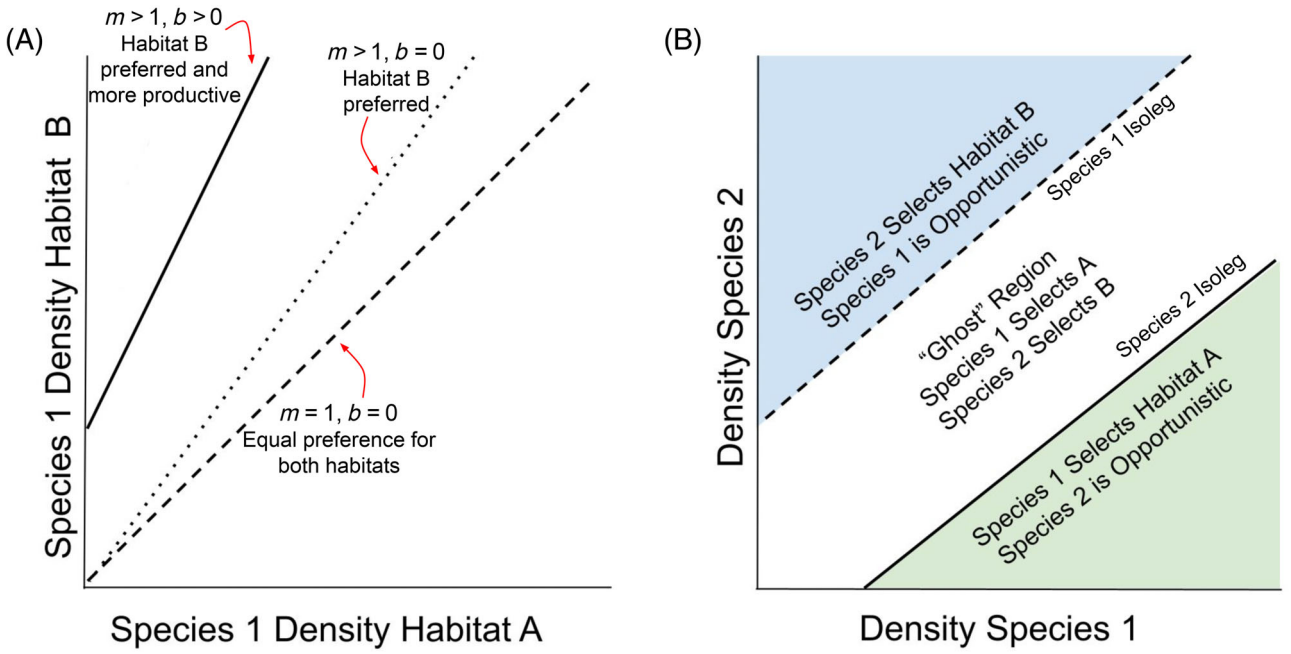

FIGURE 1 Conceptual representation of isodars and isolegs in two habitats. (A) Isodars as linear functions ($y = mx + b$), plotted from the density of a species in each habitat and compared to a 1:1 line (dashed). Slope and intercept of isodars (solid and dotted lines) describe the strength of density-dependent habitat selection (i.e., preference) (Morris, 1988). (B) Isolegs are lines within state space plots of the relative density of each species across habitats and indicate ranges of density where habitat selection switches from selective to opportunistic. Here, species 1 selects Habitat A when density ranges fall below its isoleg and species two selects Habitat B when density ranges are above its isoleg. This leads to segregation among habitats and a region in state space indicating a "ghost of competition" (Rosenzweig, 1987).

habitat types between selective and opportunistic (Figure 1B). Isolegs can quantify the range of densities over which coexistence is possible via species differences in habitat selection (Rosenzweig & Abramsky, 1997), indicating when a "ghost" may occur. Isolegs can be generated from data by analyzing the selectivity of each species across habitats (Abramsky et al., 1990), and can then be calculated and plotted in the density state space (Figure 1B) (Abramsky et al., 1990; Pimm et al., 1985; Pimm & Rosenzweig, 1981; Rosenzweig & Abramsky, 1997). When there is habitat selection showing distinct preferences, isolegs usually diverge, indicating that there is a ghost of competition (Morris, 1988, 1999a). Despite the usefulness of isodars and isolegs, they are rarely used to describe habitat selection in systems with high-profile species, such as those that are of conservation interest (Kotler et al., 2016; Malone & Polivka, 2022).

Shared habitat preferences can occur between ecologically similar species that occur in sympatry (Dehnhard et al., 2020; Ziv et al., 1995). Such a situation can highlight the importance of combining habitat selection theory with descriptive approaches to analyze similarities in habitat preferences and, more importantly, mechanisms that permit coexistence within shared habitats (Indermaur et al., 2009). Isolegs can be applied to a wide range of species preferences and such partial-preference isolegs can be used to describe situations in which there is mutually preferred habitat (Wasserberg et al., 2006). This usually involves some sort of niche partitioning or selection of different secondary habitats (Brown, 1996; Rosenzweig & Abramsky, 1986). Isolegs that represent 100% preference (Figure 1B), however, can still describe how specialist and generalist behaviors allow coexistence in different habitats (Morris, 1999b).

In applying habitat selection theory to restoration ecology, we first note that managers and researchers often rely on functions that describe physical habitat gradients to identify important parameters along which species may be selective or opportunistic (Holbrook et al., 2019; Lele et al., 2013). Such resource selection functions (RSFs) are typically generalized linear models (GLMs) that predict species density as a function of candidate parameters (Boyce & McDonald, 1999). As such, they are not structured in a complex way, but nevertheless may require extension to describe non-linear relationships (McCabe et al., 2021). RSFs can describe habitat distribution of competitors (Santos et al., 2018) and can be coupled with isoleg analyses by defining and describing the available habitats from which study species may choose.

A common question in restoration ecology is whether habitat restoration has indeed benefited target species (Fisher et al., 2019). Some habitat actions may target more than one species with similar habitat requirements (McAfee et al., 2021), or may elicit an unexpected response in a second species (Gumm et al., 2011). Because isoleg theory describes habitat partitioning in heterogenous environments (Morris et al., 2009), it may be useful in restoration ecology when management actions increase overall habitat heterogeneity and affect more than one species (Berger-Tal et al., 2011; Berger-Tal & Saltz, 2016; Blumstein & Fernández-Juricic, 2010). Despite this potential, isolegs have only rarely been applied in such studies (Kotler et al., 2016; Morris, 2003a; Shochat et al., 2005; Török & Helm, 2017). Moreover, the few previous applications have focused almost exclusively on terrestrial animals (O'Neil et al., 2020), but will emerge from any system with significant isodars. Despite this terrestrial bias, isolegs can likely aid in interpreting data on fish because habitat partitioning has been observed to reduce competition in many fish species (Nunn et al., 2020; Persson & Greenberg, 1990; Werner et al., 1977).

A key application of habitat selection theory emerges in fish restoration ecology given that habitat manipulations often lead to heterogeneity in habitat quality. Here, we show that the effects of those manipulations can actually be quantified using isodars and isolegs to analyze observational data on fish in those habitats. One such manipulation involves the addition of woody debris such as engineered log jams (ELJs) to create stream pools to aid the growth and survival of species with strong affinity for pool habitat (Roni et al., 2002; Roni, Beechie, et al., 2015). ELJ-treated pools have been shown to modulate competition in some cases (Hasegawa & Maekawa, 2008, 2009), suggesting that it is a restoration strategy that can be evaluated using isolegs.

The freshwater habitats of juvenile Chinook salmon (*Oncorhynchus tshawytscha*) and steelhead (*Oncorhynchus mykiss*) overlap across their range of co-occurrence in rivers and streams across the Pacific Northwest of the United States and in British Columbia, Canada (Everest & Chapman, 1972; Hillman et al., 1987). These two species compete strongly for resources (Harvey & Nakamoto, 1997; Hearn, 1987; McMichael et al., 1997) resulting in the partitioning of their habitats into deeper, slow-current pools favored by Chinook versus shallower, fast-current pools, glides, or riffles favored by steelhead. Habitat selection in adults of some salmonids has been analyzed using isodars (Huntsman et al., 2017; Rodríguez, 1995), establishing the applicability of theory to these study systems. Previous work has shown that ELJs are effective in improving the habitat capacity for the two species (Polivka & Claeson, 2020; Polivka, 2020) in part by improving

growth of individuals (Polivka et al., 2020). An initial isodar analysis in that study system showed that the two species had similar preferences for ELJ-treated habitat (Polivka, 2022), indicating that following up with an isoleg analysis would help identify how competition shapes habitat partitioning between them.

Here, we combined isodars and isolegs with RSFs and a movement experiment to ask whether habitat selection in Chinook salmon and steelhead is driven by competition and whether habitat restoration mediates behavior. We did this first by updating the isodars presented in Polivka (2022) with more complete data, showing that there is a shared preference for ELJ-treated habitat by Chinook salmon and steelhead juveniles, thereby confirming that isolegs would be useful for understanding habitat selection in these species. We then used RSFs at the habitat scale to identify a physical gradient along which habitat selection could occur which formed the basis of a subsequent isoleg analysis. Next, we constructed isolegs using a selectivity index (Abramsky et al., 1990) that described selection for deep versus shallow ELJ-treated pools and partitioning indicative of a ghost of competition. Finally, we used an experiment to measure movement in and out of treated and untreated pools to test the hypotheses that (1) interspecific competition for space affects the short-term immigration of at least one of the two species into a given habitat type, and (2) these competitive effects on habitat selection (movement into habitats) might be mitigated by habitat restoration with ELJs. This integration of theory, observation, and experimentation allows us to describe the effects of restoration on competition at multiple scales (Figure 2).

