

# Beaver activity increases habitat complexity and spatial partitioning by steelhead trout

Gus Wathen, Jacob E. Allgeier, Nicolaas Bouwes, Michael M. Pollock, Daniel E. Schindler, and Chris E. Jordan

**Abstract:** Freshwater habitat restoration is a major conservation objective, motivating efforts to restore habitat complexity and quality for fishes. Restoration based on the engineering activities of beavers (*Castor canadensis*) increases fish habitat complexity, but how this affects fish habitat use and movement behaviours is not well known. We used a network of passive integrated transponder antennas to quantify small-scale movement and microhabitat use of 175 individual juvenile steelhead (*Oncorhynchus mykiss*) in a stream channel with a complex bathymetric profile resulting from a beaver impoundment and in a simplified channel devoid of beaver activity. Our results show that juvenile steelhead exploit microhabitat heterogeneity by employing a range of behaviours that maximizes available habitat via spatial and temporal partitioning among individuals. These results suggest spatial resource partitioning as a potential mechanism for the previously established positive correlations among steelhead density, survival, and production with beaver-based restoration within the study watershed. More broadly, our findings provide insight as to how populations can exploit habitat complexity through spatial partitioning that can be informative for planning restoration and management actions.

**Résumé :** La restauration des habitats d'eau douce constitue un important objectif de conservation à l'origine d'efforts pour rétablir la complexité et la qualité d'habitats pour les poissons. Si la restauration reposant sur les activités de génie civil des castors (*Castor canadensis*) accroît la complexité des habitats de poissons, son incidence sur l'utilisation de l'habitat et les comportements de déplacement des poissons demeure méconnue. Nous avons utilisé un réseau d'antennes à radio-étiquettes passives intégrées pour quantifier les déplacements à petite échelle et l'utilisation de microhabitats par 175 truites arc-en-ciel (*Oncorhynchus mykiss*) juvéniles dans le chenal d'un cours d'eau au profil bathymétrique complexe causé par une digue de castor, et dans un chenal simplifié exempt d'activité de castors. Nos résultats montrent que les truites arc-en-ciel juvéniles exploitent l'hétérogénéité des microhabitats en ayant recours à un éventail de comportements qui maximise l'habitat disponible grâce au partage spatial et temporel de l'habitat entre individus. Ces résultats suggèrent que le partage spatial des ressources est un mécanisme qui pourrait expliquer les corrélations positives déjà établies entre la densité, la survie et la production de truites arc-en-ciel et la restauration reposant sur les castors dans le bassin versant étudié. Plus largement, nos constatations fournissent de l'information sur la manière dont les populations peuvent exploiter la complexité de l'habitat grâce au partage spatial de ce dernier, qui peut éclairer la planification d'interventions de restauration et d'aménagement. [Traduit par la Rédaction]

## Introduction

Habitat degradation is one of the principal threats to freshwater populations worldwide (Dudgeon et al. 2005), with over a third of the rivers in the United States designated as impaired (US Environmental Protection Agency 2000). Such concerns have precipitated the spending of over \$1 billion annually on river restoration efforts throughout the US (Bernhardt et al. 2005). A primary objective of restoration is enhancing habitat complexity, but efforts are often undertaken with a lack of understanding of underlying processes that make more complex habitats more suitable for freshwater fish populations (Palmer et al. 2010).

Previous research has shown habitat complexity to be an important driver of resource diversity for wildlife (Kovalenko et al. 2012). These ideas are rooted in theory whereby increased population-level dietary niche diversity (the diversity of resources that the population feeds on) promotes increased resource partitioning among individuals (Roughgarden 1972; Bolnick et al.

2007). In turn, the reduced competition for resources associated with resource partitioning can lead to increased carrying capacity (Harrison et al. 2017) and population resilience to environmental stochasticity (Wolf and Weissing 2012). Resource partitioning among individuals has been linked directly to habitat complexity. For example, intrapopulation resource partitioning has been shown to increase along a continuum of increased habitat complexity in mangrove ecosystems (for gray snapper (*Lutjanus griseus*); Layman et al. 2007) and tropical montane forests (for vampire bats (*Desmodus rotundus*); Layman et al. 2007; Streicker and Allgeier 2016). Yet, a mechanistic link between improved habitat and increased resource partitioning is still missing, in part because of our lack of understanding of the influence of habitat complexity on how individuals differentially utilize the habitat (i.e., spatial partitioning).

The promotion of dam building by beavers (*Castor canadensis*), either naturally or through building of beaver dam analogs

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(BDAs), is being used as a tool to restore streams and improve fish habitat by reversing the negative effects of channel incision via sediment aggradation and floodplain reconnection (Pollock et al. 2014; Bouwes et al. 2016). Recently, Bouwes et al. (2016) demonstrated that juvenile steelhead (anadromous *Oncorhynchus mykiss*) abundance, survival, and production increased dramatically following the introduction of BDAs and a subsequent increase in dam building activity by beaver, relative to a control watershed. They hypothesized that the increase in these responses were, in part, due to the increase in habitat complexity in beaver dam complexes. However, the manner in which the juvenile steelhead behaviour changed to affect how they use microhabitats following an increase in dam complexes is unknown.

A growing body of research is revealing the importance of complex habitat use patterns in juvenile steelhead and other salmonids at various temporal periods (see Gowan et al. 1994). Steelhead are known to prefer shallow, slow-moving water as fry and shift towards deeper habitats with greater velocities as they age (Everest and Chapman 1972). However, juvenile salmonids often display diel shifts in habitat use in response to predatory pressures (Metcalfe et al. 1999), for energy sequestration (Reeves et al. 2010; Sloat et al. 2013), and for utilizing thermal refugia (Brewitt and Danner 2014). Further, diverse movement behaviours exist within populations, which may indicate alternate survival strategies (Steingrímsson and Grant 2003; Myrvoold and Kennedy 2016). These movement behaviours are important for conservation because they may provide clues about survivorship, but research to date has been inconclusive as to potential mechanisms. We aim to develop a better understanding of habitat use that can inform future restoration actions by gaining detailed information on small-scale movement patterns of a threatened cold-water species during a survival bottleneck (i.e., warm water, low discharge).

Here we test the hypothesis that spatial partitioning among individuals will increase with increased habitat heterogeneity. We do so by monitoring the movement and habitat use behaviour of individuals within a threatened population of juvenile steelhead for a week in two study reaches within a stream: one that is impounded by a beaver dam with high diversity in habitat characteristics and the other in a simplified channel with a homogeneous bathymetric profile. We conducted this study during midsummer, where high water temperatures and decreased discharge create a potential survival bottleneck for juvenile steelhead in our study system. Specifically, we were interested in two questions:

- (1) How do beaver complexes affect habitat use by juvenile steelhead with respect to microhabitat selectivity and time of day?
- (2) Does habitat heterogeneity increase spatial partitioning by affecting movement and habitat use behaviours?

