

Individual behaviour and resource use of thermally stressed brook trout *Salvelinus fontinalis* portend the conservation potential of thermal refugia

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Abstract

Individual aggression and thermal refuge use were monitored in brook trout *Salvelinus fontinalis* in a controlled laboratory to determine how fish size and personality influence time spent in forage and thermal habitat patches during periods of thermal stress. On average, larger and more exploratory fish initiated more aggressive interactions and across all fish there was decreased aggression at warmer temperatures. Individual personality did not explain changes in aggression or habitat use with increased temperature; however, larger individuals initiated comparatively fewer aggressive interactions at warmer temperatures. Occupancy of forage patches generally declined as ambient stream temperatures approached critical maximum and fish increased thermal refuge use, with a steeper decline in forage patch occupancy observed in larger fish. These findings suggest that larger individuals may be more vulnerable to stream temperature rise. Importantly, even at thermally stressful temperatures, all fish periodically left the thermal refuge to forage. This indicates that the success of refugia at increasing population survival during periods of stream temperature rise may depend on the location of thermal refugia relative to forage locations within the larger habitat mosaic. These results provide insights into the potential for thermal refugia to improve population survival and can be used to inform predictions of population vulnerability to climate change.

KEYWORDS

brook trout, climate change, personality, *Salvelinus fontinalis*, thermal refugia

1 | INTRODUCTION

Climate change and landscape disturbance have resulted in substantial increases in stream temperatures worldwide (Isaak *et al.*, 2012; Nelson & Palmer, 2007). Stream temperature rise is most commonly exemplified by increased average summer water temperatures, but shifting thermoclines can also result in earlier warming in spring, delayed onset of cooling in autumn, and an increase in the number of days that exceed physiological thresholds for the native fish community (Pederson *et al.*, 2010). As temperature directly affects freshwater fish bioenergetics, reproductive and competitive ability, and survival

(McCullough *et al.*, 2009; Pankhurst & Munday, 2011; Woodward *et al.*, 2010), shifts towards warmer thermal regimes have often been accompanied by reduction or extirpation of native fish populations and increased invasion by native and non-native species with higher thermal tolerances (Comte *et al.*, 2013; Moyle *et al.*, 2013).

Thermal habitat loss has been most significant for obligate coldwater species, including stream salmonids (Comte *et al.*, 2013; Muhlfeld *et al.*, 2018). In recent decades there has been a marked shift in the distribution of stream salmonids towards increasingly lower order and higher elevation streams as species distributions contract down to include the coldest remaining habitats in a watershed

(Almodóvar *et al.*, 2012; Comte & Grenouillet, 2013). Long-term viability of headwater-isolated populations is threatened by reduced population size and connectivity (Carim *et al.*, 2016), but near-term survival is also expected to decline with continued stream temperature rise (Albouy *et al.*, 2012; Buisson *et al.*, 2008). While the rate of warming may be reduced in high-elevation, mountainous catchments (Isaak *et al.*, 2016), stream temperatures in some catchments could rise approximately 1.5°C for every 2°C increase in air temperature (Null *et al.*, 2013).

Stream temperature rise will likely result in continued declines in the distribution of coldwater fishes (Comte *et al.*, 2013); however, recent evidence suggests that predictive models may provide overly pessimistic conclusions about population vulnerability (Isaak *et al.*, 2016). Often, this is because data used to construct predictive models are collected at spatial scales that are not commensurate with the scale at which fish use habitat (Fullerton *et al.*, 2018; Snyder *et al.*, 2015). Consider maximum summer temperature or maximum 30day average temperatures, which are often used to estimate reach-level occupancy probability for a fish species of interest (DeWeber & Wagner, 2018). These metrics summarise ambient conditions and can provide insights into occupancy probabilities for an entire stream reach, but they fail to account for fine-scale spatial heterogeneity in stream temperature that can increase local survival (Ebersole *et al.*, 2003; Kanno *et al.*, 2014; Snyder *et al.*, 2015; Torgersen *et al.*, 1999). For example, areas of groundwater upwelling are common in mountainous streams (Dugdale *et al.*, 2015; Ruesch *et al.*, 2012) and provide areas of thermal refugia that are upwards of 14°C colder than ambient stream temperatures (Baird & Krueger, 2003).

Observational studies have documented rapid movement of fish to thermal refugia as ambient stream temperatures become physiologically stressful (Ebersole *et al.*, 2001; Sutton *et al.*, 2007). Accordingly, many have hypothesised that occupancy of thermal refugia can decrease physiological stress, increase fish growth and reproduction, and ultimately allow for population persistence despite widespread loss of thermal habitat (Aunins *et al.*, 2015; Fullerton *et al.*, 2018). This has motivated the inclusion of thermal refugia into species distribution and vulnerability models, and it is often found that the presence of thermal refugia can predict coldwater fish occupancy (Isaak *et al.*, 2017). However, these models make the overly simplistic assumption that the presence of thermal refugia is enough to significantly influence population persistence, when still little is known about how fish use and compete for access to this limiting resource. For example, observational studies have documented individuals readily moving into and out of a thermal refuge, even when ambient water temperatures exceed the species' thermal tolerance (Goniae *et al.*, 2006). One hypothesis for this behaviour is that competition for space inside the refuge limits occupancy to include only dominant individuals (Biro, 1998; Ebersole *et al.*, 2001). Under this hypothesis, larger individuals with more aggressive personality types may be the most successful at defending territory within the refuge and thus most successful at surviving periods of thermal stress. Alternatively, another hypothesis is that refuge habitats are devoid of necessary resources and individuals must frequently move among several habitat patches to feed, avoid

predators, or conserve energy during high flows (McCullough *et al.*, 2009). With this hypothesis, larger individuals may have reduced survival as longer periods of time spent out of the refuge are expected to be more metabolically demanding for individuals with larger body sizes (Norin & Clark, 2016; Sheridan & Bickford, 2011). Conversely, because smaller individuals are less affected by thermal stress, they may be able to move around the environment more freely, provided they are not competitively excluded from thermal refugia.