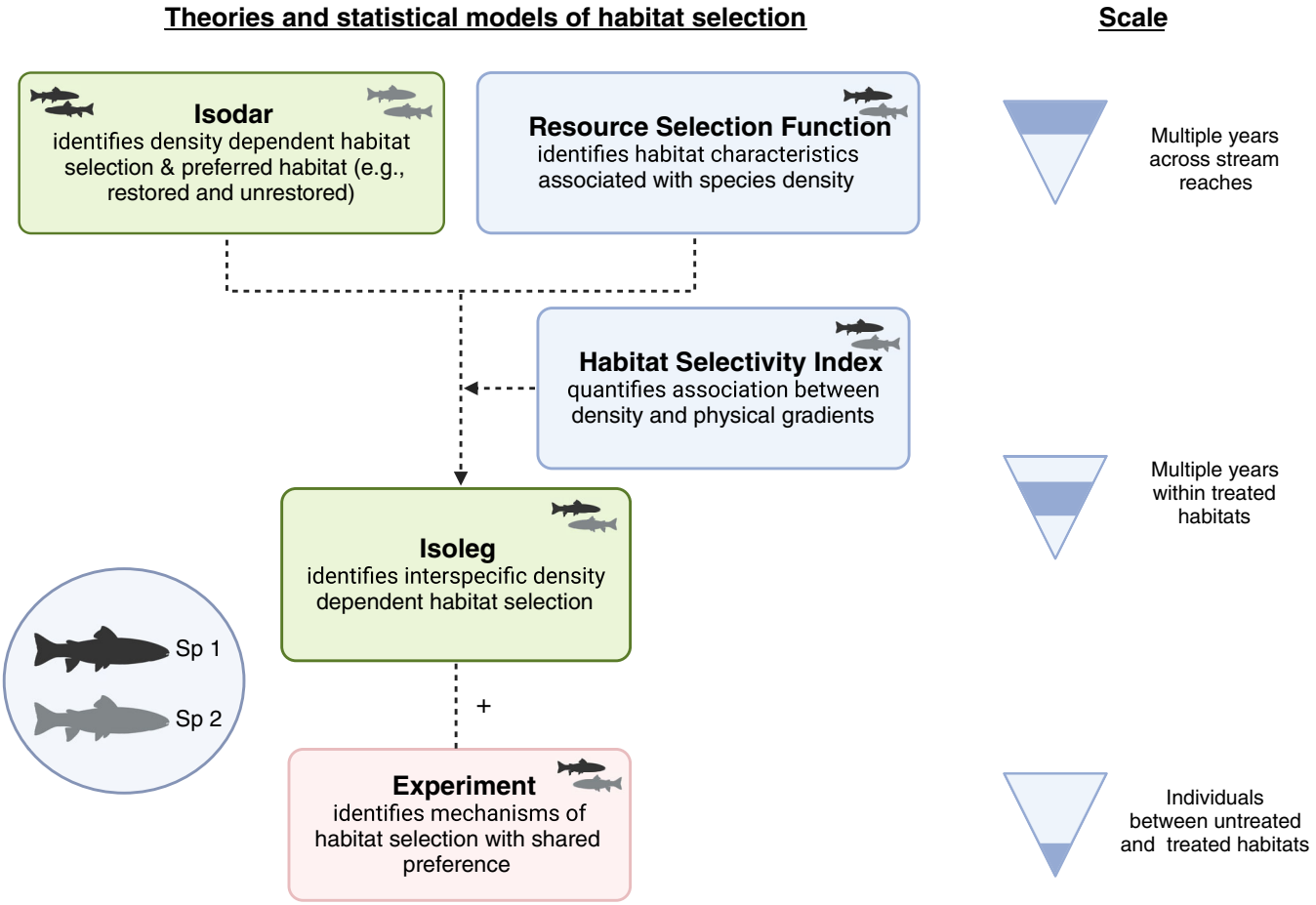

FIGURE 2 Combination of behavioral ecology theory (green boxes) and statistical models (blue boxes) used in this study to demonstrate how distribution and movement data can be analyzed to determine multispecies habitat selection at multiple scales. Isodars incorporate intraspecific competition to identify broad-scale habitat preferences (e.g., restored vs. unrestored habitat). Resource selection functions (RSFs) identify species associations with habitat characteristics. From the resultant statistical model, gradients in important characteristics can be identified and used to determine habitat selectivity. Isolegs are then derived from habitat selectivity models. Isolegs, combined with experiments at the habitat scale, describe both interspecific density-dependent habitat selection and dynamics related to shared habitat preferences (Figure made using Biorender.com).

MATERIALS AND METHODS

Data collection

We built on studies that documented the effects of ELJs on Chinook and steelhead populations in the Entiat River, WA, USA (Polivka, 2020; Polivka et al., 2015; Polivka & Claeson, 2020). The Entiat is a sub-basin of the Columbia River with its confluence at 49.657° N, 120.224° W. Sub-yearling Chinook spend 1 year in pools in rivers and streams before emigrating to the ocean (Hillman et al., 1987), whereas anadromous steelhead spend 1–3 years in pools before emigrating to the ocean. For this study, we focused on five reaches in the lower valley segment of the Entiat River, in which ELJs were installed beginning in 2008, but with most installations being carried out in reaches in 2014 (Figure 3, and see Appendix S1). Four untreated reaches provided a comparison of behavior in untreated habitat in reaches with no ELJ-enhanced habitat. Fish density varies considerably across ELJ-enhanced pools, but unrestored pools have similar fish density whether they occur in a treated or untreated reach (Polivka & Claeson, 2020).

We estimated fish density by counting fish visually while snorkeling, thereby avoiding the effects on behavior that result from electrofishing (Mesa & Schreck, 1989). Underwater visibility in the Entiat River is 4–5 m, so visual counts are very accurate and have been shown to be comparable to capture-recapture methods (Polivka et al., 2015). For the reach restored in 2008, we carried out sampling in post-treatment years 2009, 2011–2016. For the reaches restored in 2014 (Appendix S1), we carried out sampling in post-treatment years 2014–2016, with all surveys taking place in late July when river discharge decreased to a level at which data collection was feasible (<200 cfs).

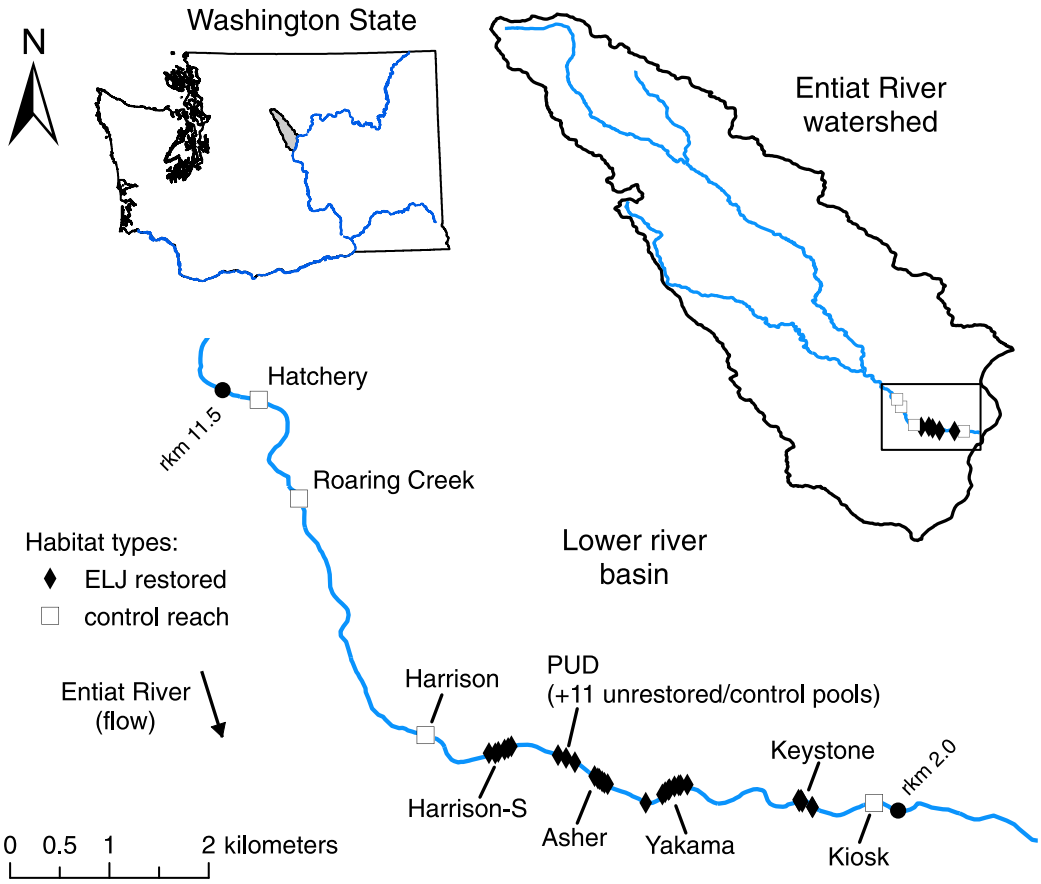

FIGURE 3 Map of Washington State (USA) showing the location of the Entiat River sub-basin (in gray) and its confluence with the Columbia River (blue line on map). The sub-basin is shown with inset identifying the lower basin segment in which the study reaches occur. The inset shows the study reaches in the Entiat River, all of which occur between river km 2.0 and 11.5 relative to the confluence with the Columbia River. Reaches with an open square are control reaches untreated with engineered log jams (ELJs); those with diamonds are treated with each diamond representing a separate ELJ. See Appendix S1 for site details including restoration dates and number of ELJs present.

In ELJ-treated pools, we calculated density (fish per square meter) by dividing counts by the surface area of the pool. For estimates of density in untreated habitat, we used a spatial randomization procedure to select 15 untreated habitats in treated reaches (Polivka & Claeson, 2020). Sub-yearlings of the two species are uncommon in mid-channel habitats (Beechie et al., 2005), and so our surveys were always carried out on the stream margins, usually in pools or glides with moderate current velocity. We standardized the survey area of each untreated habitat to 15 m^2; this area is somewhat smaller than most ELJ-enhanced pools, but previous work in this study system has shown that fish abundance increases linearly with water surface area (Polivka et al., 2015). We measured depth and current velocity at every survey and we used the same method to sample untreated habitat in untreated reaches. Because reaches are occupied by new cohorts of sub-yearlings each year, in our analyses we treated data for different years as independent. The few (<5 per year) age 1+ steelhead that we observed were omitted from our analyses.

