

Turning Night into Day: Effects of Stress on the Self-Feeding Behaviour of the Eurasian Perch *Perca fluviatilis*

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Keno Ferter and V. Benno Meyer-Rochow (2010) Turning night into day: effects of stress on the self-feeding behaviour of the Eurasian perch *Perca fluviatilis*. *Zoological Studies* 49(2): 176-181. Effects of stress on the feeding behaviour of the Eurasian perch *Perca fluviatilis* were investigated. Over a period of 32 d, the self-feeding patterns of a group of 4 fish were monitored with a light-dark cycle of 12:12 h. As the perch could obtain food by triggering a feeding apparatus at any time, food availability likely did not govern the feeding activity pattern. During the light phase, when the perch were exposed to an illumination of 2.4 W/m², they were repeatedly (but at irregular times) disturbed through surface-transmitted vibrations and shadows. Monitoring of the self-feeding pattern over a 24 h period showed that the fish changed their feeding activity from diurnal to nocturnal when exposed to this type of stress in combination with the relatively bright illumination during daytime hours. In order to show that the perch associated the trigger with food and pulled it intentionally rather than randomly, the feeding apparatus was emptied while trigger activation was monitored for a further 6 d. As soon as food was no longer available from the feeding apparatus the perch decreased their pulling activity until they had completely lost interest 6 d later. <http://zoolstud.sinica.edu.tw/Journals/49.2/176.pdf>

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The Eurasian perch *Perca fluviatilis* L. is a widely distributed freshwater species of northern Europe and Asia that prefers shallow and moderately productive waters of a wide range of environments from slow rivers to lakes 40 m deep. Due to its tolerance of brackish water, it can even be found in the Baltic Sea. It was also introduced to the Azores, South Africa, Australia, and New Zealand (Craig 2000). The temperature tolerance of the Eurasian perch, which ranges from 4 to 31°C, determines its geographic distribution (Rougeot and Toner 2008).

The species is carnivorous and its diet is highly variable. Whereas young larvae feed mainly on zooplankton like rotifers, cladocerans and copepods, juvenile and adult perch feed on insect larvae and small fish. Larvae and young juveniles live in groups and in order to optimize their

feeding success, they are known to perform diel vertical migrations (Kratochvil et al. 2008). Adult individuals lead solitary lives (Rougeot and Toner 2008).

Earlier studies involving self-feeding on demand and radio transmitter tagging had confirmed that the Eurasian perch is a diurnally active species with peaks at dawn, dusk, and midday (Anthouard and Fontaine 1998, Jacobsen et al. 2002). Interestingly, these peaks coincide with the activity maxima known for aquatic insects (Csabai et al. 2006). Furthermore, a seasonal activity rhythm was identified that possessed a maximum in summer and a minimum in winter (Craig 1977).

Depending on their preference for a certain light intensity level for feeding activity to occur, most fish can be classified as either diurnal

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or nocturnal. While nocturnal species show photoreceptor adaptations to generally increase their sensitivity to light, diurnal species show adaptations to increase colour discrimination as well as temporal and spatial acuity (Ali et al. 1977, Munz 1990). However, that a switch from a diurnal to a nocturnal life style is indeed possible, has been reported for several species (Greenwood and Metcalfe 1989, Riehle and Griffith 1993, Fraser and Metcalfe 1997). For example, juvenile Atlantic salmon *Salmo salar* are predominantly diurnal during the summer, but become nocturnal in winter. This switch is temperature dependent and only occurs at temperatures of $< 10^{\circ}\text{C}$.

The anatomical organization of the eye of perches conforms to the general design of the teleost eye, which owing to screening pigment migrations and/or cellular movements, permits adjustments to different ambient light intensities (Yew et al. 2001, Meyer-Rochow and Coddington 2003, Kunz 2006). Based on comparative values of scotopic and photopic thresholds for a variety of teleost species, e.g., scotopic thresholds for goldfish (Powers and Easter 1978) and the cichlid *Haplochromis burtoni* (Allen and Fernald 1985) of 6.14×10^{-9} and 6.31×10^{-8} $\mu\text{E/s}$, respectively, and a photopic threshold of 1.87×10^{-2} $\mu\text{E/s}$ for the New Zealand torrentfish *Cheimarrichthys fosteri* (Meyer-Rochow and Coddington 2003), we can assume the *P. fluviatilis* visual thresholds do not greatly differ from those values.