Determining the dynamics that control refuge use is important for understanding the potential for thermal refugia to increase population persistence and mediate population dynamics. If competition for position inside the refuge is high, then it could suggest that the number and size of refuge habitats is a significant predictor of reach carrying capacity (Ebersole *et al.*, 2001; Ebersole *et al.*, 2003). Alternatively, if fish must leave a thermal refuge in search of resources, then the location of a refuge within the larger habitat mosaic could predict the value of that refuge for increasing population survival (George *et al.*, 2016). For example, if refugia exist in a highly fragmented landscape, then the presence of refugia may not significantly increase population survival as fish will either become trapped within a forage-deficient refuge or will spend an excess of time migrating through thermally unsuitable habitat in search of resources (Torgersen *et al.*, 1999).

The objective of this research was two-fold. The first goal was to determine whether individual attributes could predict how fish compete for access to thermal refugia in a controlled experimental stream laboratory. To do this, individual average aggression and change in aggression with increased temperature were quantified as a function of fish size and personality (specifically exploration, which is one of the major axes of personality and is correlated to aggression (Adriaenssens & Johnsson, 2011; Pike *et al.*, 2008)). The hypothesis was that larger, more exploratory individuals would be the most aggressive and would outcompete smaller fish for access to the most energetically profitable locations in the stream. However, another hypothesis was that the most energetically profitable patches in the stream would change with increasing stream temperatures, and fish would shift resource use away from a forage patch and towards a thermal refuge as stream temperatures increased. Therefore, the second objective was to explore how fish size and personality influenced average resource use, as well as change in resource use, with increasing stream temperatures.

This study was conducted using brook trout *Salvelinus fontinalis* (Mitchill 1814), a stream salmonid native to eastern North America. Brook trout optimal growth occurs between 13 and 16°C, with cellular stress responses initiated at approximately 20°C (Chadwick *et al.*, 2015; Chadwick & McCormick, 2017). Native brook trout populations have experienced significant declines in recent decades due, in part, to stream temperature rise (Hudy *et al.*, 2008). Empirical and analytical evidence suggests that thermal refugia can increase brook trout population persistence (Baird & Krueger, 2003; Petty *et al.*, 2012; Aunins *et al.*, 2015), and some have attempted to incorporate thermal refugia into species distribution models that predict future reach-level occupancy (Snyder *et al.*, 2015).

2 | MATERIALS AND METHODS

All experimental protocols were approved by the Pennsylvania State University Institutional Animal Care and Use Committee under protocol # 47545.

2.1 | Experiment set-up

This study was conducted in an indoor stream laboratory at the U.S. Geological Survey Leetown Science Center in Kearneysville, West Virginia, USA. A detailed description of the artificial streams can be found in Hitt *et al.*, (2017). Briefly, there were four 7.6m gravel-bottom stream channels, each consisting of three pools and two riffles. The four streams were divided into two pairs, and each pair of streams shared a common sump and filtration system. Fish could freely swim among pools within a stream, but movement between streams was not possible. A belt feeder located in the upstream riffle periodically delivered 5 mm floating pellets (Finfish G pellets, Zeigler Brothers, Inc.; www.zeiglerfeed.com) during daylight hours (Figure 1). Brook trout readily compete for access to food and space, but to ensure food was a limiting resource and that competition for territories near the belt feeder was high, the amount of food in each stream was restricted to 1% of fish biomass per day. This forage density is higher than wild brook trout streams (Ensign *et al.*, 1990), but too low to satiate fish and reduce competition.

Ambient stream temperatures were manipulated from 14 to 23°C (see §2.3) using a combination of controlled heating (Aqua Logic 12 kW in-line heater; www.aqualogicinc.com) and cooling (Aqua Logic 17.4 kW chiller barrel). To provide thermal heterogeneity in the stream channel, an area of groundwater upwelling was simulated by introducing 14°C spring water into the last pool (this pool is herein referred to as the thermal refuge) following Hitt *et al.*, (2017). Spring water was delivered to the thermal refuge at a continuous rate of 3 l min⁻¹ using flexible tubing buried in the substrate. Importantly,

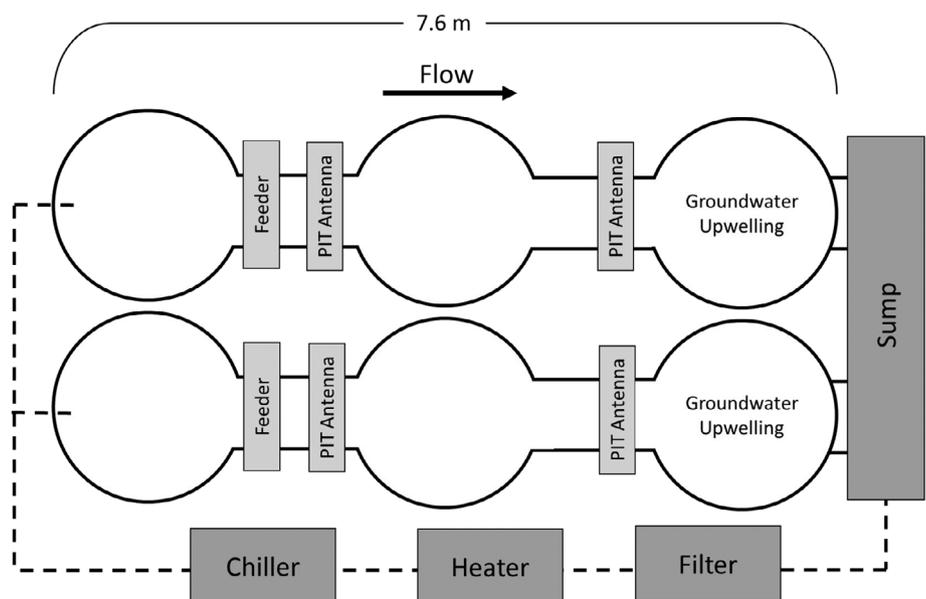
because water density decreases at warmer temperatures, there was a vertical temperature cline in the thermal refuge with the stream bottom maintaining approximately 14°C, but temperatures approximating ambient stream temperature near the water surface. Stream temperatures were monitored in every pool using continuous temperature data loggers (Onset ProV2; www.onsetcomp.com).

