

Light-mediated host searching strategies in a fish ectoparasite, *Argulus foliaceus* L. (Crustacea: Branchiura)

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SUMMARY

Argulus foliaceus, an obligate fish ectoparasite, can search for its hosts in both light and dark conditions and uses vision in the light. We have examined what searching mode is used at night, when the infection rate was at its highest, and which stimuli produced by the fish are most important. A change of illumination produced a clear difference in the searching behaviour of adult *Argulus* females. The mean swimming speed and the area explored were 3–4 times higher in the dark, when the parasite employed a cruising search strategy. This changed to an ambush (hover-and-wait) strategy in the light. The swimming activity is accompanied by changes in metabolic costs; the activity of the electron transport system being approximately 25% lower in the light. The most pronounced light-induced differences in host-searching behaviour took place in moderately hungry parasites (starved for 24–96 h). Less motivated (just having left a fish) or exhausted animals did not exhibit any clear differences in swimming speed. Among the external signals tested, fish smell, from both perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*), induced an elevated swimming speed of the parasite. Periodic water movements caused similar but weaker effects. The effects of these stimuli were observed under both light and dark conditions. We conclude that host-searching behaviour of *A. foliaceus* is under internal (state of hunger) and external (illumination and host-induced signals) control and involves all its sensory equipment (vision, olfaction and mechanoreception). Perch (but not roach) reduced their swimming speed in the dark, which make them more susceptible to cruising *Argulus*. Thus the behavioural interplay between hosts and parasites can also influence the infection rate of *A. foliaceus* found on perch and roach in Finnish lakes.

Key words: searching behaviour, *Argulus foliaceus*, ectoparasite, fish host.

INTRODUCTION

Searching for food is one of the most costly activities in aquatic animals, especially if the resources are distributed unpredictably in time and space and the threat of predation is high. In fresh waters, such a situation is common for small free-swimming organisms like crustaceans, fish larvae and insect larvae. Some animals are able to endure periods of scarce resources which considerably lower their activity and metabolism. Others are active permanently, using every opportunity for finding food and avoiding predators.

A. foliaceus, an obligate blood-feeder on many freshwater fishes (Herter, 1927; Kollatsch, 1959; Stammer, 1959), while free-swimming, faces essentially the same problems as most aquatic predators. The parasites can survive without the host for less than 2 days at the larval stage and usually for no more than 1 week when adults (Kollatsch, 1959; our observations). Adults spend

most of their life attached to fish; however, they leave their hosts on a number of occasions, such as during the search for a mating partner, egg laying, at the death of the host, etc. (Kollatsch, 1959; Stammer, 1959). During the period of high reproductive and feeding activity, *A. foliaceus* cannot afford a reduction in its metabolism and, therefore, has to rely on behavioural mechanisms to meet its demands. However, learning would provide no advantage when resources are unpredictable and schooling has never been observed in argulids. Fish blood is the only food source for this parasite and, thus, a widening of the diet is restricted by adding more fish species to their host spectrum. From the viewpoint of the parasite potential hosts are very scarce. Even if the fish is encountered, the success of *A. foliaceus* attacks is low (Mikheev, Valtonen & Rintamäki-Kinnunen, 1998). To extend a 'net of infectivity' (Rea & Irwin, 1995), i.e. to increase encounter rate with a potential host, a solitary searcher like *A. foliaceus* has to maintain a high level of searching activity all the time.

The behaviour of *A. foliaceus* during the light period has been studied previously, and the important role of mechanoreception (Herter, 1927) and

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vision (Mikheev *et al.* 1998) has been demonstrated. On the other hand, the highest rate of infection was recorded in the dark (Mikheev *et al.* 1998). Herter (1927) and Stammer (1959) did not find olfactory cues to be of noticeable importance for host searching. However, it hardly seems possible that host searching in the dark is based only on mechanoreception. Consequently, the need for direct observations on the behaviour of *A. foliaceus* in the dark is evident.

The low host specificity of *A. foliaceus* was mentioned by a number of authors (Kollatsch, 1959; Petrushevski, 1970; Shulman, 1970). Nevertheless, the parasite's preference for juvenile roach, *Rutilus rutilus*, was observed in the light, while juvenile perch, *Perca fluviatilis*, were preferred in the dark (Mikheev *et al.* 1998). The higher reflectivity of the roach provides efficient visual cues in the light, but what causes the high preference for perch in the dark?

