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ARTICLE

Quantifying the Foodscape for Stream-Dwelling Cutthroat Trout Reveals Spatial and Temporal Ranges of Resource Exploitation and Energy Intake

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Abstract

Food availability is a primary factor limiting the abundance of wild populations, but quantifying it requires an understanding of when and where prey are vulnerable to predators. Salmonid fishes in streams are commonly thought to forage on drifting aquatic invertebrates during daylight hours. However, past studies also report benthic and nocturnal foraging despite the predominant view of salmonids as diurnal drift-feeding predators. We used instream videography to assess foraging mode and energy intake for stream-dwelling Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri*. We recorded the foraging behavior of wild fish with a waterproof video camera and estimated energy intake based on fish size, foraging rate, retention rate, and caloric values of prey. Fish captured prey primarily from the water column and surface, targeting drifting invertebrates during daytime hours; however, they also foraged from the stream benthos and during nighttime. Yellowstone Cutthroat Trout foraging rate was most strongly related to foraging location in the stream, diel period, and month. Energy intake was highest from daytime drift-foraging behavior and exceeded a modeled metabolic limit of food intake during October and November. Nocturnal and benthic foraging contributed the smallest proportion of total foraging attempts but was observed over all months of our study and sometimes comprised up to 30% of estimated energy intake. Our results indicate that Yellowstone Cutthroat Trout in streams acquire most of the food intake as daytime drift-feeding predators.

In wild populations, food availability is a primary factor limiting the growth, survival, and reproduction of individuals (Boutin 1990; Newton 1998; Sibly and Hone 2002). As animal abundance is intrinsically related to food availability, density-dependent competition for food and space is a common factor regulating animal populations (Fowler 1981; Grant 1990; Anholt and Werner 1995; Ward et al. 2006). In some instances, populations have declined under food stress and may reach sufficiently small numbers to increase the risk of extinction (Becker and Beissinger 2006; Rosen 2009). While measuring prey availability is critical in evaluating the extent to which prey can limit the abundance of predator populations, quantifying food availability in natural ecosystems requires an understanding of a predator's ability to exploit prey (Johnson and Sherry 2001; Searle et al. 2007; Prevedello et al. 2013).

Prey may avoid predation by using temporal and spatial asynchrony with predator activity or by defense mechanisms against predators (Abrams 1984). In response, predators can optimize their energy intake by altering foraging behavior to increase prey consumption during different times of the day or season or by moving to areas with greater prey abundance (Sih 1982; Dill 1983; Kramer 2001; Sims et al. 2006). Adaptive flexibility of foraging strategies can compensate for habitat heterogeneity and the corresponding access to prey over different temporal, regional, and seasonal scales (Dill 1983; Baird et al. 1992). Although the frequency of different prey taxa in the diet of a predator can be used to quantify their relative importance as food, measuring the abundance of prey can be misleading if prey are only accessible to predators during particular times or locations. Behavioral assays of foraging animals can be used to refine when, where, and how

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frequently different prey sources are encountered and consumed. By quantifying the availability of food sources in a foraging animal's environment and the factors that restrict an animal's ability to exploit prey, the "foodscape" can be defined as the range of edible prey types and locations available to foraging animals from the broader landscape it occupies (Searle et al. 2007). Given the relationship between food availability and growth, survival, and reproduction, it is critical to understand how effective predators are at exploiting different sources of prey in their foraging environment and how prey availability can influence an organism's energy budget.

In stream ecosystems, invertebrates are a principal source of prey for many fishes (Keeley and Grant 2001; Quinn 2018). Aquatic and semiaquatic invertebrates typically have all or part of their life cycle associated with the stream substrate as benthos (Merritt et al. 1996) but can also enter the stream current as invertebrate drift. Invertebrate drift is the flux of aquatic and terrestrial invertebrates carried by water currents through behavioral movements during dispersal or by accidental entry into the water column (Waters 1972; Allen and Castillo 2007). While numerous studies on the diet of stream fishes document the importance of invertebrates as prey, their source as benthic versus drifting prey is often unknown because of the difficulty in assessing the relative importance of where prey are consumed (Ringler and Brodowski 1983; Johansen et al. 2010; Anderson et al. 2016). Given that invertebrate abundance from benthic and drifting sources can differ dramatically (Waters 1961, 1972), assessing the availability of food for stream fishes can depend on the degree to which different species of fish rely on benthic and drifting invertebrates.

Salmonid fishes are commonly thought of as drift-feeding predators in stream ecosystems. They often maintain foraging stations in streams by swimming against the current and scanning the water column to target and capture invertebrates drifting past (Kalleberg 1958; Keenleyside 1962; Bachman 1984; Grant et al. 1989; Hughes and Dill 1990). While many species of salmonids have terminally oriented mouths, perhaps making benthic foraging difficult, behavioral observations indicate a shift towards benthic foraging under experimentally reduced levels of drift abundance (Fausch et al. 1997). In addition, salmonids are typically viewed as diurnal foragers, feeding during daylight hours when drift can be observed and targeted in the water column (Kreivi et al. 1999; Neuswanger et al. 2014; Di Prinzio et al. 2015) and because they have a reduced detection and capture success of invertebrates in darkness (Fraser and Metcalfe 1997; Rader 1997; Miyasaka and Nakano 1999; Elliott 2011). Although food availability has long been thought to be one of the main limits of salmonid abundance in streams (Chapman 1966; Grant and Kramer 1990; Allen and Castillo 2007; Railsback and Harvey 2011), and departures from diurnal drift-foraging behavior are acknowledged in the literature, the extent and importance to which benthic and nocturnal foraging contribute to food intake are largely unknown (Harvey and Railsback 2014).