We hypothesized that fish “select” for certain microhabitats within study reaches and that this selection is driven by the availability of favorable water depths and velocities. Further, we expect increased spatial partitioning by individuals in the beaver dam complex, resulting from increased habitat heterogeneity.

## Materials and methods

This study was conducted on Bridge Creek, a 710 km<sup>2</sup> watershed flowing into the John Day River in a semi-arid portion of central Oregon, USA. Mean discharge of Bridge Creek is 0.78 m<sup>3</sup>·s<sup>-1</sup>, with a mean monthly discharge range of 0.11 m<sup>3</sup>·s<sup>-1</sup> (September) to 1.94 m<sup>3</sup>·s<sup>-1</sup> (May; USGS Gauge 14046778, 2006–2016). Stream gradient in the lower 32 km of Bridge Creek ranges from 1% to 3%, with active channel widths between 4 and 8 m. Water temperatures in Bridge Creek often approach the thermal survival threshold for its steelhead population (29 °C; Rodnick et al. 2004) during midsummer months (Weber et al. 2017). The fish community of Bridge Creek is dominated by steelhead, dace (*Rhinichthys* spp.), and suck-

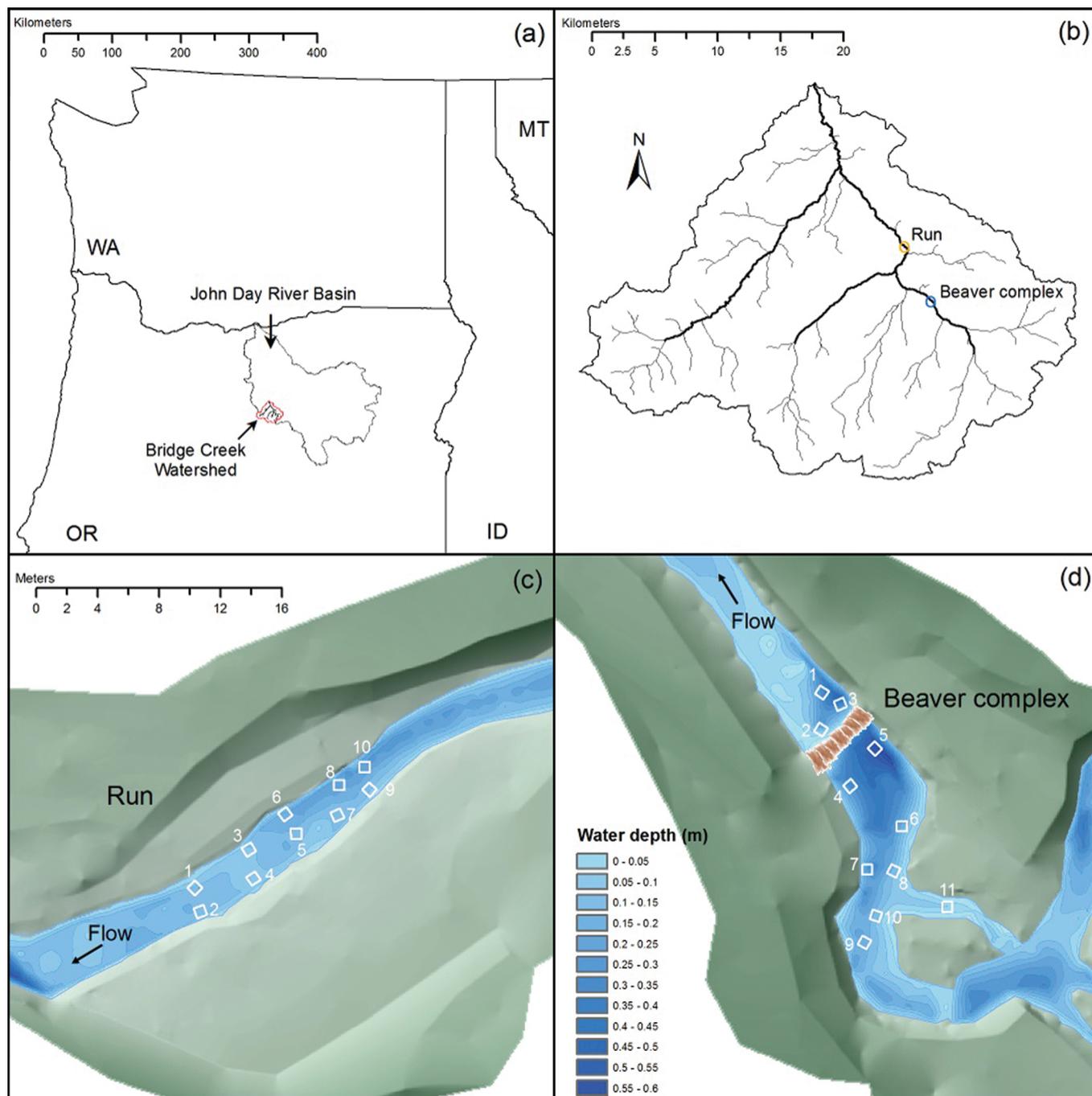
ers (*Catostomus* spp.). Common potential predators of the juvenile steelhead are great blue heron (*Ardea herodias*), belted kingfisher (*Megaceryle alcyon*), garter snakes (*Thamnophis elegans*), and occasionally river otters (*Lontra canadensis*). Riparian vegetation is primarily composed of willow species (*Salix* spp.), with dogwood (*Cornus sericea*), alder (*Alnus* spp.), and cottonwood (*Populus* spp.) present in patches.

The lower 32 km of Bridge Creek is part of a long-term ecosystem experiment testing how beaver dam persistence and abundance in a highly degraded, incised stream channel affects the freshwater production of steelhead (Bouwes et al. 2016). This experiment involves promoting beaver activity and building artificial beaver dams in incised plane-bed channels characterized by homogeneous depth and velocity profiles, with the goal to stimulate pool creation, channel aggradation, and floodplain reconnection (Pollock et al. 2014). Our objective was to document spatial utilization behaviours of juvenile steelhead in a stream channel with high depth complexity (coefficient of variation (CV) of depth = 0.8) resulting from beaver activity and a plane-bed channel with relatively homogeneous depths (CV of depth = 0.34) reflective of degraded reaches on Bridge Creek. For this study, we define habitat heterogeneity as variation in the bathymetric profile of the stream channel, which also influences water velocity and fish cover.

