



Seasonal variations of activity pattern of brown trout (*Salmo trutta*) in a small stream, as determined by radio-telemetry

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Abstract

Nine brown trout (27.9–42.8 cm FL, 234–995 g) from the Aisne stream (Belgian Ardenne) were tagged with surgically implanted radio transmitters, and their activity patterns were studied at 10-min intervals during twenty-six 24-h cycles from October 1995 to May 1997. The duration and intensity of activity were mainly proportional to water temperature and day length but some differences appeared between individuals. The daily home range in summer was also 3.2 times longer than in winter, and was exploited 2.5 times more intensively. At all seasons, trout were most active at dusk, and seasonal variations in diel patterns consisted mainly in a progressive shift from more crepuscular activity in autumn and winter to more homogenous and intensive activity during spring and summer, but still with a predominance of activity at dusk. This relative consistency of activity rhythm throughout the year was interpreted within the context of foraging risk and efficiency, in view of the scarcity of predators in the Aisne stream, and of drifting macroinvertebrates being consistently more abundant at dusk at all times of the year. However, activity patterns varied substantially between individuals living in different microhabitats, including when fish were investigated on the same day. This suggests that activity patterns are also subordinated to local factors such as habitat structure or abundance of drifting prey.

Introduction

Rhythmicity is an intrinsic component of all ecosystems and animals, including fish, the circadian rhythms of which are synchronised by environmental cues (syntheses in Palmer, 1976; Thorpe, 1978; Helfman, 1986; Boujard & Leatherland, 1992). Arrhythmia in fish is exceptional and only takes place in pathological situations reflecting an extreme perturbation of the animal by environmental unpredictability or degradation (Hambrick & Hibbs, 1977; El-Shamy, 1978; Baras, 1997). Although reproductive activity and social interaction may alter the activity rhythm of fish, it is generally admitted that diel rhythms correspond to foraging and feeding activities.

Many authors have investigated the activity patterns of brown trout *Salmo trutta* L. and documented different patterns. Hoar (1942) reported that trout were

active throughout the day whereas others studies concluded that they were essentially nocturnal (Chaston, 1968, 1969; Jenkins, 1969; Eriksson, 1978), diurnal (Swift, 1962, 1964), or crepuscular (i.e. active during twilight (dawn and dusk); Bachman et al., 1979). However, some of these studies were conducted in controlled environments, or relied on stomach content analysis, as an attempt to determine the periods of the day when the fish had been active. Recent studies using scuba diving (e.g. Heggenes et al., 1993), and hourly positions of radio-tagged fish (Schulz & Berg, 1992; Bunnell et al., 1998) revealed that trout changed their daily activity pattern depending on season and water temperature. Other similar telemetry studies (Clapp et al., 1990; Young et al., 1997a; Young, 1999) indicated that large brown trout were largely nocturnal and/or crepuscular during summer. In small salmonid streams, however, foraging does not

require long-range movements from the home (Neveu, 1991). Additionally, brown trout, like most predators, do not need to forage over long periods of time (Elliott, 1994). As a corollary, the analysis of trout activity through the study of their movement on an hourly basis may combine biases that restrict considerably our understanding of the fine scale variations of fish activity with respect to environmental conditions. The conclusions of more recent studies on the activity of salmonids with respect to drift rates (cutthroat trout, *Oncorhynchus clarki pleuriticus* Richardson; Young et al., 1997a; brown trout, Giroux et al., 2000) support this statement. Similarly, scuba diving or other methodologies relying on direct observation may be limited, for example, by turbidity or low light levels that interfere with the detection of fish all day long throughout the year.

This study aimed to investigate the seasonal variations of activity rhythms of brown trout in a small stream of the Belgian Ardenne (where brown trout are naturally present), to analyse the relationships between activity patterns and environmental factors, to determine the possible adaptive significance of these changes, and whether different individuals adopted similar behavioural responses to similar environmental changes. In contrast with the aforementioned studies, the study relied on most frequent (once every 10-min) sampling of activity level in radio-tracked individuals.

