

## Movement Patterns of Large Brown Trout in the Mainstream Au Sable River, Michigan

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**Abstract.**—We used radiotelemetry to monitor spring and summer movements of 11 brown trout *Salmo trutta* (442–584 mm) for up to 904 d in a Michigan stream. Individual brown trout used a few specific locations near cover (referred to as home sites) as resting locations during the day, moved across various distances at night, and generally returned to the same home site the next morning. Home sites were predominantly artificial cover (88%) rather than natural sites, as natural cover was very limited in the study area. Some fish used multiple home sites, and the average separation between multiple home sites for individual fish was over 500 m. Fish tracked for more than 1 year used the same home sites each summer and generally exhibited similar behavior each year. Fish belonged to two general categories of daily movement behavior: mobile or stationary. Mobile fish tended to move frequently and were found within their home sites only 43% of the time at night. Stationary fish did not move far from home sites, even at night. There was a negative correlation between the average gradient and the maximum distance fish moved from their home sites during nocturnal periods. Stationary fish resided in areas of steeper gradient (usually about 0.20%) and moved less often nocturnally than did mobile fish. Three fish were tracked extensively over 36 d to quantify diel activity patterns. The hourly activity of fish increased dramatically at dusk, continued at a lower level overnight, and then increased again at dawn before declining to near zero during the day. This behavior pattern was similar among all individuals tracked and also between the months of June, July, and August for an individual fish. Nocturnal movements involved significantly greater distances than diurnal movements for these fish. The relationship between movement and gradient may indicate energetic tradeoffs between the cost of moving against a current and the energy gained during active foraging. Also, the dominant use of artificial home sites has implications for the value of habitat improvements meant to increase abundance of large brown trout.

The movements of stream-dwelling brown trout *Salmo trutta* have been estimated with a variety of techniques applied to various sizes of fish. Studies of smaller individuals (<400 mm) indicate that these fish are largely residential, with limited long-range movements (Jenkins 1969; Bachman 1984; Ovidio et al. 2002). Larger individuals appear to demonstrate more nomadic movements, including long-range displacements, which often occur at night. The fish then return to the same or another home site the following day (Clapp et al. 1990). These nomadic movements are believed to be foraging related (Jenkins 1969; Young 1999; Ovidio et al. 2002), because nocturnal searches for fish

prey may require more active searching patterns than the drift feeding commonly observed for young trout (Eckhardt 1979). Diel patterns of activity have been described but not well defined, and the extent of foraging movements has not been well documented. Factors that vary through the diel period, such as light level, food availability, and water temperature, may influence diel foraging activity of large brown trout (Clapp et al. 1990; Ovidio et al. 2002). If these movements are foraging related, then the distances moved could also be influenced by foraging success, because individuals that find food early in a displacement might truncate that movement for the night.

Movements by stream-dwelling fishes are not only determined by foraging constraints but also by energetic costs of movement against a current. These energetic costs may influence the foraging strategy used by stream-dwelling fish. Velocity-dependent activity modes have been described for

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small rainbow trout *Oncorhynchus mykiss* (Johnson et al. 1987), cutthroat trout *Oncorhynchus clarki* (Johnson et al. 1987), and brown trout (Gosse and Helm 1982). Gradient is often a good correlate of average velocity in a stream, and many fishes show distribution patterns limited by elevation and gradient, as well as by temperature. For example, Guillory (1982) found that species in a warmwater Louisiana stream were restricted to sites based on gradient. Other studies in locations with a wider distribution of temperature and gradient conditions have shown combined effects of these two factors on fish distributions (Barber and Minckley 1966; Hocutt and Stauffer 1975; Rahel and Hubert 1991). These studies indicate that the costs of swimming against a current may be important to species persistence in a location. Energetic costs also vary with temperature (Brett and Groves 1979; Diana 1995). Seasonal changes in food abundance and availability, current velocity, and temperature could obviously alter the regularity and extent of nocturnal movements by large trout (Bunnell et al. 1998). Few studies have quantitatively analyzed the energetic constraints on piscivores living in a stream environment. Modeling work by Hayes et al. (2000) derived energetic models for drift-feeding brown trout, which largely reside in local pools; energy costs were calculated based on duration of exposure to currents during foraging. Rand and Hinch (1998) demonstrated strong relationships among current velocity, energetics, and migrations of anadromous salmonids.