The Cutthroat Trout *Oncorhynchus clarkii* is a salmonid fish species native to western North America. Like other stream salmonids, Cutthroat Trout in streams appear to feed primarily on invertebrates (Nakano et al. 1992; Leeseberg and Keeley 2014), but the degree to which invertebrates are captured from the drift versus benthos during day and night has yet to be examined. In this study, we quantified the foraging behavior of free-ranging Yellowstone Cutthroat Trout *Oncorhynchus clarkii bouvieri*, a subspecies of Cutthroat Trout with populations native to the upper Snake River and Yellowstone River, draining portions of Idaho, Nevada, Utah, Wyoming, and Montana (Behnke 2002). In doing so, we estimate temporal and spatial variation in foraging behavior to determine if Cutthroat Trout are primarily predators of drifting invertebrates during daylight hours or whether food intake occurs from other locations in the stream and at night. We examined seasonal variation in foraging behavior throughout the summer–fall growing season and assessed the degree to which foraging occurs from the benthos, water column, and surface during day and night. We also measured foraging distance and ingestion rate to understand the effectiveness of foraging behavior under day and night conditions. Finally, we used measures of foraging rate to estimate energy intake for different foraging modes and compared them to a maximum daily ration to quantify the relative importance of different foraging strategies.

METHODS

We quantified the foraging behavior of Cutthroat Trout in three first-order tributary streams to the Portneuf River in southeastern Idaho (Supplemental Figure 1 provided in the online version of this article). Inman Creek, Harkness Creek, and Goodenough Creek contain populations of Yellowstone Cutthroat Trout as the only species of fish present. This ecosystem of midelevation streams (1,670–2,000 m) is a mix of sagebrush steppe and montane flora and fauna (Sleeter et al. 2012). Streams follow typical high-elevation seasonal patterns of runoff-fed streams in this semiarid region (Minshall and Andrews 1973). Mean monthly air temperatures range from –8.9°C to 31°C, with a mean annual precipitation of 308.1 mm (National Oceanic and Atmospheric Administration 2019).

Behavioral observations.— To quantify the diel foraging behavior of Yellowstone Cutthroat Trout, we used a waterproof digital video camera to record video segments at systematic intervals over a 24-h period. In order to record focal animal observations, we placed the camera in

a haphazard selection of locations where fish had been observed to forage. We positioned the camera's field of view to capture the cross-sectional area of a stream pool. In the three study streams, the maximum pool volume was about 2.6 m^3 and a typical stream width was 0.5–1.5 m. The video camera system consisted of a single GoPro Hero 3+ camera (GoPro, San Mateo, California) and water-tight housing bolted to a 5-mm-thick steel plate (40 by 40 cm) used to anchor the camera in the stream current. To power the camera over a 24-h period, we replaced the standard camera battery with a battery eliminator wired to pass through the camera's housing with a watertight seal and connected it to a 10,000 mAh external battery pack placed outside the stream, 3–5 m away (Voltaic Systems, Brooklyn, New York). The camera was triggered to record a 10-min video segment every hour over a 24-h period using a Raspberry Pi microcomputer (Raspberry Pi Foundation, Cambridge, UK), which was connected to the camera's wireless signal with a coaxial cable that also passed through the camera housing and brought the signal from underwater and into proximity to the computer's wireless antenna. Video segments were triggered on the camera using a Python computer program (Python Software Foundation, Delaware) that issued wireless commands to turn the camera on and off and record video at desired intervals. Video files could then be collected from the field after a single 24-h period by removing the camera's storage card. Additional cards and batteries could be exchanged to deploy a camera on consecutive days. A cell phone served as an external monitor during camera placement using the GoPro capture application.

We replaced the video camera's factory-installed lens with a lens sensitive to infrared light to enable the camera to record at night. To make nighttime observations, we used eight LED infrared lights (12 W, wavelength = 850 nm) powered by a 12 V battery and controlled with a programmable switch. Salmonid fishes, as well as invertebrates, are unable to see the infrared spectrum, making this method a suitable study tool to sample behavior during nighttime and low-light conditions (Heise 1992; Dirnwoeber et al. 2012). We attached a HOBO Pendant Temperature/Light 8 K data logger (Onset, Cape Cod, Massachusetts) on the camera mount to record light and water temperature in the foraging area. We defined night as light levels <4.5 lx (lm/m^2). Video sampling occurred from the beginning of August through November in 2017 and 2018.

Behavioral analyses.— In the laboratory, we reviewed video segments on a computer monitor to quantify the foraging behavior of focal fish. For focal animal observations, a foraging attempt was defined as a sudden movement of the fish towards an object in their field of view, ending with the fish opening and closing its mouth to engulf a prey item. Foraging attempts were included in the total number observed per unit time, even if the prey item was rejected by fish and ejected from the mouth. Foraging attempts were classified within the stream according to foraging location as either benthic, water column, or water surface. When video included multiple fish, we distinguished individuals by their length, spotting pattern, and position in the group (Bachman 1984). Fish size was estimated using a reference video segment collected initially after camera placement by moving a meter stick through the camera's field of view and used to convert distances on the screen into distances in centimeters.

For behavioral comparisons, each 24-h observation period at a single stream location was divided into day and night periods where 10-min video segments were collected once per hour. We counted foraging attempts of focal individuals and the location of each attempt as benthic, water column, or surface. We then used the counts to calculate overall foraging rate per minute and for benthic, water column, and surface feeding. The foraging rate for each 10-min video segment was then averaged to a single value for a given 24-h observation period or subdivided into two observations, one for daytime and one for nighttime. As multiple fish were sometimes observed within each 10-min video collected, we averaged foraging behavior across all fish observed in each segment and used the average measure to ensure that we did not inflate the number of independent observations. For comparisons of foraging rate by fish size, most video segments contained only one fish; however, in some segments we estimated multiple fish if more were present on screen. A single sampling site was sometimes revisited within the 4-month period, but these visits were treated as statistically independent observations when they did not occur within the same month. A total of three to four pools were recorded from each stream within a month. Behavioral observations were only included in data analyses if fish were present for greater than 60 s.

