Title:

Native Fish Abundance and Habitat Selection Changes in the Presence of Nonnative Piscivores

Running Title: Nonnative predators impact native fishes

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Data availability:

Our data is publicly available and archived on the Open Science Framework (OSF): https://osf.io/3j2kp/

Disclosure statement:

No potential conflict of interest was reported by the authors of this study.

Ethics statement:

No animals were subjected to handling and observations were carried out in a manner that caused minimal disturbance.

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ABSRACT:

We compared abundance patterns and developed resource selection models for imperiled native southwestern (U.S.A.) fishes in the presence and absence of Black Bass (*Micropterus spp*.) to evaluate how fishes alter their selection for habitats when sympatric with a nonnative piscivore. We collected data using snorkel surveys and in-stream habitat sampling in Fossil Creek (AZ), upstream (native fish only) and downstream (native and nonnative fish) of a fish barrier. The abundance of all Roundtail Chub (*Gila robusta)*, small (≤ 127 mm total length (TL); vulnerable to predation) Sonora Sucker (*Catostomus insignis)*, and Speckled Dace (*Rhinichthys osculus)* was significantly reduced, but the abundance of both small and large (>127 mm TL; invulnerable to predation) Desert Sucker (*Catostomus clarkii)* was similar in sampling reaches with and without Black Bass. When sympatric with Black Bass, small Roundtail Chub increased their selection for riffles by 2.57 times and small Desert Sucker reduce their selection for pools by 6.90 times while also selecting for faster flow velocity and finer substrates in lotic mesohabitats. Large native fishes altered selection least, notwithstanding an increased selection for canopy cover in sampling reaches with Black Bass. Observed shifts in resource selection are consistent with predator avoidance strategies. Our study highlights the behavioral consequences of nonnative piscivores on native fish communities and stresses the importance of maintaining lotic mesohabitats as potential refugia for vulnerable native fishes when nonnative piscivores are present.

Key words:

Native Fish, Stream Ecology, Desert Southwest, Roundtail Chub, Habitat Selection, Nonnative Species

Freshwater ecosystems and the species they support are globally imperiled due to resource overexploitation, water pollution, flow regime modification, climate change, the widespread loss of habitat, and the proliferation of nonnative species (Xenopoulos et al. 2005; Dudgeon et al. 2006; Tickner et al. 2020). Freshwater vertebrate populations have declined at more than twice the rate of terrestrial populations and wetlands are being lost at three times the rate of forest environments (Dudgeon et al. 2006; Comte et al. 2013; Tickner et al. 2020). Endemic freshwater fishes are particularly vulnerable and 28% of species investigated by the IUCN are at significant risk of extinction (IUCN 2019; Tickner et al. 2020).

Fundamental to the conservation of freshwater fishes is the identification of the physical features of the stream (e.g., depths, substrate, flow, cover, food) that collectively constitute habitat for a target species, and then to maintain that habitat in sufficient quantity to sustain viable populations (Rosenfeld and Hatfield 2006; Turner and List 2007). Assuming that higher quality habitats support a greater density of individuals (Mayor et al. 2009), increasing the spatiotemporal quantity of such habitats can increase the abundance and distribution of a target species (Fretwell and Lucas 1970; Rosenfeld and Hatfield 2006). A loss of habitat or reductions in habitat quality may force individuals to occupy suboptimal environments or disperse in search of new environments (McMahon and Tash 1988; Rosenfeld 2003), both of which would have negative fitness consequences (Mannan and Steidl 2013; Davis and Wagner 2016). The availability of suitable habitats is the major driver of species distribution, abundance, and diversity across spatial scales (Bunn and Arthington 2002) including the spatial distribution of individuals within a stream (Teresa and Casatti 2013). Under ideal free distribution, individuals arrange themselves in the spatial environment to maximize their fitness by selecting specific environmental features that provide adequate resources for survival, growth, and reproduction, while minimizing external sources of mortality (e.g., predation; Fretwell and Lucas 1970; Rosenfeld and Hatfield 2006).

Modified flow regimes and other types of aquatic habitat degradation have decreased the quantity and quality of habitat available to native fishes and facilitated the spread and establishment of nonnative fishes (Bunn and Arthington 2002). Direct impacts of nonnative fishes include predation (Brown and Moyle 1991), competition (Rinne 1991), hybridization, and disease and parasite transmission (Tyus & Saunders 2000; Gozlan et al. 2010). Nonnative species can also indirectly affect native fishes. Native fishes avoid nonnative species to minimize predation risk and competition, potentially excluding individuals from previously selected resources (Brown and Moyle 1991; Bowers and Dooley 1993; Douglas et al. 1994; Mayor et al. 2009). Many studies have documented shifts in native fishes' habitat selection resulting from the presence of nonnative species across freshwater fish taxa (Brown and Moyle 1991; Rinne 1991; Bohn et al. 2008). This illustrates the importance of understanding the habitat associations and requirements of native fishes and how those associations shift in the presence of nonnative fishes.

The native freshwater fish assemblage of the southwestern United States and northern Mexico (hereafter referred to as the Southwest) is one of the most imperiled faunal groups in North America (Minckley and Deacon 1968; Rahel 2000; Schade and Bonar 2005). More than two-thirds of the fishes endemic to the Southwest are listed as endangered, threatened, or a species of concern by state or federal agencies, one species has gone extinct, and multiple others have been locally extirpated (Rinne 1994; Minckley et al. 2002; Olden and Poff 2005; Turner and List 2007). The decline of the native Southwest fishes is primarily attributed to widespread habitat loss and expansion of nonnative fishes. Previous research has found that native Southwest fishes face intense predation (Pilger et al. 2008), competition for resources (Rinne 1994), and are displaced from their trophic niche towards lower trophic positions by nonnative fishes (Marks et al. 2010; Rogosch and Olden 2020). The conservation and recovery of native Southwest fishes depends on a comprehensive knowledge of their habitat requirements and the ecological mechanisms that influence habitat selection (Rosenfeld and Hatfield 2006). Such efforts also require an understanding of how native species alter their selection for habitat in the presence of nonnative species, which are nearly ubiquitous within the Southwest (Clarkson et al. 2005; Schade and Bonar 2005).

In this study, we evaluated abundance patterns and modeled habitat selection via resource selection functions (RSFs) for native fishes of Fossil Creek, AZ in the presence and absence of nonnative Black Bass (*Micropterus spp.*) We used data collected upstream and downstream of a fish barrier which divided our study area into two sections, one exclusively occupied by native fish (upstream) and one in which Black Bass were present (downstream). We hypothesized that the abundance of fish occupying the ecological niche most similar to Black Bass would show significant differences in both abundance and habitat selection upstream and downstream of the barrier. Additionally, we hypothesized that species with less niche overlap with the nonnative Black Bass would be less impacted by its presence and would, therefore, have less need to alter their selection for habitat.

METHODS-

Study Site: -

Fossil Creek is a 23-km long spring-fed perennial river in central Arizona originating on the Mogollon Rim of the Colorado Plateau with a terminus at the Verde River (USFS 2011; Figure 1). The origin of the perennial reach of Fossil Creek, Fossil Springs, discharges 76 m^3/min, providing a steady year-round baseflow of 1.2 – 1.6 m^3/s and a relatively constant temperature of approximately 21.1° C.

From 1909 – 2005, Fossil Creek's flow was diverted to provide hydroelectricity. In 2005, the flow was restored to Fossil Creek and the river was federally designated as Wild and Scenic in 2009 (USFS 2011). As part of that restoration, a collaboration of management agencies removed nonnative fishes from the river, constructed a fish barrier 7 km upstream from the mouth of Fossil Creek, and repatriated native fishes. Two major washes (Sally May and Boulder Canyon; Figure 1) contribute loose alluvium into Fossil Creek and as a result, there is a transition from large deep pools upstream to shallower pools of finer substrates downstream of these inputs. As such, there are some differences to the physical features of the river upstream and downstream of these washes (Marks et al. 2006; Carter and Marks 2007; Marks et al. 2009).