The purpose of this study was to conduct a telemetry evaluation of the movements of brown trout in the mainstream Au Sable River, Michigan. The original intent was to compare our findings to the general behavior of brown trout observed by Clapp et al. (1990) in the South Branch of the Au Sable River. Three unique observations in the present study were the diel activity pattern of brown trout during the summer, the repeatability of locations and behavior from one year to the next in individual brown trout, and the relationship of long-range foraging activities to stream conditions in various reaches of the river. We used telemetry to quantify these patterns in the Au Sable River system and to further expand the understanding of brown trout behavior in streams.

### Methods

The mainstream Au Sable River originates 16 km north of Grayling, Michigan, and flows 26 km south and then 183 km east to Lake Huron. Six

large dams on the mainstream between Oscoda and Mio prevent fish migrations from Lake Huron into the upper Au Sable River. Brown trout in the upper river are free to range throughout the north and south branches and within the mainstream between dams in Grayling and Mio. Highly permeable glacial drift in the watershed contributes to cool, stable streamflows, and hence favorable conditions for trout.

The uppermost reach of the study site extended 1.7 km from a small dam at U.S. Route 27 in Grayling to Interstate 75. The dam creates a shallow (mean depth < 1 m), 18.6-ha impoundment. Average discharge at the dam is 2.0 m<sup>3</sup>/s, and summer water temperatures there can reach 27°C (Coopes 1974). Between U.S. Route 27 and Interstate 75, the river is swift, the bottom consists primarily of gravel, and groundwater input is relatively high. The East Branch of the Au Sable River flows into the mainstream within this reach; average discharge in the East Branch is 1.2 m<sup>3</sup>/s (Coopes 1974), and summer water temperatures are up to 4.5°C cooler than in the mainstream. The reach from Interstate 75 to Burton's Landing is 8 km long, has a low overall gradient (0.04%), receives little groundwater input, and has a bottom substrate dominated by sand. Average stream width is 27 m, and average discharge is 3.2 m<sup>3</sup>/s (Hendrickson and Doonan 1972). Maximum daily water temperature in July 1991 was 19.7°C. The remaining 14.5 km of the study site, located between Burton's Landing and Wakeley Bridge, has a higher average gradient, more groundwater input, bottom substrate composed of gravel and cobble, and greater trout production than the Interstate 75 to Burton's Landing reach. Average stream width of the reach between Burton's Landing and Wakeley Bridge is 29 m, and average discharge is 5.4 m<sup>3</sup>/s (Hendrickson and Doonan 1972). Mean maximum daily water temperature at different points within the reach varied from 16.0°C to 18.1°C in July 1991.

Eleven individual brown trout were captured with DC electrofishing gear and were successfully implanted with radio transmitters between 8 May 1990 and 8 September 1991 (fish 5 was implanted with a new transmitter on 8 September 1991 after expulsion of the original one) (Table 1). Fish were anesthetized in tricaine methanesulfonate. Transmitters were placed in the abdominal cavity through a midventral incision between the pelvic and pectoral girdles. After closure of the incisions with nonabsorptive silk or nylon sutures, oxytetracycline (55 µg/kg body weight) was injected into

TABLE 1.—Summary of radio transmitter implants in 11 brown trout tracked between 8 May 1990 and 8 May 1993 in the mainstream Au Sable River, Michigan. Number of observations includes only the observations of fish displacement, not the diel-activity observations made for fish 4, 11, and 12. Fish 5 was implanted twice; fish 7 died.