The spatial segregation of the foraging patch in the first riffle and thermal refuge in the last pool creates a realistic scenario wherein resources are fragmented across the stream and fish must choose which resource to occupy. To monitor individual resource use, a passive integrated transponder (PIT) antenna was installed in the middle of each riffle, with antennas having a read range of approximately 50 mm in both the upstream and downstream direction. With only one antenna per riffle it was not possible to monitor the directionality of movement and therefore individual movement rates are not quantifiable. However, total fish-specific detections at each antenna can be used as a metric for relative resource use on a given day. For example, more total detections at the upstream antenna suggest higher prioritisation of the forage patch, whereas increased detections at the downstream antenna indicates a shift towards increased use of the thermal refuge.

2.2 | Study fish

This study used one-year-old brook trout from the West Virginia Department of Natural Resources Ridge Creek Hatchery in Berkeley Springs, West Virginia, USA. Prior to the start of the study, fish were housed in groups of equal size in the four experimental streams at 14°C. Fish were anaesthetised in 100 mg l⁻¹ MS-222 and a PIT tag was inserted into the abdominal cavity and an external Floy tag posterior to the dorsal fin. Floy tags had a unique colour code so that individual fish could be visually identified during behavioural observations. Fish recovered from tagging for approximately one month before the start of personality assessments.

FIGURE 1 Diagram of one pair of experimental streams used to study individual response to thermal stress in brook trout. The streams were connected by a common water sump and filtration system. Each stream consisted of three pools and two riffles, with an area of groundwater upwelling located in the downstream pool. The upstream riffle contained a continuous belt feeder and there was a passive integrated transponder tag (PIT) antenna in both riffles to monitor resource use



2.2.1 | Fish personality assessments

Personality was assessed using a standard open field test (Réale *et al.*, 2007). Specifically, each individual's level of exploratory behaviour was measured, with greater distances moved during the test being indicative of fish with more exploratory personalities. All open field tests were completed in the third pool of a randomly selected stream. During open field tests, gravel and plumbing were removed from the pool and a barrier was placed to prevent fish from exiting the pool and entering the riffle.

For each open field test, a randomly selected individual fish was placed in the testing pool where it was allowed to acclimate for 15 min before the start of a 10-min test. Fish behaviour was recorded using Noldus Ethovision 11.5 software (www.noldus.com), which monitored the fish's location every 0.5 s and automatically measured the total distance (cm) a fish moved during the test.

Four replicate open field tests were conducted for each fish, with at least one week separating each test. At the conclusion of the last open field test, fish were measured for length and weight and evenly distributed among the four experimental streams resulting in 17 fish per stream, or 2.5 fish m⁻¹. This density is higher than what would be expected in natural brook trout streams, which should have increased competition for food and space. When distributing fish, the eight largest individuals were evenly distributed among the four streams and the remaining individuals were randomly distributed. Fish total length ranged from 168 to 249 mm and average fish length in each stream was 185, 190, 190 and, 196 mm.

2.3 | Temperature trials

There were three, eight-day temperature trials. Each trial started with two days at 14°C after which ambient water temperature was increased by 3°C every two days. Thus, each trial consisted of two days each at 14, 17, 20 and 23°C. Stream temperatures were always increased overnight after the second day of a treatment temperature, with approximately 1°C of warming h⁻¹. As described above, 14°C spring water was delivered to the thermal refuge throughout the duration of the trials. Previous laboratory studies suggest that prolonged exposure to temperatures above 20°C is stressful for brook trout (Chadwick *et al.*, 2015) and often induces significant mortality. However, all fish survived the duration of the study.

During temperature trials, individual agonistic interactions were documented by filming three underwater videos (GoPro HERO; www.gopro.com) in the thermal refuge of each stream. Videos were, 20 min and were recorded at approximately 08:00, 12:00 and 16:00 h every day. To minimise temporal autocorrelation and potential time-of-day effects, one randomly selected video was analysed per stream, per day. For each video, the colour-coded external Floy tags were used to score the total number of times each fish initiated an agonistic interaction. Agonistic interactions included the behaviours of nipping,

biting, chasing and lateral displays (Hartman, 1963; Keenleyside & Yamamoto, 1962).

2.4 | Data analysis

Data were analysed using Bayesian hierarchical models. Accordingly, results do not rely on frequentist *P*-values. Instead, 90% Bayesian credible intervals for the mean of the posterior distribution and the posterior probability that the parameter estimates were in the direction (positive or negative) of the hypothesis are reported (for the hypothesised effect directions see Table 1). The scale reduction factor (\hat{R}) for each parameter, trace plots and plots of posterior distributions were examined to assess convergence for all three models. All statistical analyses were completed in JAGS (www.mcmc-jags.sourceforge.net) in the jagsUI package (Kellner, 2015) using R statistical 3.5.0 (www.r-project.org). Unless otherwise noted, predictor variables in all models were scaled by subtracting by the mean and dividing by the standard deviation.