We used a network of passive integrated transponder (PIT) antennas to quantify juvenile steelhead microhabitat use and movement in an area around an active beaver impoundment (hereinafter, beaver complex) and in a plane-bed run void of proximal beaver activity (hereinafter, run). We deployed 11 antennas in the beaver complex and 10 antennas in the run. We placed antennas systematically (>1 m apart to avoid antenna cross-talk) in an attempt to cover the broad ranges of depths, velocities, substrate, and other types of fish cover at each site (i.e., microhabitats) while maintaining a consistent spacing. Each antenna operated at a frequency of 134 kHz and had a measured vertical detection range of 35–40 cm for the PIT tags (12.5 mm, 134.2 kHz, full duplex; Biomark HPT12, Boise, Idaho). We constructed antenna housing (66 cm × 66 cm; area = 0.44 m<sup>2</sup>) out of PVC (polyvinyl chloride; outer diameter = 2.6 cm). Antenna housing diameter was kept to a minimum to avoid adding a bed roughness component to the stream channel that could influence fish behaviour. We equipped each antenna with Onset temperature loggers (UTBI-001, U22-001) to record hourly temperatures. Antennas were connected to a multiplexing PIT-tag reader by cable lengths of 15 m. We used custom multiplexing modules paired with RM310 PIT-tag readers (Allflex; [www.allflexusa.com](http://www.allflexusa.com)) to activate antennas for 0.25 s per cycle. The multiplexer unit was powered by a 6 V (200 Ah) rechargeable absorbent glass mat battery pack, which, combined with a solar panel, provided continuous power. This system enables logging up to 100 000 time-stamped detections per day with an onboard data logger. To reduce the number of repetitive events, a data-repeated filter precluded the repeat reading of the same tag code, at the same antenna, within each 1 min period. Therefore, we refer to all detections as “minutes” at which fish were detected by an antenna. For this study, we define a microhabitat as equal to the area that our antennas represent (0.44 m<sup>2</sup>).

The beaver complex and run study reaches were located at river kilometres 26 and 17, respectively. Both reaches are nested within existing long-term steelhead population and habitat monitoring sites as part of an Intensively Monitored Watershed program (Bennett et al. 2016). The run study reach area was 17 m long with a surface area of 51.2 m<sup>2</sup> and located in the middle of a 57.7 m plane-bed channel feature. The 20 m beaver complex consisted of lotic conditions flowing into a lentic channel feature resulting from a beaver impoundment and a subsequent plunge pool below the impoundment. The surface area of the complex was 89.3 m<sup>2</sup> (Fig. 1). We conducted a topographic survey of stream channel morphology in both monitoring sites at baseflow conditions in

**Fig. 1.** Maps displaying Bridge Creek's location the Pacific Northwest, USA (a); location of study reaches within the Bridge Creek watershed (b); and the bathymetry and antenna locations of the run (c) and beaver complex (d) reaches. The beaver dam in panel (d) is indicated by the brown, channel-spanning obstruction. Antenna sizes and channel features in panels (c) and (d) are all to scale. (Panels (a) and (b) are modified from map data provided by Oregon Spatial Data Library, Salem, Oregon, USA). [Colour online.]



November 2015 (CHaMP 2014). We used digital elevation models generated from topographic surveys to run hydraulic models (Wheaton et al. 2017) that utilize bed roughness and a porous plate structure at the beaver impoundment to predict average water column velocity and obtain depths of our study areas at a grain size equal to that of antenna area. We georeferenced antenna locations and identified the overlapping model-predicted depth and velocity microhabitats as “sampled”, while other microhabitats were deemed “available”.

We used PIT tags to identify individual steelhead that used the study reaches. PIT tags are advantageous because they are inexpensive, have no battery, and can be used in small fish (>70 mm). However, they are susceptible to tag collision, the size limitation precludes age 0 steelhead, and they have a limited detection range. Fish were tagged as part of tri-annual surveys that utilize electrofishing catch data of juvenile steelhead to estimate abundance using mark-recapture models (Bouwes et al. 2016; Wathen et al. 2017). All capture and tagging efforts were completed by

26 June 2015, allowing for a minimum of 6 days for re-acclimation before recording of habitat use and movement patterns. We placed antennas and began data collection in study reaches on 30 June 2015, at baseflow conditions. We truncated our data set to include records from 7 full days (1 July 2015, 0600 through 7 July 2015, 0559) to accommodate a 24 h acclimation period. We chose to limit our data set to a week's time because we were interested in understanding if small-scale movement may help us understand how juvenile steelhead navigate Bridge Creek's most stressful conditions (high temperatures, low discharge) on a daily basis. We were constrained by the logistical challenges of maintaining the extensive array over extended periods of time. During observations, there was no presence by our research team in or around the study reaches to avoid a fish behavioural response to human disturbance.

## Data analysis

### Question 1: aggregate habitat selection

We were specifically interested in testing if fish "selected" for certain microhabitats defined by depth and velocity at separate times of the day. To answer this, we tested the probability that fish occupied the microhabitats where we placed our antenna, relative to the availability of all potential microhabitats within each study reach. The beaver complex and the run were divided into 201 and 116 microhabitat cells, respectively, using hydraulic model outputs to characterize habitat, hereinafter referred to as "available" microhabitats, representing all the possible areas a fish could occupy within a given reach. Antenna locations were nonrandomly chosen for each study reach and accounted for 5.4% and 8.5% of the microhabitats, respectively — hereinafter referred to as "sampled" microhabitats. To determine if fish preferred the sampled versus the available microhabitats, we estimated the depth and velocities for each available microhabitat cell. We then compared the distribution of microhabitat depths and velocities that were used by the fish (frequency that fish used one of the sampled microhabitats) to null distributions of what would be expected from random use of all available microhabitats. Specifically, to generate this null distribution, we randomly sampled depths and velocities from all available microhabitats ( $n = 564\ 480$  for the beaver complex and  $n = 315\ 360$  for the run; these values represent the total potential time in minutes that all observed fish could have been recorded within a given "sampled" microhabitat over a 7-day period). We then removed all depths and velocities from this null distribution that were different from the sampled microhabitats — creating a null distribution that describes the probability that fish "chose" the microhabitat represented by our antennas by chance. We then compared these null distributions to the observed distributions using a  $t$  test and a Kolmogorov–Smirnov test (hereinafter KS test;  $\alpha < 0.1$  for both tests).

We used a generalized linear model to test if microhabitat selection (i.e., the number of detection minutes per antennae; log-transformed to reduce skew) was predicted by either depth or velocity. To explicitly test for differences between the run and beaver complex, we used the study reach as an interaction term for both velocity and depth. We also included variables for substrate and cover in initial models, but they contributed little to the predictive power of the model and thus were not included in our final models.

To test how fish changed microhabitat use over the course of the day, we first split each day into four time bins (diel periods): morning (0600–1159), afternoon (1200–1759), evening (1800–2359), and night (0000–0559). For each diel period we counted the number of unique fish detections at each of the antenna. For visualization and qualitative purposes, we plotted the average number of unique fish detected per day at each antenna during four diel periods. We then ranked antennas, from most visited (rank = 1) to least visited, as a measure of "preference". We quantified the

magnitude of change in preference rank each antenna had over different diel periods across all days as a measure of the difference between the rank at that period and the average rank of the antenna across time (e.g.,  $\text{rank}_{\text{average}} - \text{rank}_{\text{morning}}$ ). As a measure of this variation, we calculated the CV of the changes in antenna rank across time for each antenna and used  $t$  tests and KS tests to quantify differences in the mean of CVs and their relative distribution between the two study reaches. In doing so we could assess the degree to which fish changed their utilization of antennas over the course of the day.