Fish number	Length (mm)	Weight (g)	Implant date	Last contact	Numbers of observations	Transmitter weight (% body weight)
1	470	850	8 May 1990	25 Jul 1990	44	2.12
2	452	964	9 May 1990	14 Jul 1990	37	1.87
3	500	1,100	23 May 1990	31 Jul 1990	33	1.64
4	487	1,179	23 May 1990	21 Feb 1992	80	1.53
5	566	1,942	23 Jul 1990	13 May 1991	42	0.93
5	584	2,120	8 Sep 1991	8 May 1993		0.99
6	521	1,602	24 Jul 1990	3 Nov 1990	9	1.12
8	442	1,010	6 May 1991	14 Feb 1993	52	2.08
9	457	1,120	6 May 1991	8 May 1993	53	1.88
10	480	1,200	6 May 1990	12 Dec 1992	55	1.75
11	485	1,250	7 May 1991	20 Mar 1992	76	1.68
12	472	1,110	14 Jul 1991	3 Sep 1991	40	1.89

the abdominal cavity to prevent infection. River water was sprayed over the body and gills to reduce stress during surgery, and anesthetic solution was sometimes sprayed over the gills to maintain sedation. The procedure required less than 10 min to complete, after which fish were immediately placed in the stream and allowed to recover at the capture site. In addition to the 11 fish successfully implanted, three fish died within 2 weeks of surgery and were not included in any analyses.

Radio transmitters used in this study (AVM Instrument Co.) were of two designs. Transmitters equipped with hairpin-loop antennas (six units) measured  $70 \times 20 \times 20$  mm, weighed 21 g, and were powered by a mercuric oxide battery with an expected life of 690 d. Transmitters equipped with coiled-loop antennas (six units) measured  $55 \times 15 \times 16$  mm, weighed 18 g, and were powered by a lithium thionyl chloride battery with an expected life of 700 d. Each unit was encapsulated in dental acrylic and coated with beeswax to prevent tissue reaction and expulsion (Tyus and McAda 1984). We tried to keep transmitter weight under 2% of body weight, as recommended by Marty and Summerfelt (1986). The average transmitter size was 1.61% of fish weight, and only two transmitters exceeded 2% of fish weight (fish 1 = 2.12% and fish 8 = 2.08%) (Table 1).

Movements and behavior of radio-tagged fish were monitored immediately following surgery. However, data collected during the 2 weeks post-surgery were excluded from analyses because brown trout require this time to recover from acute handling stress (Pickering et al. 1982). Fish were located from shore by triangulation (two bearings)

with a programmable scanning receiver (Challenger 200, Advanced Telemetry Systems, Isanti, Minnesota) and a 60-cm directional-loop antenna. When radio-tagged fish could be seen from shore or from underwater, telemetric locations were compared with true positions of fish. Based on these comparisons, daytime location estimates made by triangulation from a distance of less than 30 m were within 1 m of the true position. Fish were located from shore at random times during day and night and were usually found in the same reach from day to day. When a fish moved to another section of river, searches were made by canoe. Although fish movements were observed year-round (Hudson 1993), this paper focuses on movements in spring and summer (1 May to 31 August).

Fish were usually located every day or every other day to quantify daily movements and home-site use. Most fish exhibited a diel pattern of activity in summer, so daily movements and home-site use data were grouped into diurnal and nocturnal (1 h before sunset to 1 h after sunrise) periods prior to analysis.

The summer range of each fish was mapped. Maps included the locations of home sites (defined below) as well as other instream and riparian landmarks. When a fish was located, we used the landmark features to determine the fish's position on the map and noted whether the fish was in a home site. Movements beyond the range of maps were measured by use of aerial photographs.

Home sites were defined as specific cover structures or pools in which a fish was located five or more times during daytime, or sites a fish returned

to after an extended period of time (Clapp et al. 1990). Home sites were classified as artificial cover, natural cover, or pool. Natural cover consisted of aquatic vegetation or submerged riparian vegetation. Daytime and nighttime home-site use was computed as the percentage of locations during which a fish was found at a home site. A Kruskal–Wallis test was used to determine whether frequency of home-site use varied between day and night periods for all fish, as well as for individual fish.