Materials and methods

Study site

The study was conducted in the Belgian Ardenne, mainly in the lower course of the Aisne stream, a typical trout stream (mean slope 2.78‰, mean width and flow in summer: 14 m and 2.41 m³ s⁻¹, respectively) which meets the R. Ourthe in Bomal (Fig. 1). Water temperature ranges from 0 to 21 °C annually (mean: 9.2 °C in 1992–1998). In the study area, the fish assemblage is typical of the grayling zone (Huet, 1949) and consists mainly of brown trout *Salmo trutta* (61% of biomass), grayling *Thymallus thymallus* (L.) (36.5% of biomass), sculpin *Cottus gobio* (L.) and stone loach *Barbatula barbatula* (L.).

Capture and tagging

From October 1995 to October 1997, nine trout (27.9–42.8 cm and 234–995 g, Table 1) were captured by

electric fishing or caught in a fish trap at the weir of Bomal (400 m upstream of the confluence with the R. Ourthe; Fig. 1.). Trout were anaesthetised with a 0.25 ml l⁻¹ solution of 2-phenoxy ethanol, then placed ventral side up into a v-shaped support adjusted to their morphology. A mid ventral incision was made between the pelvic girdle and the anus, and an alcohol sterilised transmitter (40 MHz, internal coiled antenna) was inserted into their body cavity. The weight of the transmitter ranged from 1.6 to 4.7 g depending on trout body weight, making sure that the transmitter to fish body weight ratio in the air never exceeded 2.0%. The incision was closed by two or three separate stitches, 5–10 mm apart, using sterile plain catgut affixed to cutting needles. In order to minimise biases originating from capture and surgery, fish were released precisely at their capture site, as soon as they had recovered equilibrium and spontaneous swimming (about 10 min after surgery).

Tracking

After implantation, the trout were located to an accuracy of ± 1.5 m² by reference to labelled marks (2–20 m apart) lining the banks of the stream and triangulation using conventional methods (Baras & Cherry, 1990).

The duration ('activity budget'), rhythm patterns and precise timings of trout activity were studied over twenty-six 24-h cycles when trout were tracked continuously and fixes taken at regular intervals (10 min). We used a FieldMaster radio receiver and a loop antenna (ATS Inc.) to measure the activity of trout. Once every 10 min, trout were located in the stream to measure their daily home range (D.H.R., distances between the most upstream and downstream location during the cycle) and distance travelled (D.T., sum of distances travelled between subsequent locations during the cycle, in every direction). Each time a trout was precisely located in the stream, its activity level was quantified based on the variations of the signal intensity (ΔI) (>1 graduation on the galvanometer of the receiver) of the radio transmitters during 1 min. These ΔI corresponded to movements of the fish in relation with a fixed antenna. The intensity of the activity was deduced from the number of changes of signal intensity between successive records. In order to estimate the activity budget (percentage of time during which the trout is active, as defined by Baras, 1995), the limit between activity and inactivity was fixed at 4 ΔI min⁻¹ after measuring the signals from fixed