Today, the upper 16.5 km of Fossil Creek retains an exclusively native fish community that consists of Roundtail Chub (*Gila robusta*), Desert Sucker (*Catostomus clarkia*), Sonora Sucker (*Catostomus insignis*), Longfin Dace (*Agosia chrysogaster),* Speckled Dace (*Rhinichthys osculus*), and Spikedace (*Meda fulgida*). Since restoration, nonnative fishes have recolonized Fossil Creek from the Verde River, but are not present above the fish barrier. The only nonnative fish observed in our study were Black Bass (likely Smallmouth Bass (*Micropterus dolomieu*) and Redeye Bass (*Micropterus coosae*) hybrids (Valente et al. 2021); however, additional species (e.g., Green Sunfish (*Lepomis cyanellus*), Red Shiner (*Cyprinella lutrensis*), catfishes (*Ictaluridae spp.*)) are likely present downstream of the barrier.

We conducted snorkel surveys in seventeen sampling reaches (mean length = 102.53 m; range = 90 – 130 m) in the summer (June–August) of 2019 and 2020 while Fossil Creek was at baseflow. Nine sampling reaches were upstream of the fish barrier where no nonnative fishes were present and eight were downstream of the fish barrier where native and nonnative fish were present. Four of the "upstream" sampling reaches, and all "downstream" sampling reaches were downstream of the aforementioned Sally May Wash and Boulder Canyon (Figure 1). Because sections of Fossil Creek are extremely remote and difficult to access, we restricted sampling site selection to accessible areas. Within accessible areas, we randomly selected the start of each sampling reach. To avoid beginning a survey in the middle of a mesohabitat unit, which could induce a fright bias, we walked downstream to the start of the nearest mesohabitat unit (pool, riffle, run) upon arrival at the random point. Each sampling reach extended ~100 m upstream from the established starting point. If we snorkeled 100 m and were in the middle of a mesohabitat unit, we either shortened or extended the reach to the end of the nearest mesohabitat unit. We removed two sampling reaches located downstream of the fish barrier due to high turbidity at the time of snorkeling.

Habitat Use: -

The water within Fossil Creek was exceptionally clear and daytime snorkel surveys were effective for estimating fish abundance and habitat use in this river (Marks et al. 2010). Two observers sampled each reach concurrently, beginning 5 m below the starting point of the survey, and proceeded upstream to the upstream terminus of the survey. We snorkeled in tandem to split the stream into two equal halves and maintained communication to ensure full observational coverage as per methods described in Strakosh et al. (2003).

We placed a colored and numbered washer on the substrate directly below the location of an observed fish. We then recorded washer number and color, species common name, and an estimated fish total length (TL) on a SCUBA slate (Strakosh et al. 2003). We estimated fish size in imperial measurements and converted these measurements to metric, as technicians were more comfortable making estimations on this scale. We limited our analyses to fish with a TL $\geq$ 67 mm (3 in) because smaller individuals, especially cyprinids, are difficult to identify while snorkeling (Li 1988). We included Speckled Dace in our analysis despite this species falling below the established size threshold as their distinctive coloration and pattern aided their identification. If a group of individuals ($\geq$1) was located within a 1 m^2 area with homogenous environmental conditions, we recorded the total number of individuals observed and an estimated size for each individual but placed only one washer in the group's central location.

We measured total depth (m), flow velocity (m^3/s), substrate composition (modified Wentworth scale), canopy cover (proportion), and recorded the GPS coordinates at each washer location immediately after snorkeling. We measured water depth using a U.S. Geological Survey top-setting wading rod and flow velocity at approximately 60% of total depth using a Marsh-McBirney electromagnetic flow meter (Hach Company, Loveland, Colorado). We visually assessed the dominant substrate type within 1 m^2 of the washer using a modified Wentworth substrate classification (0 = silt < 0.062 mm; 1 = sand 0.62 – 2 mm; 2 = gravel 2 – 4 mm; 3 = pebble 4 – 64 mm; 4 = cobble 64 – 256 mm; 5 = boulder > 256 mm) and measured canopy cover with a spherical densiometer following methods in Lemmon (1956), in which four canopy measurements are taken (upstream, downstream, left bank, and right bank) and the mean canopy cover value recorded. Finally, we assigned each washer to a mesohabitat type (pool, riffle, or run).

Available Habitat: -

We measured the same five habitat measurements along transects set perpendicular to the stream thalweg within each sampling reach to characterize habitat availability. We placed the first transect one mean-stream-width upstream from the start of the sampling reach, with additional transects placed every 10 m upstream until the end of the sampling reach. We then acquired measurements at five equidistance points along each transect. If the width of the transect was greater than 10 m, we took the first measurement 1 m off the streambank and if the width of the transect was less than 10 m, we took the first measurement at 0.5 m from the stream bank. We alternated each transect's starting point between stream banks. To measure substrate, we placed a 1 m chain with demarcations every 10 cm on the streambed, perpendicular to the transect. We categorized the dominant substrate type (modified Wentworth Scale) by estimating substrate class at each 10 cm demarcation and calculating the mode of the ten substrate classes.

Data Analysis: -

We classified all fish ≤ 127 mm (5 inches) TL as small fish and all fish > 127 mm TL as large fish. This classification was based on Gaeta et al. (2018), which found that cyprinids > 127 mm TL exceed the maximum prey size of most Black Bass ≥ 300 mm TL, which was the upper range of Black Bass TL observed within Fossil Creek. We assumed large fish to be invulnerable to predation by Black Bass.

Fish Abundance

We calculated relative abundance as the number of fish per 100 m of sampled stream (n = 15). We calculated relative abundance for both small and large fish individually. We used a Wilcoxon signed-rank test to test differences in the relative abundance of each native species in the presence and absence of nonnative Black Bass. Our null hypothesis was that there was no difference in the mean abundance of species or size-classes between sampling reaches with and without nonnative fishes present. Additionally, we modeled fish abundance relative to mesohabitat (pool, riffle, run) for small and large fish, both in the presence and absence of Black Bass. We standardized observations to a single mesohabitat unit and calculated the number of fish present per mesohabitat unit in pools, riffles, and runs separately. We then compared the mean abundance of each species/size class among mesohabitats using a nonparametric Kruskal-Wallis test. Our null hypothesis was that there is no difference in the mean abundance of fish among mesohabitats: pool, riffle, and run. We conducted all analyses in Program R (v. 4.2.2, R Core Team 2022) and used $\alpha = 0.05$.

Habitat Selection (Resource selection functions):

We modeled habitat selection using resource selection functions (RSFs) which are proportional to the probability of selection and quantify the relative selection strength for habitat features (e.g., sampling points or raster pixels; Manly et al. 2002; Lele et al. 2013; Avgar et al. 2013). We estimated RSF's using a used versus available study design, where habitat covariates are measured at units used by the study species and also at random units representing the range of habitat conditions available to the study species (Manly et al. 2002; Johnson et al. 2006). In our study, used units represented sampling units where fish were observed, and available units represented measurements from our transects. We used the exponential form of the RSF (generalized linear mixed model (GLMM); e.g., logistic regression; Johnson et al. 2006; Manly et al. 2002; Warton and Shepherd 2010). Under this form, the coefficients from the binomial GLM (β) are selection coefficients describing the relative strength of selection for habitat covariate X (Avgar et al. 2017; Fieberg et al. 2021) and $W(x)$ describes the relative probability or intensity of use of a particular location within the stream:

$$W(x) = \exp(\beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_n X_n) \quad [1]$$

Prior to analysis, we z-score standardized continuous covariates to facilitate comparing the selection strength of each covariate. We weighted used points based on the count of individuals present at each sampling unit (e.g., washer location). We also assigned large weights (5000) to each available point because previous studies have demonstrated the equivalence between a binomial GLM with highly weighted available points and an inhomogeneous Poisson point process model which facilitates the interpretation of RSF coefficients as relative selection strength and provides better estimates of relative intensity of use (Warton and Shepherd 2010; Fithian and Hastie 2013; Fieberg et al. 2021). We used a mixed-modeling framework and specified random intercepts by sampling reach (n = 15) to account for differences among sampling reaches and pseudo-replication (Gillies et al. 2006). We fit our RSFs using a GLMM with a binomial error distribution and logit link using the glmmTMB package (Brooks et al. 2017) in R.