In two reaches, we carried out mark–recapture studies in late July, the time of peak fish density, in 2009, 2012, 2013, and 2016. Missing years resulted when we had to avoid concurrent studies in the same reaches, when the stream discharge in July was too high to allow us to snorkel safely or to capture fish efficiently, or when nearby forest fires led to sediment deposition that made it impossible to see and capture the fish. In the mark–recapture study, we used 11 ELJ-treated pools in the "Asher" reach and in a set of 11 unrestored pools in the "PUD" reach (Figure 3, Appendix S1: Table S1), but we did not include ELJ-treated pools that were added to the "Asher" site in 2014.

We captured fish using a 3 × 1.5 m seine with a 3-mm mesh, again to avoid the known problems of electrofishing (Mesa & Schreck, 1989). Because the cobble and rock substratum of the river makes pulling a seine ineffective, two field-crew members stood at the downstream end of the pool and held the seine open as two other members used large hand nets while snorkeling to either capture fish individually or to chase fish into the seine. As with the fish counts, the clarity of the water in the Entiat made captures straightforward. Moreover, the structural complexity of ELJs does not appear to affect capture efficiency for behavioral (Polivka, 2020) or growth (Polivka et al., 2020) studies.

Captured fish were anesthetized using MS-222 (<0.1 g/L) for 2–3 min; this level of anesthetic exposure has only a mild effect on the fish. We marked anesthetized fish with a subcutaneous injection of visible implant elastomer (VIE; Northwest Marine Inc.). To ensure that only sub-yearlings were considered, we measured the standard length (SL) of all fish (all Chinook were sub-yearlings; steelhead less than 70 mm SL were considered sub-yearlings, following Everest & Chapman, 1972). Following measurement and marking, fish were then moved to insulated, aerated buckets and allowed to recover from anesthesia for at least 10 min, or until they righted themselves and became alert and responsive. Following recovery, fish were released into the capture pool. We then resampled the pool 24 h later, recording the number of recaptured, marked fish and newly captured, unmarked fish. The marks can last for at least 60–65 days (Polivka et al., 2020), and it therefore seems likely that mark loss did not affect recapture numbers.

Habitat selection theory: Isodars, resource selection functions, and isolegs

We generated updated isodars using all years of post-treatment density data from all treated reaches in the Entiat River (Figure 3). The previous isodar study in this system (Polivka, 2022) generated isodars from only a single set of ELJ-treated pools in the "Asher" reach compared with a single set of untreated pools in the "PUD" reach (see Appendix S1) over time. To calculate the isodar for each species, we first calculated the average density of that species within each habitat type (treated vs. untreated) within each treated reach, with data for untreated habitats coming from the randomly selected set of surveys in the treated reaches and data for the treated habitats coming from ELJ-treated pools. This calculation produced a set of average densities in treated vs. untreated habitats within each reach ($N = 4$ reaches × 2 years of post-treatment data; plus 1 site, "Asher," with 8 years of post-treatment data). These values were then used as the coordinates of the points plotted in the density phase plane. We then fit a regression line to the paired habitat densities (treated vs. untreated) for each species, such that each data point represents a different reach in a different year, again with independence following from the fact that, in each year, each site contained different cohorts of sub-yearlings. The isodars are thus the regression lines through the data.

To calculate regression lines, we used Deming regression, which allows for measurement error on both axes (Linnet, 1990). We performed the analysis using the default assumption that the error ratio was $\lambda = 1$. Following Polivka et al. (2020) and Polivka (2022), who showed that there is little difference in habitat selection when either species is at low density, and after confirming that *y*-intercepts were not meaningfully different from zero (Polivka, 2022), we set the intercepts in our regression models to zero. If the slope of the regression line for a given species was greater than 1, we concluded that the fixed proportional use of habitat favored ELJ-treated

habitat over untreated habitat (Figure 1A). To allow for uncertainty in our estimates of the slope, we only considered a slope to be meaningfully greater than 1 if the lower value of its 95% credible interval was greater than 1. We also allowed for the unlikely possibility that fish prefer untreated habitat, which would have led to slopes less than 1, but in practice both slopes were indeed greater than 1 (see *Results*).

Because the isodars show shared species preferences (Polivka, 2022, and see *Results* below), and because we wanted to identify physical characteristics of restored and unrestored habitats that are associated with habitat selection, we used Bayesian GLMs as RSFs. Specifically, we quantified the density of each species in terms of pool depths (D) and current velocities (C), which were shown to be the key covariates in previous studies (Polivka et al., 2015; Polivka & Claeson, 2020), and heterospecific density (H) to determine whether competition was evident. Explicitly, the model structure is then:

$$\text{Density} = \alpha_0 + \alpha_1 D + \alpha_2 C + \alpha_3 H. \quad (1)$$

To understand how fish choose habitat in the absence of restoration, we first analyzed data from the reaches without ELJ-enhanced pools (Figure 3, Appendix S1). To understand the effects of restoration, we performed a second, identical analysis of data from ELJ-enhanced pools.

To fit the GLMs to the data, we used the Bayesian software *stan* and the `brms` package in the **R** programing language (R Core Team, 2017; Stan Development Team, 2017a, 2017b). We used weakly informative priors, in the form of the defaults provided by `brms`, and a Gaussian error structure. For each model we ran four chains for 2000 iterations, using the first 1000 iterations as a warm-up and thinning by one iteration, giving a total of 4000 samples (1000 per chain). In all cases, the Gelman–Rubin statistic $\widehat{R} < 1.1$ (Gelman, 2008), indicating that the chains had converged.

Because we found that the two species differ in the extent to which they use treated habitats at different depths (see *Results*), we built isolegs for the two species based on the species' habitat selectivity for deep and shallow ELJ-treated pools in restored reaches. Chinook and steelhead post-treatment density data collected during 2014 and 2015 were used for analysis because total number of deep and shallow treated pools with fish present in those years best allowed for the calculation of habitat selectivity. To categorize a pool as deep or shallow in each year, we used the median pool depth for that year (2014, median = 36.5 cm; 2015, median = 38.7 cm; see Appendix S1 for variation in depth among sites and years). All pools deeper than the median were classified as "deep." We then calculated the habitat selectivity index for each species using the ratio of species density in deep habitat to the total species density in both deep and shallow habitat (e.g., Chinook selectivity = [density Chinook deep]/[total density Chinook]).

A high selectivity score indicates that a species prefers deep habitats, whereas a low score indicates that the species prefers shallow habitats. Selectivity scores of 1 indicate densities at which a species prefers deep habitat. Low selectivity scores indicate densities at which a species uses shallow and deep pools opportunistically. We quantified the relationship between each species' habitat selectivity index and the total density of Chinook and steelhead via generalized linear regression, using the *glm* function in the lme4 package in R (Bates et al., 2007). Selectivity for each species was modeled separately as a function of both species' density:

$$\text{Selectivity} = \beta_0 + \beta_1 C + \beta_2 S, \quad (2)$$

where C is Chinook density and S is steelhead density. To allow for the overdispersion that is often present in proportional data, we used a quasibinomial error structure.

To generate the isolegs for each species, we obtained the selectivity equations from the generalized linear regression models using the *extract_eq* function in the package `equatiomatic` in R (Anderson et al., 2021). Coefficients for the isoleg equations consisted of significant β_1 and β_2 values in the GLM results from analyzing the selectivity index as described in Equation (2). We then set each species' habitat selectivity at ≈1 (the distinction between selectivity on deep habitats and opportunistic habitat selection) and algebraically solved for the isolegs of each species by rearranging the selectivity equations (see *Results*).

Immigration and emigration models for understanding mark–recapture data

The goal of our mark–recapture experiment was to test whether density-dependent movement into and out of different habitat types identified space competition as a mechanism behind the patterns apparent in the isoleg analysis. To analyze the mark–recapture data, we constructed models that described small-scale movement into pools (immigration) and out of pools (emigration), which are built upon the model described in Polivka et al. (2020). Our immigration model is

$$I = \alpha_0 + \alpha_1 R e^{-\alpha_2 R}, \quad (3)$$

where I is the density of immigrating fish and R is the initial (log) density of fish in a pool calculated from

the number of recaptured individuals. Our emigration model is

$$E = \beta_0 + \beta_1 R e^{-\beta_2 R}, \quad (4)$$

where E is the number of fish marked but not recaptured, and thus assumed to be emigrants (predation is negligible in this system on the 24 h time scale of the experiments), and R is again the total density of fish recaptured in a pool on Day 2. In these models, when initial density is low, so that R is zero or close to it, the baseline density-independent immigration and emigration rates are α_0 and β_0 respectively. Immigration and emigration in the models increase with increasing recapture density R; at very high densities, however, immigration and emigration again approach their respective baseline values of α_0 and β_0. The parameters α_1 and β_1 then represent the rate at which immigration and emigration rise with increasing density, while α_2 and β_2 represent the rate at which density-dependence reduces immigration and emigration. Immigration and emigration are thus maximized at intermediate values of recapture density R. The maximum levels of immigration and emigration, and the densities at which these maxima occur, can then be calculated using elementary calculus, for example, for the immigration model the peak immigration level is $I = \frac{\alpha_1}{\alpha_2 e}$, which occurs at $R = \frac{1}{\alpha_2}$.

We fit the models to immigration and emigration data for both Chinook and steelhead. To allow for the possibility that immigration or emigration may depend on either the density of conspecifics or the density of heterospecifics, for each species we first fit the models assuming that R represents conspecifics, and second that R represents heterospecifics. To similarly allow for the possibility that immigration depends on habitat type, first, we fit the models to data from restored habitat, and second, we fit the models to data from unrestored habitat.

In fitting the immigration and emigration models, we again used a Bayesian statistical approach. In this case, we used Gibbs sampling as implemented in the JAGS software package (Plummer, 2003). We used a Poisson likelihood, as is appropriate for count data. As in our GLMs, the Gelman–Rubin statistic $\widehat{R} < 1.1$, indicating that the chains had converged in all cases.

RESULTS

Isodars, resource selection functions, and isolegs

The isodars show that both species had higher density in ELJ-treated habitats across sites and years (Figure 4). The Chinook isodar has slope 3.96, with 95% credible interval 2.38–5.54, whereas the steelhead isodar has slope 2.07 and credible interval 1.13–3.00. The slopes for the isodars and lower bounds on the credible intervals for both species are thus >1, indicating a shared preference for ELJ-treated habitat.