Movements from home sites into midstream occurred frequently at night and were believed to be movements in search of prey. Two types of movements were measured: displacements and diel movement patterns. Displacement was measured for every fish (when possible) to quantify the number and distances of locations away from home sites; the most common observation was for fish to be at a home site. Displacement was measured as the distance between each telemetric location of an individual and its nearest home site. For displacements, daytime locations of individual fish were made at least every 3 d; nighttime locations were attempted every 3 d, but sometimes did not occur for up to 8 d because not all fish could be found every night. The median daytime, median nighttime, and maximum displacement distances were computed for each fish. Based on nocturnal displacement, fish were categorized as mobile (median displacement = 13–375 m) or stationary (median displacement = 0 m). Frequency distributions of foraging distances were developed for mobile and stationary fish and for diurnal and nocturnal periods. Distributions were compared by mobility group and time of day with a Kolmogorov–Smirnov test.

Gradient was measured within the range (distance between extreme upstream and downstream locations over the entire tracking record) of each brown trout to determine whether gradient was an important factor influencing the extent of foraging displacements. Stream gradient was measured within a reach by use of a level, was computed as the total drop in stream surface elevation (mm) over the mid-channel length of a reach (nearest dm), and was then converted to percent slope over the entire range. Simple linear regression was used to examine whether median nighttime displacement and maximum foraging displacement were related to gradient for nine fish (fish 2 and fish 5 were eliminated from the analysis due to aberrant behavior described later).

The second method for analyzing movements

involved quantifying the timing, extent, and pattern of diel movements of three fish (4, 11, and 12) during 36 monitoring sessions over 24 h each in summer 1991. These three fish were chosen for diel studies because their locations in the river were in areas with good access to facilitate observations, particularly at night. During a session, an attempt was made to locate the fish each hour from the initial sighting until that same time the following day (extreme movements were difficult to pinpoint on an hourly basis and sometimes not completely measured). Distance moved from one hour to the next represented the linear distance between locations and not necessarily the total distance moved during the hour. Diel range and hourly movement rates were computed for each session. Diel range was computed as the distance between the extreme upstream and downstream locations recorded during the 24-h period. Hourly movement rates were computed as the linear distance displaced each hour and were categorized into diurnal or nocturnal periods. Wilcoxon's signed rank test was used to compare mean daytime and nighttime movement rates for individual fish. A Kruskal–Wallis test, and in some cases a Mann–Whitney *U*-test, was used to examine whether daytime and nighttime movement rates varied by month for fish 4 and fish 11. All statistical analyses were performed with SYSTAT and the Statistical Package for the Social Sciences (Wilkinson 1989; SPSS 2002), and results were considered statistically significant at *P*-values less than 0.05.

## Results

Brown trout were tracked for 67 and 904 d (mean = 327 d) from May 1990 to May 1993 (Table 1). Altogether, 521 locations were plotted for these fish, averaging 47 locations per fish (range = 9–80 locations). Only data collected through May 1992 were used to compute home-site use, because locations after that date were taken sporadically. Four brown trout were tracked on a limited basis between May 1992 and May 1993 to determine whether these fish used the same areas and home sites as compared to the previous two summers.

Radio contact with four fish was lost 79–175 d after surgery. Transmitters in two of these fish exhibited signs of premature failure prior to the loss of contact. Five transmitters were recovered in working condition 11–68 d after the last detected movement, and no sign of fish remains were observed near recovered transmitters. The transmitter

TABLE 2.—Summer home-site use by nine brown trout tracked between May 1990 and May 1992 in the Au Sable River, Michigan. Distance between home sites represents mean separation (m). Home-site type represents the number of artificial cover (A), natural cover (N), and pool (P) home sites. Fish 2 and 5 were excluded from this analysis because of their use of the Grayling Fish Hatchery pool.

Fish number and statistic	Number of home sites	Distance between sites	Home-site type	Home-site use (%)	
				Day	Night
1	3	3,503	3A	63	26
3	3	14	3A	97	100
4	4	42	3A, 1N	84	43
6	1		1P	100	40
8	2	17	1A, 1N	87	71
9	1		1A	96	72
10	2	160	2A	91	87
11	3	68	3A	86	8
12	5	166	5A	76	33
Total	24		21A, 2N, 1P		
Mean	2.7	567		87	54
SD	1.3	1,296		12	31