We used a hierarchical approach to modeling habitat selection. We first modeled mesohabitat selection, and then modeled selection of microhabitat resources within each mesohabitat. We modeled mesohabitat selection with a RSF model which included the categorical covariate (i.e., X) mesohabitat (pool, riffle, run with ‘run’ acting as the reference level in all models) and the random intercept for sampling reach. We then subset our used and available data by mesohabitat and modeled microhabitat (depth, flow velocity, substrate composition, canopy cover) selection within pools, riffles, and runs separately. For each of these two analyses we fit two models, one using data above the barrier (Black Bass absent) and one using data below the barrier (Black Bass present). We identified significant differences to resource selection between sampling reaches with and without Black Bass with non-overlapping 95% confidence intervals for a given coefficient. We were unable to evaluate changes in habitat selection for Sonora Sucker and Speckled Dace due to insufficient sample sizes.

We evaluated RSF models for mesohabitat selection using *k*-fold cross validation following Johnson et al. (2006), where we divided our data into *k* folds with each sampling reach serving as a fold. We then refit our RSF using *k*-1 randomly selected folds (training data) and predicted relative intensity of use for both used and available points in the withheld fold (testing data) using Equation 1 and calculated the observed proportion of used observations within each suitability bin and the expected proportion of available observations within each bin. A well-calibrated RSF will show a 1:1 relationship between the observed and expected proportions. We repeated this process *k* times and used Lin's (Lin 1989) concordance correlation coefficient (CCC) to quantify the deviation of observed and expected proportions from a line with intercept = 0 and slope = 1. We considered models with a CCC value < 0.50 to be a poor fit.

RESULTS

Fish Abundance:

We observed and recorded the location of 1,999 fish of five species: 1,793 native fishes (63.4 % small fish / 36.5 % large fish) and 206 nonnative Black Bass (75.2 % small fish / 24.8% large fish; Table 1). We observed no nonnative fishes upstream of the fish barrier and Black Bass was the only nonnative fish observed downstream of the fish barrier. Black Bass accounted for 32.2% of total fish abundance downstream of the fish barrier.

Roundtail Chub Gila robusta

Small Roundtail Chub were significantly more abundant in sampling reaches without Black Bass ($P < 0.01$; Figure 2). In sampling reaches without Black Bass, small Roundtail Chub abundance was not different among mesohabitat units, and marginal evidence ($P = 0.09$) suggests that small Roundtail Chub abundance was greater in riffles with Black Bass present (Table 2). Small Roundtail Chub selected for pools and riffles more than runs and significantly increased their selection for riffles by 2.57 times when Black Bass were present (Figure 3; Table S1). Selection for microhabitat remained similar in locations with and without Black Bass, although small Roundtail Chub increased their selection for canopy cover in runs with Black Bass (Figure 4; Table S2). We were unable model small Roundtail Chub microhabitat selection in pools due to low abundance when Black Bass were present.

Large Roundtail Chub were significantly less abundant in sampling reaches with Black Bass ($P < 0.01$; Figure 2). The abundance of large Roundtail Chub was not different among mesohabitats, and this distribution remained consistent regardless of Black Bass presence ($P = 0.38$; Table 2). In sampling reaches without Black Bass, we found no selection for mesohabitat; but marginal evidence suggests large Roundtail Chub increased their selection for pools by 4.10 times when sympatric with Black Bass (Figure 5; Table S1). In general, large Roundtail Chub used microhabitats within pools in proportion to their availability, but selected deep water, avoided fast flow velocities, and used a range of substrates and canopy cover in riffles and runs. We only modeled change to microhabitat selection in riffles due to insufficient observations and poor model convergence in other mesohabitats. Microhabitat selection in riffles remained consistent regardless of Black Bass presence (Figure 6; Table S2).

Desert Sucker Catostomus clarkii

The abundance of small Desert Sucker was similar between sampling reaches with and without Black Bass ($P \geq 0.95$; Figure 2). Small Desert Sucker abundance was not related to mesohabitat in sampling reaches without Black Bass, however; some evidence suggests ($P = 0.06$) that the abundance of small Desert Sucker was less in pools with Black Bass (Table 2). When Black Bass were absent, small Desert Sucker did not select for mesohabitat, but when sympatric with Black Bass, small Desert Sucker were 6.90 times more likely to avoid pools (Figure 3;Table S1). In general, small Desert Sucker selected for deep water of slower flow velocity in riffles and runs, selection that remained consistent regardless of Black Bass presence. Small Desert Sucker selected for smaller substrates in riffles, and larger substrates and increased levels of overhead cover in runs when sympatric with Black Bass (Figure 4; Table S2). Desert Sucker were generally not found in pools with Black Bass and microhabitat selection was not modeled in these environments due to insufficient sample sizes.

The abundance of large Desert Sucker was not significantly different between sampling locations with and without Black Bass ($P = 0.95$; Figure 2) and we found no significant differences to the abundance of large Desert Sucker among mesohabitats ($P = 0.61$; Table 2). Large Desert Sucker selected for riffles, and some evidence suggests this selection for riffles increased by 3.40 times in sampling reaches with Black Bass (Figure 5; Table S1). We were only able to model change to microhabitat selection in riffles due to insufficient observations in runs and pools with Black Bass present. In riffles, large Desert Sucker selected for deep water of slow flow velocity and large substrates, selection that remained consistent in sampling reaches with and without Black Bass (Figure 6; Table S2). Large Desert Sucker did, however, significantly increase their selection for canopy cover in riffles with Black Bass.

Sonora Sucker Catostomus insignis and Speckled Dace Rhinichthys osculus

The abundance of small Sonora Sucker was significantly reduced in sampling reaches with Black Bass (P = 0.02); however, the abundance of large Sonora Sucker was not different (P = 0.51; Figure 2). The abundance of Sonora Sucker of either size-class was not different among mesohabitats with or without nonnative Black Bass ($P \geq 0.14$; Table 2). The abundance of Speckled Dace was significantly reduced in sampling reaches with Black Bass present (P = 0.01). In sampling reaches with exclusively native fishes, the abundance of Speckled Dace was greatest in riffles than other mesohabitats (P = 0.01; Table 2).

Black Bass Micropterus spp.

Black Bass were restricted to sampling reaches downstream of the fish barrier. Small Black Bass abundance did not differ among mesohabitats (P = 0.58; Table 2); however, small Black Bass selected pools 3.33 times and riffles 2.08 times more than runs (CCC = 0.56; Figure 3; Table S1). Small Black Bass did not selectively use microhabitats in pools but selected deep and slow environments with smaller substrates and less canopy cover in riffles (Figure 4; Table S2). We could not model microhabitat selection in runs due to insufficient observations.

Large Black Bass abundance was unrelated to mesohabitat (P = 0.87; Table 2), but large Black Bass selected pools 7.01 times more than they selected runs (Figure 5; Table S1). Large Black Bass did not selectively use microhabitats, notwithstanding a strong selection for canopy cover in pools and riffles (Figure 6; Table S2). We were unable to model large Black Bass microhabitat selection in runs due to poor model convergence and small sample sizes.