2.4.1 | Individual personality

Individual exploratory behaviour was quantified by fitting a Bayesian hierarchical regression where the response variable y_i was total distance moved (cm) by fish j during each of the four open field tests. Intercepts ι_j and slopes ζ_j were allowed to vary by individual fish, thus giving:

$$y_i \sim N(\iota_{j(i)} + \zeta_{j(i)}x_i, \sigma_y^2), \text{ for } i = 1 \dots n$$

$$\begin{pmatrix} \iota_j \\ \zeta_j \end{pmatrix} \sim MVN \left[\begin{pmatrix} \mu_\iota \\ \mu_\zeta \end{pmatrix}, \begin{pmatrix} \sigma_\iota^2 & \sigma_{\iota\zeta} \\ \sigma_{\iota\zeta} & \sigma_\zeta^2 \end{pmatrix} \right], \text{ for } j = 1 \dots J$$

As suggested by Dingemanse and Dochtermann (2013), prior to analysis trial number was scaled by subtracting by the mean and dividing by two standard deviations. Thus, the posterior mean of each fish-specific intercept (ι_j) can be interpreted as the measure of each individual's exploratory behaviour and was used as the personality predictor in models for agonistic interactions and resource use described below.

Fish-specific intercepts and slopes were assumed to come from a multivariate normal distribution (MVN), where μ_ι and μ_ζ are the grand mean intercept and slope, respectively. The parameters σ_ι^2 , σ_ζ^2 and $\sigma_{\iota\zeta}$ are the variances among intercepts, slopes and their covariance, respectively. Diffuse normal priors were used for μ_ι , μ_ζ and σ_y and the variance-covariance matrix was modelled using the scaled inverse-Wishart distribution (Gelman & Hill, 2007). Three parallel Markov chains were run, beginning each chain at a different random starting value. Each chain was run for 10,000 iterations, from which the first 5,000 samples were discarded resulting in 15,000 samples used to summarise posterior distributions.

TABLE 1 Summary statistics for Bayesian hierarchical Poisson models. Fish aggression and location were modeled as a function of personality and total length. Intercepts indicate average values and slopes the effect of temperature on fish response. For each response, the posterior mean for the estimate slope, 90% Bayesian credible interval (BCI), and the posterior probability that the effect is in the direction of the estimated posterior mean (Pr(direction of posterior mean)) are reported

Model and response variable	Predicted direction of correlation	Posterior mean of the estimated parameter	90% BCI	Pr(direction of posterior mean)
Fish aggression				
Personality (intercept, $\varphi_{\alpha 1}$)	+	0.22	-0.004, 0.44	0.95
Personality (slope, $\varphi_{\beta 1}$)	±	-0.02	-0.15, 0.11	0.60
Total length (intercept, $\varphi_{\alpha 2}$)	+	0.32	0.09, 0.55	0.99
Total length (slope, $\varphi_{\beta 2}$)	-	-0.10	-0.24, 0.04	0.88
Fish movement				
Personality (intercept, $\tau_{\nu 1}$)	±	-4.12	-16.16, 7.96	0.72
Personality (slope, $\tau_{\psi 1}$)	±	-1.27	-6.04, 3.49	0.67
Total length (intercept, $\tau_{\nu 2}$)	+	43.81	31.48, 55.99	1.00
Total length (slope, $\tau_{\psi 2}$)	-	-16.62	-21.33, -11.86	1.00

2.4.2 | Agonistic behaviour

A Bayesian hierarchical Poisson regression was used to model counts of individual aggressive behaviour. The response variable C_i was the number of aggressive interactions during the i^{th} observation. As before, slopes and intercepts (α_j and β_j , respectively) were allowed to vary by individual fish, giving the model:

$$C_i \sim \text{Pois}(\lambda_i)$$

$$\lambda_i = e^{\alpha_{i(i)} + \beta_{j(i)} \cdot \text{Temperature}_i + \epsilon_i + \gamma_{k(i)} + \delta_{l(i)} + \eta_{m(i)} + \text{offset}(i)}$$

$$\begin{pmatrix} \alpha_j \\ \beta_j \end{pmatrix} \sim \text{MVN} \left[\begin{pmatrix} \mu_\alpha + \phi_{\alpha 1} \text{Personality}_j + \phi_{\alpha 2} \text{Length}_j \\ \mu_\beta + \phi_{\beta 1} \text{Personality}_j + \phi_{\beta 2} \text{Length}_j \end{pmatrix}, \begin{pmatrix} \sigma_\alpha^2 & \sigma_{\alpha\beta} \\ \sigma_{\alpha\beta} & \sigma_\beta^2 \end{pmatrix} \right],$$

for $j = 1 \dots J$

To accommodate overdispersion, an observation-level random effect, ϵ_i , was included and assumed $\epsilon_i \sim N(0, \sigma_\epsilon^2)$. Additionally, all data were pooled across streams and trials and so the model included random effects for stream γ_k ($\gamma_k \sim N[0, \sigma_\gamma^2]$), trial number δ_l ($\delta_l \sim N[0, \sigma_\delta^2]$) and day of the study η_m ($\eta_m \sim N[0, \sigma_\eta^2]$). To account for differences in the amount of time each individual fish was observed during a video, an offset was included in the model, which was equal to the \log_e of the time spent in the thermal refuge during a video.

To understand how fish personality and length influenced agonistic behaviour, fish-specific intercepts and slopes were modelled as a function of fish personality and length, where μ_α , $\phi_{\alpha 1}$ and $\phi_{\alpha 2}$ are the intercept and slopes for the effects of personality and length on average agonistic behaviour and μ_β , $\phi_{\beta 1}$, and $\phi_{\beta 2}$ are the intercept and slopes for the effects of fish personality and length on the temperature-aggression relationship (i.e., change in aggression across temperatures) for each fish, respectively.