implanted in fish 5 was recovered in a pool at the Grayling Fish Hatchery in May 1991; however, the fish was recaptured in the same pool 119 d later and re-implanted (Table 1). The original incision had healed completely, and a scar was present near the fish's left pectoral fin, where the transmitter was apparently expelled. Fish 5 had grown in length (18 mm) and weight (178 g) in the 413 d following initial implantation. Fish 1 was also recaptured and re-implanted when the first transmitter began to fail 4 d after surgery. Three fish that died following surgery were probably injured during surgery or capture; in one case, high water temperature (26°C) may have contributed to the fish's death. Brown trout successfully implanted in this study did not appear to be adversely affected by transmitters. Fish implanted with transmitters were observed on spawning redds, chasing and capturing prey, and fleeing from predators such as osprey *Pandion haliaetus*. Fish revisited their earlier-detected home sites in the same year and in multiple years; multiple home sites were not sequentially used but were often revisited.

#### Home Sites

Most brown trout used home sites as daytime resting locations and were also commonly found there at night. Fish observed in home sites appeared lethargic and were sometimes found lodged within or resting against debris so that swimming or fin movements were not required for maintaining position. Home sites used by radio-tagged fish were also used by brook trout *Salvelinus fontinalis*, rainbow trout, white sucker *Catostomus commersoni*, and other brown trout. Nine fish tracked in summer used a total of 24 home sites (Table 2).

Individual fish used from one to five home sites (mean 2.7), with an overall mean separation of 567 m between sites. Fish 2 and fish 5 were excluded from home-site analysis because of residence in the Grayling Fish Hatchery pool. Three of the four fish tracked during more than one summer between May 1990 and May 1993 used the same home site(s) from year to year (fish 10 was the exception). Home-site occupation varied among individual fish, ranging from 63% to 100% in daytime and from 8% to 100% during the nighttime (Table 2). When data were combined for all fish, the percentage of total locations occurring in home sites was significantly greater ( $P < 0.05$ ) during daytime (87%) than nighttime (54%). Home-site use at night was probably overestimated because several fish moved only short distances (<5 m) from home sites at night, making it difficult to determine their exact locations relative to the home sites.

Twenty-one home sites were classified as artificial cover, two as natural cover, and one as pool. Artificial cover appeared to be more abundant than natural cover in the study area; in many areas, it was the only cover type available. Most artificial home sites (95%) were structures built specifically as trout cover. Eight fish used at least one of these artificial structures as a home site, including six fish that used them exclusively. Artificial structures consisted of log jams, log rafts, stump complexes, or undercut banks. An undercut retaining wall was the only artificial structure used that was not built specifically as trout cover. Pools were used as home sites by three fish; two of these fish (2 and 5) resided at the Grayling Fish Hatchery and were provided artificial food on a daily basis. The two home sites classified as natural cover were

TABLE 3.—Summary of daytime and nighttime foraging displacements (m) of nine brown trout tracked during spring and summer between May 1990 and May 1992 in the Au Sable River, Michigan. Gradient represents average percent gradient in the section occupied.

Fish number	Day		Night		Maximum displacement	Gradient (%)
	N	Median displacement	N	Median displacement		
<b>Mobile fish</b>						
1	44	0	16	13	125	0.12
6	10	0	5	90	170	0.20
11	94	0	26	119	643	0.08
12	43	0	5	45	135	0.14
<b>Stationary fish</b>						
3	35	0	8	0	5	0.15
4	131	0	49	0	415	0.14
8	54	0	14	0	143	0.19
9	62	0	21	0	37	0.20
10	52	0	17	0	96	0.19