An increase in the predation risk during daytime foraging in winter was advanced as a possible reason, for fish to be ectothermic and become more and more sluggish as temperatures decrease. Consequently, they would face greater difficulties escaping from endothermic predators like, for instance, diurnally active piscivorous birds. By restricting feeding forays to nighttime, salmon can, thus, shelter and hide from predators during the day and use the safer time for food procurement (Fraser and Metcalfe 1997).

This study on demand feeding in the Eurasian perch was performed in order to determine if individuals of this species can shift from a diurnal to a nocturnal pattern, given stress conditions that simulated predation risk. Using a self-feeding apparatus, these perch could feed on demand at any time of the day or night. This allowed us to test whether the fish were capable of modifying their feeding pattern when external factors (like disturbances of various kinds) made adjusting their feeding rhythm a desirable option.

Animal acquisition and care

For the experiment, a group of 4 adult *Perca fluviatilis* (ranging in total length from 10 to 12 cm) was used. The fish were caught with a fishing rod in Oct. 2007 from a medium-sized channel in Norden, Germany. The channel was approximately 1.5 m deep and 40 m wide. The water of the channel was static or slowly moving and of low translucency due to severe eutrophication.

Following capture, the fish were kept in an 80 L aquarium. The aquarium water was filtered at a rate of 757 L/h (AquaClear®, Power Filter50) and its temperature was maintained at 20°C . In order to simulate a semi-natural environment, the bottom of the aquarium was covered with pebbles and small plants, among which the perch could find places to hide. Once the fish had acclimated to the new environment, they were fed mealworms on a daily basis at different times of the day. This irregular feeding was important so that the perch would not get used to a certain feeding time.

The photoperiod was set to a constant light-dark cycle of 12:12 h (lights on at 07:00 and off at 19:00) using an energy-saving plant lamp (Megaman®, Plantlamp PAR38). The light intensity during the light phase was set to 2.4 W/m^2 . During the dark phase, the intensity of the remaining light was $25 \mu\text{W/m}^2$. The light intensities were measured at the surface of the water using a J18 Photometer (Tektronix, Beaverton, OR, USA).

In order to expose the perch to forms of stress resembling a predation risk during the day, the aquarium was placed in a frequently used hallway, which connected two research laboratories with each other. Since the light period was set to regular working hours, the perch were frequently (but at irregular times) disturbed during this period by people walking past the tank. During the dark phase, no people passed down this hallway. Therefore, there were no disturbances from 19:00 to 07:00.

Self-feeding apparatus and data acquisition

The fish were fed using a self-feeder for 32 d. This allowed the fish to feed on demand 24 h a day. The self-feeding system consisted of a modified food timer (FOODTIMER, Mie University, Tsu City, Japan) and a sensor. The sensor was connected to a triggering string. The trigger itself was made from a 3 cm piece of wool, which was weighted with a piece of lead. The trigger was placed about 15 cm below the water

surface. When a fish pulled the trigger, the sensor activated the food timer and 4 or 5 mealworms were released from the feeder. The signal from each trigger activation was recorded using a line recorder (Servogor 110, Kipp and Zonen, Goerz, Delft, Holland). The feeding apparatus was refilled every day. An illustration of the experimental setup is shown in figure 1.

Control experiment

After feeding the fish for 32 d using a self-feeder, a control experiment was performed. This was done in order to prove that the fish had associated the trigger with food and did not randomly pull the trigger in darkness. For this part of the investigation no food was placed in the self-feeder, and trigger activation was recorded for 6 d.

Data analysis

The recording paper of the line recorder moved at a speed of 6 cm/h. Thus, by counting the number of lines per 6 cm interval, it was possible to calculate the total number of pulls per hour. Due to a malfunction of the system on day 12, this day and the 4 following days were excluded from the results. On day 17, the fish had returned to a normal feeding rhythm. From this day onward, the data were included in the results. The average and standard deviation of pulls per hour were calculated using Microsoft Excel for every hour of the 27 d. For statistical analysis, the software SPSS (SPSS, Chicago, IL, USA) was used. In order to test that there was a significant difference between different times of day, one-way analysis of variance (ANOVA) for repeated measures was used and in order to test for differences between

different times of day, pair-wise comparisons were performed with the significance level set at 0.05 (95% confidence interval for differences).