Diffuse normal priors were used for intercept and slope parameters and diffuse uniform priors were used for random effect standard deviations. The variance-covariance matrix was modelled using the scaled inverse-Wishart distribution. Three parallel Markov chains were run, beginning each chain at a different random starting value. Each chain was run for 50,000 iterations, from which the first 30,000 samples were discarded and every second sample was retained, resulting in 10,000 samples used to summarise posterior distributions. After analysis, estimates for the random effects were examined for equal variance to confirm that pooling across streams and trials was appropriate.

2.4.3 | Resource use

Recall that individual resource use was measured by subtracting the number of detections at the PIT antenna near the downstream thermal refuge from the number of detections at the PIT antenna in the upstream forage patch (i.e., upstream detections - downstream detections). As such, positive numbers indicate higher occupancy at the forage patch and negative numbers indicate higher occupancy at the thermal refuge. Because the PIT receivers were programmed with a quick read rate, it was not uncommon for slow-moving fish to be detected multiple times during a single pass through the antenna. Therefore, prior to analysis, consecutive detections that occurred within 3 s by the same fish, at the same antenna, were removed. Occasionally a single fish would establish a territory within the read range of the antenna, and so it was possible for consecutive detections to occur over longer time periods. While detections within the same three-second timeframe were still removed, additional consecutive detections were retained for the analysis. As PIT tag detections are interpreted as a measure of resource use, not movement and because it was not possible for more than one trout to establish territory within the read range of the antenna, retaining these data has a negligible effect on the interpretation of the results.

Similar to the aggression model described above, a Bayesian hierarchical Poisson regression was used to model resource use (M_i) as a

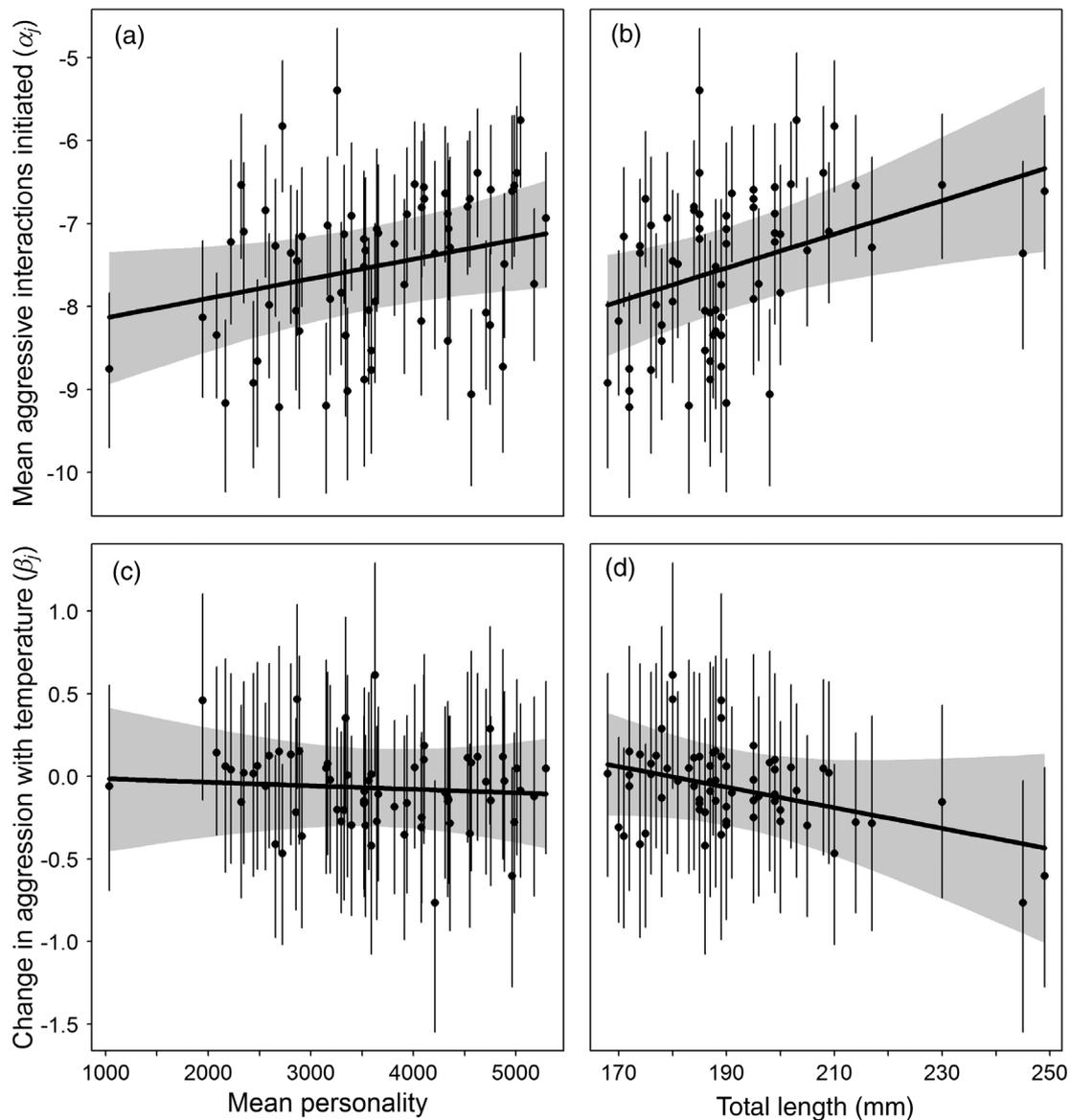


FIGURE 2 Effect of individual personality (a) and length (b) on the number of aggressive interactions a fish initiated at average stream temperatures (α_j) and the effect of fish personality (c) and length (d) on the slope of the aggression-temperature relationship (β_j). Individual-specific slopes for the effect of temperature on aggression capture individual change in aggression across temperatures with, for example, negative numbers indicating declines in aggressive interactions at warmer ambient stream temperatures. Points represent fish-specific estimates for intercepts and slopes and 90% credible intervals are shown as vertical bars. The 90% credible region for the hierarchical Bayesian Poisson regression is shown in grey