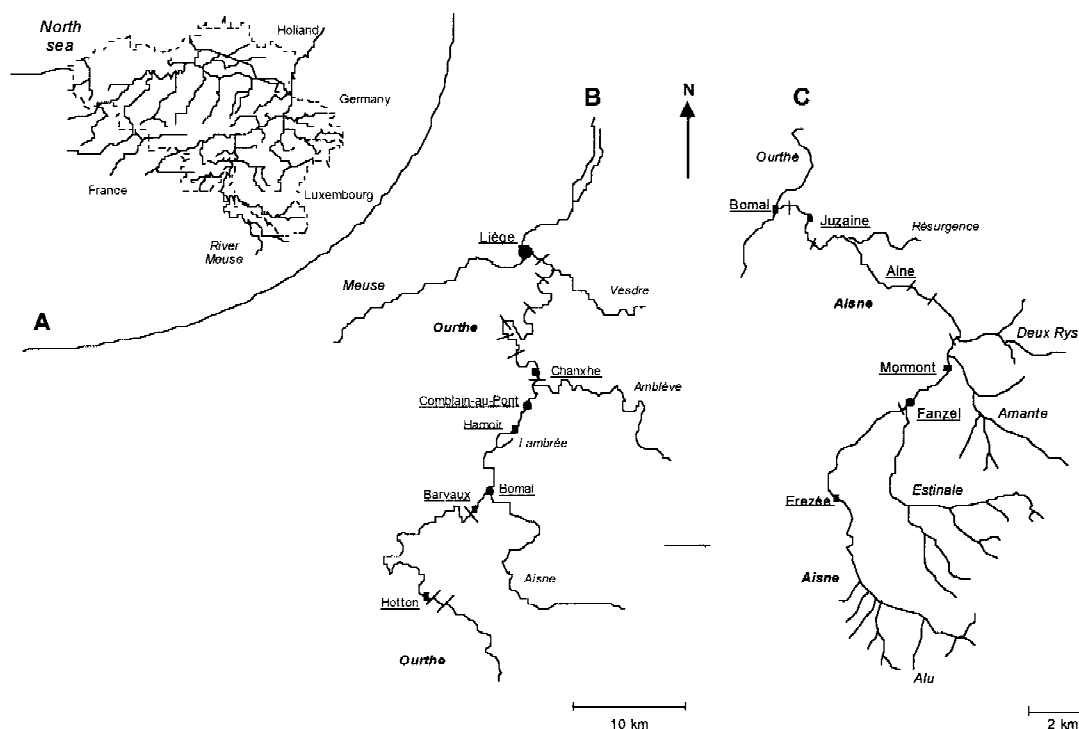


Figure 1. Location of the study area, the Aisne Stream (tributary of the river Ourthe) in the Belgian Ardennes.

transmitters placed in the Aisne stream. This is because the signal strength of an immobile radio transmitter is not strictly constant, due to the passage of other fish and obstacles to signal propagation (e.g. leaves, branches) in the stream or other sources of inaccuracy while measuring signal strength (Baras, 1997). The activity budget can be calculated on different time scales (hourly, crepuscular, daily...). In order to test for within individual variability, trout no 1 was monitored for 10 cycles and trout no 2 for six.

Trout activity was analysed over the entire 24-h cycle, and separately during dawn, day, dusk and night. In order to compare between cycles at different seasons, dawn and dusk periods were fixed at two hours each (± 1 h v. the times of sunrise and sunset, respectively). For each period of the 24-h cycle, the intensity and the duration (budget) of the activity were later compared to environmental variables and fish size by stepwise multiple-regression analyses. Environmental variables taken in account were day length, day length variations between consecutive days, water temperature (daily thermal range, mean, minimum and maximum), water level. These environmental variables were also transformed (log, square) for logarithmic and exponential relationships.

Two relevant variables (temperature and season or day length) were categorised and tested for analysis of variance. Variations of D.H.R., D.T. and exploitation (D.T./D.H.R.) over environmental conditions were determined by non-parametrical tests (Kruskal–Wallis and Mann–Whitney tests).

Results

Daily home range and distance travelled

During a 24-h cycle, trout occupied distinct resting and foraging places (up to five), and frequently travelled between them. Both the numbers of places and distances between places varied considerably between 24-h cycles (two to five places, 2 to ≥ 100 m). The longitudinal extension of the daily home range (D.H.R.) of radio-tagged trout in the Aisne stream ranged from 6 to 480 m (mean: 48 m) over the annual cycle. No significant relationships were found between the size of the D.H.R. the D.T. and the size of the trout. During spawning migrations in autumn, trout tended to occupy larger D.H.R. but the huge variation between 24-h cycles caused these differences to be non-significant (Kruskal–Wallis test: $H=5.66$, $P=0.1293$, and $H=5.41$,

Table 1. Lengths, weights and tracking periods of radio-tagged brown trout

Trout no	Size (cm)	Weight (g)	Date of release	Days tracked	Starting dates of the 24-h cycles
1	39.9	611	13 Oct. 1995	302	25 Oct 95–08 Nov 95–06 Dec 95–10 Jan 96–14 Feb 96–07 Mar 96–10 May 96–11 Jun 96–24 Jul 96–24 Sep 96 (<i>n</i> =10)
2	28.5	275	22 Apr. 1996	466	29 May 96–03 Jun 96–19 Jun 96–10 Jul 96–24 Sep 96–11 Mar 97 (<i>n</i> =6)
3	27.9	234	04 Jun. 1996	70	19 Jun 96–10 Jul 97 (<i>n</i> =2)
4	42.0	995	20 Jun. 1996	26	03 Jul 96 (<i>n</i> =1)
5	28.8	271	14 Aug. 1996	107	04 Sep 96 (<i>n</i> =1)
6	29.5	287	19 Sep. 1996	84	24 Sep 96–09 Oct 96 (<i>n</i> =2)
7	42.8	755	25 Feb. 1997	215	18 Jun 97 (<i>n</i> =1)
8	30.4	288	20 Mar. 1997	203	15 Apr 97–13 May 97 (<i>n</i> =2)
9	29.9	290	18 Apr. 1997	256	29 Apr 97 (<i>n</i> =1)