To estimate foraging distance and the rate of prey rejection according to diel period, we measured the distance traveled by fish when targeting potential prey items and the number of items that were rejected following prey capture attempts. Measures of foraging distance and rejection rate were collected from a subsample of video that had satisfactory camera placement to measure distance and record whether a fish retained a prey item or rejected it. Foraging distance was estimated in body lengths (±0.5 body lengths) to standardize measurements from fish of different body sizes. We measured foraging distance as the initial position of the fish's snout while scanning for prey to the location in the stream where the prey item was captured or attempted to be captured (Grant et al. 1989; Grant 1990). The rejection rate of prey items was

quantified by noting whether the fish rejected the item after initially capturing it.

Invertebrate sampling.— We estimated food availability in each stream by sampling invertebrates from the stream current and the stream substrate. Invertebrate sampling occurred in habitats directly downstream of areas used for videography. We estimated drifting aquatic invertebrate abundance by anchoring a drift net in the center of the stream for 30 min. The drift net was constructed from a rectangular metal collar (25×25 cm) and attached to an elongated net 75 cm in length with a mesh size of 300 μm. Daytime invertebrate drift samples were collected within a period ranging from 2 h after sunrise until 2 h before sunset. Nighttime samples were collected beginning 0.5 h after sunset, initiated during astronomical twilight. At this time, the horizon line is visible but details in the environment are not distinguishable by the observer. Sampling ended in the period of true night. The two sampling periods were selected to capture differences between day and night invertebrate availability. While daytime drift samples were collected during the day following an observation period, a single nighttime sample was collected for each week of observations from a given stream. Benthic invertebrate samples were collected using a 0.072-m^2 Hess sampler placed onto the substrate, fitted with a 200-μm mesh net following the methods described by Delong and Brusven (1998). Drifting invertebrate abundance was calculated as the number per meter cubed of water sampled, and benthic invertebrate abundance was calculated as the number per meter squared of stream substrate (Smock 1996). Following collection from the stream, all invertebrate samples were concentrated into plastic bags, preserved with 5% formalin, and returned to the laboratory for counting and identification. In the lab, each invertebrate was identified to family or order level of taxonomy and measured for maximum length and width (±0.1 mm) using a dissecting microscope and digitizing system.

Statistical analyses.— To test for differences between the main effects of diel period (day versus night) on foraging rate, we used a *t*-test to compare mean daytime and nighttime foraging rate averaged across sampling sites. To investigate combined factors of diel period as well as seasonal changes in foraging rate (July to November), we used a two-factor analysis of variance (ANOVA) to test for differences in foraging rate. Total or overall foraging rate was estimated per minute based on all foraging attempts observed for each focal animal observed. In addition, we also estimated location-specific foraging rates as the number of attempts per minute that were directed to the benthos, water column, or surface. As foraging can occur from any of the three locations during the same observation period, we treated each foraging rate in separate analyses to avoid the issue of pseudofactorialism, which occurs when a single response variable (such as foraging rate) is subdivided into multiple categories, artificially inflating the degrees of freedom available (Hurlbert 2013). When we tested for differences between foraging rates by location, we calculated percent difference between location-specific foraging rates to create a single response variable. We used Bonferroni-corrected *P*-values to control for multiple pairwise comparisons, with alpha = 0.05/3 or $P = 0.017$ as a critical level of significance. We used measures of foraging rate based on individuals observed at sampling locations over 24-h sampling periods. We separated sampling observations over the three different study streams such that no sampling location on a single stream was observed on consecutive days and no stream was observed for more than three consecutive days before a different stream was visited. In doing so, we assume that the behavior of focal animal observations made at individual pools was independent of other pools in the set of observations.

To compare the relative importance of foraging effort from different areas of the stream, we estimated energy intake (J/min) based on foraging rate from stream surface, water column, and benthos. Energy intake levels were estimated using location and time-specific foraging rates multiplied by the average energy content of prey items encountered from the stream and estimated prey rejection rates observed, where estimated energy intake = foraging rate (number/min) × prey energy content (J) × (1 – rejection rate). Prey energy content was based on invertebrate length collected from samples and was calculated using the following equation (Cummins and Wuycheck 1971; Smock 1980):

$$\text{Prey energy content(J/prey)} = 0.3818(\text{mean length of prey in mm})^{2.46}$$

We also compared estimated energy intake to maximum intake rates based on Elliott's (1976) model of maximum ration (Cmax) for Brown Trout *Salmo trutta*. Because ration size is strongly dependent on fish size, we used a commonly observed fish length from our study streams of 10 cm, converted to mass based on a length–mass regression equation for Cutthroat Trout (Jenkins and Keeley 2010). Fish mass was then used to calculate the maximum daily ration for a Cmax from Elliott's (1976) model using the following equations:

$$\text{if temperature} < 6.6^{\circ}\text{C, Cmax} = \left[2.902(\text{fish mass in grams})^{0.762}\right] \times \left[e^{0.418(\text{temperature in }^{\circ}\text{C})}\right],$$

$$\text{or if temperature} > 6.6°C, \text{Cmax} = \left[15.018(\text{fish mass in grams})^{0.759}\right] \times \left[e^{0.171(\text{temperature in } °C)}\right].$$

Daily Cmax was then converted to an intake rate by dividing the ration by the number of minutes in a 24-h period.

RESULTS

Foraging Environment

Prey available to Yellowstone Cutthroat Trout varied between day and night and from August through November. Based on a total of 43 drifting invertebrate samples from the day and 27 samples from the night, invertebrate abundance declined from August to November for both diel periods (Figure 1A; ANOVA: $F_{3,68} = 5.23$, $P = 0.0019$). However, there was no significant diel difference in drifting invertebrate concentrations when integrated over the 4-month period (Figure 1A: ANOVA: $F_{1,68} = 0.55$, $P = 0.46$). Drifting invertebrate abundance was higher during August at nighttime and daytime but decreased at night over daytime samples by November, producing a significant month × diel period interaction (Figure 1A; ANOVA: $F_{3,68} = 3.49$, $P = 0.018$). Based on 43 daytime samples and 31 nighttime samples, benthic invertebrate abundance also declined from August to November for both diel periods (Figure 1B; ANOVA: $F_{3,71} = 4.34$, $P = 0.0060$). Benthic invertebrate abundance tended to be higher at night than during the day in August and September and lower at night in October and November, producing no significant difference between diel periods (Figure 1B; ANOVA: $F_{1,71} = 0.76$, $P = 0.38$) and no significant interaction between month and diel period (Figure 1B; ANOVA: $F_{3,71} = 1.49$, $P = 0.22$). Drift abundance was positively correlated to benthic invertebrate abundance ($\log_{10}$ drift abundance versus $\log_{10}$ benthic abundance; $r = 0.28$, $P < 0.0001$).