RESULTS

The self-feeding behaviour of the test perch is displayed in figure 2. Since data were obtained for 27 d, the average number of pulls per hour is shown for every hour and day.

Except for 13:00, 18:00, and 09:00 no feeding activity occurred during the illumination phase. However, as soon as the light was switched off, the perch began feeding. The highest feeding rate was measured during the first hour after the light had been switched off (about 8 pulls per hour on average).

ANOVA comparisons showed that there was a significant difference between the different times of day. The pair-wise comparison revealed that the feeding activity in the first hour after the light was switched off was significantly higher than at any other time of the 24 h cycle ($p < 0.001$ for every time point). After 20:00, the feeding activity significantly decreased. From 22:00 until 07:00,

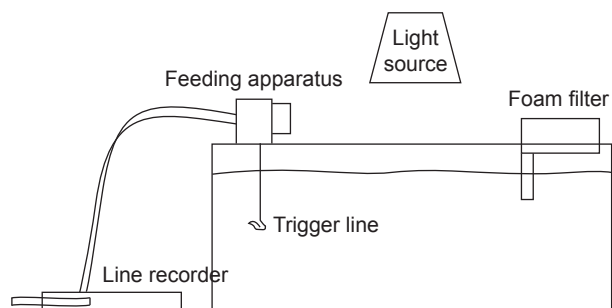


Fig. 1. General experimental setup showing the position of the filter, the light source, and feeding apparatus. Upon pulling the trigger line, 4 or 5 mealworms were released from the feeding apparatus. Each pull was recorded by a line recorder, which was connected to the feeding apparatus.

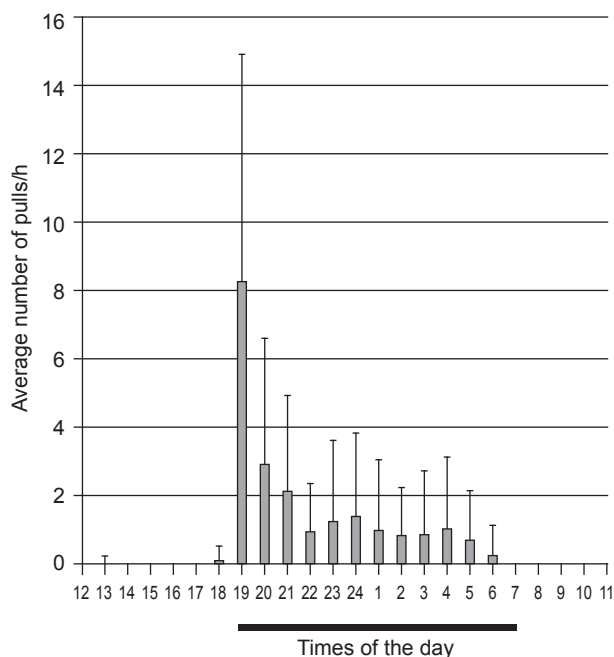


Fig. 2. Self-feeding behaviour of the Eurasian perch on a 24 h cycle with stress conditions during the illumination phase. The average number of pulls per hour for 27 d is displayed. The standard deviations are shown as vertical bars. The black bar indicates darkness from 19:00 to 07:00.

the average number of pulls did not exceed more than 2 pulls per hour. The pair-wise comparison further showed that there was no significant difference in feeding activity between 22:00 and 07:00 ($p > 0.05$), and that the feeding activity in the last hour of the dark phase did not significantly differ from that during the light phase. In summary, the perch only fed during hours of darkness and showed no feeding activity during the light phase.

After 2 d of normal operation, all food was removed from the self-feeder, but the recording was still run for 6 d more. The results are displayed in figure 3.

On the 1st d after the food had been removed from the feeding apparatus, a normal amount of trigger-pulling activity was recorded (24 pulls in 1 dark phase). However, on the 3rd d after food removal, a decrease in trigger activation was observed (18 pulls per night). This trend continued until the fish pulled only 2 times in one dark phase on day 6. This shows that the perch associated the trigger with food and pulled it intentionally and not just randomly. As soon as food was no longer available from the feeding apparatus, the perch decreased their pulling activity until they completely lost interest.