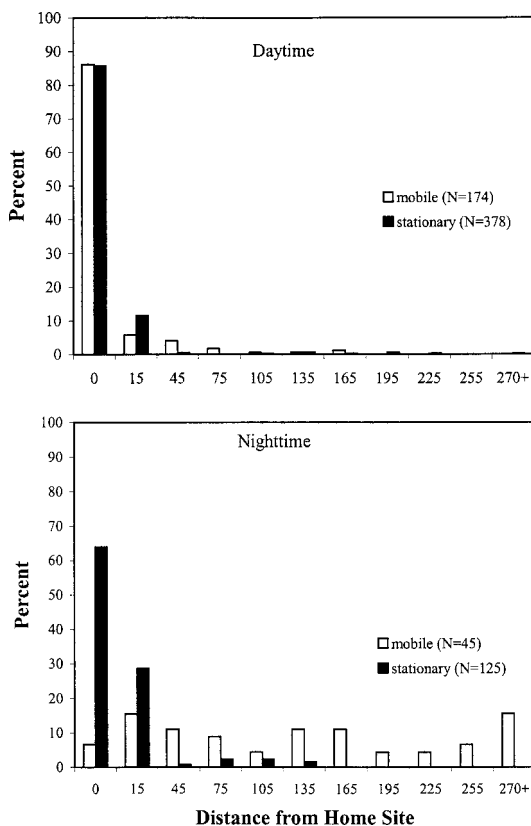


FIGURE 1.—Distributions of day and night displacement from home sites for four mobile and five stationary radio-tagged brown trout located 525 times during daytime and 161 times during nighttime in the Au Sable River, Michigan. Distances were divided into 30-m intervals, listed as the mean of each interval.

an aquatic macrophyte bed *Elodea* spp. and a partially submerged stand of alders *Alnus* spp.

#### Daily Movements

Individual fish appeared to use one of two movement patterns (Table 3). Mobile fish (four individuals) appeared to be more active. At night, they moved frequently or continuously, were found within home sites only 42% of the time, and often moved more than 100 m from home sites (Figure 1). Stationary fish (five individuals) held positions at night in midstream, were found within a home site 94% of the time, and were never found more than 150 m from a home site at night. Two tagged fish, however, were often observed or located in midstream even during the day. Home-site use during the day was only 63% for fish 1. This fish and two large, untagged brown trout were often observed away from cover in daytime. We observed these fish individually herding small prey fish from midstream toward a retaining wall, where they attempted to capture the fish. During the day in August 1990 and 1991, fish 4 was often located outside of its home site, and sometimes appeared to be wandering in midstream. The two fish residing at the hatchery were provided food pellets and remained active throughout the day, although they did not displace from their home pool.

As stream gradient increased, the length of nocturnal movements decreased. There was a significant negative relationship ( $y = -3,343x + 720$ ;  $r^2 = 0.6$ ;  $P < 0.05$ ) between percent gradient ( $x$ ) and maximum nocturnal displacement ( $y$ ; m). There was no significant relationship between gradient and median diurnal displacement ( $P > 0.05$ ). Four mobile fish lived in low to moderate gradients



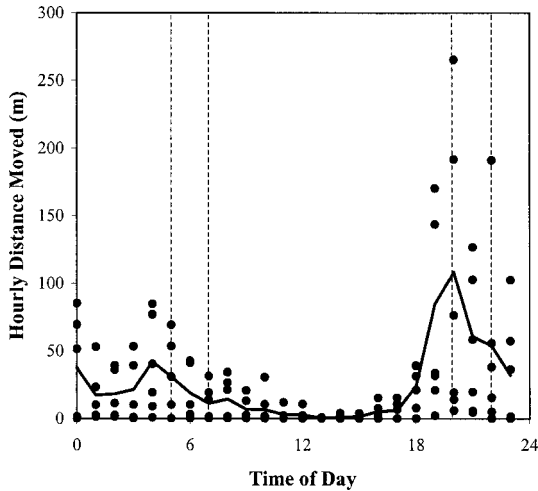


FIGURE 2.—Diel pattern of monthly averages for hourly distances moved by two radio-tagged brown trout (fish 3 and fish 4) in the Au Sable River, Michigan, from June through August (dots), and the overall mean values (solid line). Intervals between dashed lines represent dawn and dusk periods approximately 1 h before and after sunrise and sunset.

(0.05–0.12%) in the upper and middle reaches and were regularly observed 50–1,000 m away from home sites at night. Three of the stationary fish lived in higher gradients (0.19–0.20%) in the lower reach and were rarely found more than 15 m from a home site at night. Most remaining fish were considered stationary and lived in areas with moderate water gradients (0.14–0.19%).