Temperature and light levels in foraging areas varied between diel periods and seasonally. Over the 4-month study period, daytime temperatures (mean ± SD) averaged 11.2 ± 2.5°C compared with 8.4 ± 1.7°C at night (Supplemental Figure 2). Temperature declined over the 4 months, dropping from 14.8°C (range = 12.5–15.1°C) during the day and 13.2°C (range = 11.7–14.6°C) at night in August to 5.2°C during the day (range = 3.9–6.1°C) and 2.6°C at night (range = 2.2–4.8 °C) in November (Supplemental Figure 2). In August, 53% of each 24-h interval occurred during the day, whereas by November, only 42% of the hours were daytime. Outside of seasonal declines in the number of daylight hours, further decreases occurred in the intensity of light levels. Daylight intensity (lux) decreased by half from August to November (Supplemental Figure 3).

A total of 76 24-h intervals of video were collected from 31 different pool sites over the three study streams, producing about 233 h of video and totaling 721 daytime and 673 nighttime 10-min video segments. At least one fish was observed in half of the video segments (713 or 51.5%), but some had up to five fish in the field of view. Of the video segments with fish present, 77.3% had one fish and 15.1% had two fish. Fish were captured in the camera's field of view for an average of 7.1 ± 1.7 min (mean ± SD) in each 10-min segment. A total of 713 focal animal observations were scored and analyzed in the study. The smallest size-class of fish observed were young-of-the-year Yellowstone Cutthroat Trout (3–5 cm), occurring in 72 video segments or 10% of observations. The most common sizes of fish observed measured 5–10 cm in fork length, which occurred in 314 videos or 43.9% of observations.

Foraging Behavior

We observed Yellowstone Cutthroat Trout occupying foraging positions during the day and at night, as well as throughout summer and fall seasons. Fish were recorded in video segments in 69.7% of total time during daytime hours and in 67.7% during nighttime hours (Supplemental Figure 4). While Yellowstone Cutthroat Trout were observed to forage during both day and night periods, the foraging rate during the day (0.86 attempts per minute) was 72% higher than during the night (0.24 attempts per minute; Supplemental Figure 5; $t_{103} = 5.38$, $P < 0.0001$). During the day, foraging was located primarily in the water column as drift feeding (Figure 2). A smaller proportion of daytime feeding also occurred as drift foraging from the water surface, and when combined, daytime drift foraging occurred at an average of 0.79 foraging attempts per minute, comprising 69% of the total foraging effort. A much smaller proportion of benthic feeding was observed across study sites during the day (Figure 2). At night, Yellowstone Cutthroat Trout foraged at lower rates that were similar among benthic, water column, and surface locations but tended to be higher in the water column (Figure 2).

For a subset of video segments, we estimated foraging distance and rejection rate of captured items to evaluate diel differences in foraging abilities. During the day, fish were found to move, on average, 0.89 body lengths to intercept prey compared with 0.7 body lengths during nighttime (Figure 3; t-test: $t_{19} = 3.35$, $P = 0.034$). Conversely, fish rejected 21.01% of captured items during daytime and 71.3% at night (Figure 3; $t_{12} = 6.05$, $P < 0.001$).