### Question 2: individual behaviour

We tested whether fish occupying a heterogeneous habitat partition the spatial niche in a more discrete manner than those in a more homogeneous environment. To do so, we quantified the degree of spatial partitioning (i.e., specialization in movement and habitat use behaviours — described below) of individuals residing in the run and beaver complex reaches. To remove fish with little habitat use information from behavioral analyses, we imposed a residency criterion where fish had to be observed in 2 or more days and at least 20 times for inclusion. There were 65 fish in the beaver complex and 19 fish in the run that met the residency criterion.

We generated transition matrices for each fish, recording the number of detections per antenna and the directionality of use (i.e., the antennas fish moved towards and away from) at unique 1 min intervals. Fish movement was characterized according to activity or boldness. Activity describes the number of transitions made between discrete antennas, as well as the use of these antennas (i.e., multiple detections of the same fish at the same antenna). Boldness describes how a fish is to travel further between detections (potentially more risky behaviour) and is quantified as the number of transitions multiplied by the physical distance (metres) between antennas. For each study reach, we quantified the proportion of antennas utilized by each fish (the number of antennas used relative to the number available) as a measure of home range size.

We calculated the degree of spatial partitioning (i.e., specialization in movement behaviour as a measure of the degree in overlap among individuals) by modifying analyses of individual-level dietary specialization from Bolnick et al. (2002). Specifically, we calculated the proportional similarity index ( $PS_i$ , a specialization measure) per individual:

$$PS_i = 1 - 0.5 \sum_j |p_{ij} - q_j|$$

where,  $\mathbf{P}$  is a proportional matrix (used by Bolnick et al. (2002) as an individual (row) by dietary item (column) matrix, here converted from the raw transition matrices for each fish creating an individual by antenna matrix),  $p_{ij}$  is the proportion (number of discrete transitions / total number of transitions) of the  $j$ th antenna that the individual  $i$  used, and  $q_j$  is the proportion of the  $j$ th antenna used by the entire population (Bolnick et al. 2002).  $PS_i$  is a value from 0 to 1 where the lower the value, the smaller amount of spatial overlap that individual has with others (i.e., they are more specialized in their movement). This metric is typically used in the context of a dietary niche (Bolnick et al. 2003, 2007), but can be applied for additional measures of niche space (Allgeier et al. 2017), as well as spatial partitioning as applied herein. This metric was calculated for the activity (the amount of movement between antennas as well as the use of these antennas) and boldness (distance of movement; i.e., the number of transitions multiplied by the physical distance) for each individual. Both  $t$  tests and KS tests were used to compare the means and spread of the distribution of individual  $PS_i$  values between study reaches. Because there were only 19 individuals that met the residency criteria in the run,

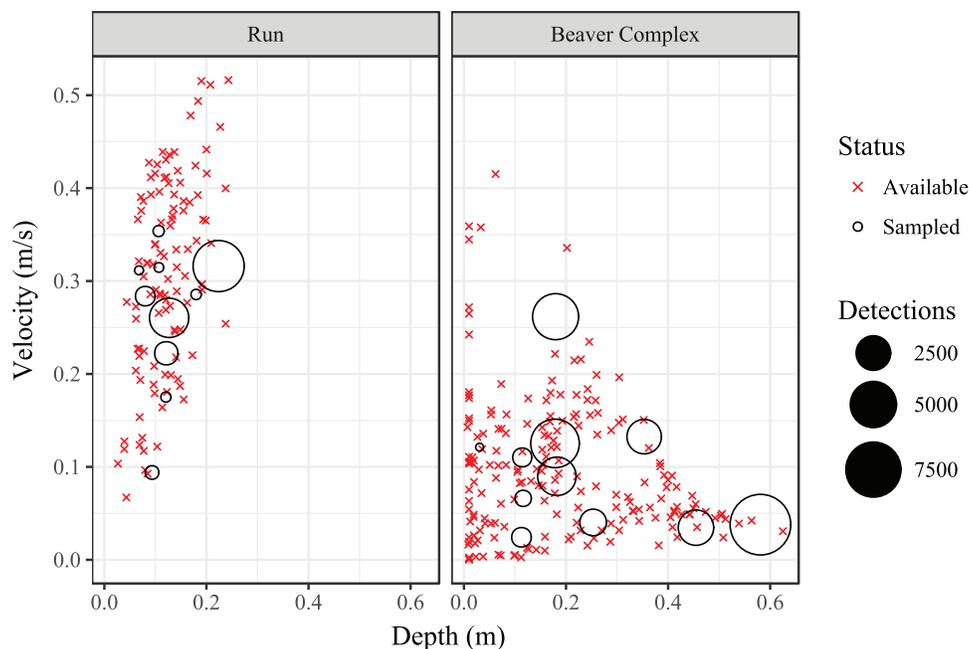
**Table 1.** Descriptive information of beaver complex and run reaches and the juvenile steelhead that utilized respective study reaches.

Study reach	Area (m <sup>2</sup> )	No. of antennas	Estimated density (fish·m <sup>-1</sup> )*	Percentage tagged (%)	Mean fork length (range; mm)	Individuals detected	Individual residents
Beaver complex	89.3	11	3.2	36	111.0 (80–190)	96	65
Run	51.2	10	1.3	51	110.9 (77–180)	79	19

Note: Individual residents reflect the number of fish observed in 2 or more days and detected at least 20 times.

\*Units are fish per linear metre.

**Fig. 2.** Scatterplots representing the depth (x axis) and water velocity (y axis) microhabitats present in each study reach. Here, “available” represents all the different microhabitats (equal to antenna area; 0.44 m<sup>2</sup>) within each study reach; and “sampled” represents the depths and velocities at which our antennas were placed. The size of the open circles representing sampled locations denotes the number of detections at each antenna.



bootstrapping was used to resample 19 individuals from the beaver complex to make equal sample size comparisons — this process was reiterated 100 times per statistical test, the average *p* value is reported with significance at  $\alpha < 0.1$ . We included results from both original and bootstrapped data sets for all comparisons.

To test if individual spatial partitioning (i.e., behaviours) changed throughout the day, we subdivided the day into the four diel periods mentioned previously and quantified the proportion of antenna locations used by individual fish and the degree of specialization of activity that occurred at each diel period. Again, a bootstrapping technique was used to resample 19 individuals from the beaver complex to make equal sample size comparisons — this process was reiterated 100 times, for which comparisons were made using *t* tests and KS tests.