The hunger of a predator may affect its searching behaviour in various ways, to the extent of switching between ambush (sit-and-wait) and active (cruising) searching (Bell, 1991). Whether food deprivation modifies host finding in actively searching parasites is unknown. *A. foliaceus* appears to be a suitable experimental animal for such a study.

The main objectives of this paper are to answer the following 3 questions. (1) What behaviour of *A. foliaceus* is responsible for the highest infection rate in the dark? (2) How do external stimuli associated with the presence of fish and hunger influence the host searching activity of *A. foliaceus*? (3) Which behavioural traits of *A. foliaceus* and its hosts result in different host preference in the dark and light?

MATERIALS AND METHODS

Parasite and host species

Parasites were collected from perch, *P. fluviatilis*, of various sizes which were caught weekly in Rutalahti Bay (Lake Päijänne in Central Finland) during July–August 1997. In the laboratory, *A. foliaceus* were gently detached with forceps and held in 20 l glass aquaria filled with filtered lake water under simulated natural photo-periods. Water temperature varied from 18 to 22 °C. Perch of various sizes were used as a host fish. Adult females with a body length 4.3 ± 0.24 mm (mean \pm S.D.) were selected for the tests.

Recording swimming activity

Swimming behaviour of an individual parasite was recorded in a 3 l aquarium with a grid drawn on the bottom and enumerated in X–Y coordinates. The grid consisted of 9 \times 12 squares of 22 \times 22 mm. The

observation aquarium was lined with black plastic to avoid the high reflectivity of glass walls, which were shown to produce numerous secondary local light sources causing fast, erratic movements of the parasites (Mikheev *et al.* 1998). The position of individual *A. foliaceus* was estimated visually in X–Y coordinates every 5 s during a standard 5 min period. In the light experiments, a white-cool tube suspended 1 m above the aquarium provided illumination of 140 lux at the surface. In the dark, a night vision tube and infrared illumination were used. The readings of the parasite position were dictated by an observer to a computer operator who input them using a specially designed recording programme. Subsequently, the data were treated using EXCEL 5.0 and STATISTICA programmes. Swimming speed (mm/s) as an index of the parasite activity was calculated for every 5 min period.

Acclimation experiments

During the pilot observations, it was noted that after an abrupt change of illumination and handling disturbance, the swimming activity of parasites changed and then gradually stabilized. To estimate how long it takes *A. foliaceus* to reach a stable level of activity, a series of 5 trials with 1 parasite in each was carried out. Swimming activity of *A. foliaceus* was recorded for 5 min periods every 15 min starting from the light regime just after the parasite had been detached from its host. After half an hour the light was switched off, and the same sequence of 3 \times 5 min recordings was performed. Then 3 \times 5 min recordings were done after switching the light on. A typical pattern of changes in swimming induced by handling and alterations in the illumination is shown in Fig. 1. Handling resulted in an increased swimming activity, which gradually decreased and stabilized within 30 min in the light. In the dark, initially low activity increased within 15 min of acclimation. After the light had again been switched on, swimming activity returned to the previous low level. Significant differences in swimming speed between subsequent 5 min recordings were observed only within 15 min after the conditions were altered (Wilcoxon matched-pairs test: $n = 5$, $P < 0.05$). For further experiments, tested animals were allowed a 30 min period of acclimation.

Testing external stimuli

The effects of mechanical and olfactory stimuli, as well as the presence of live fish, on the swimming speed of the parasite were tested in both light and dark situations. Mechanical stimulation was produced by sending a shock wave through the aquarium with a piece of semi-rigid plastic tubing (frequency 2 Hz). Chemical stimuli (odour of juv-