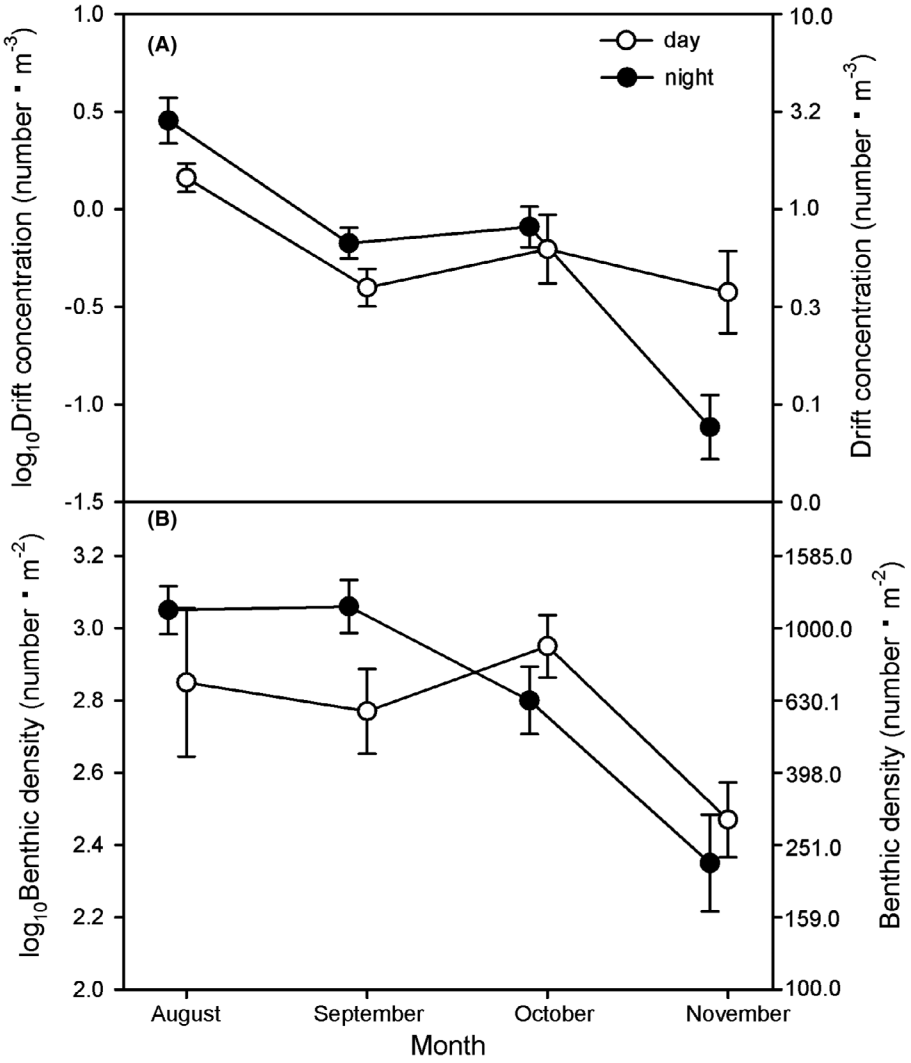

FIGURE 1. Log_{10} mean (error bars show $\pm$ 1 SE) **(A)** drifting invertebrate abundance and **(B)** benthic invertebrate abundance by month. Open circles represent day observations, and solid circles represent night observations. The right-hand vertical axis is provided as a reference for conversion to untransformed values of invertebrate drift.

Over the 4-month observation period, overall foraging rate (benthic + water column + surface attempts) was significantly higher during the day than at night (Figure 4; Supplementary Table 1 [available in the online version of this article]; ANOVA: $F_{1,\ 101} = 25.47$, $P < 0.0001$). We did not detect any significant difference in foraging rate among months (Figure 4; ANOVA: $F_{3,\ 101} = 2.44$, $P = 0.069$), and there was no significant interaction between month and diel period (ANOVA: $F_{3,\ 101} = 0.44$, $P = 0.73$). When we examined foraging rate by location in the stream, foraging rate in the water column was significantly higher during the day than at night (Figure 4; ANOVA: $F_{1,\ 101} = 32.99$, $P < 0.0001$). Although foraging in the water column during the day appeared to decline from August to November, we did not detect a significant effect of month (ANOVA: $F_{3,\ 101} = 1.10$, $P = 0.36$) or a significant interaction between diel period and month (ANOVA: $F_{3,\ 101} = 0.48$, $P = 0.70$). Foraging from the benthos did not differ between diel period (Figure 4; ANOVA: $F_{1,\ 101} = 0.12$, $P = 0.73$), by month (ANOVA: $F_{3,\ 101} = 2.24$, $P = 0.088$), or by interaction between month and diel period (ANOVA: $F_{3,\ 101} = 1.01$, $P = 0.39$). Surface foraging rate did not differ by diel period (Figure 4; ANOVA: $F_{1,\ 101} = 0.01$, $P = 0.92$) but did differ among some of the months compared (ANOVA: $F_{3,\ 101} = 2.97$, $P = 0.035$). Surfacing foraging rate in September was higher than in November (Tukey test: $P = 0.031$). There was no interaction between diel periods and month on surface foraging rate (ANOVA: $F_{3,\ 101} = 0.45$, $P = 0.72$).

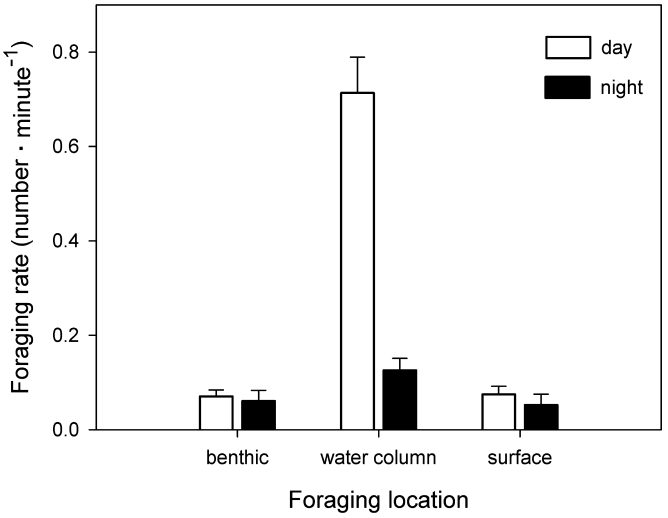

FIGURE 2. Mean (error bars show ± 1 SE) foraging rate of Yellowstone Cutthroat Trout during day (open bars) or night (solid bars) diel periods and according to foraging location in the stream.

Size-Related Effects on Foraging Behavior

Based on overall foraging rate (benthic + water column + surface attempts), fish of different size-classes fed at a lower rate at night than during the day (Figure 5; Supplementary Table 2; ANOVA: $F_{1,\ 146} = 5.02$, $P = 0.027$). Foraging rate did not differ by size-class (ANOVA: $F_{3,\ 146} = 0.64$, $P = 0.59$), and there was no significant interaction between fish size and diel period (ANOVA: $F_{3,\ 146} = 0.51$, $P = 0.68$). Daytime drift feeding from the water column was the principal location of foraging activity across all fish sizes (Figure 5A). Water column foraging rate was significantly higher during the day than at night (Figure 5; ANOVA: $F_{1,\ 146} = 5.65$, $P = 0.0002$). There was no effect of fish size on foraging rate from the water column (ANOVA: $F_{3,\ 146} = 0.58$, $P = 0.63$), and there was no interaction between size-class and diel period (ANOVA: $F_{3,\ 146} = 0.36$, $P = 0.78$). Benthic foraging rate did not differ between day and night (ANOVA: $F_{1,\ 146} = 5.02$, $P = 0.027$). However, there was a difference among different size-classes of fish (ANOVA: $F_{3,\ 146} = 4.34$, $P = 0.0058$), with the smallest or young-of-the-year size-class differing from the 10–15-cm and >15-cm size-classes (Tukey test: $P < 0.05$). No interaction between fish size and month was observed (ANOVA: $F_{3,\ 146} = 0.72$, $P = 0.54$) for benthic foraging rate. Surface foraging rate of fish did not differ between day and night periods (ANOVA: $F_{1,\ 146} = 0.16$, $P = 0.69$), and there was no effect of the size-class factor (ANOVA: $F_{3,\ 146} = 1.52$, $P = 0.21$). However, a significant interaction between size-class and month (ANOVA: $F_{3,\ 146} = 3.54$, $P = 0.016$) revealed that the largest size-class of fish had a higher foraging rate at night than during the day (Tukey test: $P = 0.029$).