## Results

From abundance surveys, we estimated the densities of juvenile steelhead to be 3.2 fish per linear metre (fish·m<sup>-1</sup>) in the monitoring site with beaver activity and 1.3 fish·m<sup>-1</sup> in the site containing the run (Table 1). Over the 7 days of observation, we recorded 96 unique individuals in the beaver complex and 79 individuals in the run. In the complex, 27% of recorded fish were only present for 1–2 days; 22% were recorded in 3–4 days; and 51% were recorded in 5–7 days. Conversely, most fish (50%) in the run were recorded for

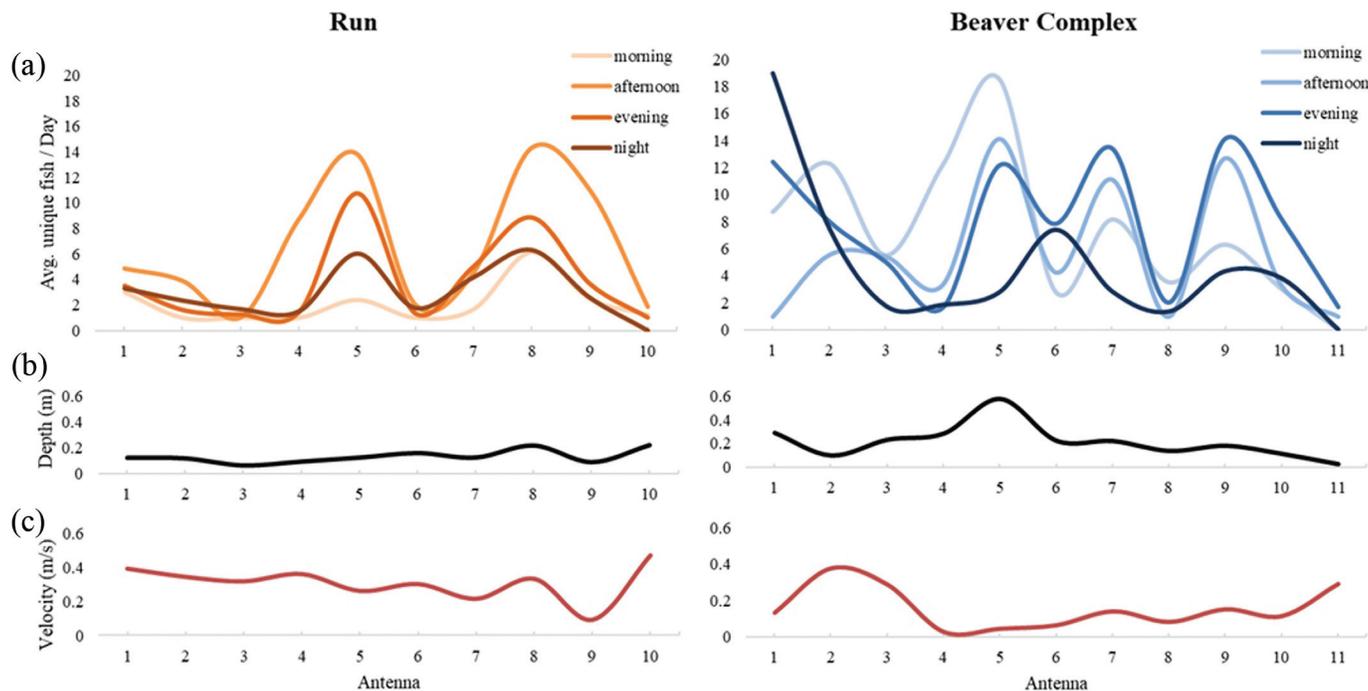
1–2 days; 26% were recorded 3–4 days; and 24% were recorded 5–7 days. The mean number of unique fish detected at individual antennas was 42.8 in the beaver complex and 32.1 in the run. The highest percentage of time accounted for by any one individual was 22.3% in the beaver complex and 29.7% in the run. Water temperature averaged 19.7 °C (range = 15.1–25.9 °C; CV = 0.028) in the beaver complex and 22.2 °C in the run (range = 17.6–27.7 °C; CV = 0.007).

### Question 1: aggregate habitat selection

Comparing individual-level site use with the relative availability of sites showed strong site selectivity in both study reaches. We found that fish “selected” for certain microhabitats, and this selection was driven by attributes of the habitat (i.e., depth and velocity) and time of day (Figs. 2 and 3). First, we found that fish occupancy of the “sampled” microhabitats (as defined by the depth and water velocity at a given antenna) significantly differed from random site occupancy (*t* test and KS test:  $p < 0.001$ ). We found that distributions of microhabitats used based on depth in both study reaches tended to be skewed right, indicating greater selectivity for deeper locations (refer to online Supplemental material, Fig. S1<sup>1</sup>). Distributions of microhabitats used based on velocity were more similar in shape to the available microhabitats in both study reaches, but slightly skewed left, suggesting preference for slower-moving water.

<sup>1</sup>Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2018-0171>.

**Fig. 3.** Row (a) depicts the mean number of unique fish detected per day at each antenna within the two study reaches, during four diel periods. Diel periods are defined as follows: morning (0600–1159), afternoon (1200–1759), evening (1800–2359), and night (0000–0559). Rows (b) and (c) represent the mean depths and water velocities, respectively, at each antenna calculated from water depth digital elevation models and hydraulic models. [Colour online.]



We extended this analysis using a linear model to directly test for the importance of depth and velocity for microhabitat selection in both study reaches. There was a significant effect of both depth (positive) and velocity (negative) for microhabitat selection by fish, but this relationship differed among study reaches (i.e., there was a significant interaction between depth and study reach and between velocity and study reach;  $p < 0.001$ ; Table 2). These factors explained ~60% of the variation in the data and were better predictors for selection in the run than in the beaver complex.

Differences were visually apparent in the preference of certain microhabitats throughout the day by the two populations (Fig. 3). For example, antennas five and eight were always the most visited antennas in the run, regardless of time of day — these antennas were characterized by deeper water and the presence of velocity shear zones created by large substrate; however, antenna preference seemed to change substantially through diel periods in the beaver complex. Differences in CV values per antenna preference rank were apparent between the two reaches, though only marginally significant ( $p = 0.1$ ). The mean antenna CV in the beaver complex was 0.34, with a range of 0–0.97 (antennas eleven and five, respectively). Mean antenna CV in the run was 0.19 with a range of 0.09–0.31 (antennas nine and seven, respectively; Fig. 4). The trend toward higher CVs in the beaver complex suggests that individuals tended to shift preference for a given antenna more over the course of the day in the beaver complex than in the run.