function of fish-specific slopes and intercepts (v_j and ψ_j , respectively), which were allowed to vary by individual fish. The final model was:

$$M_i \sim \text{Pois}(\omega_i)$$

$$\omega_i = e^{\rho_{\psi(i)} + \psi_{\psi(i)} \cdot \text{Temperature}_i + \varepsilon_i + \gamma_{k(i)} + \delta_{l(i)} + \eta_{m(i)}}$$

$$\begin{pmatrix} v_j \\ \psi_j \end{pmatrix} \sim \text{MVN} \left[\begin{pmatrix} \rho_v + \tau_{v1} \cdot \text{Personality}_j + \tau_{v2} \cdot \text{Length}_j \\ \rho_\psi + \tau_{\psi1} \cdot \text{Personality}_j + \tau_{\psi2} \cdot \text{Length}_j \end{pmatrix}, \begin{pmatrix} \sigma_v^2 & \sigma_{v\psi} \\ \sigma_{v\psi} & \sigma_\psi^2 \end{pmatrix} \right],$$

for $j = 1 \dots J$

As with the aggression model, fish-specific intercepts were modelled as a function of ρ_v , τ_{v1} , and τ_{v2} , which represent the intercept

and slopes for the effects of fish personality and length on average resource use. Likewise, fish-specific slopes were modelled as a function of ρ_ψ , $\tau_{\psi1}$ and $\tau_{\psi2}$ which represent the intercept and slopes for the effects of fish personality and length, respectively, on the temperature-resource use relationship (i.e., how resource use changed across temperatures) for each fish.

Because of the large number of detections and variability of detections among individual fish, the difference in PIT detections was divided by 10 prior to analysis to improve model convergence. The random effects portion of this model was identical to that of the agonistic interaction model. The only exception was that the resource use model did not include an offset term, as all fish were capable of being detected throughout the day. The model took

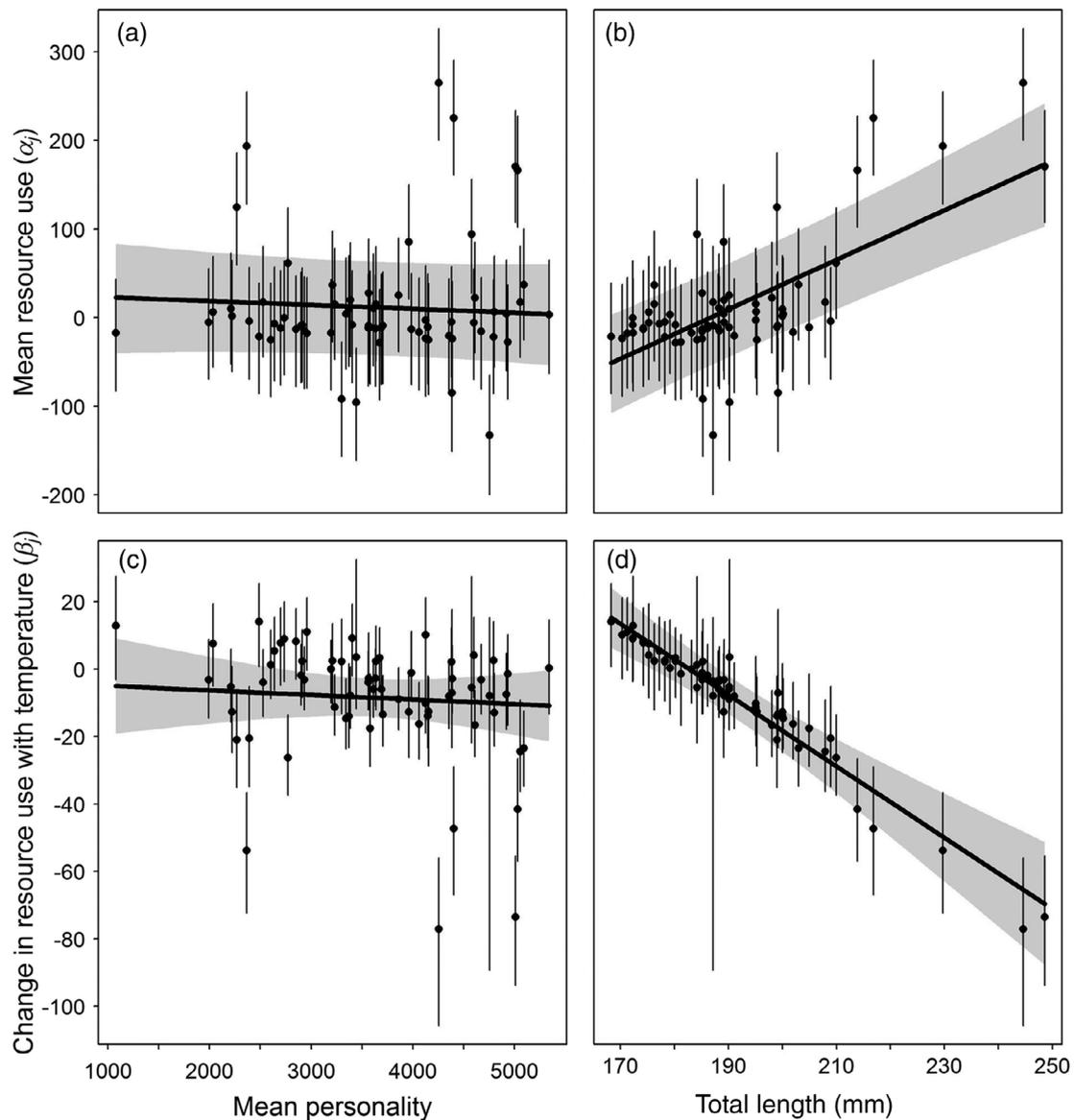


FIGURE 3 Effect of individual personality (a) and length (b) on resource use at average stream temperatures (α_j) and the effect of fish personality (c) and length (d) on the slope of the resource use-temperature relationship. Individual-specific slopes for the effect of temperature on resource use capture individual change in resource use across temperatures with, for example, negative numbers indicating declines in forage patch occupancy at warmer ambient stream temperatures (see Supplementary Information Figure S2 for further description). Points represent fish-specific estimates for intercepts and slopes and 90% credible intervals are shown as vertical bars. The 90% credible region for the hierarchical Bayesian Poisson regression is shown in grey