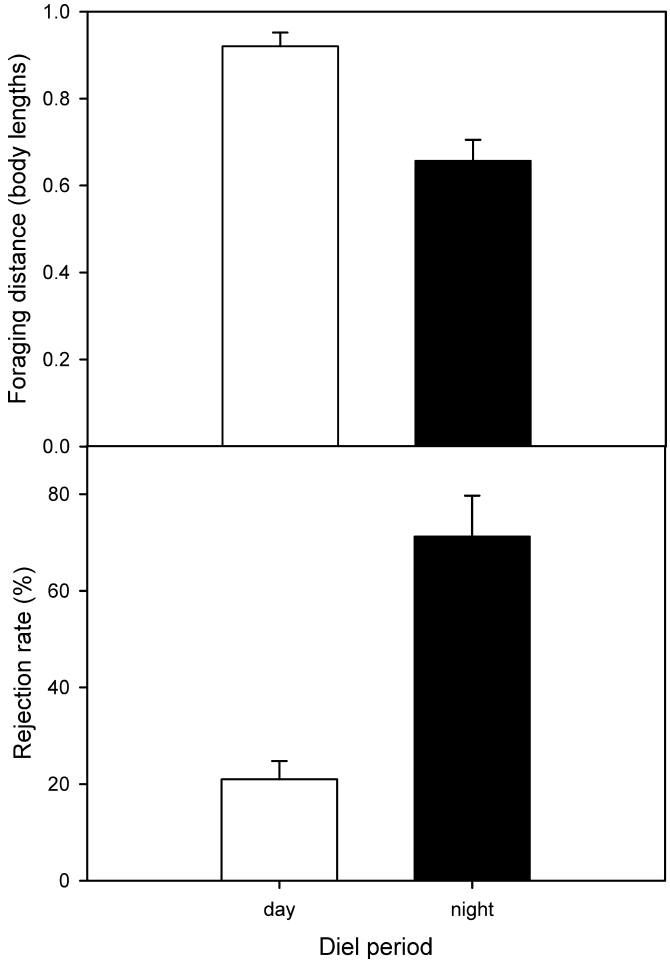

FIGURE 3. Mean (error bars show ± 1 SE) foraging distance of Yellowstone Cutthroat Trout in body lengths (top panel) and mean rejection rate of foraging attempts (bottom panel), measured during the day (open bars) and night (solid bars).

Estimated Measures of Energy Intake

Daytime drift foraging accounted for the largest component of estimated energy intake, over nighttime drift and benthic foraging behaviors. Estimated energy consumption from drift foraging differed between day and night due to differences in foraging rate between the two periods and due to reduced prey retention rates at night (Figure 6). Energy intake declined seasonally from an average of 3.1 J/min during the day and 1.2 J/min at night in August to only 2.1 J/min during the day and 0.24 J/min at night in November.

To understand the implications of energy intake for fish throughout the study period, the maximum daily ration was estimated for a 10-cm fish. Maximum daily energy intake was much higher in August, starting at 13.9 J/min, before dropping over fall months (Figure 6). Estimated energy intake from daytime and nighttime drift and

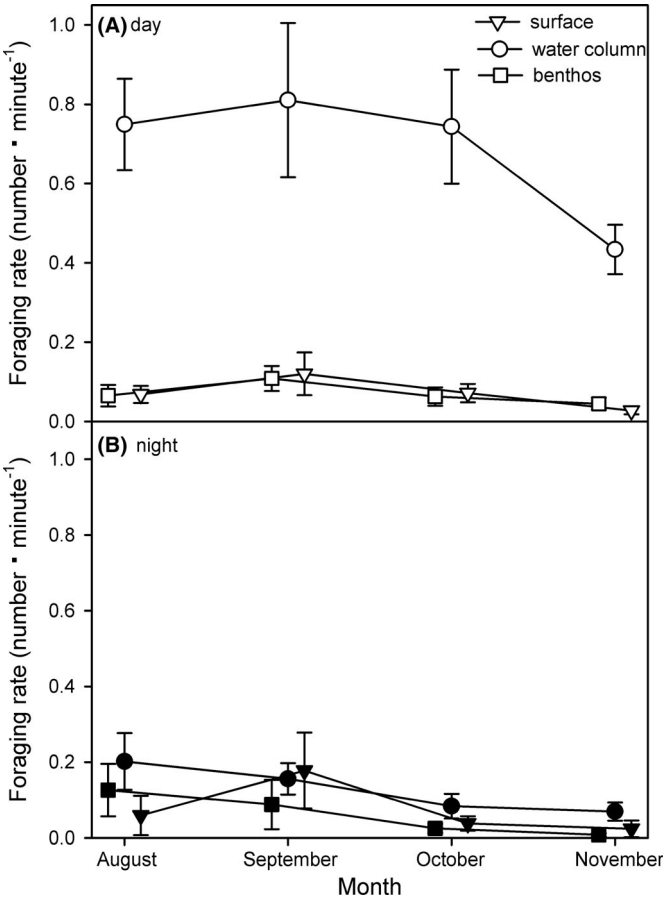

FIGURE 4. Mean (error bars show ± 1 SE) monthly foraging rate of Yellowstone Cutthroat Trout observed during **(A)** diurnal periods or **(B)** nocturnal periods and according to foraging location (square = benthic, circles = water column, triangle = surface).