DISCUSSION: -

Our results support the hypothesis that native fishes alter their habitat selection in the presence of a nonnative predator (i.e., Black Bass) in a manner consistent with predator avoidance. Additionally, the abundance of many species (e.g., Roundtail Chub, Sonora Sucker, Speckled Dace) was lower in the presence of Black Bass, presumably because of their susceptibility to Black Bass predation (Pilger et al. 2008). Black Bass are one of the most problematic nonnative species for native fishes of the Colorado River Basin (Johnson et al. 2008). Roundtail Chub, Sonora Sucker, and Speckled Dace lack behavioral and morphological adaptations to avoid predation and are increasingly vulnerable to predation (Schlosser 1987; Marsh and Brooks 1989; Rees et al. 2005; Pilger et al. 2010; Arena et al. 2012; Ward and Figiel Jr. 2013). Additionally, predation risk is a strong determinant in habitat selection decisions because predation has more immediate and stronger fitness consequences than a temporary resource deficit (Hugie and Dill 1994; Mayor et al. 2009). Large Black Bass selected for pools over other mesohabitats, and as such, small (i.e., vulnerable) Desert Sucker reduced their selection for pools by 6.9 times (avoidance) and small Roundtail Chub increased their selection for riffles by 2.5 times in the presence of Black Bass. Predator-induced shifts in habitat selection can reduce the availability of suitable habitats by forcing individuals to occupy suboptimal environments (Brown and Moyle 1991; Douglas et al. 1994; Barret and Maughan 1995), which affects individual fitness and population viability (Werner et al. 1983; Werner and Hall 1988).

The abundance of both small and large Roundtail Chub was significantly reduced when Black Bass were present, which supports our initial hypothesis that species that were ecologically similar to Black Bass would be most impacted. Roundtail Chub and Black Bass often occupy the highest trophic level within their resident stream environment (Arena et al. 2012); however, Roundtail Chub have been shown to reduce their trophic position when sympatric with nonnative fishes indicating a competitive inferiority (Marks et al. 2010; Rogosch and Olden 2020). Additionally, Black Bass become piscivorous within their first-year post-hatch.

Small Roundtail Chub likely experience high levels of predation from, and competition with, Black Bass. The reduced abundance of Roundtail Chub suggests that predator-induced shifts to habitat selection insufficiently offset negative interactions with Black Bass (Schlosser 1987; Schlosser 1988; Brown and Moyle 1991). Roundtail Chub might not have the capacity to alter their selection of resources or behavior to adequately segregate from Black Bass because of the species' ecological similarity. Vulnerable Roundtail Chub did, however, increase their selection for riffles when Black Bass were present. Bestgen and Propst (1989) similarly found that small Roundtail Chub were restricted to nearshore shallow environments when nonnative fishes were present but used midchannel environments when nonnative fishes were removed by a natural flow event. This highlights the importance of riffle habitat as potential refuge habitat when Black Bass are present. The low abundance of large Roundtail Chub likely reflects reductions in Roundtail Chub recruitment. Predation by nonnative fishes on young native fishes can result in recruitment failure and is a primary cause for the decline of native Southwest fishes (Tyus and Saunders 2000; Clarkson et al. 2005).

We were unable to compare Sonora Sucker and Speckled Dace meso- and microhabitat selection between sampling locations due to the significant reduction in abundance of both species in sampling reaches with Black Bass. Sonora Sucker were observed in a relatively low abundance regardless of sampling reach. The overall low abundance of Sonora Sucker might reflect their preference for slow and deep waters (Minckley 1973) which are characteristic of larger mainstem rivers. Sonora Sucker abundance was similarly low in neighboring tributaries (Wet Beaver Creek, West Clear Creek, Sycamore Creek; Gahl 2022, unpublished data). Nevertheless, the reduced abundance of small Sonora Sucker in sampling reaches with Black Bass is indicative of predation and/or competitive exclusion. The abundance of large Sonora

Sucker was not different between sampling reaches with and without Black Bass, suggesting that some Sonora Suckers are recruiting into larger size-classes or emigrating from locations upstream of the fish barrier where Black Bass are not present. Source-sink population dynamics of an artificially fragmented river (Rahel 2013) would warrant further investigation. Speckled Dace larvae are smaller than larvae of other native species with poorer swimming abilities (Robinson et al. 1998), contributing to this species' vulnerability to predation. Even as adults, Speckled Dace never achieve a size that exceeds the gape limitation of most Black Bass, exposing this species to predation at all life stages.

Small and large Desert Sucker abundance was unrelated to Black Bass presence, supporting our hypothesis that fish with less ecological overlap with the nonnative Black Bass would be least impacted. Less ecological niche overlap between these species is likely to reduce opportunities for negative interspecific interactions. Desert Sucker further reduced the opportunity for negative interspecific interactions via shifts to habitat selection. Small Desert Sucker strongly avoided pools in sampling reaches with Black Bass, while also altering microhabitat selection in riffles and runs, behaviors assumed to reduce spatial overlap with the largest and most piscivorous Black Bass (Schlosser 1988; Gaeta et al. 2018). Desert Sucker are known riffle and run inhabitants (Ward et al. 2003; Minckley and Marsh 2009). Their increased selection for lotic environments likely resulted in fewer fitness consequences than would be experienced by species less adapted to these environments. We did, however, observe a Black Bass consuming a small Desert Sucker, confirming some predation on this native fish.

Habitat selection is behavioral and inherently hierarchical (Johnson 1980; Mayor et al. 2009). Microhabitat selection is conditional upon the available habitat features within a given mesohabitat, yet mesohabitat use is a product of selection at a higher hierarchical level (Bowers and Dooley 1993). Modeling habitat selection at a single spatial scale is likely to result in misleading inferences by ignoring selection at larger spatial scales (Owen 1972; Mayor et al. 2009). For example, when we pooled microhabitat data across all mesohabitats, as is often done in fisheries studies, we found that small Desert Sucker selected deep waters with slow flow velocity, implying a selection for pools. However, our multi-scale, hierarchical approach found that small Desert Sucker avoided pools and instead selected deep areas with slow flow velocity in riffles and runs; conditions that are consistent with "pocket-water" and previously described habitat selection for this species (Shipley and Booth 2012). Ignoring the hierarchical nature of habitat selection in native stream fishes, particularly in the presence of nonnative piscivores, may underestimate the value of these important environments for conserving native fishes.

Our study was observational, and we cannot derive causal relationships between the presence of Black Bass, observed shifts to native fish abundance, and habitat selection from this study, alone. However, our results combined with evidence from previous research (Gilliam and Frazier 1987; Brown and Moyle 1991; Barrett and Maughan 1995), strongly suggest that native fishes shift habitat to avoid Black Bass, specifically by shifting their selection from pools towards more lotic mesohabitat types. Alternatively, observed shifts in habitat selection might represent the selective removal of individuals from riskier environments rather than individual behavioral shifts. Finally, habitat selection was not modeled for Sonora Sucker and Speckled Dace due to limited observations and we were unable to model the impact of other native species as they were not present in Fossil Creek at the time of sampling. Possibly due to periodic flooding (Minckley and Meffe 1987), other nonnative species have been slow to recolonize the lower reaches of Fossil Creek.

Our study underscores the importance of protecting riffles and runs as within-stream refuges for native fishes when Black Bass are present (Rahel 2000; Schade and Bonar 2005). The desert Southwest is currently amid a ≥ 21-year megadrought (Williams et al. 2022) and lotic mesohabitats are being lost via lentification (i.e., the transformation of lotic river environments into a series of disconnected lentic environments via surface water reductions; Sabater 2008; Sabo et al. 2010). As surface waters recede, fishes will become increasingly concentrated into pools, mesohabitats dominated by nonnative fishes, exposing native fishes to greater predation risk (Bestgen and Platania 1991; Gibson et al. 2015). A reduction to surface water has not been observed in Fossil Creek, however, streamflow throughout the Verde River Basin has declined considerably since the mid-20th century (Serrat-Capdevilla et al. 2012; Jaeger et al. 2013; Schenk et al. 2022), with concurrent declines to native fish populations (Rinne et al. 1998; Neary and Rinne 1998; Rinne 2005; Rinne and Miller 2006). While studies have found that the enhancement of instream habitat is likely to benefit native fishes, most have concluded that habitat enhancements alone are insufficient to restore native fish populations if nonnative fishes remain (Marks et al. 2010; Walsworth and Budy 2015). Our study provides more evidence of this as habitat and flow conditions are similar throughout Fossil Creek (Marks et al. 2010); however, the abundance of native fishes was reduced and their selection for habitats altered when Black Bass were present. The removal of nonnative species combined with the intentional fragmentation of the stream preventing natural recolonization by nonnative fishes (Rahel 2013), as done in Fossil Creek, appears to be a viable solution to preserve native fish populations. When segregation from, or suppression of nonnative fish populations is not tenable, maintaining flows at a level that preserves or enhances the spatial availability and extent of lotic mesohabitats would provide some refuge to an imperiled native fish community.