DISCUSSION

The experimental results suggest that *Perca fluviatilis* individuals changed their feeding activities from diurnal to nocturnal when exposed to stress. This result is not in line with several earlier observations on the Eurasian perch in its natural environment, in which this species was described as being diurnal with peaks at dusk, dawn, and midday (Alabaster and Stott 1978, Rask 1986, Huusko et al. 1996). Moreover, laboratory observations of the self-feeding activity on demand under non-stress conditions, showed a clear and distinct diurnal feeding activity in this species (Anthouard and Fontaine 1998), but feeding patterns can change when additional predatory species are present (see below: Schleuter and Eckmann 2006).

Although not demonstrated with demand-feeding, a shift from diurnal to nocturnal feeding activities (similar to what we observed) had been reported for the European minnow (Greenwood and Metcalfe 1998, Metcalfe and Steele 2001) and several salmonid species (Fraser et al. 1993, Heggnes et al. 1993, Riehle and Griffith 1993, Metcalfe et al. 1999). Those species display considerable flexibility in their daily feeding activity patterns and change from diurnal to nocturnal when

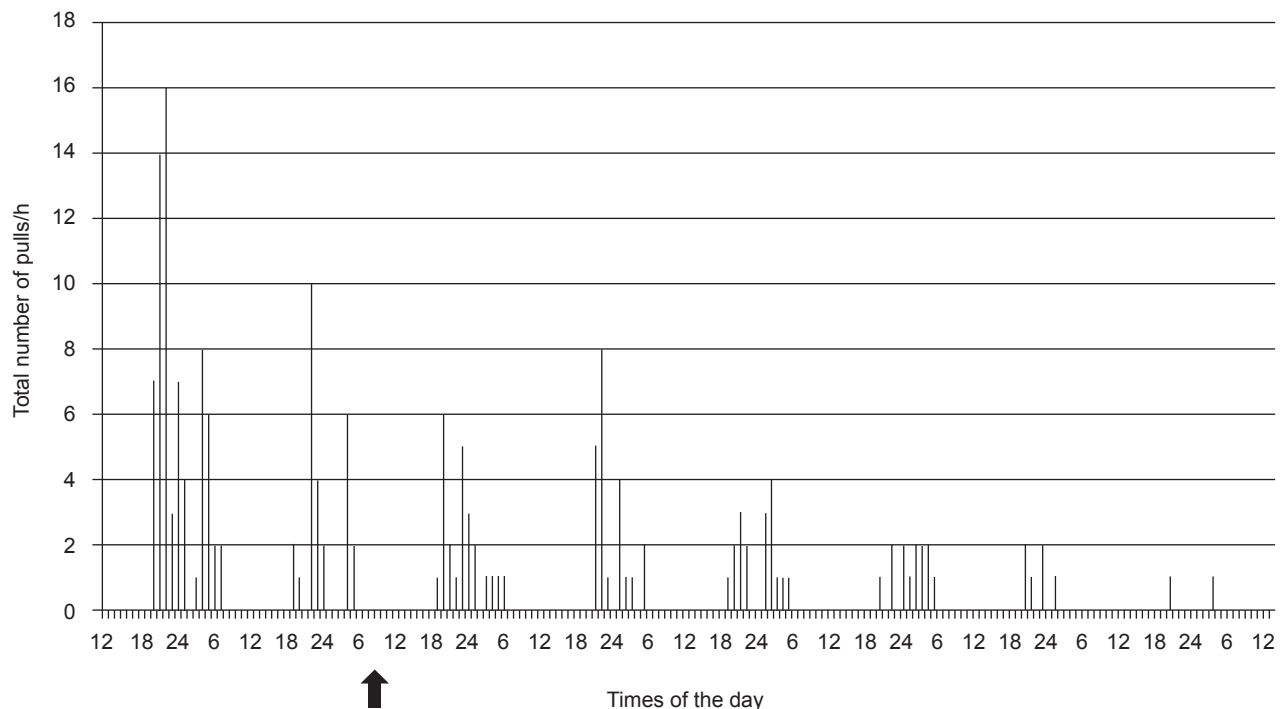


Fig. 3. Results of the control experiment. The blue arrow indicates the time when all food was removed from the self-feeder. The recording of trigger pulls was done for 6 d more after the food had been removed from the feeding apparatus.

water temperatures drop in winter. The change is thought to minimize exposure to predators during the day, because fish are ectothermic and become increasingly slow as temperatures fall. Thus, they would find it harder to escape from endothermic diurnal predators like fish-eating birds, for instance (Fraser and Metcalfe 1997).