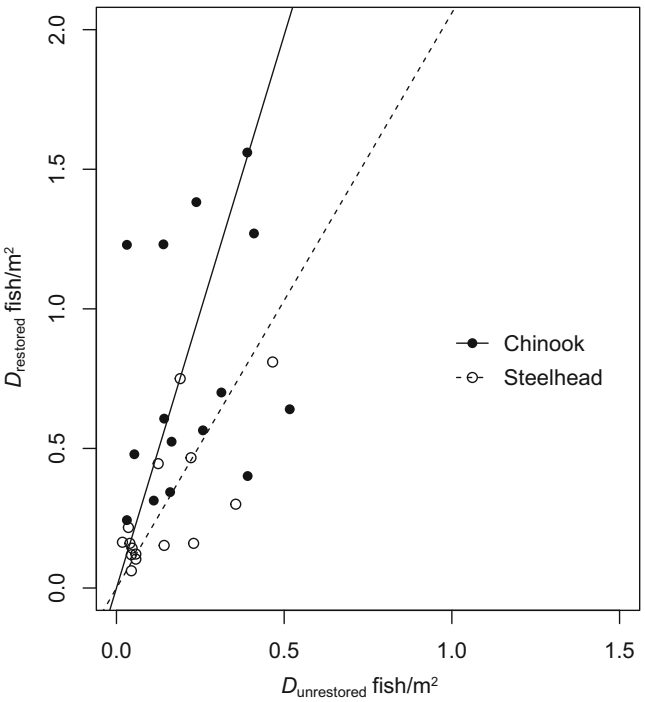

FIGURE 4 Isodars for juvenile Chinook salmon (black circles, solid line) and steelhead (open circles, dashed line) in restored versus unrestored habitat. The 95% CIs of the slopes overlap, thus showing a shared preference for restored habitat.

RSFs show that depth influences habitat distribution in both untreated and treated habitat. In untreated reaches, steelhead density did not vary much with depth, whereas Chinook densities increased with depth (Table 1). In ELJ-treated reaches, densities of both species were correlated with depth, with steelhead being associated with shallower ELJ pools, and Chinook with deeper ELJ-treated habitats (Table 2). RSFs thus provide initial evidence for distinct preferences within ELJ-treated habitats, with partitioning occurring along a depth gradient.

Within treated habitats, the calculated selectivity index for Chinook indicated a preference for deeper pools (Table 3A, Figure 5). Chinook selectivity for deeper ELJ pools was thus consistent with the depth gradient indicated by the RSF (Table 2). The generalized linear regression model analyzing selectivity within ELJ-treated habitats (Table 3A) resulted in the following equation describing the relationship between Chinook selectivity and the densities of Chinook and steelhead:

TABLE 1 Resource selection functions (generalized linear models [GLMs] fitted using a Gaussian error structure) for (A) Chinook density and (B) steelhead density in untreated habitat.

Effect	Posterior mean	Error	Lower 95%	Upper 95%
(A) Chinook salmon				
Intercept	0.019	0.061	−0.099	0.139
Steelhead density	−0.106	0.098	−0.297	0.086
Depth	0.537	0.127	0.283	0.776
Current velocity	−0.198	0.072	−0.335	−0.055
(B) Steelhead				
Intercept	0.266	0.057	0.151	0.381
Chinook density	−0.122	0.114	−0.343	0.101
Depth	−0.030	0.149	−0.323	0.265
Current velocity	−0.219	0.081	−0.378	−0.054

Note: Depth, current velocity, and heterospecific density were modeled as effects on habitat selection. Posterior distribution for GLM coefficients and 95% credible interval indicate that both species overlap with respect to current velocity. Chinook occupy deeper untreated habitat, whereas steelhead do not show habitat selection with respect to depth.

TABLE 2 Resource selection functions (generalized linear models [GLMs] fitted using a Gaussian error structure) for (A) Chinook density and (B) steelhead density in ELJ-treated habitat.

Effect	Posterior mean	Error	Lower 95%	Upper 95%
(A) Chinook salmon				
Intercept	0.130	0.168	−0.203	0.459
Steelhead density	−0.020	0.079	−0.179	0.134
Depth	1.025	0.354	0.343	1.735
Current velocity	−0.445	0.280	−0.991	−0.102
(B) Steelhead				
Intercept	0.783	0.178	0.442	1.122
Chinook density	−0.028	0.111	−0.247	0.193
Depth	−0.865	0.413	−1.664	−0.048
Current velocity	−0.322	0.334	−0.978	0.323

Note: Depth, current velocity, and heterospecific density were modeled as effects on habitat selection. Posterior distribution for GLM coefficients and 95% credible interval demonstrate meaningful separation along the depth gradient, with steelhead occupying shallower ELJ pools (B) and Chinook occupying deeper ELJ pools (A).

$$\log\left[\frac{P_c}{1-P_c}\right] = -0.9 + 0.8(C) + 0.05(S), \quad (5)$$

where P_c is the Chinook selectivity index, C is Chinook density, and S is steelhead density.

The isoleg is obtained by solving algebraically the equation for $P_c = 0.999$, that is, effective 100% preference for deep habitat due to the logistic nature of our selectivity model (Equation 5). The Chinook behavioral isoleg is then:

$$C = -0.0625(S) + 4.874. \quad (6)$$

The Chinook isoleg is therefore a straight line with negative slope with y-intercept = 4.874 (Figure 6). Above the isoleg, Chinook are predicted to be selective for deep ELJ pools; below the isoleg, Chinook are predicted to occupy shallow ELJ pools opportunistically (see Appendix S2).

TABLE 3 Results from generalized linear regression model with quasibinomial error structure assessing the relationship between Chinook selectivity for deep habitat (A), steelhead selectivity for deep habitat (B), and total densities of Chinook and steelhead in 2014 and 2015 ($n = 76$, Chinook; $n = 75$, steelhead).

Effect	β	SE	*t* value	*p*
(A) Chinook salmon				
Intercept	−0.8986	0.3722	−2.414	**0.018**
Chinook density	0.7970	0.2569	3.103	**0.003**
Steelhead density	0.0468	0.2548	0.184	0.855
(B) Steelhead				
Intercept	0.4133	0.3684	−1.122	0.121
Chinook density	0.5360	0.2343	2.288	**0.025**
Steelhead density	−0.0912	0.2611	0.349	0.141

Note: Species density with significant effect on species selectivity shown in bold.

Steelhead habitat selectivity is also dependent on Chinook densities (Table 3B) such that steelhead preference for deep habitat increases with increased Chinook densities. The generalized linear regression model results in the following equation describing the relationship between steelhead selectivity and the densities of Chinook and steelhead:

$$\log\left[\frac{P_s}{1-P_s}\right] = -0.4 + 0.54(C) - 0.09(S), \quad (7)$$

where P_s is steelhead selectivity index, S is steelhead density, and C is Chinook density. Solving as before gives the steelhead behavioral isoleg:

$$C = 0.1667(S) + 6.294. \quad (8)$$

The steelhead isoleg is thus a straight line with positive slope. Above the species isoleg, we predict habitat selection for deep ELJ pools, while below the species isoleg there is increasing selection for shallow ELJ pools with increasing steelhead density (see Appendix S2).

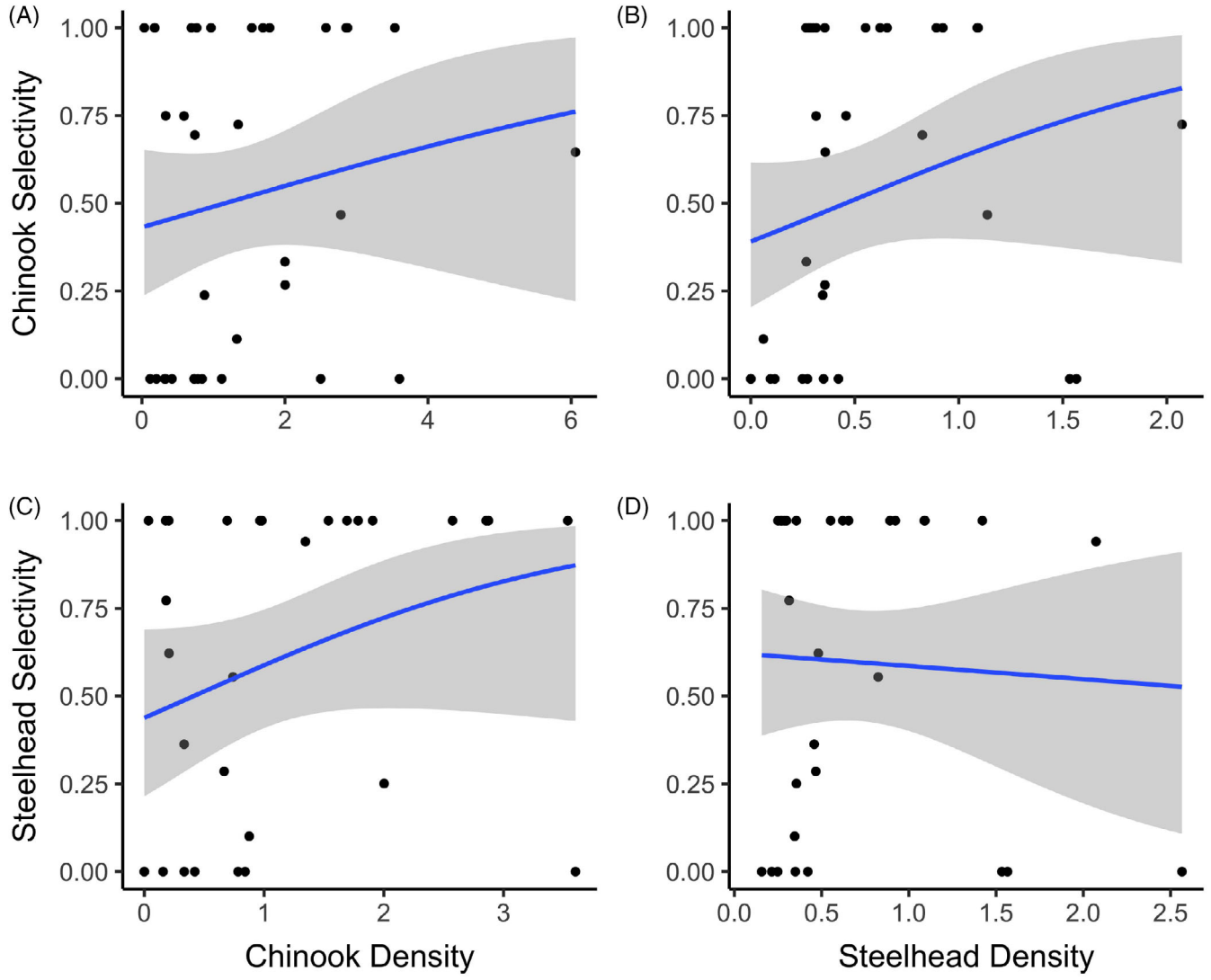

FIGURE 5 Habitat selectivity graphs depicting the relationship between Chinook selectivity for deep habitat as a function of Chinook density (A) and steelhead densities (B). Chinook habitat selectivity is impacted by Chinook density, but not steelhead density. Steelhead habitat selectivity graphs depicting the relationship between steelhead habitat selectivity and Chinook (C) and steelhead densities (D). Blue lines represent logistic regression model with 95% CIs.