long MCMC runs to converge so a total of 20 million samples were run, with the first 5 million removed. Of the remaining 15 million, every 40th sample was kept for a total of 375,000 samples retained to summarise the posterior distributions. As before, estimates for stream-level random effects were examined to ensure pooling of data across streams and trials was warranted.

3 | RESULTS

3.1 | Individual personality

Fish-specific intercepts quantifying individual exploratory behaviour (μ_j) ranged from 1035.58 to 5293.79 (SD = 936.09), suggesting

considerable among-individual variation in personality. There was no correlation between individual personality and fish length ($R^2 = 0.24$).

3.2 | Agonistic behaviour

On average, fish with more exploratory personalities initiated more aggressive interactions (Figure 2a), with a 95% probability for a positive relationship between personality and aggression ($\phi_{\alpha 1} = 0.22$, 90% CI 0.00, 0.44). Average aggression also increased with fish length (Figure 2b), with a 99% probability that larger fish initiated more aggressive interactions ($\phi_{\alpha 2} = 0.32$, 90% CI 0.09, 0.55).

Overall, across all individuals, there was a 70% probability that aggression declined with increased ambient stream temperature ($\beta_j = -0.06$, 90% CI $-0.29, 0.18$). Individual personality was not correlated with change in aggressive behaviour in response to temperature ($\phi_{\beta 1} = -0.02$, 90% CI $-0.15, 0.11$; Figure 2c), but there was an 88% probability that larger fish had decreased aggression at warmer temperatures ($\phi_{\beta 2} = -0.10$, 90% CI $-0.24, 0.04$; Figure 2d).

3.3 | Resource use

At average stream temperatures, individual resource use was not influenced by fish personality ($\tau_{v1} = -4.12$, 90% CI $-16.16, 7.96$; Figure 3a). However, there was an over 99% probability that larger fish were more likely to occupy territories near the feeder ($\tau_{v2} = 43.81$, 90% CI $31.48, 55.99$; Figure 3b).

Across all fish, there was a more than 99% probability that forage patch use declined with increasing ambient stream temperature ($\psi_j = -8.55$, 90% CI $-14.18, -2.90$). For example, when ambient stream temperatures were 14°C, each stream had, on average, 250 more detections at the upstream antenna. When ambient stream temperatures were 23°C, there were five fewer detections at the upstream antenna representing a 102% decrease in PIT tag detections near the forage habitat patch during periods of thermal stress (Supporting Information Figures S1).

While forage patch occupancy generally declined with increased temperature, there was considerable individual variation in the effect of temperature on forage patch occupancy. Some individuals were either unaffected by temperature or increased the amount of time spent in the forage patch at higher stream temperatures, while others spent considerably more time in the thermal refuge (Supporting Information Figure S2). Fish personality was not correlated with change in resource use with stream temperature ($\tau_{\psi 1} = -1.27$, 90% CI $-6.04, 3.49$; Figure 3c), but there was an over 99% probability that fish size negatively influenced forage patch use with increasingly stream temperatures ($\tau_{\psi 2} = -16.62$, 90% CI $-21.33, -11.86$; Figure 3d). Posterior means and directional posterior probabilities for the aggression and resource models are found in Table 1.

4 | DISCUSSION

Loss of thermal habitat is one of the most significant threats to stream fish communities and could lead to widespread extirpation of cold water fish populations (Isaak & Rieman, 2013). However, estimates of stream isotherm shift rates used to predict future species distributions often do not account for the potential for thermal refugia to enable population persistence (Snyder *et al.*, 2015). Even then, it is usually assumed that the presence of refugia will enable survival when understanding the dynamics controlling resource use (competition, refuge location, size, *etc.*) is necessary before accurate predictions about the population-level benefits of refugia can be made.

This study provides some insights into fine-scale variation in individual behaviour and resource use in a thermally variable stream

channel. Results suggest that fish size can be used to predict variation in behaviour and resource use among individuals during periods of stream temperature rise, with larger individuals experiencing more significant declines in aggression and forage patch occupancy at warmer temperatures. Conversely, smaller individuals demonstrated little change in behaviour with increased temperature and some even increased occupancy of a thermally stressful forage patch when temperatures were at critical maxima. While the effect of length on aggression and resource use was influenced by only a few large individuals, it is important to note that their behaviour was repeatable across trials (as indicated by the small 90% credible intervals). Additionally, the largest fish were evenly distributed among the four streams and so their responses to temperature were independent. The size distribution of fish in each experimental stream (*i.e.*, right-skewed by only one or two large individuals) is also similar to what would be expected in natural brook trout populations. Accordingly, it is reasonable to assume that the observed trends are indicative of the behaviour of wild trout populations. Taken together, these results help elucidate significant uncertainties from field-based observations of individual thermal refuge use and provide an improved understanding of the potential conservation benefits of thermal refugia for coldwater fish populations.