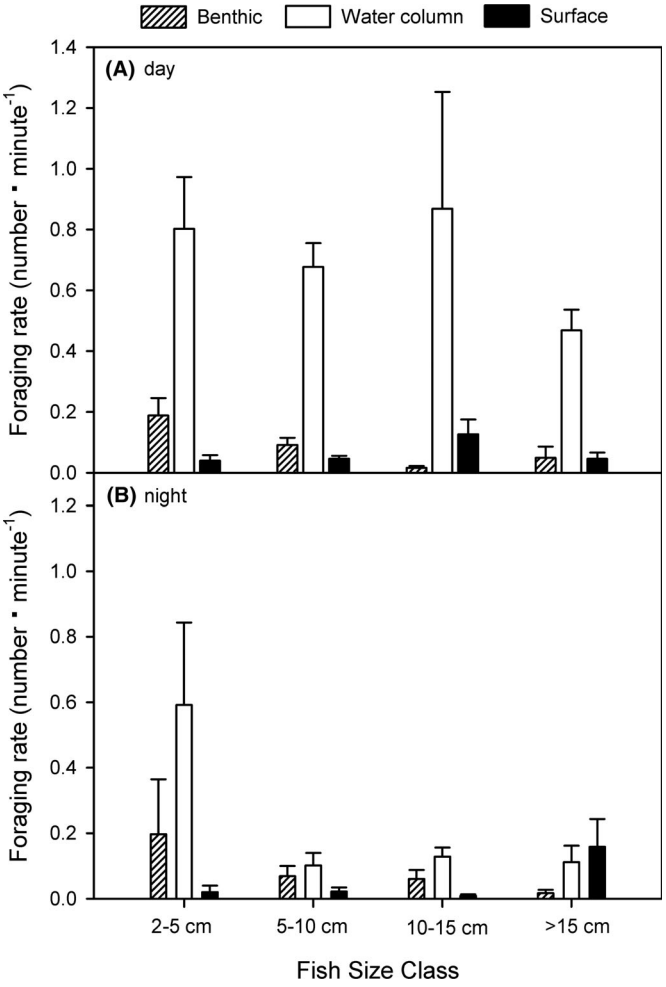

FIGURE 5. Mean (error bars show ± 1 SE) foraging rate of Yellowstone Cutthroat Trout during **(A)** day and **(B)** night, partitioned by fish size and according to foraging location (hatched bars = benthic, open bars = water column, hatched bars = surface).

benthic foraging remained less than the maximum daily ration in August and September; however, diurnal drift foraging became higher than this value during October and November. Energy consumed during October and November as estimated by foraging rate in our study was higher than predicted by a maximum ration rate of food intake based on Elliott's (1976) model for Brown Trout.

DISCUSSION

Salmonid fishes in streams have long been observed to be daytime drift-feeding predators, but little comparative data exist to determine the importance of different feeding strategies used to capture invertebrate prey. In this study, we quantified the foraging effort over daily and seasonal cycles to compare the relative importance of benthic, water column, and surface foraging in streams. As past observations have suggested, we found that daytime drift feeding is the predominant form of food intake for stream-dwelling Yellowstone Cutthroat Trout. However, we also observed a low frequency of benthic foraging and foraging at night. While our data indicate that drift foraging is the main source of energy intake, salmonids can also exploit food sources from the benthos and capture prey during nighttime. Secondary feeding locations and prey sources may sustain their energy intake to maintain a positive energy balance during periods when drift foraging is more constrained by day length or by cold temperatures that limit metabolic activity.

Stream-dwelling salmonid fishes are commonly observed to forage from holding stations in the current, where they move from to capture prey from the water column and then return to continue searching (Keenleyside 1962; Grant et al. 1989; Hughes and Dill 1990; Keeley and Grant 1995; Nislow et al. 1998; Neuswanger et al. 2014). However, past studies also suggest that salmonids

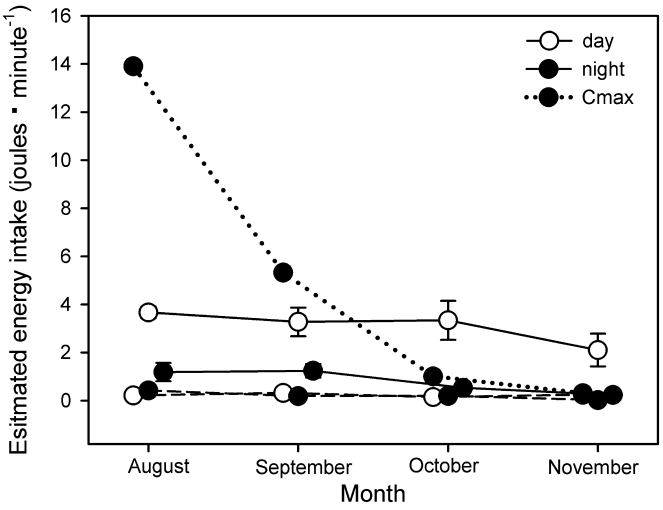

FIGURE 6. Mean (error bars show ± 1 SE) estimated energy intake (J/min) for a 10-cm Yellowstone Cutthroat Trout by month from the drift (solid lines) or benthos (dashed lines) (day = open circles, night = solid circles). Average maximum daily ration (Cmax) for a 10-cm salmonid is shown by the dotted line and expressed as a rate of energy intake needed per minute to achieve Cmax.

can feed from the benthos by picking invertebrates off the stream substrate (Tippets and Moyle 1978; Grant and Noakes 1987; Fausch et al. 1997; Nislow et al. 1998; Tunney and Steingrímsson 2012). High densities of benthic invertebrates may provide substantial food sources, but our data indicate that Yellowstone Cutthroat Trout only feed at low rates from the stream bottom in comparison to the water column and surface drift. As most salmonids (trout, salmon, and char species) have terminally oriented mouths, capturing invertebrates off of the stream substrate may not provide sufficient encounter and consumption rates of prey compared with intake rates from drift feeding. It may be that salmonids in streams more commonly exploit invertebrates directly from the benthos when faced with intense interspecific competition for drifting prey (Fausch et al. 1997) or during periods with very limited flow or cold temperatures that may limit access to invertebrate drift (Metcalfe et al. 1999).