Since no actual predators were present during the current experiment, one might argue that the experimental setup of this study was inappropriate. However, wild fish possess inherent behaviours that prepare the fish for the eventuality of an attack by a predator. These behavioural patterns are sensitive to the perceived risk in a fish's surroundings, even if no actual predator is present. Therefore, fish, which have evolved nocturnal feeding activity as an anti-predator response towards diurnal predators, remain nocturnal even if placed in an environment without predators (Metcalfe et al. 1999). Moreover, if the animals are generally inexperienced, they tend to overestimate predation risk, since this is safer than the reverse (Bouskila and Blumstein 1992). With numerous disturbances by people passing the aquarium during the light phase and the associated surface-transmitted vibrations from footsteps, the perch may have interpreted these as a hazard. Since after 19:00 disturbances no longer occurred, it seems that the fish consequently shifted their feeding activity from the 'dangerous' day to the 'safer' night: the diurnal fish became nocturnal.

Another factor which ought to be taken into account is the relatively bright illumination of the experimental aquarium during the illuminated phase (2.4 W/m^2). The perch used in this study were captured from water with very low translucency. Thus, they were adapted to low light levels during the day. Craig (1977) suggested that there might be an optimal light level under which perch feed. Light levels above or below this value could possibly inhibit feeding. He observed the natural activity pattern of the Eurasian perch in Windermere (England), and found that perch were still active at very low light intensities. When the translucency of the water became too high during the winter, and light could penetrate deeper into the water, the perch limited their activity to dusk and dawn. During May, Aug., and Sept., light intensities never reached the critical illumination level due to the high productivity of the water body. Consequently, the translucency of the water remained low. During this time, all perch stayed active throughout the day.

Contrary to this, Jacobsen et al. (2002)

observed that there was no significant difference in the activity between midday and dawn/dusk. Only on day one was there a significant difference when the maximum activity occurred at midday. Moreover, earlier self-feeding experiments with perch have shown a clear diurnal feeding rhythmicity, although the light intensity during the light phase was comparable to that used in our experiment (Anthouard and Fontaine 1998). Jacobsen et al. (2002) suggested that perch feed whenever food is available during daylight. Thus, one reason for activity rhythms to occur would be diel changes in food availability (cf., Csabai et al. 2006). However, since in this study food availability was kept constant, availability should not have had an influence on the feeding activity pattern. This study showed that there must have been factors other than food availability, possibly stress, perceived predation risk, or excessive light intensities during the day, which led to the absence of food uptake during the illuminated phase of the day and the shift to nocturnal feeding.

In this context, it is of importance to note that some fish can display extraordinary individual differences and flexibility with regard to their daily patterns of behaviour. As shown by Sanchez-Vazquez et al. (1996) for goldfish, some individuals were diurnal while others were nocturnal; some changed their feeding behaviours readily while others did not, so the authors concluded that "flexibility in phasing and a certain degree of independence between locomotor and feeding activities could be an adaptive response of the highly adaptable circadian system of fish". For perch, there apparently is a flexibility in response readiness, as shown by Schleuter and Eckmann (2006), that is strongly influenced by interspecific competition during nighttime, but not daylight hours when ruffe (*Gymnocephalus cernuus*) were present together with the perch. Yet, it must be remembered that in our study only perch and no other species were involved.

Additional experiments, similar to those that had involved rainbow trout *Oncorhynchus mykiss* (Mizusawa et al. 2007), need to be carried out to determine the minimum light level below which perch are no longer able (or willing) to feed. By keeping fish under total darkness during the dark phase and, thus, making it impossible for them to visually locate food, it should be possible to show whether perch can become diurnal despite disturbances during the light phase. Studies like the latter were performed on the European minnow by Metcalfe and Steele (2001). Another possible

approach would be to restrict food availability in the feeding apparatus and make food available from it only during the day. The perch would then have to balance their need to increase diurnal feeding against the risk of exposure and fear of attack from predators. At the moment, however, we do not have the answer.

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