The two isolegs plotted in state space create a behavioral map, dividing the density state space into three regions of habitat selection for Chinook and steelhead (Figure 6). When Chinook density is low, the isolegs indicate that the two species behave opportunistically (lower region). The negative slope of the Chinook isoleg indicates that Chinook are the competitively subordinate species so that Chinook density decreases as steelhead density increases in the shallower pools. This result is consistent with the RSF for ELJ-treated habitat (Table 2). At high Chinook densities (top region), the isolegs show that Chinook and steelhead have a shared preference for deep habitats. At these densities, the positive slope of the steelhead isoleg indicates that steelhead are the dominant competitors in treated habitats. As Chinook density increases, steelhead at these densities increasingly select deep pools as their density increases. Finally, when Chinook are at moderate densities we expect habitat partitioning to occur as a strategy to reduce the effects of competition (middle region). Above the Chinook isoleg, Chinook will increasingly select deep pools, and below the steelhead isoleg, steelhead will increasingly select shallow pools, effectively creating a "ghost of competition" region of the behavioral map.

Immigration model

Our immigration model provides a mechanistic explanation for the habitat partitioning evident from the RSFs

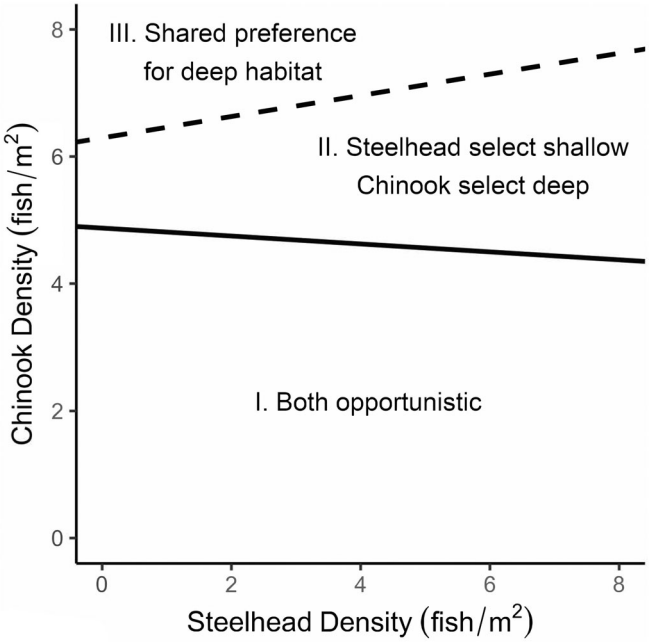

FIGURE 6 Isolegs for Chinook salmon (solid line) and steelhead (dashed line) in density state space. Isolegs were calculated using 2014 and 2015 density data in deep and shallow engineered log jam (ELJ)-treated pools. Chinook and steelhead isolegs indicate a shared preference for deep pools. Above the isolegs, each species prefers deep pools, and below the isolegs, each species behaves as a habitat opportunist and will increasingly prefer shallow pools. Regions of habitat selection are indicated by Roman numerals). Region II represents a region where habitat preferences diverge from one another. In that region, steelhead are progressively more likely to be found in shallow pools while Chinook are more likely to be found in deep pools, indicating a "ghost of competition."

and suggests a ghost of competition at the scale of treated and untreated habitats. First, in untreated habitat, Chinook immigration into pools falls strongly as steelhead density increases (Figure 7, bottom left panel). Chinook densities are thus low in untreated pools with high steelhead densities because high steelhead densities discourage Chinook immigration into pools. This conclusion is strengthened by the result that, in untreated habitats, Chinook immigration increases sharply with increasing conspecific density (Figure 7, top left panel); the main reason why Chinook avoid untreated pools is thus because of high steelhead densities rather than because of an inherent bias against untreated pools. Within treated pools, this result is also consistent with the Chinook isoleg that has a negative slope implying that Chinook are less likely to use shallow pools as steelhead density increases (Figure 6).

In treated habitats, in contrast, Chinook immigration is unaffected by steelhead density, and is also largely unaffected by conspecific density (Figure 7, right panels). Accordingly, when Chinook are at high density, they are very likely to colonize treated pools even if the treated pools have high densities of steelhead, again consistent with the isolegs. ELJs, therefore, greatly reduce the response of Chinook immigration to high densities of steelhead, helping to explain why treated pools often have high densities of both species, as indicated by the isodars (Figure 4) and by the top region of the isoleg map (Figure 6). Total levels of Chinook immigration were higher in treated pools than in untreated pools (difference in means 11.4, 95% HDI $[-17.3, -5.51]$; Appendix S3: Figure S1; means comparisons estimated by Bayesian Estimation Supercedes the T-test; Kruschke, 2013). Log-jam-treated pools thus enabled higher levels of density-dependent immigration by Chinook, which may partially explain the overlapping isodars.

Steelhead immigration similarly declined with increasing Chinook density, while increasing with increasing steelhead density (Figure 8). In the case of steelhead, however, these effects were similar in treated and untreated habitat; steelhead immigration was generally higher in restored than unrestored pools, but the difference was much smaller than it was in Chinook (difference in means −2.41, 95% HDI $[-4.83, -0.173]$, Appendix S3: Figure S2). The bottom panels of Figure 8 show that there was a weakly negative effect of higher Chinook density on steelhead immigration, an effect that was qualitatively similar in treated and untreated pools. These results suggest that steelhead immigration is unaffected by Chinook density, suggesting, in turn, that the effects of the ghost of competition are manifest exclusively through constraints on Chinook immigration.

We report the details of the analysis of movement out of the pools (emigration) in Appendix S3. In general, Chinook emigration was not affected by steelhead density, but saturated as Chinook density increased (Appendix S3: Figure S3). Chinook emigration did not differ with the presence or absence of ELJ treatments, suggesting that competitive pressure has no effect on Chinook emigration. Steelhead emigration rates were also unaffected by Chinook densities, nor were they affected by steelhead densities in untreated pools (Appendix S3: Figure S4). There was, however, a clear positive relationship between steelhead density and steelhead emigration from treated pools.

DISCUSSION

Isodars and isolegs are theories used to assess habitat selection within and between species as a strategy to mitigate competitive interactions. Here, we showed that these theories, combined with correlative analyses and

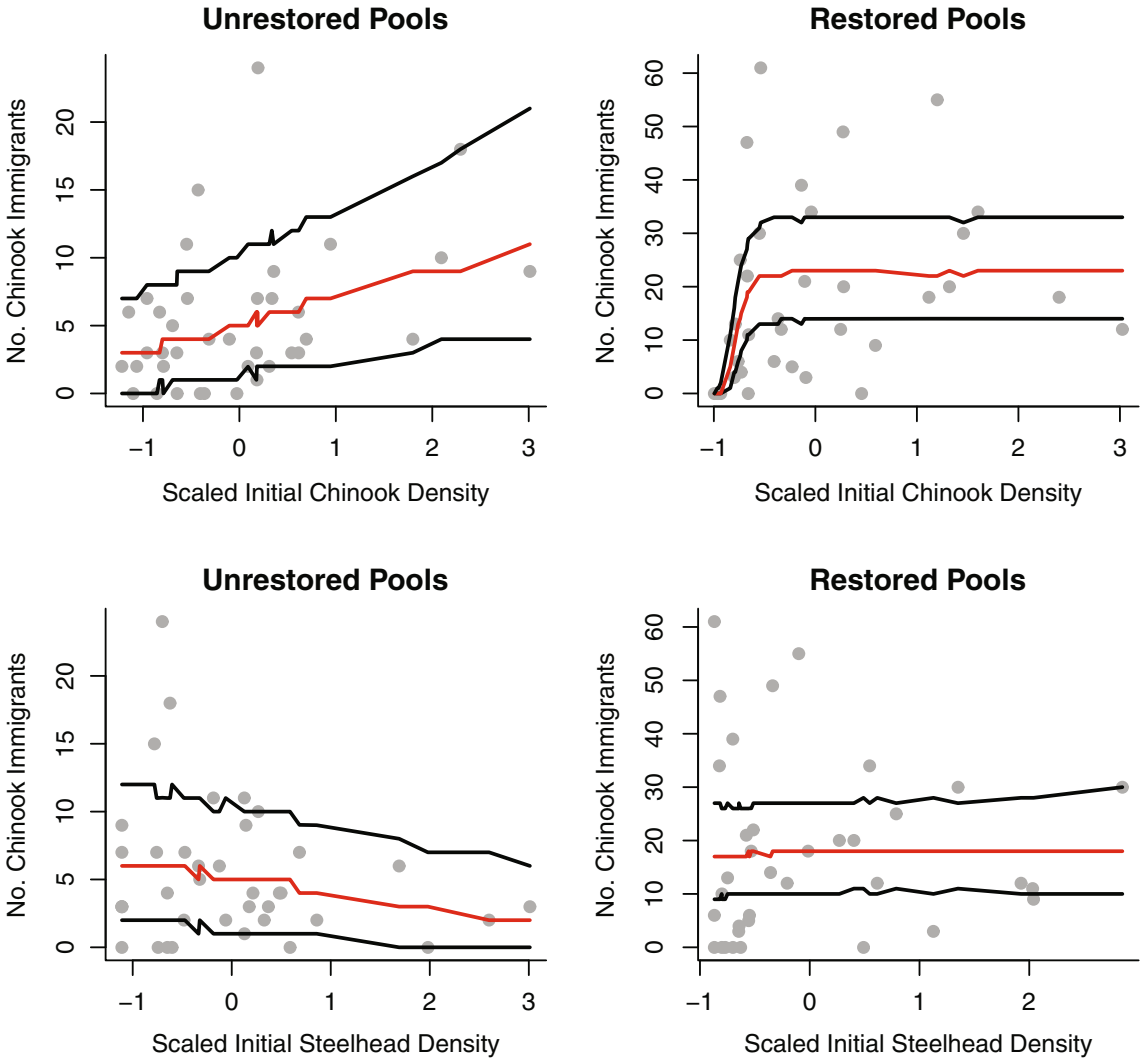

FIGURE 7 Chinook salmon immigration movements into untreated (left) and engineered log jam (ELJ)-treated (right) pools as a function of conspecific (top) and heterospecific (bottom) density (log scale) in restored (right) and unrestored (left) study pools, with mean immigration (red line) and 95% CIs (black lines).