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Author Contributions:

CJ and SB conceived and designed the investigation and performed all laboratory and field work. CJ and JB analyzed the data. CJ, JB, and SB wrote the manuscript.

Data availability:

Our data is publicly available and archived on the Open Science Framework (OSF): https://osf.io/3j2kp/

Disclosure statement:

No potential conflict of interest was reported by the authors of this study.

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TABLES:

Table 1: Number of fish (standard deviation in parentheses) observed per 100 m snorkeling reach (n = 15) in Fossil Creek, Arizona where a fish barrier divides the river into two sections, one with only native fishes, and one where nonnative Black Bass are present. Fish ≤127 mm TL were classified as small (S, vulnerable to predation) and fish > 127 mm TL were classified as large (L, invulnerable to predation). Significant *P*-values (α = 0.05) are bolded.

Species / Size	**Native Fish Only**	**Black Bass Present**	**Wilcoxon *P*-value**
Roundtail Chub (S)	60.68 (30.20)	13.83 (15.43)	**0.01**
Roundtail Chub (L)	31.33 (19.76)	4.33 (2.25)	**<0.01**
Desert Sucker (S)	20.89 (29.03)	33.50 (47.23)	1.00
Desert Sucker (L)	11.58 (9.30)	14.17 (16.44)	0.95
Sonora Sucker (S)	2.89 (3.86)	0.17 (0.10)	**0.02**
Sonora Sucker (L)	7.67 (10.58)	5.16 (7.60)	0.51
Speckled Dace (S)	10.44 (12.46)	0.33 (0.52)	**0.01**
Black Bass (S)	*not present*	20.67 (20.18)	-
Black Bass (L)	*not present*	8.33 (5.01)	-

Table 2: Relative abundance (standard deviation in parentheses) of fish per mesohabitat type: pool, riffle, or run in sampling reaches with exclusively native fishes and in sampling reaches with nonnative Black Bass present. We analyzed data from areas without Black Bass and areas with Black Bass separately. Small fish are those under ≤ 127 mm TL (vulnerable to predation) and large fish are those >127 mm TL (invulnerable to predation). Speckled Dace and Sonora Sucker were not present in sufficient abundance in sampling reaches with Black Bass, and Black Bass were only present downstream of the fish barrier. Bolded numbers show *P*-values ≤ 0.05 from the Kruskal-Wallis tests.

Species		**Native Fish Only**				**Nonnative Black Bass Present**			
	Sz	**Pool**	**Riffle**	**Run**	***P*-value**	**Pool**	**Riffle**	**Run**	***P*-value**
Desert Sucker	S	0.39(0.87)	0.39(0.54)	0.52(0.59)	0.48	0.02(0.04)	0.57(0.73)	0.77(1.22)	0.06
	L	0.13(0.27)	0.33(0.32)	0.23(0.30)	0.12	0.12(0.20)	0.42(0.51)	0.15(0.32)	0.26
Roundtail Chub	S	2.14(2.64)	1.38(1.20)	0.94(0.37)	0.95	0.04(0.10)	0.45(0.52)	0.09(0.10)	0.09
	L	0.55(0.89)	0.71(0.45)	0.68(0.41)	0.38	0.12(0.21)	0.14(0.17)	0.04(0.06)	0.40
Sonora Sucker	S	0.05(0.11)	0.02(0.04)	0.08(0.08)	0.14	*not present*			
	L	0.11(0.13)	0.09(0.13)	0.18(0.31)	0.61	0.25(0.61)	0.12(0.19)	0.06(0.13)	0.61
Speckled Dace	S	0.02(0.03)	**0.41(0.47)**	0.12(0.17)	**0.01**	*not present*			
Black Bass	S	*not present*				0.12(0.20)	0.29(0.38)	0.16(0.16)	0.58
	L	*not present*				0.92(1.77)	0.11(0.08)	0.10(0.11)	0.87

FIGURE CAPTIONS:

Figure 1: Map of Fossil Creek, Arizona, and the location of the fish barrier and 15 sampling reaches (~100 m) snorkeled during summer of 2019 and 2020. Six reaches were located downstream of the fish barrier (nonnative fishes are present) and nine snorkeling reaches were located upstream (native fishes only) of the fish barrier. Two reaches were removed due to poor visibility at the time of snorkeling. Fossil Creek is a tributary of the Verde River, AZ. Two major washes, Sally May and Boulder Canyon, are also pictured.

Figure 2: Relative abundance of small ≤127 mm TL (panel a.) and large > 127 mm TL (panel b.) fish per 100 m sampling reach. Grey boxes show abundance in sampling reaches with Black Bass present and white boxes show abundance in sampling reaches with native fishes only. Significance of the Wilcoxon-signed rank test is symbolized as follows: P <0.01 *** | 0.01 < P < 0.05 ** | 0.05 < P < 0.10 *

Figure 3: Small fish (≤ 127-mm TL; vulnerable to predation) mesohabitat selection. Coefficient estimates and 95% confidence intervals from resource selection functions (RSF) for mesohabitat selection of small fish in the presence and absence of Black Bass. “Run” was the reference level for the explanatory categorical varia' le mesohabitat (levels: pool, riffle, run). Coefficients estimate relative selection strength of pools and riffles relative to runs. White shapes represent selection in sampling reaches with native fish and grey shapes represent selection when Black Bass are present. Significant change to selection is represented by non-overlapping 95% confidence intervals.

Figure 4: Small fish (≤ 127-mm TL; vulnerable to predation) microhabitat selection. Coefficient estimates and 95% confidence intervals from resource selection functions (RSF) for microhabitat features (depth (m), flow velocity(m3/s), substrate composition (modified Wentworth Scale, and canopy cover (proportion)) for small fish within each mesohabitat (pool, riffle, and run). White shapes represent selection in sampling reaches with native fish and grey shapes represent selection when Black Bass are present. Insufficient observations of small native fishes in pools and small Black Bass in runs prevented the modeling of microhabitat selection in those areas. Significant change to selection is represented by non-overlapping 95% confidence intervals.

Figure 5: Large fish (> 127-mm TL; invulnerable to predation) mesohabitat selection. Coefficient estimates and 95% confidence intervals from resource selection functions (RSF) for large fish in the presence and absence of Black Bass. Run was the reference level for the RSF, so coefficients estimate relative selection strength of pools and riffles relative to runs. White shapes represent selection in sampling reaches with native fish and grey shapes represent selection when Black Bass are present. Significant change to selection is represented by non-overlapping 95% confidence intervals.

Figure 6: Large fish (> 127-mm TL; invulnerable to predation) microhabitat selection. Coefficient estimates and 95% confidence intervals from resource selection functions (RSF) for microhabitat features (depth (m), flow velocity (m3/s), substrate composition (modified Wentworth Scale, and canopy cover (proportion)) large fish within each mesohabitat (pool, riffle, and run). White shapes represent selection in sampling reaches with native fish and grey shapes represent selection when Black Bass are present. Insufficient observations of large native fishes in pools and runs and poor model

convergence for Black Bass in runs prevented the modeling of microhabitat selection in those areas. Significant change to selection is represented by non-overlapping 95% confidence intervals.