Studies of salmonids have also reported foraging during moonlit nights and nocturnal activity during winter, or have inferred nocturnal foraging based on increases in stomach contents during nighttime, indicating that salmonids can feed during low-light periods (Jenkins 1969; Cunjak 1988; Metcalfe et al. 1999; Johnson et al. 2016). While our data did reveal that Yellowstone Cutthroat Trout make foraging attempts in darkness, the low frequency, higher rejection rate, and shorter distances moved to forage indicate that they are not very effective predators at night. Behavioral studies of salmonids in streams also indicate a reduced ability to capture prey at night, given lower foraging distance and feeding rates (Jenkins 1969; Watz et al. 2014). Although Yellowstone Cutthroat Trout appeared to have more limited ability to detect and capture prey at night, our video recording revealed that fish did seem to react to particles moving past them in the stream current at night. Our qualitative observations of fish reacting to particles moving past them in the current (at night) suggest that fish can respond to particles that touch them or detect pressure differences in the stream current as particles move past them. We detected a higher abundance of drifting and benthic invertebrates at night, during some months, as other studies have found from a range of stream ecosystems (Elliott 1970; Ramírez and Pringle 1998). Higher drift rates and activity patterns of stream invertebrates at night are thought to reduce the risk of predation from visual predators like salmonids (Rader 1997). While Yellowstone Cutthroat Trout attempted to feed at night, perhaps because of an increased number of invertebrates, their success rate was much lower than during daytime. It may be that salmonids in streams can supplement their energy intake with some night feeding, but our data indicate that night feeding is a minor component of food intake.

Assessing the foraging effort of free-ranging animals provides a means of quantifying the temporal and spatial distribution of food resources by determining which prey are vulnerable to foraging individuals. Behavioral observations of foraging animals can describe a foodscape by identifying where food is consumed from the range of habitats available (Searle et al. 2007). In streams, aquatic invertebrates are often a primary source of prey for many fishes (Allan 1981; Angradi and Griffith 1990). However, the vulnerability of stream invertebrates can differ between different areas of the stream and can significantly influence how much prey is available as food. The surfaces of the stream bottom and the interstitial spaces formed among rocks provide a diversity of foraging and shelter habitats for stream invertebrates. As a result, the highest densities of invertebrates are often found as stream benthos (Covich et al. 1999). Benthically oriented fishes like suckers (family Catostomidae) or sculpins (family Cottidae) may forage from the substrate surface or among the spaces of stream substrate, but trout, salmon, and char species appear to rely mainly on drifting aquatic invertebrates captured from the water column and surface (Miyasaka and Nakano 1999; Syrjänen et al. 2011).

Our estimate of energy intake based on foraging rate indicates that Yellowstone Cutthroat Trout feed below or near the level needed to acquire a maximum ration for two of the summer months we observed fish but above the rate needed during the two fall months. In small streams like the ones we observed Yellowstone Cutthroat Trout in, resident salmonids are often limited in the maximum size they can achieve (Meyer et al. 2003; Leeseberg and Keeley 2014).

Living in small streams may constrain the encounter rate of prey by reducing the cross-sectional area that fish can forage from and limit energy intake, growth, and maximum body size. Our data support this idea because fish foraged at a rate lower than that needed for maximum growth during summer months when temperatures were optimal for growth. Curiously, fish foraged at a higher rate during colder months than predicted by Cmax, perhaps because they forage for limited time periods before becoming inactive and slowly metabolizing the food they acquire away from foraging stations. Whether such activity patterns match the strategies used by wild fish will require more detailed monitoring of fish behavior in natural streams than we were able to observe in our study.

By measuring the behavior of Yellowstone Cutthroat Trout over a 24-h period, we were able to compare how foraging rate changed over day–night periods and quantify where prey are targeted in the stream. Although filming and videography have a long history in the study of animal behavior, the need to control a camera by an operator has often limited how long the investigator could be present, especially for underwater applications (Keeley and Grant 1995; Hughes et al. 2003). The availability of open-source software and hardware allowed us to develop a customized system of recording fish behavior. We used an inexpensive adventure camera that was controlled with a battery-powered microcomputer capable of hosting a UNIX computer operating system and executing a simple Python software program. By combining the camera and computer components, we were able to systematically record the behavior of fish in a natural stream without being present at the stream for extended periods of time. The trends toward miniaturization, affordability, and open-source custom control of video recording technology offer promising avenues for future studies of animal behavior and activity for which long-term observer presence is logistically untenable or would disturb the focal species. In the future, many different devices using low-cost, open-source hardware and software can be imagined and developed by researchers to facilitate when, where, and how frequently data can be collected (Greenville and Emery 2016; Hereward et al. 2021).

Modeling approaches are becoming more widely used to evaluate the effects of different management scenarios for stream fishes. Studies to evaluate the effect of restoration efforts or predict future consequences of climate change are commonly based on the availability of suitable habitat for salmonid fishes (Jenkins and Keeley 2010; Urabe et al. 2010; Carmichael et al. 2020; Railsback et al. 2021b). At the core of many such models, fish foraging behavior and estimates of food consumption are used to calculate energy intake and habitat suitability (Hughes and Dill 1990; Rosenfeld and Taylor 2009; Dodrill et al. 2016; Hayes et al. 2016; Railsback et al. 2021a). Despite the importance of behavior in estimating foraging location, food intake, and constraints of when fish can forage, relatively few behavioral data have been used to parameterize models. The miniaturization and availability of inexpensive high-quality video systems may allow behavioral data to be collected for a variety of field conditions, fish species, and life stages. While drift foraging was the predominant foraging mode for Yellowstone Cutthroat Trout in small headwater streams, the extent to which benthic and nocturnal foraging provides energy intake for salmonids may differ for different species, in larger rivers, or in seasons outside of the range we studied. Future studies may reveal that the sources of food consumption and feeding strategies can differ substantially over what we observed. Additional behavioral data could be used to refine models and improve their predictive ability of habitat suitability and help researchers better understand the factors that limit the distribution and abundance of stream fishes.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.