experiments, are useful in restoration ecology for comparing both selection of restored versus unrestored habitat and partitioning of restored habitat. In this specific application, isodars showed that two ecologically similar fish species preferred restored habitat. That shared preference motivated further analysis of density-dependent habitat selection using isolegs applied to a physical habitat gradient—specifically stream pool depth—identified by RSFs. The experiment and isolegs ultimately showed that a "ghost of competition" arises in restored habitat and is derived from the competition that occurs in unrestored habitat. Therefore, we have shown how habitat selection theory informs restoration ecology, despite its rare use in this context (Morris, 2003a), especially in fish conservation studies (Malone & Polivka, 2022). Our application of theory to a fish restoration system is novel and provides a concrete example of the usefulness of theory in that context.

There are two major implications of isodar theory as applied in this study. First, restoration that targets ecologically similar species may result in each species showing increased use of the restored habitat type (Santos et al., 2018). Previously (Polivka, 2022), isodars indicated that steelhead had equal preference for treated and untreated habitat (isodar slope not different from 1), but the multiple treated reaches over multiple years that we included here strengthened the analysis and showed that steelhead share a preference for restored habitat with Chinook. This is despite the apparent superiority of steelhead in competing for space in unrestored habitat indicated by the experiment. Second, isodars enabled analysis of the effects on the two fish species of restoration across stream reaches, as opposed to previous studies that only showed the effect at the scale of habitat units (Polivka et al., 2015; Polivka & Claeson, 2020). The application of isodar

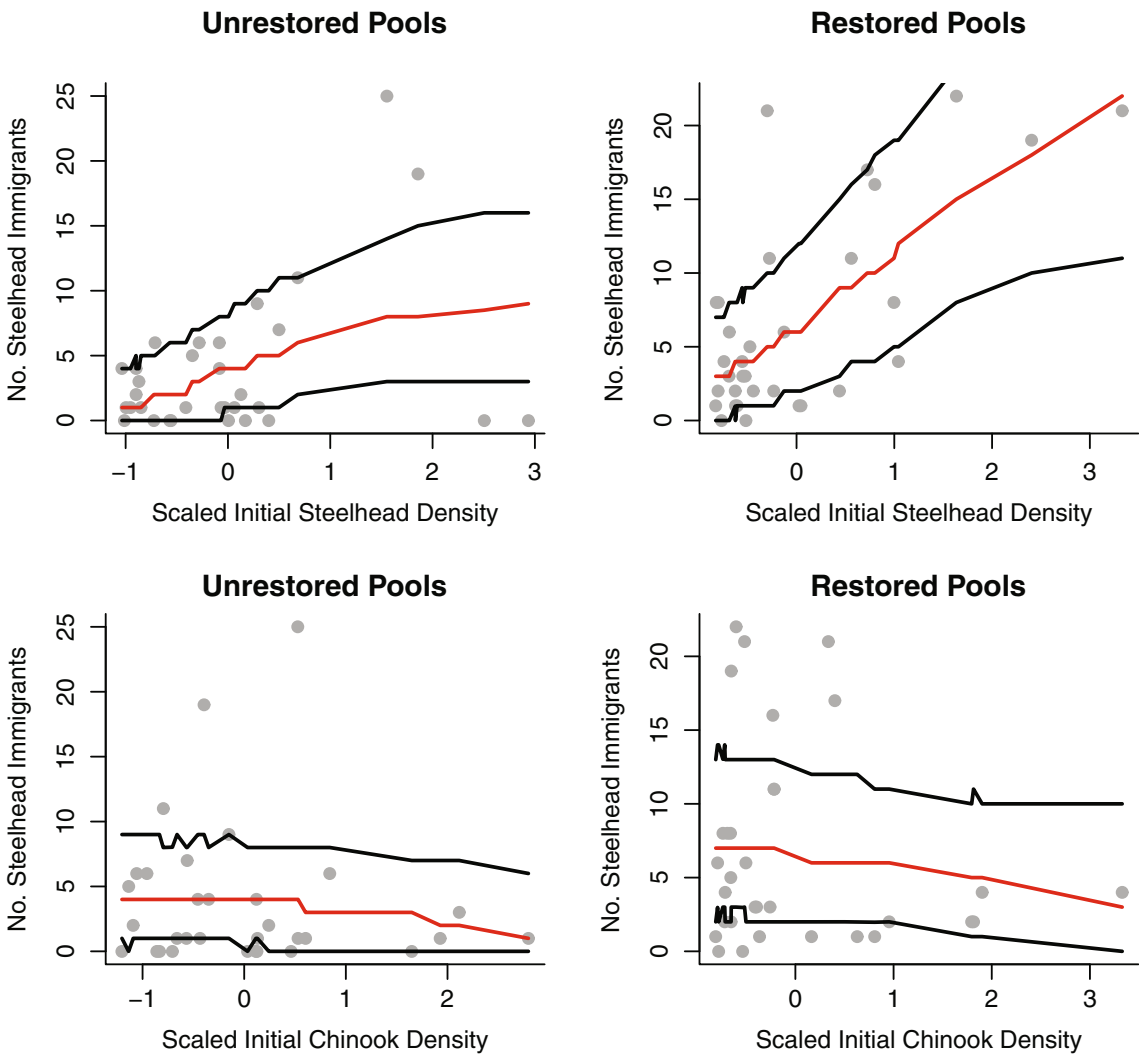

FIGURE 8 Steelhead immigration movements into untreated (left) and engineered log jam (ELJ)-treated (right) pools as a function of conspecific (top) and heterospecific (bottom) density (log scale) in restored (right) and unrestored (left) study pools, with mean immigration (red line) and 95% CIs (black lines).

theory thereby represents a novel approach to an elusive question in salmonid restoration ecology in the Pacific Northwest, USA—that of detecting effects at larger spatial scales (Roni, Jordan, & Pess, 2015).

Fish select habitats along a depth gradient in ELJ-treated habitat, as indicated by both the RSFs (Table 2) and behavioral isolegs (Figure 6). Together, these results suggest that while both species have similar preferred habitats, steelhead are the competitive superior and a range of deep and shallow pools can facilitate coexistence between the two species at a larger spatial scale (i.e., whole reach vs. habitat units). On average, steelhead were associated with shallow pools whereas Chinook were associated with deeper pools. In contrast with the selectivity analysis that generated the isolegs (Table 3), the RSFs did not show the effect of one species on the density of the other. The RSFs show density correlations with shallow (steelhead) versus deep (Chinook) pools, resulting from habitat partitioning. Use of the selectivity analysis generates isolegs showing densities at which those associations are likely to occur and lead to a ghost of competition (region II of Figure 6).

The disadvantages of RSFs is that they tend to be nonmechanistic (Moorcroft & Barnett, 2008), and do not always allow for density dependence (McLoughlin et al., 2010). Consideration of deep versus shallow ELJ pools through isoleg analysis addressed these disadvantages by showing that habitat selection is density-dependent, meaning that some densities lead to the existence of a ghost of competition, that is, each species being selective on one habitat type. Ultimately, the isolegs help explain the shared preferences indicated by the isodars in showing that although both Chinook and steelhead prefer ELJ-treated pools, variation in pool depth facilitates

coexistence. Use of the two years (2014 and 2015) with all available study sites led to a selectivity analysis with an approximately consistent median for the classification of pools as "deep" or "shallow." Although depth variation among sites and years can be higher (Appendix S1), our isoleg results were not affected by excessive variation in depth in those two years. It is possible that years with higher discharge or management strategies that create deeper ELJ pools might result in higher habitat diversity which further promotes species coexistence.

Isoleg theory has previously shown its usefulness in salmonid systems (Young, 2004) in which it was demonstrated that Coho salmon (*Oncorhynchus kisutch*), behave similarly to Chinook, by specializing on deeper pools compared with steelhead. One important contrast with that study is that our isolegs are based on observational data, whereas Young (2004) based the isolegs on experiments in an artificial stream system. Isolegs based on observational data have higher uncertainty than those based on experimental data (Rosenzweig & Abramsky, 1997). Another issue with using field observations is that the range of observed densities in our study may still be below the carrying capacity of the environment so that the extent of actual partitioning is underrepresented in the data. Higher observed densities of both species may therefore lead to the expansion of region II in the isoleg plot.

A given study system may also consist of more than two isolegs, particularly if a centrifugal pattern of habitat selection can be identified (Brown, 1996; Wasserberg et al., 2006) where there is a shared preferred habitat and two alternative habitats. In our case, it may be possible to introduce selection of unrestored habitats into the behavioral map, to possibly show circumstances under which steelhead are selective and Chinook are opportunistic on that habitat. More than two habitat alternatives can also lead to "partial" ghosts where there is stable coexistence owing to one species using two or more habitats (Wasserberg et al., 2006). However, an exploratory selectivity analysis did not show density dependence in the selectivity at the scale of ELJ-treated versus untreated habitat (unpublished data), therefore additional isolegs including unrestored habitat would be overly speculative, pending more data.