Figures for manuscript: "Native fish abundance and habitat selection changes in the presence of nonnative piscivores"

Figure 1:

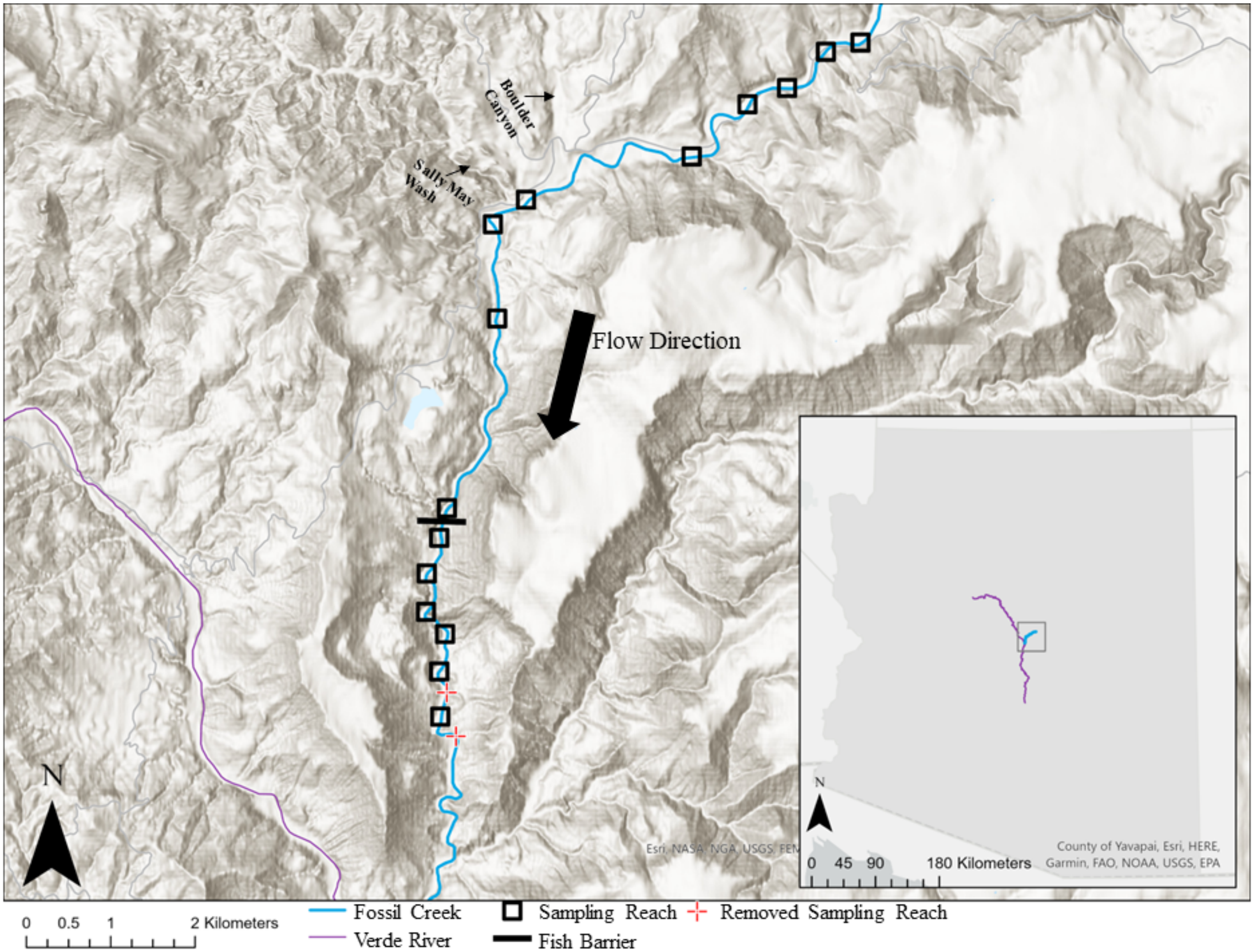


Figure 2:

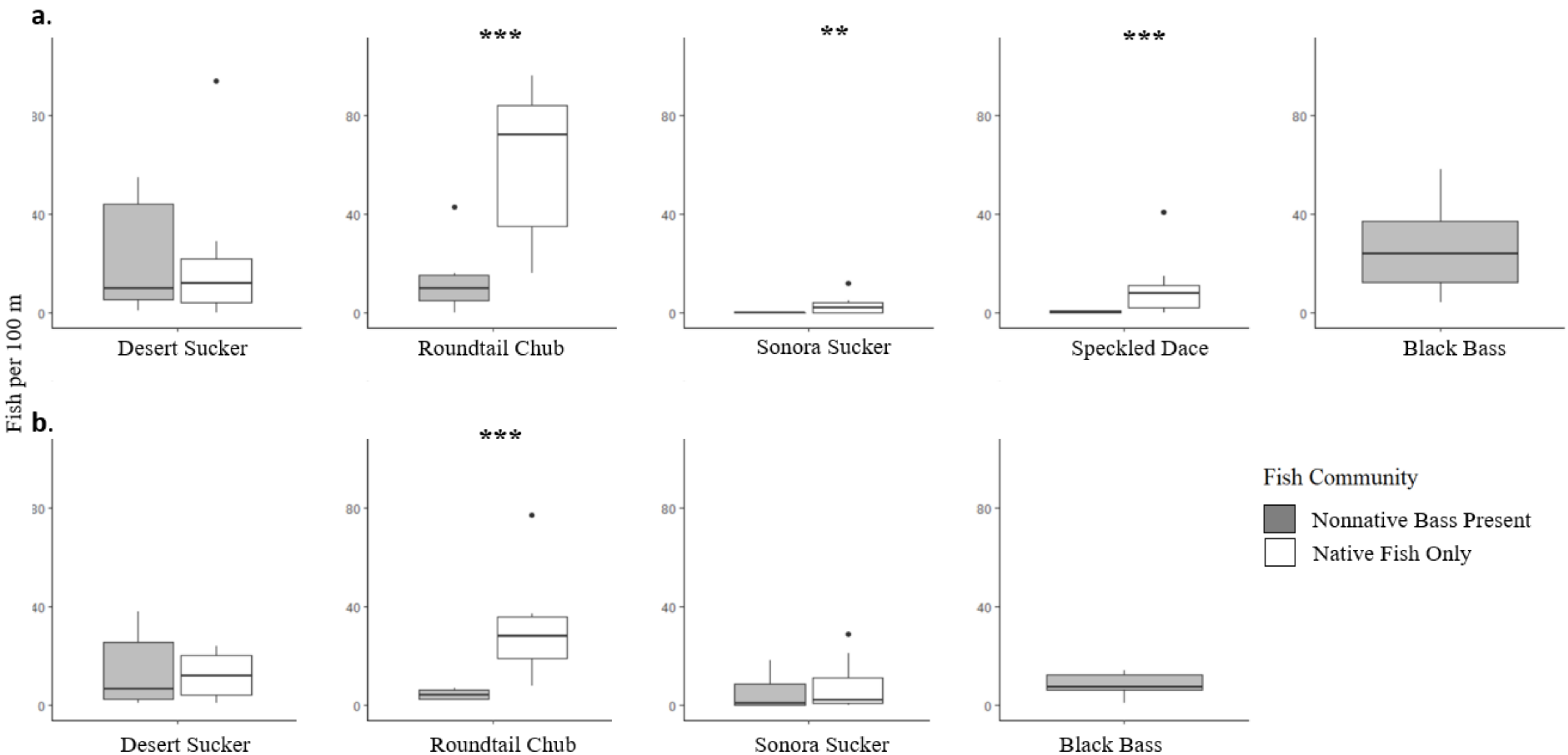
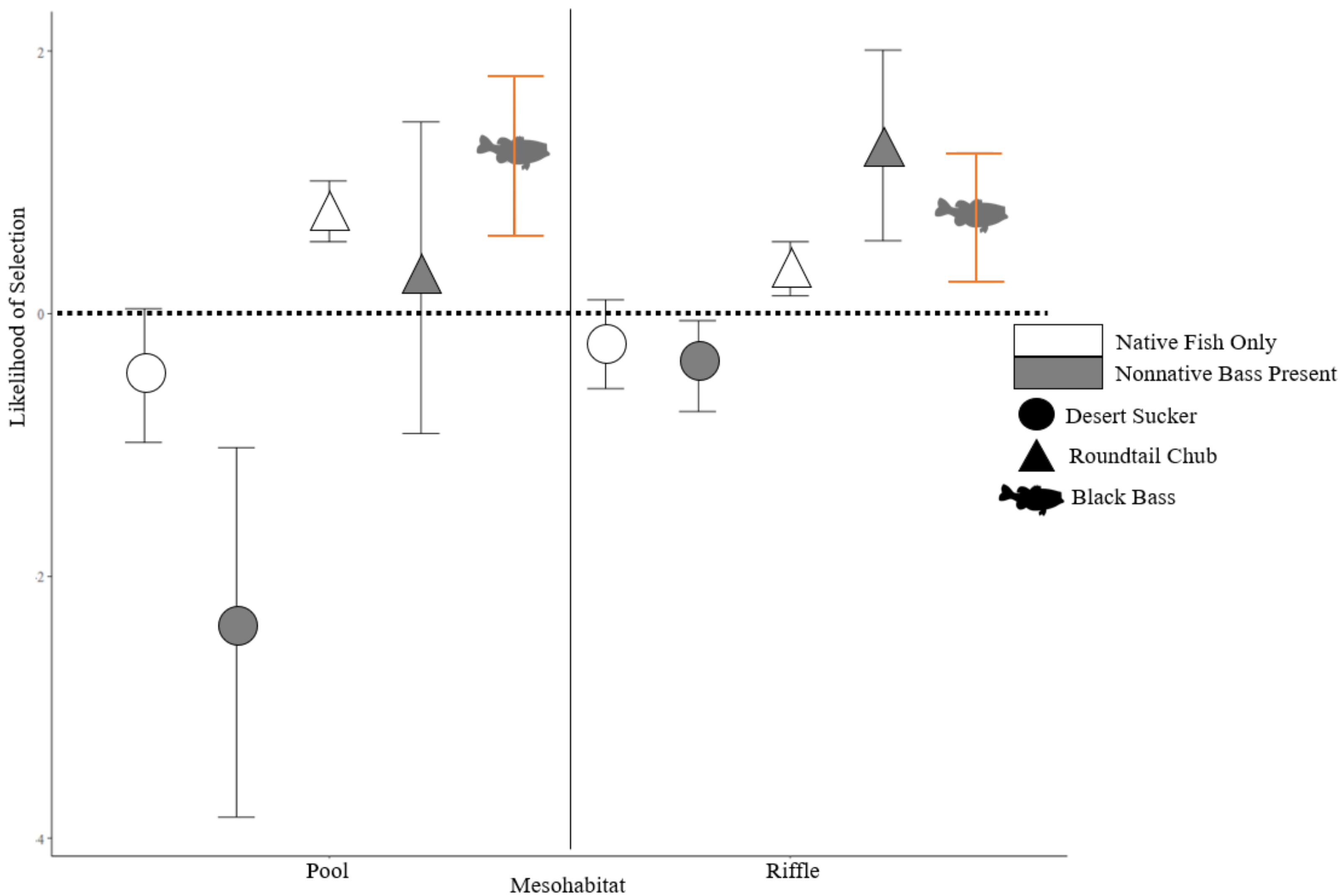
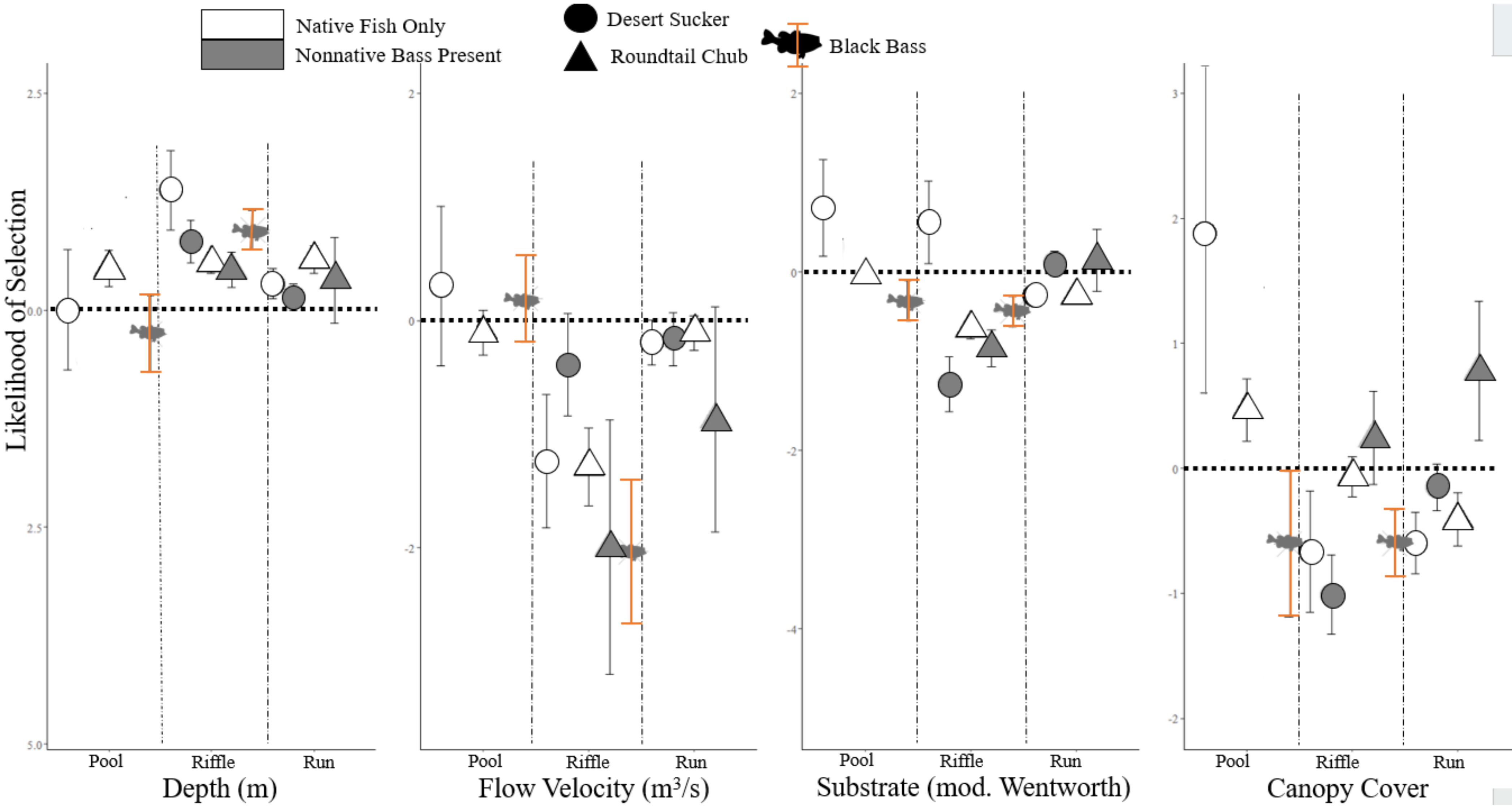

a.
b.
Fish per 100 m
***
**
***
***
Desert Sucker
Roundtail Chub
Sonora Sucker
Speckled Dace
Black Bass
Desert Sucker
Roundtail Chub
Sonora Sucker
Black Bass
Fish Community
Nonnative Bass Present
Native Fish Only

Figure 3:



2
0
-2
-4
Likelihood of Selection
Native Fish Only
Nonnative Bass Present
Desert Sucker
Roundtail Chub
Black Bass
Pool
Mesohabitat
Riffle

Figure 4:



Native Fish Only
Nonnative Bass Present
Desert Sucker
Roundtail Chub
Black Bass
Likelihood of Selection
Pool
Riffle
Run
Depth (m)
Flow Velocity (m³/s)
Substrate (mod. Wentworth)
Canopy Cover

Figure 5:

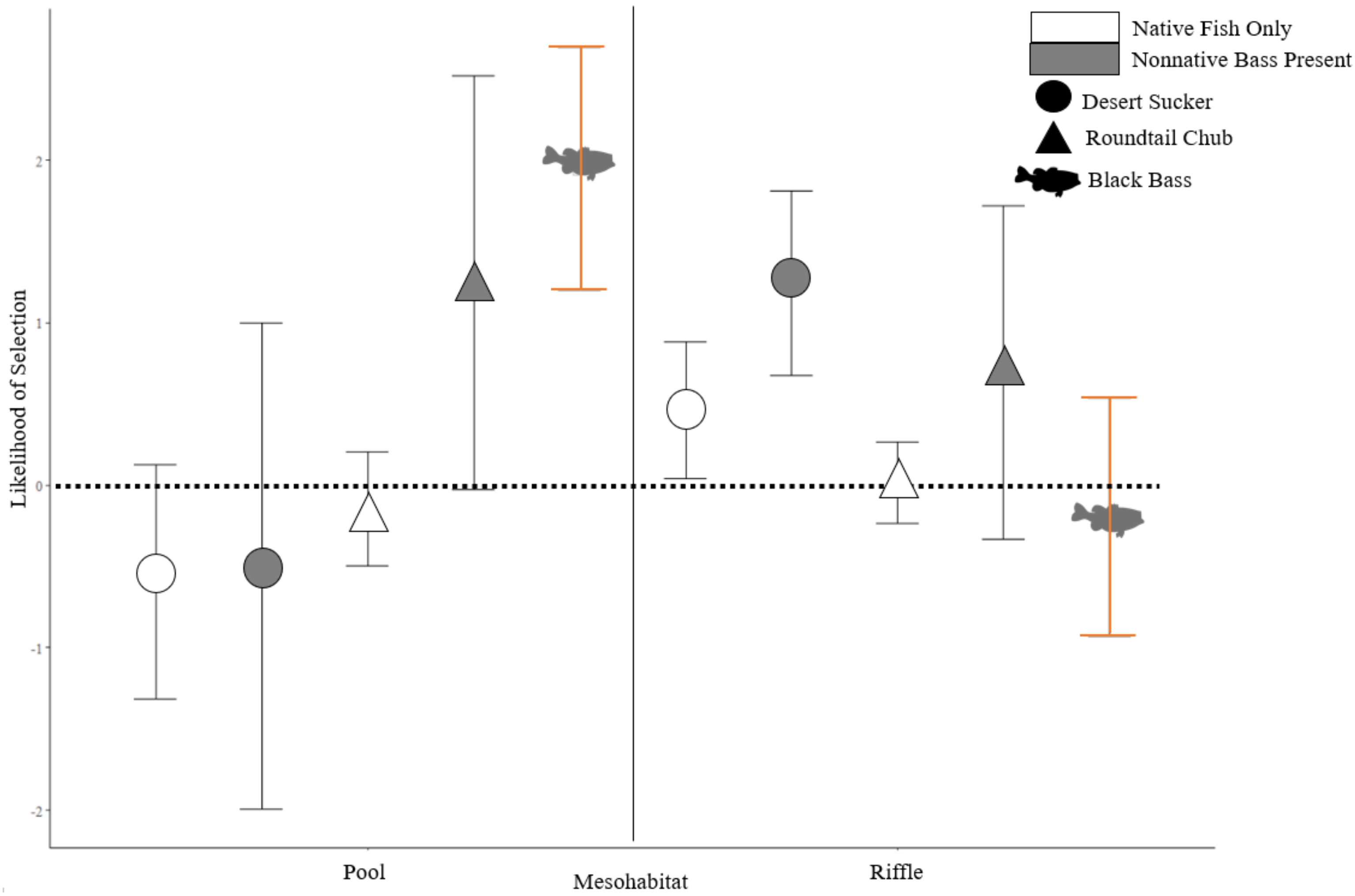
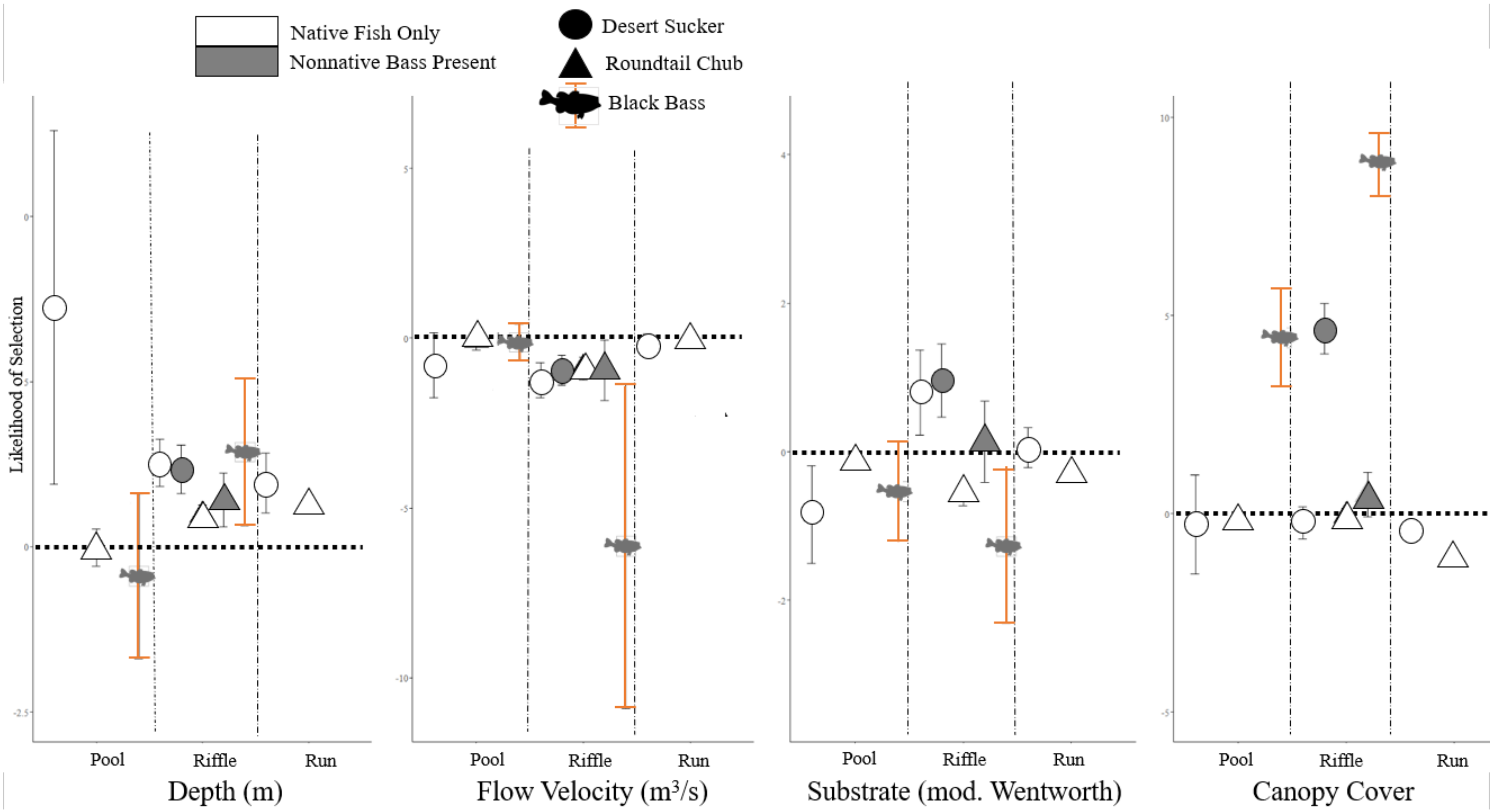

Native Fish Only
Nonnative Bass Present
Desert Sucker
Roundtail Chub
Black Bass
Likelihood of Selection
2
1
0
-1
-2
Pool
Mesohabitat
Riffle

Figure 6:


Native Fish Only
Nonnative Bass Present
Desert Sucker
Roundtail Chub
Black Bass
Likelihood of Selection
Pool
Riffle
Run
Depth (m)
Flow Velocity (m³/s)
Substrate (mod. Wentworth)
Canopy Cover