Table 2. Variations of daily home range, mobility and exploitation (mean \pm SD) of habitat by brown trout in the Aisne stream. The values sharing at least one common superscript (a or b) do not differ at the 0.05 level of significance (Mann–Whitney *U* test)

Water temperature ($^{\circ}$ C)	Daily home range (D.H.R., m)	Distance travelled over 24 h (D.T., m)	Exploitation (D.T./D.H.R.)
<4	12 \pm 3	21 \pm 9	1.77 \pm 0.41 ^a
4–8	199 \pm 247	258 \pm 376	1.43 \pm 1.06 ^a
8–12	18 \pm 11	48 \pm 28	3.27 \pm 1.74 ^a
>12	38 \pm 36	122 \pm 90	4.43 \pm 3.59 ^b

$P=0.1442$, for D.H.R. and D.T., respectively; Table 2). Outside of the spawning period, the D.H.R. of trout was proportional to water temperature, but was always restricted to less than 40 m. Compared to the size of their D.H.R, trout travelled over significantly longer distances when temperature was $>12^{\circ}$ C (Mann–Whitney *U*-test; Table 2), suggesting that they exploited their D.H.R. more intensively during the warmest days of the year.

Activity rhythms and budgets

The activity budget of trout varied substantially with water temperature (Fig. 2). At temperatures $<4^{\circ}$ C, during autumn and winter, the activity budget of trout averaged less than 10%, and on some occasions, trout showed no activity at all. Activity took place mainly at dusk, and was lowest at dawn. At temperatures from 4 to 8° C, activity still predominantly took place at dusk. Trout were also active at night, dawn and during

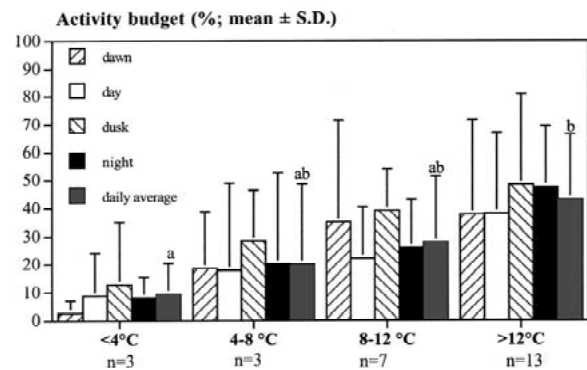


Figure 2. Variation of activity budget of brown trout in the Aisne Stream, depending on water temperature ($1.6\text{--}17.2^{\circ}$ C). Values are means \pm standard deviations (S.D.) for each period of the 24-h cycle (and daily average). Values are daily means \pm S.D. For the daily average bars, values sharing at least one common superscript (a or b) do not differ at the 0.05 level of significance (Scheffe *F*-tests).

the day, but activity was less intense than at dusk. At

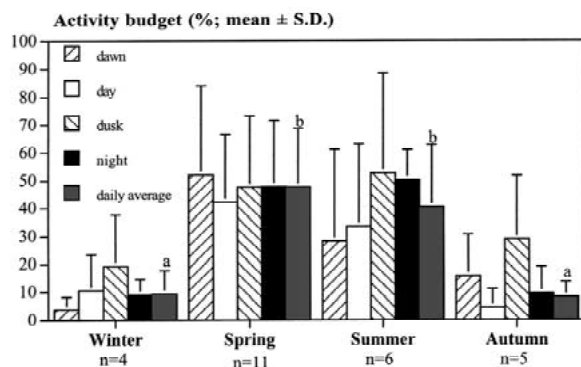


Figure 3. Variation of activity of brown trout in the Aisne Stream, depending on season. Values are means \pm standard deviations (S.D.) for each period of the 24-h cycle and for the entire 24-h cycle (and daily average). Values are daily means \pm S.D. For the daily average bars, values sharing at least one common superscript (a or b) do not differ at the 0.05 level of significance (Scheffe *F*-tests).