Although few have studied personality-specific response to thermal stress, exploratory personality is often correlated with increased aggression and low glucocorticoid stress response (Baker *et al.*, 2018; Réale *et al.*, 2007). As such, it was initially hypothesised that increased aggression by exploratory fish would result in occupancy of preferred resource patches, and that exploratory fish would be less sensitive to changes in stream temperature (Briffa *et al.*, 2015). As predicted, fish with more exploratory personality types did, on average, initiate more aggressive interactions. However, increased aggression did not translate into access to preferred habitat patches, as there was no relationship between personality and average resource use. Even at low ambient temperatures, fish with more exploratory personalities did not spend more time in the forage patch and personality did not influence changes in resource use or aggression during the eight-day temperature trials. Unlike studies of rainbowfish *Melanotaenia duboulayi* (Castelnau 1878) (Colléter & Brown, 2011), results suggest fish size is likely more important than exploratory personality in determining the outcome of competitive interactions in brook trout, as larger, less exploratory fish, outcompeted more exploratory individuals for access to preferred habitat patches.

Compared with personality, fish size was a more important predictor for how brook trout altered their behaviour in response to rising ambient water temperatures. While temperature had little effect on resource use of smaller individuals, larger fish responded to increased ambient temperatures by spending considerably more time in the thermal refuge (Supporting Information Figure S2). Others have noted that refuge occupancy is associated with active territory defence by larger individuals (Biro, 1998), but the present study found overall decreased aggression inside the refuge. This was surprising, as the density of fish in the refuge far exceeded that which would be expected in wild brook trout streams (Wagner *et al.*, 2014) and was

higher than other laboratory studies of aggression in brook trout (Hitt *et al.*, 2017). Reduced aggression may explain why refugia are often occupied by high densities of fish (Ebersole *et al.*, 2001) and would suggest that small areas of thermal refugia can have large influences on fish abundance and population dynamics.

The negative effect of fish size on forage patch use and aggression across temperatures suggests that larger fish may experience higher levels of physiological stress at warmer temperatures. Body size is positively correlated with metabolic demand (Woodward *et al.*, 2010), and metabolic demand generally increases with temperature (Norin & Clark, 2016). Therefore, it is plausible that the behavioural changes observed here are the product of a heightened cellular stress response in larger fish. In contrast, smaller fish often responded to rising temperatures by spending more time outside of the thermal refuge and in the forage patch (as evidence by individuals with slopes greater than zero in Figure 3d). This reaction could be indicative of a muted stress response, wherein the slower metabolisms of smaller fish buffered them against cellular stress during periods of increased temperature. Another, possibly concordant, hypothesis is that the displacement of larger fish to the thermal refuge resulted in competitive release of the forage patch, which allowed smaller fish more opportunity to forage. Regardless of the mechanism, smaller fish demonstrated more choice in resource selection, which probably resulted in increased energetic intake. In a natural setting, ability to move more freely among habitat patches could increase survival of smaller individuals following a period of thermal stress. Ultimately, reduced energetic intake and increased stress response of larger individuals could lead to a reduction in average body size in brook trout populations, which could have long-term effects on population vital rates (Daufresne *et al.*, 2009; Sheridan & Bickford, 2011).

Across all fish there was a decline in forage patch occupancy with increasing stream temperature (Figure 3b). However, all fish still spent significant amounts of time outside of the thermal refuge, even when ambient temperatures were 23°C (Supporting Information Figure S2). Studies have shown that brook trout exposed to temperatures exceeding 20°C for several hours show increased cellular stress, decreased movement, and increased mortality (Chadwick *et al.*, 2015). While individual-based models have found that fish prioritise movement and resource selection decisions that will maximise energy reserves for reproduction (Railsback & Harvey, 2002), temperature trials were not long enough for fish to lose considerable body mass and prioritise food intake over exposure to thermal stress. Additionally, behavioural observations inside the thermal refuge suggest fish were not being competitively excluded from the thermal refuge. This observation is concordant with others (*e.g.*, Ebersole *et al.* 2001), and indicates that individuals choose to only intermittently occupy a thermal refuge while continuously searching for additional resources in the environment. Interestingly, it was common for fish to make extended forays lasting up to several hours before returning to the thermal refuge. This could be because fish were using warmer temperatures to metabolise food after feeding (Armstrong *et al.*, 2013). Alternatively, it could support hypotheses that temporary occupancy of refugia is enough to significantly reduce cellular stress, which allows fish to

spend prolonged periods of time in what would otherwise be lethal conditions.

Results from this study help elucidate the potential influence that thermal refugia can have on coldwater fish populations. For streams that experience periodic warming, the size of a thermal refuge will probably affect reach carrying capacity (Ebersole *et al.*, 2001). However, decreased aggression and high individual turnover inside the refuge suggest that refugia can probably support higher densities of fish than habitat patches of equal size. Conversely, high emigration outside of the refuge indicates that the location of refugia within the larger habitat mosaic is likely important for determining the population-level effect of refugia. Refugia in highly fragmented landscapes may do little to increase population survival, as fish will need to spend extended periods of time moving among habitat patches to access resources. Continued stream temperature rise will likely exacerbate the negative effects of fragmentation, as streams will reach warmer maximum temperatures and exceed critical thermal maxima for longer consecutive periods of time (Fullerton *et al.*, 2018).

Future research would benefit from more explicit study of whether periodic occupancy of thermal refugia is sufficient to reduce cellular stress to baseline levels. If so, fish may be able to survive extended periods of thermal stress, provided that habitat connectivity is sufficient enough to allow for frequent access to a refuge. Alternatively, if baseline physiological conditions are not reached in the refuge, then each foray into thermally stressful temperatures may have an additive effect resulting in local extirpation. Ultimately, the present study, along with future field and laboratory investigations of individual-level use of thermal refugia, can be used for improving long-term predictions of species distributions with future climate-induced stream temperature rise.

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CONTRIBUTIONS

S.W., N.H. and T.W. developed the research idea and designed the experiment; S.W., B.K and N.H. collected data; S.W., B.K. and T.W. analysed the data; S.W. wrote the manuscript with significant contributions from B.K. N.H. and T.W.

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SUPPORTING INFORMATION

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

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