The joint mark–recapture experiment at the scale of individuals within habitats provided the most definitive evidence that competition was mitigated by restoration. Restored habitat had a higher capacity for immigration by Chinook and settlement by new individuals even when high density of steelhead was present, whereas unrestored habitat showed that space competition is the mechanism behind habitat selection at the scale of treated versus untreated habitat. Combined with the isoleg analysis, the experiment therefore shows that the competition observed in untreated habitat vanished in ELJ-treated habitat, becoming a ghost, caught or "busted" by the experiment (Schmidt et al., 2000). Furthermore, the potential for competition verified by the experiment at the scale of individuals within habitats can be extended to the reach scale by the isoleg analysis.

Mark–recapture methods have only rarely been used to estimate the effect of interspecific competition on habitat selection in fishes (Yackulic et al., 2018). We improved upon standard approaches by constructing a model of density-dependent immigration. Crucially, Bayesian model fitting techniques were found to be useful, despite relatively low sample size, even allowing estimation of a heterospecific density parameter. Another advance was that we observed a positive effect on immigration into pools, and therefore on total habitat capacity, for both species instead of only for Chinook, as was previously indicated (Polivka, 2020). This capacity increase is quantifiable by comparing the α_1 term across restored and unrestored habitat in Equation (3).

We show that the combination of experiments with habitat selection theory expands the inferences that can be made from long-term, habitat-specific data typically collected in post-restoration monitoring studies (Polivka, 2022). Few fish habitat restoration efficacy studies rely on mechanistic approaches that explicitly incorporate habitat selection theory, density dependence, or experimental evidence to evaluate efficacy as we applied them in this study (Malone & Polivka, 2022; Polivka, 2022; Roni et al., 2010). We highlight the potential for these approaches to be applied to observational data commonly collected in post-restoration monitoring studies, simply by analyzing such data in new ways. More broadly, this study supports the conclusion that habitat selection theory can have substantial explanatory power in restoration ecology despite only sometimes being applied in this way (Morris, 2003a).

ACKNOWLEDGMENTS

This work was supported in part by the US Bureau of Reclamation, Bonneville Power Administration (Integrated Status and Effectiveness Monitoring Program), and Pacific Northwest Research Station (USDA FOREST SERVICE). Administrative support for field technicians and for MM was provided by Cascadia Conservation District. We thank S. Eichler, R. Logan, A. Bushy, K. Tackman, J. West, J. Novak, K. Logan, J. Jorgensen, H. Porter, B. Miland, R. Hosman, S. Kaech, and C. Raine for collection and curation of field data during the various years of the study. A. Bushy was supported by the American Fisheries Society Hutton Junior Fisheries Biology Scholarship. S. Claeson designed Figure 2. B. Kotler and J. Brown provided helpful

discussions on earlier drafts of the manuscript. We also thank D. Morris and an anonymous reviewer for further improvement of the manuscript. All fish handling was conducted under US Department of Commerce, NOAA-Fisheries, Permit No. 1422 and is consistent with guidelines published by the American Fisheries Society.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Malone, 2024) are available in Zenodo at https://doi.org/10.5281/zenodo.13623121.

ORCID

Carlos M. Polivka https://orcid.org/0000-0001-9021-240X
Margaret A. Malone https://orcid.org/0000-0001-8853-7096

REFERENCES

Abramsky, Z., M. A. Bowers, and M. L. Rosenzweig. 1986. "Detecting Interspecific Competition in the Field: Testing the Regression Method." *Oikos* 47: 199–204.

Abramsky, Z., M. L. Rosenzweig, B. Pinshow, J. Brown, B. Kotler, and W. Mitchell. 1990. "Habitat Selection: An Experimental Field Test with Two Gerbil Species." *Ecology* 71: 2358–69.

Anderson, D., A. Heiss, and J. Sumners. 2021. "Equatiomatic: Transform Models into 'LaTeX' Equations."

Bates, D., D. Sarkar, M. D. Bates, and L. Matrix. 2007. "The lme4 Package." R Package Version 2:74.

Beechie, T., M. Liermann, E. Beamer, and R. Henderson. 2005. "A Classification of Habitat Types in a Large River and their Use by Juvenile Salmonids." *Transactions of the American Fisheries Society* 134: 717–729.

Berger-Tal, O., T. Polak, A. Oron, Y. Lubin, B. P. Kotler, and D. Saltz. 2011. "Integrating Animal Behavior and Conservation Biology: A Conceptual Framework." *Behavioral Ecology* 22: 236–39.

Berger-Tal, O., and D. Saltz. 2016. *Conservation Behavior: Applying Behavioral Ecology to Wildlife Conservation and Management*. Cambridge, UK: Cambridge University Press.

Blumstein, D. T., and E. Fernández-Juricic. 2010. *A Primer of Conservation Behavior*. Sunderland, MA: Sinauer Associates.

Boyce, M. S., and L. L. McDonald. 1999. "Relating Populations to Habitats Using Resource Selection Functions." *Trends in Ecology and Evolution* 14: 268–272.

Brown, J. S. 1996. "Coevolution and Community Organization in Three Habitats." *Oikos* 75: 193–206.

Dehnhard, N., H. Achurch, J. Clarke, L. N. Michel, C. Southwell, M. D. Sumner, M. Eens, and L. Emmerson. 2020. "High Inter- and Intraspecific Niche Overlap among Three Sympatrically Breeding, Closely Related Seabird Species: Generalist Foraging as an Adaptation to a Highly Variable Environment?" *Journal of Animal Ecology* 89: 104–119.

Everest, F. H., and D. W. Chapman. 1972. "Habitat Selection and Spatial Interaction by Juvenile Chinook Salmon and Steelhead Trout in Two Idaho Streams." *Journal of the Fisheries Research Board of Canada* 29: 91–100. https://doi.org/10.1139/f72-012.

Fisher, J., J. Cortina-Segarra, M. Grace, D. Moreno-Mateos, P. R. González, S. Baker, J. Frouz, et al. 2019. "What is Hampering Current Restoration Effectiveness?"

Fretwell, S. D., and H. Lucas. 1970. "On Territorial Behavior and Other Factors Influencing Habitat Distribution in Birds. I. Theoretical Development." *Acta Biotheoretica* 19: 16–36.

Gelman, A. 2008. "Scaling Regression Inputs by Dividing by Two Standard Deviations." *Statistics in Medicine* 27: 2865–73. https://doi.org/10.1002/sim.3107.

Gumm, J. M., J. L. Snekser, J. Leese, K. Little, J. Leiser, V. Imhoff, B. Westrick, and M. Itzkowitz. 2011. "Management of Interactions Between Endangered Species Using Habitat Restoration." *Biological Conservation* 144: 2171–76.

Harvey, B. C., and R. J. Nakamoto. 1997. "Habitat-Dependent Interactions Between Two Size-Classes of Juvenile Steelhead in a Small Stream." *Canadian Journal of Fisheries and Aquatic Sciences* 54: 27–31. https://doi.org/10.1139/f96-249.

Hasegawa, K., and K. Maekawa. 2008. "Potential of Habitat Complexity for Mitigating Interference Competition Between Native and Non-Native Salmonid Species." *Canadian Journal of Zoology* 86: 386–393. https://doi.org/10.1139/Z08-015.

Hasegawa, K., and K. Maekawa. 2009. "Role of Visual Barriers on Mitigation of Interspecific Interference Competition Between Native and Non-Native Salmonid Species." *Canadian Journal of Zoology* 87: 781–86. https://doi.org/10.1139/z09-071.

Hearn, W. E. 1987. "Interspecific Competition and Habitat Segregation Among Stream-Dwelling Trout and Salmon: A Review." *Fisheries* 12(5): 24–31. https://doi.org/10.1577/1548-8446%281987%29012%3C0024%3AICAHSA%3E2.0.CO%3B2.

Hillman, T. W., J. Griffith, and W. Platts. 1987. "Summer and Winter Habitat Selection by Juvenile Chinook Salmon in a Highly Sedimented Idaho Stream." *Transactions of the American Fisheries Society* 116: 185–195.

Holbrook, J. D., L. E. Olson, N. J. DeCesare, M. Hebblewhite, J. R. Squires, and R. Steenweg. 2019. "Functional Responses in Habitat Selection: Clarifying Hypotheses and Interpretations." *Ecological Applications* 29: e01852.

Huntsman, B. M., J. A. Falke, J. W. Savereide, and K. E. Bennett. 2017. "The Role of Density-Dependent And–Independent Processes in Spawning Habitat Selection by Salmon in an Arctic Riverscape." *PLoS One* 12: e0177467.

Indermaur, L., T. Winzeler, B. R. Schmidt, K. Tockner, and M. Schaub. 2009. "Differential Resource Selection Within Shared Habitat Types Across Spatial Scales in Sympatric Toads." *Ecology* 90: 3430–44.

Kotler, B. P., D. W. Morris, and J. S. Brown. 2016. *Conservation Behavior: Applying Behavioral Ecology to Wildlife Conservation and Management, Chapter Direct Behavioral Indicators as a Conservation and Management Tool*. Cambridge: Cambridge University Press.

Kruschke, J. K. 2013. "Bayesian Estimation Supersedes the t Test." *Journal of Experimental Psychology: General* 142: 573–603.

Lele, S. R., E. H. Merrill, J. Keim, and M. S. Boyce. 2013. "Selection, Use, Choice and Occupancy: Clarifying Concepts in Resource Selection Studies." *Journal of Animal Ecology* 82: 1183–91.

Linnet, K. 1990. "Estimation of the Linear Relationship Between the Measurements of Two Methods With Proportional Errors." *Statistics in Medicine* 9: 1463–73.

Malone, M. A., and C. M. Polivka. 2022. "The Behavioural Ecology Toolkit for Fish Management and Conservation." *Fish and Fisheries* 23: 1485–1506.

Malone, M. A. 2024. "MarineBioMeg/Isolegs: Isolegs (Isolegs)." Zenodo. https://doi.org/10.5281/zenodo.13623121.

McAfee, D., C. Larkin, and S. D. Connell. 2021. "Multi-Species Restoration Accelerates Recovery of Extinguished Oyster Reefs." *Journal of Applied Ecology* 58: 286–294.

McCabe, J. D., J. D. Clare, T. A. Miller, T. E. Katzner, J. Cooper, S. Somershoe, D. Hanni, et al. 2021. "Resource Selection Functions Based on Hierarchical Generalized Additive Models Provide New Insights into Individual Animal Variation and Species Distributions." *Ecography* 44: 1756–68.