**Question 2: individual behaviour**

In the run, 24% of unique individuals met the residency criteria for inclusion in behavioural analyses, opposed to 68% of individuals detected in the beaver complex (Table 1), suggesting that most of the fish in the beaver complex spent a good deal of time in that habitat feature, while many fewer fish ended up spending significant time in the run. No difference was found between the beaver complex and the run with respect to the proportion of antennas individuals used with the bootstrap approach (Fig. 5);

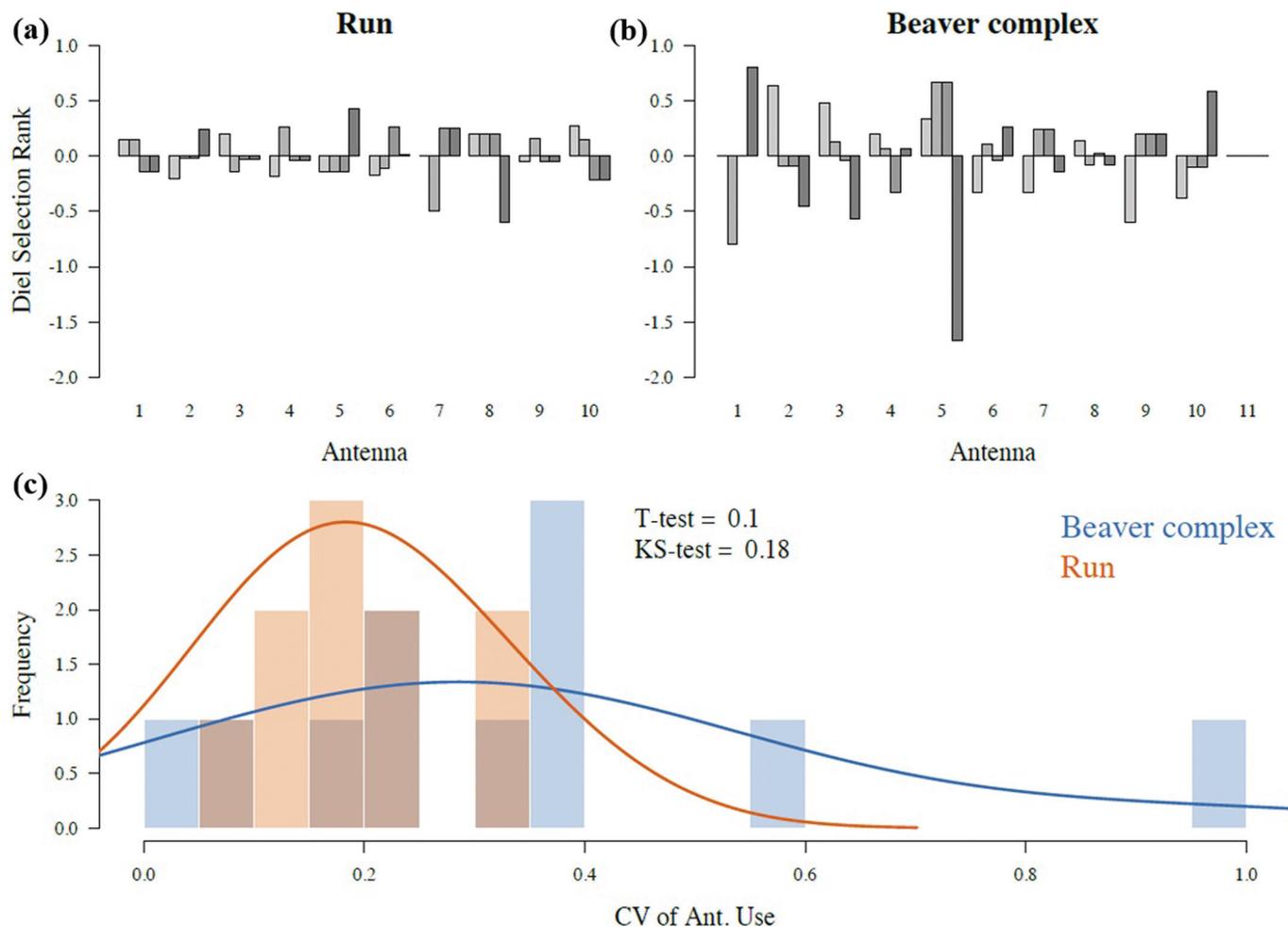
**Table 2.** Output from the generalized linear model that tested the importance of depth, velocity, and study reach for microhabitat selection.

Variable	Estimate	Standard		
		error	<i>t</i>	<i>p</i>
Interaction	4.12	1.60	2.57	0.02
Study reach	0.33	1.87	0.18	0.86
Velocity	-23.89	10.76	-2.22	0.04
Depth	47.53	12.16	3.91	<0.01
Reach × velocity	39.78	14.41	2.76	0.01
Reach × depth	-32.26	12.57	-3.05	0.01
$R^2 = 0.60$				

however, differences were significant ( $p = 0.1$ ) when making comparisons with uneven sample sizes (i.e., the beaver complex had more residents). Significant differences were found in individual specialization metrics between the two study reaches for both activity (mean  $p = 0.02$ , spread  $p < 0.01$ ) and boldness (mean  $p < 0.01$ , spread  $p = 0.01$ ), with the beaver pond individuals displaying less spatial overlap (i.e., higher levels of spatial partitioning) in both regards (Fig. 5). This means that individual fish in the beaver complex displayed more unique behaviours (relative to the run) in terms of both what antennas they moved towards and the distances they traveled across the reach.

The proportion of antennas used by individuals and their degree of spatial overlap was highly variable throughout the four diel time blocks (Fig. 6). Individuals in the beaver complex used a large proportion of the sampled microhabitats in the morning (not significant when applying the more conservative bootstrap), but a smaller proportion of sampled microhabitats in the afternoon and night time. Individuals were more specialized (higher degree of spatial partitioning) in the beaver complex only in the afternoon (Fig. 6).

**Fig. 4.** Bar charts (a and b) represent population-level changes in the rank of antenna preference by juvenile steelhead over four diel periods (average rank – rank at a given diel period) for beaver complex and run study reaches. A positive value indicates an antenna is more popular in the specified diel period compared with average popularity of the antenna. The histogram (c) depicts the frequency of coefficient of variation (CV) of antenna preference rank within diel periods, whereby the larger the CV indicates greater changes between diel periods of antenna preference. A *t* test indicates a difference in means variation between the two study reaches; a trend of increased CV can be noted in the beaver complex relative to the run. [Colour online.]