temperatures from 8 to 12 °C, the activity budget rose to 28%, and trout adopted a bimodal dusk and dawn rhythm pattern. At temperatures optimal for growth (≥ 12 °C), the activity budget of trout exceeded 40%, activity was at least twice as high as at lower temperatures, and it took place essentially at dusk and during the night.

On a seasonal basis (Fig. 3), the activity budget averaged 40% during spring, summer and fall and was less than 10% during late autumn and winter. Seasonal variations of the activity rhythm pattern closely matched those outlined for different ranges of water temperatures. In winter, the activity took predominantly place at dusk. In summer and autumn, trout adopted a bimodal activity (dusk and night in summer and dawn and dusk in autumn). In spring, the activity was spread over the entire day cycle (close to 40%). Seasonal variations also were also conspicuous at the individual level.

Distinct stepwise multiple-regression analyses on the behaviour of trout 1 and 2 revealed that their behaviours were influenced differently by environmental factors (Table 3). Trout 2, which lived downstream of a small weir, was little influenced by day length, except for its nocturnal activity, which lasted longer during summer days. Trout 1, which lived in a more typical pool-riffle sequence, was influenced by day length, water level and temperature, with the latter variable acting exclusively at dawn and dusk, which normally are the colder and warmer periods of the daily cycle.

A similar between fish difference was observed between trouts 2 and 3, that lived, respectively, down-

stream and upstream of a small weir (Bomal, Fig. 1) during spring–summer 1996, and could be tracked simultaneously on two occasions (19 June and 10 July 1996; Table 1). During both 24-h cycles, trout 2 was essentially active at night but its activity budget varied from 18.6 to 38.6%. By contrast, trout no 3 showed similar activity budgets (circa 30%) but changed its acrophase of activity from diurnal to crepuscular and nocturnal.

Discussion

Surgical implantation is probably the best attachment procedure for long term telemetry studies on fish, including salmonids (Clapp et al., 1990; Young, 1994; Ovidio, 1999b; Lucas & Baras, 2000; Baras et al., in press). During this study, trout were recaptured on several occasions. Healing was completed within four to six weeks, and no inflammation, pathological outbreak or necrosis was observed, thereby suggesting that the behaviours described here were not influenced by tagging artefacts.

Except for spawning migrations, when trout moved over several hundreds of metres or tens of kilometres (for comparisons in the same stream, see also Ovidio et al., 1998; Ovidio, 1999a,b), the daily home range (D.H.R.) ranged from 8 to 480 m (mean 48 m). These values are similar to those observed in southern Appalachian (0–357 m, Bunnell et al., 1998) and southeastern Wyoming rivers (mean of 41 m, Young, 1999) but smaller than those of brown trout in a Michigan river (mean of 193 m, Hudson 1993) and in an Idaho stream (mean of 105 m, Young et al., 1997b). This discrepancy may originate from differences in habitat structure, hydrologic characteristics, climatic conditions and different positioning frequency of the fish (Ovidio et al., 2000).

We observed no clear-cut relationship between D.H.R. and environmental factors or fish size, presumably because brown trout are predators (e.g. Elliott, 1967; Cada et al., 1987) that do not need to extend largely their foraging area when their appetite increases (Clapp et al., 1990), especially in small streams. Trout usually move in between calm resting places and neighbouring faster flowing sites, where drift is more abundant (Schuler et al., 1994; Rousset & Bardonnet, 1995; Giroux et al., 2000). These observations corroborate the fact that brown trout are not necessarily strict sit-and-wait predators (Clapp et al., 1990). As observed in the present study, they may

Table 3. Environmental variables influencing the activity of brown trout (no 1 and 2) in the Aisne stream, as identified by stepwise multiple-regression analyses on activity budget. Trout as in Table 1 *: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$; ****: $P < 0.0001$