A total of 14 diel monitoring sessions were completed for fish 4, 18 for fish 11, and 4 for fish 12. Due to the limited number of sessions, fish 12 was eliminated from further analysis. The majority of movements occurred at night, especially near dawn and dusk (Figure 2). The typical diel pattern of behavior was for fish to leave home sites at dusk, hold stationary positions in midstream or move throughout midstream during the night, then return to the same or a nearby home site at dawn. Peaks in mean hourly movement occurred around sunrise and sunset and varied in magnitude from 9 to 68 m/h at dawn and from 22 to 181 m/h at dusk (Figure 2). Overall, movements at night were significantly larger than during the day for each fish, and the same was true for monthly averages for each fish, except fish 4 in August (Kolmogorov–Smirnov test,  $P < 0.05$ ). Nocturnal movements were significantly different between fish, with fish

11 showing more extensive nighttime movements, but did not differ significantly among months for a given fish. Finally, diurnal movements were not significantly different either between fish or among months, except for significantly elevated diurnal movements by fish 4 in July.

## Discussion

Large brown trout in this study showed considerable variation in displacements. This variation appeared to be related to differences in stream gradient. We observed large brown trout moving long distances and traveling between home sites. Other authors have described similar long-range movements of large, stream-dwelling brown trout (Clapp et al. 1990). Though we believe the long movements were related to active foraging, we have no data on the foraging of our study fish. However, studies by Ovidio et al. (2002) and Bunnell et al. (1998) both found similar movements and also believed them to be foraging related. Movements and behavior we observed for some fish were different from those described above. Several fish rarely moved far from home sites. These fish appeared to use a sit-and-wait strategy, maintaining midstream positions within 30 m of a home site in moderate- to high-gradient areas. Other fish appeared to use an active-search strategy characterized by frequent or continuous movements, and they regularly displaced themselves by more than 30 m from home sites at night. Most of these fish lived in areas with low to moderate gradients and were often observed moving 150–2,000 m at night. Individual brown trout tracked during two or more years mainly used the same home sites and movement patterns from one year to the next.

Range of movement in summer reflected movements between home sites or movements away from home sites, which were presumably related to foraging. Home-site use and displacement of most fish were similar to those reported for large brown trout in the South Branch of the Au Sable River (Clapp et al. 1990). In both studies, brown trout used specific cover structures as bases for nighttime foraging, were relatively inactive during daytime, moved away from cover near sunset, and returned to the same or a nearby home site by sunrise.

This is the first study to quantify diel movements of large, stream-dwelling brown trout. Three brown trout monitored over diel periods moved primarily at night, with distinct peaks in hourly movement rates near dawn and dusk. Other fish

that were not monitored hourly over the diel period were nocturnally active, moving into midstream at dusk and returning to daytime resting sites at dawn. Crepuscular activity in small brown trout has been noted by several authors (Swift 1962; Chaston 1969; Priede and Young 1977; Oswald 1978; Bachman et al. 1979; Ovidio et al. 2002), and activity patterns in brown trout may be controlled either by absolute light intensity or by changes in light intensity (Oswald 1978; Bachman et al. 1979; Regal 1992). Clapp et al. (1990) and Regal (1992) found activity levels were correlated with light levels, but were possibly related to food availability also. Dawn and dusk peaks in hourly movement rates in this study may be related to greater availability or vulnerability of prey at these times. Invertebrate drift densities are known to peak near sunrise and sunset (Waters 1962; Jenkins 1969; Elliott 1970). Large brown trout may time their foraging movements in response to greater availability of invertebrate drift or drift-feeding forage fish. Timing and extent of diel movements in our study were not well correlated with other environmental factors.

Home sites used by brown trout in this study were qualitatively similar to habitat used by brown trout in the South Branch of the Au Sable River (Clapp et al. 1990). These sites apparently were used for resting during the day and provided overhead cover and possibly reduced water velocities. Home sites also provided low-light conditions, which are selected by brown trout (Devore and White 1978; Fausch and White 1981; Gosse and Helm 1982). The majority of fish in this study used artificial cover, and other studies in the Au Sable River system indicate the importance of artificial cover to trout (Nuhfer 1979; Fausch and White 1981), which is due mainly to limited natural cover.