## Discussion

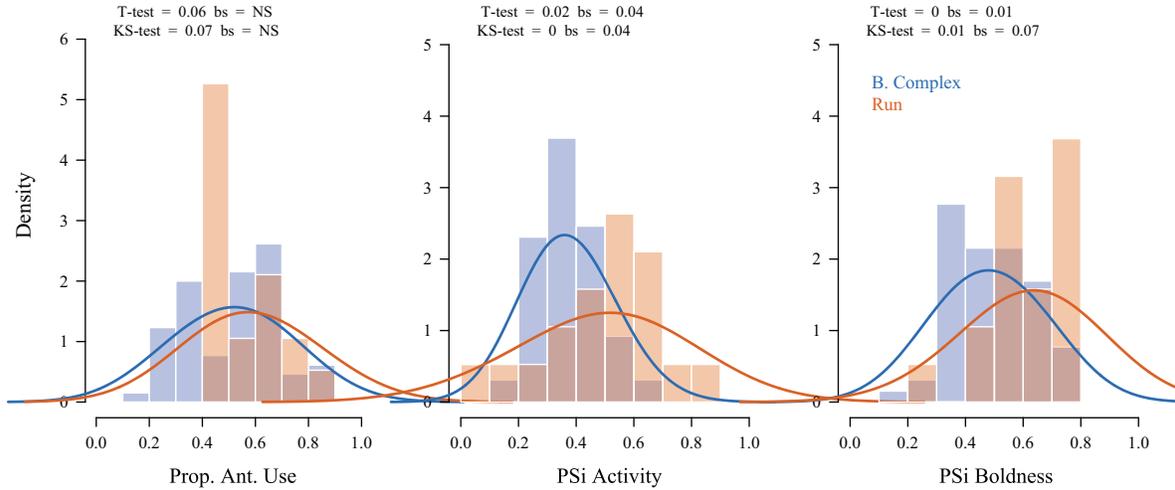
The structure of a habitat influences fish population productivity (Van Horne 1983), but the mechanisms by which this occurs are not well known. Understanding how individuals that share physical space modify their behaviour in relation to the complexity of their habitat may offer insight into how individuals partition resources and the ecological interactions of a species (Bolnick et al. 2002; White et al. 2014). Previous research in our study system (the Bridge Creek watershed) demonstrated that beaver-based restoration increased habitat complexity, density, and survival of juvenile steelhead (Bouwes et al. 2016). More broadly, beaver activity and BDAs are being promoted as a potential restoration tool to remediate channel incision (Pollock et al. 2014) and increase habitat complexity for the benefit of fish populations (Bouwes et al. 2016; Dauwalter and Walrath 2017). Our research provides important new insights into the mechanisms that may lead to enhance population productivity. We showed that improved habitat quality (increased heterogeneity due to beavers) enhances the degree to which individuals partition the physical space of the habitat, with implications for improved resource use efficiency and population productivity (Kovalenko et al. 2012).

More juvenile steelhead used the beaver complex for longer durations, compared with the run. From our fish capture surveys,

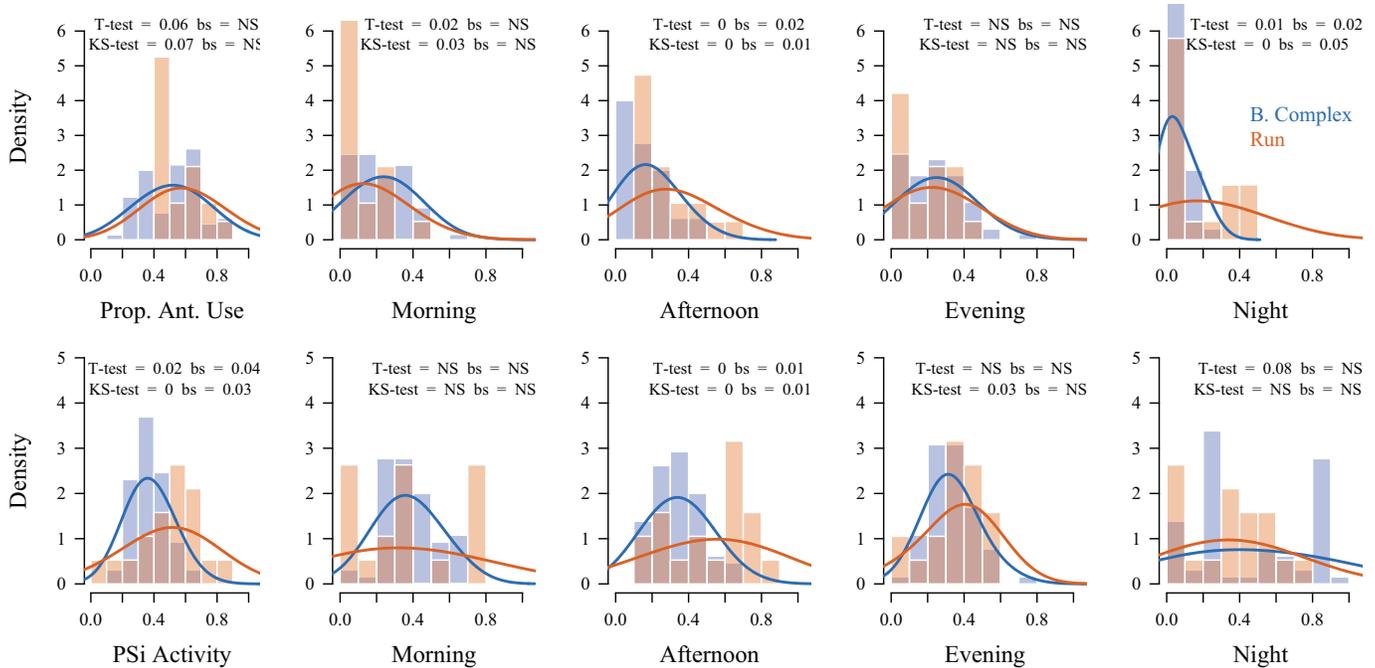
we know that the density of juvenile steelhead was almost three times higher in the site impacted by beaver activity, and, on average, these fish spent longer amounts of time within this habitat than in the more homogeneous run. Our findings are consistent with other studies documenting increased biomass of juvenile anadromous salmonids in beaver-impacted tributaries whereby the presence of beavers increased habitat heterogeneity, providing a larger range of growth opportunities for juvenile salmon (Malison et al. 2015). Beaver ponds accommodate higher densities of some fish species (Bylak et al. 2014) because of the increased microhabitat complexity associated with changes in depth and velocity (Dauwalter et al. 2014; Bouwes et al. 2016). Depth and velocity have long been considered key drivers of habitat selection in stream fishes (Everest and Chapman 1972), and their availability, in the form of suitable microhabitats for stream-dwelling salmonids, can limit a system's carrying capacity of those fish (Ayllón et al. 2012).