		Trout no 1	Trout no 2
Number of cycles		10	6
Budget	24-h	$R^2=0.924$ ****	$R^2=0.590$ *
		day length (+) water level (-)	daily thermal range (+)
	dawn	$R^2=0.921$ ***	—————
		day length (+) water temperature (+) daily thermal range (-)	
	day	$R^2=0.756$ **	—————
		day length (+)	
	dusk	$R^2=0.844$ **	—————
		water temperature (+)	
	night	$R^2=0.827$ **	$R^2=0.682$ *
		day length (+) water level (-)	day length (+)

adapt to higher temperatures by occupying these fast flowing sites (Ovidio, unpublished data) over longer periods, or by foraging there more intensively. In these circumstances, experience may be a key to the efficient exploitation of drift, and this may also account for the consistent fidelity of trout to their home range or territory during the growing season (spring and summer; Ovidio et al., 1998; Ovidio, 1999a,b). In a south central Wyoming stream, Young (1994) found fish length-home range dependence for large brown trout (>340 mm). In southern Appalachian rivers, Bunnell et al. (1998) observed that brown trout >375 mm occupied larger home range than smaller trout, and explained this phenomenon by a possible shift from drift feeding to piscivory when trout approach 350 mm. However, in the Aisne stream, large brown trout are essentially drift feeders (Giroux et al., 2000) and in our study, only three brown trout were >340 mm.

During spring and summer, brown trout have been characterised as a nocturnal (Chaston, 1968; Clapp et al., 1990; Young, 1999) or crepuscular species (Bachman et al., 1979; Bunnell et al., 1998), and sometimes as a typically diurnal species (Swift, 1962, 1964). This study demonstrated that rhythm patterns may vary substantially between individuals in different habitats, as well as between seasons or days for a single individual. As Eriksson (1978), Heggenes et al. (1993) and Bunnell et al. (1998), we found that trout were pre-

dominantly crepuscular or nocturnal during winter and autumn, possibly because nocturnal foraging minimises predation risks (Heggenes et al., 1993; see parallel for nocturnal migration in Jonsson & Jonsson, 1993), but also because drift is more abundant during the scotophase (Brittain & Eikeland, 1988). Trout can detect prey at low light intensities (0.03–0.1 lx; Tanaka, 1970; Robinson & Tash, 1979; Henderson & Northcote, 1985), and several studies provided evidence that trout can feed at night (Jenkins, 1969; Oswald, 1978; McIntosh & Townsend, 1995), especially when drift is more abundant at night than during the day (Giroux et al., 2000).

In contrast to most authors who documented activity shifts depending on season and water temperature, we observed that trout in the Aisne stream were most active at dusk throughout the year, including at water temperatures corresponding to the optimum for growth (12–16 °C; Elliott, 1994). Apparently they adapted to warmer temperatures simply by being more active, over longer periods of time and over a slightly longer activity area. This contrasts with other studies on trout (Heggenes et al., 1993) or other species (the cyprinid *Barbus barbus*, Baras, 1995), where the activity pattern changed substantially with season and temperature. Hypotheses accounting for this relative consistency include the (almost) absence of piscine and avian predators in the Aisne stream, and

the abundance of drifting macroinvertebrates peaking almost systematically at dusk (Giroux et al., 2000). When predation pressure is low, trout could thus be predominantly active at times of the day when prey are abundant enough to permit efficient foraging. In a high elevation stream of Wyoming (U.S.A.), Young (1999) observed a predominance of nocturnal activity of large brown trout in late summer, despite temperatures from 13 to 23 °C. Young (op cit.) suggested that the summer nocturnalism is perhaps a vestige of juvenile behaviour, a consequence of the absence of diurnal predators or a recent response to human predation.

Despite this apparent stability, we observed substantial within individual variations between activity patterns over successive weeks during the same season, and that trout living in distinct habitats showed contrasting activity patterns on the same day. These discrepancies probably reflect local variations in the timing and abundance of drifting prey, which may both govern the activity pattern of salmonids (cutthroat trout, Young et al., 1997a; brown trout; Giroux et al., 2000) or differences in foraging tactics between individuals. This interpretation, which is based on the behaviours of individuals, may also account for why so many different activity patterns were observed in trout in different rivers and streams.

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