McLoughlin, P. D., D. W. Morris, D. Fortin, E. Vander Wal, and A. L. Contasti. 2010. "Considering Ecological Dynamics in Resource Selection Functions." *Journal of Animal Ecology* 79: 4–12.

McMichael, G. A., C. S. Sharpe, and T. N. Pearsons. 1997. "Effects of Residual Hatchery-Reared Steelhead on Growth of Wild Rainbow Trout and Spring Chinook Salmon." *Transactions of the American Fisheries Society* 126: 230–39. https://doi.org/10.1577/1548-8659%281997%29126%3C0230%3AEORHRS%3E2.3.CO%3B2.

Mesa, M. G., and C. B. Schreck. 1989. "Electrofishing Mark–Recapture and Depletion Methodologies Evoke Behavioral and Physiological Changes in Cutthroat Trout." *Transactions of the American Fisheries Society* 118: 644–658.

Moorcroft, P. R., and A. Barnett. 2008. "Mechanistic Home Range Models and Resource Selection Analysis: A Reconciliation and Unification." *Ecology* 89: 1112–19.

Morris, D. W. 1988. "Habitat-Dependent Population Regulation and Community Structure." *Evolutionary Ecology* 2: 253–269.

Morris, D. W. 1989. "Habitat-Dependent Estimates of Competitive Interaction." *Oikos* 55: 111–120.

Morris, D. W. 1999a. "Has the Ghost of Competition Passed?" *Evolutionary Ecology Research* 1: 1.

Morris, D. W. 1999b. "A Haunting Legacy from Isoclines: Mammal Coexistence and the Ghost of Competition." *Journal of Mammalogy* 80: 375–384.

Morris, D. W. 2003a. "How Can we Apply Theories of Habitat Selection to Wildlife Conservation and Management?" *Wildlife Research* 30: 303–319.

Morris, D. W. 2003b. "Toward an Ecological Synthesis: A Case for Habitat Selection." *Oecologia* 136: 1–13.

Morris, D. W., B. P. Kotler, J. S. Brown, V. Sundararaj, and S. B. Ale. 2009. "Behavioral Indicators for Conserving Mammal Diversity." *Annals of the New York Academy of Sciences* 1162: 334–356.

Nunn, A., L. Vickers, K. Mazik, J. Bolland, G. Peirson, S. Axford, A. Henshaw, and I. Cowx. 2020. "Dynamic Competition and Resource Partitioning During the Early Life of Two Widespread, Abundant and Ecologically Similar Fishes." *Hydrobiologia* 847: 2211–24.

O'Neil, S. T., J. A. Vucetich, D. E. Beyer, Jr., S. R. Hoy, and J. K. Bump. 2020. "Territoriality Drives Preemptive Habitat Selection in Recovering Wolves: Implications for Carnivore Conservation." *Journal of Animal Ecology* 89: 1433–47.

Persson, L., and L. A. Greenberg. 1990. "Juvenile Competitive Bottlenecks: The Perch (*Perca fluviatilis*)-Roach (*Rutilus rutilus*) Interaction." *Ecology* 71: 44–56.

Pimm, S. L., and M. L. Rosenzweig. 1981. "Competitors and Habitat Use." *Oikos* 37: 1–6.

Pimm, S. L., M. L. Rosenzweig, and W. Mitchell. 1985. "Competition and Food Selection: Field Tests of a Theory." *Ecology* 66: 798–807.

Plummer, M. 2003. "JAGS: A Program for Analysis of Bayesian Graphical Models Using Gibbs Sampling." In *Proceedings of the 3rd International Workshop on Distributed Statistical Computing*, Vol. 124, 1–10. Vienna.

Polivka, C. M. 2020. "Habitat Affinity and Density-Dependent Movement as Indicators of Fish Habitat Restoration Efficacy." *Ecosphere* 11: e03166.

Polivka, C. M. 2022. "'If You Build It...': Methodological Approaches to Detect Postrestoration Responses in Stream Fishes." *Fisheries* 47: 346–355.

Polivka, C. M., and S. M. Claeson. 2020. "Beyond Redistribution: In-Stream Habitat Restoration Increases Capacity for Young-of-the-Year Chinook Salmon and Steelhead in the Entiat River, Washington." *North American Journal of Fisheries Management* 40: 446–458.

Polivka, C. M., J. Mihaljevic, and G. Dwyer. 2020. "Use of a Mechanistic Growth Model in Evaluating Post-Restoration Habitat Quality for Juvenile Salmonids." *PLoS One* 15: e0234072.

Polivka, K. M., E. A. Steel, and J. L. Novak. 2015. "Juvenile Salmon and Steelhead Occupancy of Stream Pools Treated and Not Treated With Restoration Structures, Entiat River, Washington." *Canadian Journal of Fisheries and Aquatic Sciences* 72: 166–174.

R Core Team. 2017. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. https://www.R-project.org/.

Rodríguez, M. A. 1995. "Habitat-Specific Estimates of Competition in Stream Salmonids: A Field Test of the Isodar Model of Habitat Selection." *Evolutionary Ecology* 9: 169–184.

Roni, P., T. Beechie, G. Pess, and K. Hanson. 2015. "Wood Placement in River Restoration: Fact, Fiction, and Future Direction." *Canadian Journal of Fisheries and Aquatic Sciences* 72: 466–478.

Roni, P., T. J. Beechie, R. E. Bilby, F. E. Leonetti, M. M. Pollock, and G. R. Pess. 2002. "A Review of Stream Restoration Techniques and a Hierarchical Strategy for Prioritizing Restoration in Pacific Northwest Watersheds." *North American Journal of Fisheries Management* 22: 1–20.

Roni, P., C. Jordan, and G. Pess. 2015. "Basin Scale Monitoring of River Restoration: Recommendations from Case Studies in the Pacific Northwest USA." In *American Fisheries Society, Symposium*, Vol. 78, 73–98. Bethesda, MD, USA: American Fisheries Society.

Roni, P., G. Pess, T. Beechie, and S. Morley. 2010. "Estimating Changes in Coho Salmon and Steelhead Abundance From Watershed Restoration: How Much Restoration Is Needed to Measurably Increase Smolt Production?" *North American Journal of Fisheries Management* 30: 1469–84.

Rosenzweig, M. L. 1974. "On the Evolution of Habitat Selection." In *Proceedings of the First International Congress of Ecology*,

Vol. 401, 404. Netherlands: Center for Agricultural Publishing and Documentation.
Rosenzweig, M. L. 1981. "A Theory of Habitat Selection." *Ecology* 62: 327–335.
Rosenzweig, M. L. 1987. "Habitat Selection as a Source of Biological Diversity." *Evolutionary Ecology* 1: 315–330.
Rosenzweig, M. L. 1991. "Habitat Selection and Population Interactions: The Search for Mechanism." *The American Naturalist* 137: S5–S28.
Rosenzweig, M. L., and Z. Abramsky. 1986. "Centrifugal Community Organization." *Oikos* 46: 339–348.
Rosenzweig, M. L., and Z. Abramsky. 1997. "Two Gerbils of the Negev: A Long-Term Investigation of Optimal Habitat Selection and Its Consequences." *Evolutionary Ecology* 11: 733–756.
Santos, J. M., R. Rivaes, I. Boavida, and P. Branco. 2018. "Structural Microhabitat Use by Endemic Cyprinids in a Mediterranean-Type River: Implications for Restoration Practices." *Aquatic Conservation: Marine and Freshwater Ecosystems* 28: 26–36.
Schmidt, K. A., J. M. Earnhardt, J. S. Brown, and R. D. Holt. 2000. "Habitat Selection Under Temporal Heterogeneity: Exorcizing the Ghost of Competition Past." *Ecology* 81: 2622–30.
Shochat, E., M. A. Patten, D. W. Morris, D. L. Reinking, D. H. Wolfe, and S. K. Sherrod. 2005. "Ecological Traps in Isodars: Effects of Tallgrass Prairie Management on Bird Nest Success." *Oikos* 111: 159–169.
Stan Development Team. 2017a. "RStan: the R Interface to Stan." http://mc-stan.org/.
Stan Development Team. 2017b. "Stan Modeling Language Users Guide and Reference Manual." http://mc-stan.org/.
Tarjuelo, R., J. Traba, M. B. Morales, and D. W. Morris. 2017. "Isodars Unveil Asymmetric Effects on Habitat Use Caused by Competition Between Two Endangered Species." *Oikos* 126: 73–81.
Török, P., and A. Helm. 2017. "Ecological Theory Provides Strong Support for Habitat Restoration." *Biological Conservation* 206: 85–91.
Wasserberg, G., B. P. Kotler, D. W. Morris, and Z. Abramsky. 2006. "A Specter of Coexistence: Is Centrifugal Community Organization Haunted by the Ghost of Competition?" *Israel Journal of Ecology and Evolution* 52: 123–140.
Werner, E. E., D. J. Hall, D. R. Laughlin, D. J. Wagner, L. A. Wilsmann, and F. C. Funk. 1977. "Habitat Partitioning in a Freshwater Fish Community." *Journal of the Fisheries Research Board of Canada* 34: 360–370. https://doi.org/10.1139/f77-058.
Yackulic, C. B., J. Korman, M. D. Yard, and M. Dzul. 2018. "Inferring Species Interactions through Joint Mark–Recapture Analysis." *Ecology* 99: 812–821. https://doi.org/10.1002/ecy.2166.
Young, K. A. 2004. "Asymmetric Competition, Habitat Selection, and Niche Overlap in Juvenile Salmonids." *Ecology* 85: 134–149.
Ziv, Y., B. P. Kotler, Z. Abramsky, and M. L. Rosenzweig. 1995. "Foraging Efficiencies of Competing Rodents: Why Do Gerbils Exhibit Shared-Preference Habitat Selection?" *Oikos* 73: 260–68.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Polivka, Carlos M., Margaret A. Malone, Spencer A. Carran, and Greg Dwyer. 2024. "Understanding How Restoration Reduces Competition for Habitat by Combining Theory, Observation, and Experiment." *Ecological Applications* 34(8): e3033. https://doi.org/10.1002/eap.3033