Habitat heterogeneity generates opportunities for stream fish to use a range of microhabitats depending on daily needs (i.e., foraging, predator avoidance, energy conservation; Schlosser 1991). We found that juvenile steelhead selected for greater depths and slower water velocities in both study reaches, but selection was stronger in the run (indicated by the importance of reach in

**Fig. 5.** Kernel density plots of the relative frequency of habitat use metrics for all individuals with the beaver complex (B. Complex) and run: Prop. Ant. Use = proportion of antennas used; Psi Activity = the degree of niche overlap (or specialization as measured by the  $PS_i$  index) in terms of the amount of movement between and use of discrete antennas; and Psi Boldness = the degree of spatial overlap in terms of the relative distance individuals move between antennas. Statistical differences between study reaches are tested with *t* tests (mean) and KS tests (spread). In all cases the distributions were compared with unequal samples sizes between the two study reaches (there are more fish in the beaver complex) and with a bootstrapped approach to compare equal sample sizes, indicated as “bs”. “NS” indicates the mean *p* value of the comparisons that were greater than 0.1. See Materials and methods for further details. [Colour online.]



**Fig. 6.** Kernel density plots of habitat use (proportion of antennas used) and specialization in movement between and use of antennas (Psi Activity) for all individuals across the entire day (far left plots) and broken into distinct diel periods. Statistical differences between study reaches are tested with *t* tests (mean) and KS tests (spread). In all cases the distributions were compared with unequal samples sizes between the two study reaches (there are more fish in the beaver complex) and with a bootstrapped approach to compare equal sample sizes, indicated as “bs”. “NS” indicates the mean *p* value of the comparisons that were greater than 0.1. See Materials and methods for further details. [Colour online.]



the linear habitat use model; Table 1), indicating limited desirable depth and velocity conditions within that reach. Specifically, in the run the two deepest antennas were always the most selected for, regardless of the time of day, and the preference for other antennas differed little between periods of the day (Figs. 3 and 4). In contrast, the time of day was important for antenna preference in the beaver complex (Figs. 3 and 4). For example, the deepest portion of the pool (antenna five) was the most popular location

when the sun was highest (i.e., morning and afternoon), but it was almost devoid of fish during nights — presumably as a response to the increased threat of diurnal avian predation (Metcalfe et al. 1999). Conversely, the tail-out of the plunge pool below the impoundment (antenna one; Fig. 1) was generally avoided during the day, but became the most selected for antenna at night, as many salmonids will make nocturnal moves to shallower areas away from cover (Jakober et al. 2000; Albrecht and Gotelli 2001; Reeves

et al. 2010; Hines et al. 2017). Diel shifts in habitat use can occur due to crepuscular foraging (Bradford and Higgins 2001); predator avoidance (Metcalfe et al. 1999); minimizing respiration at high water temperatures (Sloat et al. 2013); and reducing swimming cost at night (Reeves et al. 2010). In the run, the limited availability of desirable habitat dictated habitat use — allowing for only slight habitat use variation in response to diverse daily needs of fish — whereas in the beaver complex, the shrinking proportion of antennas used in the afternoon and night indicates there were very specific and desirable places to be during those discrete diel periods (Fig. 6). Therefore, we can conclude that availability of quality habitat constrains the degree to which fish can vary their daily habitat preference and that habitat heterogeneity allows variation in habitat selection over the diel cycle.

Understanding how individuals partition an ecological niche has a long history in ecology (Roughgarden 1972) and has been a central tool used to understand competition and coexistence among individuals — with the central idea being that higher rates of niche partitioning can reduce competition and enhance coexistence (Huston 1994). Our study showed that within the beaver complex, individual fish established more distinctive patterns of spatial use of microhabitats than in the run. This pattern is reflected in increased specialization in activity and boldness behaviours and variation in diel movement patterns of individuals in the beaver complex relative to those in the run, where individuals showed less variation in their habitat selection strategies. In the run, individuals either established use patterns at the two deepest antennas or used other habitat in seemingly random ways, presumably as if they are searching for quality microhabitat (Figs. 2 and 4). In the beaver complex, individuals display more specialized habitat use and movement patterns that changed through the day, presumably allowing individuals to fulfil daily needs (i.e., foraging, digestion, predator avoidance) in different physical space at different times. These findings identify increased spatial partitioning (i.e., specialized movement behaviour) as a potential mechanism that allows the coexistence of increased abundance of steelhead in habitats altered by beavers.

In addition to physical alterations, beaver impoundments can change the structure of the invertebrate community within a stream by replacing the lotic species with a lentic community (McDowell and Naiman 1986), thereby diversifying the potential prey base for fishes, with implications for increased numbers of population-level dietary niches (Tinker et al. 2008). The movement specialization we observed within the beaver complex could represent segregation of foraging behaviours such as drift foraging for lotic invertebrates flowing into the complex and pelagic foraging for lentic invertebrates within the complex. Such diversification is unlikely in the run because consistently higher water velocities may exclude lotic prey items found in beaver ponds (e.g., water boatmen and amphipods), making pelagic foraging behaviours ill-suited for that habitat.

Interestingly, there appears to be no apparent cost in growth rates for highly mobile juvenile steelhead compared with stationary individuals, indicating the potential importance of two disparate movement behaviours as a viable means to expanding population-level resource base and to reduce intraspecific competition for resources (Kahler et al. 2001; Steingrímsson and Grant 2003; Myrvold and Kennedy 2016). Collectively, our findings in conjunction with previous work suggests that the diversity in beaver complex movement behaviours could be a manifestation of dietary niche expansion (Harrison et al. 2017). Further, juvenile steelhead have shown strong diel movement capabilities to exploit thermal refuge (Brewitt and Danner 2014). Beaver impoundments can contain an increased diversity of near-bed water temperatures (Weber et al. 2017), which our study confirms, as variation in temperatures between antennas in the beaver complex was four times that observed in the run. Diel utilization of

thermal refuge may also be a key to survival during thermally stressful periods often observed in our study watershed.

Grids of PIT antennas are increasingly being used to understand individual fish behaviour and habitat use at fine scales (Johnston and Bergeron 2009; Roy et al. 2013a, 2013b). The use of this system helped us compile a unique and comprehensive data set on 175 individual fish locations over a 7-day period. However, two aspects of our study represent important caveats. First, the lack of replication at the site level limits our ability to make generalizations of how juvenile steelhead utilize beaver complexes versus runs, because the structure of beaver complexes are variable, and fish responses change as beaver complexes age (Bylak et al. 2014). Second, our antenna setup provided incomplete spatial and temporal coverage of the habitats we sampled. This was especially apparent at night in the beaver complex, as many fish detected by day were not detected by night. This detection limitation was particularly apparent via visual observations (G. Wathen) of fish occupying the beaver complex tail-out at night that were not otherwise detectable in our data set due to the absence of antennas in that respective area.

Our study provides new insights in how habitat complexity can affect individual-level behavioural traits of habitat utilization and specialization. This study adds to the growing body of research highlighting the utility of understanding individual-level variation in ecological traits (in our case, movement) for ecological processes. This study also provides further support to the idea that habitat quality positively affects population viability — a presumed, but generally untested, expectation for restoration efforts. Future efforts to integrate individual-level movement behaviour into a broader set of tools used to assess habitat restoration will likely improve future restoration efforts.

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