The nocturnal displacements of brown trout in this study suggested that individual fish were using one of two search modes. Previous work has classified the search mode or foraging strategy of other predators as sit and wait (Pianka 1966) or active search (Eckhardt 1979), based on the frequency of movements per unit time (Huey and Pianka 1981) or the probability of moving over a given time period (Pietruszka 1986). We classified individual movements based on behavior and extent of nocturnal movements away from home sites. The behavior and range of stationary fish were consistent with those of smaller brown trout in other studies (Jenkins 1969; Bachman

1984; Bunnell et al. 1998; Burrell et al. 2000), and our findings generally agreed with those of studies conducted in the Au Sable River by Shetter (1968) and Favro et al. (1986), in which large brown trout were captured and recaptured within the same general area. Mobile fish appeared to use an active-search strategy characterized by frequent nocturnal movements. The majority of mobile fish lived in areas with low to moderate gradients and were often observed moving 150–2,000 m in one night. The strategy used by individual brown trout in this study may be related to prey abundance, type of prey consumed, or the energetic costs associated with an active-search strategy in flowing water.

The foraging strategy used by a predator generally reflects prey mobility (Huey and Pianka 1981). Thus, the active-search strategy used by some brown trout in this study is consistent with a piscivorous diet, whereby relatively sedentary prey (small fish) are more likely to be discovered by actively searching predators. Although fish contribute the bulk of their diet, large brown trout in the Au Sable River system are known to consume insects (Alexander 1977; Stauffer 1977). However, large brown trout may not be able to meet metabolic needs on a diet of insects alone (Bachman 1982; Hayes et al. 2000). The energetic costs of searching for prey in flowing water also appear to influence the strategy used by large brown trout. Median and maximum foraging displacements of large brown trout decreased with increasing gradient. Higher gradients were strongly correlated to higher average water velocities, and brown trout in high-gradient areas generally used a sit-and-wait strategy, while fish in low-gradient areas generally used an active-search strategy. Clapp (1988) suggested that the energetic demands of swimming in fast water may prevent fish from making long-range foraging movements.

The foraging behavior of large brown trout in this study may also reflect a certain degree of opportunism. We observed brown trout taking advantage of “artificial” situations, such as the retaining walls used to assist in capture of prey, and the availability of food pellets at the Grayling Fish Hatchery.

An important assumption in telemetry studies is that transmitters do not influence behavior of radio-tagged fish (Clapp et al. 1990). Young (1999) observed that brown trout and other salmonids resumed feeding less than 15 min after surgery. Brown trout in this study did not appear to be adversely affected by transmitters over the long



term, as implanted individuals were observed actively foraging and spawning; one individual that was recaptured appeared healthy and had grown normally since implantation. Transmitter expulsion was documented for one fish, and several other transmitters recovered may have been expelled by fish. Meyers et al. (1992) also recovered several transmitters with no signs of fish remains. Expulsion of dummy transmitters occurs rapidly and without infection in rainbow trout (Lucas 1989) and Atlantic salmon *Salmo salar* (Moore et al. 1990) and does not affect growth, swimming performance, or maturation (Moore et al. 1990). The fish that expelled its transmitter in this study appeared healthy and had grown in length and weight since initial implantation.

The diel patterns of long-range movements, coupled with relationships between distance moved and stream gradient, suggest that the movement of large brown trout is tied to several proximate environmental conditions (water velocity, light level, and temperature) that will ultimately influence energetic success of the fish (food consumption, metabolism, and growth). Though such changes in behavior with multiple cues have often been described in energetic terms (Brett 1971; Diana 1995), actual studies linking behavioral and energetic concepts are rare. Empirical and modeling studies of foraging choices and consequences could dramatically improve our knowledge of stream fish behavior. Such studies have been accomplished in laboratory situations related to optimal foraging (Werner and Hall 1974), but they have not been applied well to fish behavior in natural settings with variable prey abundance, temperature, or current velocity.

One final management implication of this study is the importance of artificial cover to the residence of brown trout. Virtually all of the trout tracked in this study used artificial cover as a home site, and all trout occupied home sites with cover. If artificial cover had not been added to the study area, it is likely that far fewer large brown trout would have occupied home sites in that region, and that the overall abundance of large brown trout would have declined dramatically.

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