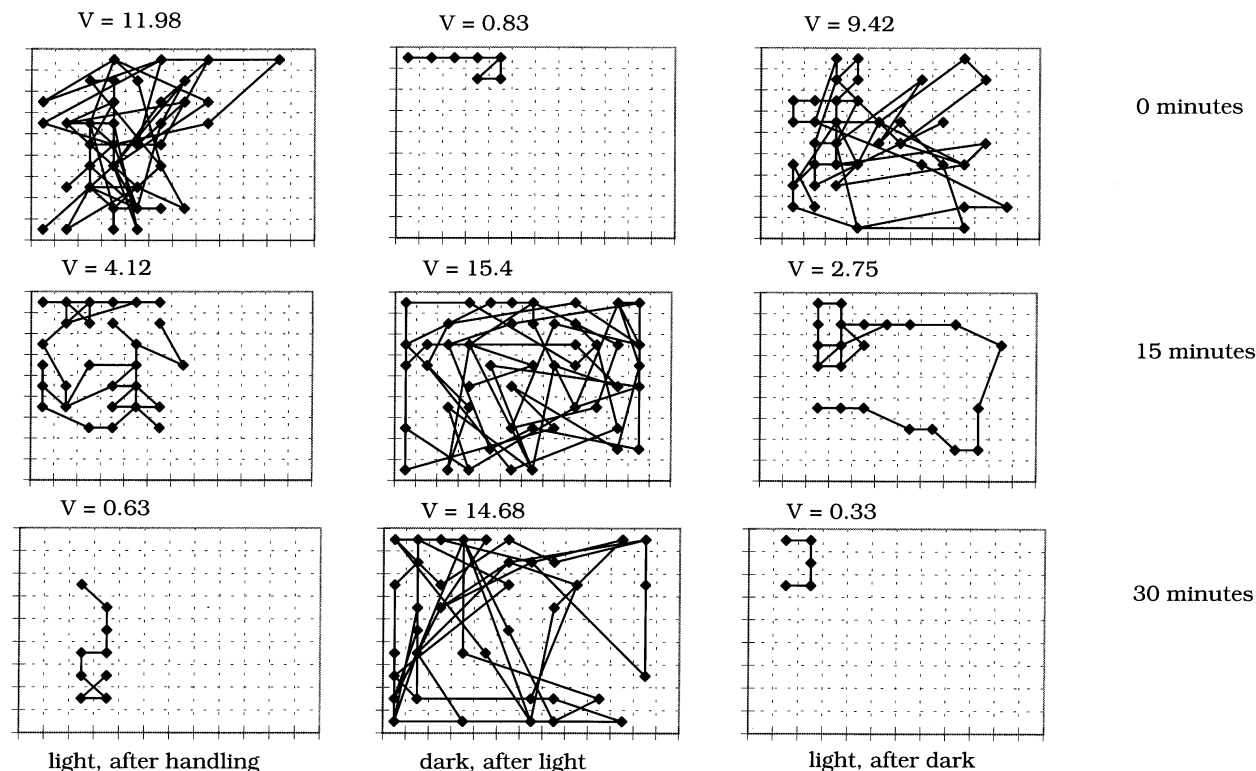


Fig. 1. Acclimation of *Argulus foliaceus* to handling and changes of illumination (an example trial). Each swimming path was obtained from a 5 min recording. V, average swimming speed, mm/s.

enile roach and juvenile perch) were obtained by placing four 0+ fish in 60 ml of filtered lake water for 30 min. Then the fish were removed, and the water was used immediately in the chemical stimulation trial.

An experiment comprised of a sequence of trials. Each trial consisted of 2×5 min periods of recording with a 5 min break in-between. One non-gravid female pre-starved for 2 days was released into the observation aquarium. Recording began after 30 min acclimation. The first trial with no stimulation served as a control. Immediately after that the mechanical stimulation trial was performed. Then the sequence was interrupted by another period of acclimation before the perch odour stimulation trial. Prior to the recording, water with fish odour (60 ml) was gently poured through the plastic tube of 1.5 cm in diameter with the bottom end covered with a fine mesh. After that, the experimental animal was removed, the water changed and the aquarium walls and bottom were thoroughly rinsed. After the period of acclimation, the second control trial was performed for the same parasite. After that one 0+ live perch from the holding tank was introduced into the aquarium, and the standard recordings were performed. The trial was terminated if the parasite attached to the fish. Experiments testing roach odour were carried out as a separate sequence of trials as described above using another set of 8 parasites. The only difference was an addition of a trial to check for a possible effect of the pouring water while introducing

the fish odour. This trial was performed just after the control. All experiments were carried out under both the light and dark conditions. Eight *A. foliaceus* females were tested in both experimental series.

Food deprivation experiments

Six non-gravid females were tested daily for their swimming activity after they had been detached from the host fish. Observations were performed in both light and dark conditions and lasted for 7 days. On the last day only 5 parasites were left.

Swimming activity of the fish hosts in the dark and light

0+ roach and perch were caught in a bay of Lake Päijänne and kept in a holding tank for 3–4 days in order to acclimate them. Recordings were performed in the same observation aquarium under dark and light conditions in the same manner as with *A. foliaceus*. A group of 3 fish were released into the aquarium and the activity of the focal fish was monitored for 10 min, following a 15 min period of acclimation. Nine perch (total length 31 ± 0.38 mm; mean \pm S.D.) and 9 roach (30 ± 0.42 mm) were tested.

Electron transport system activity measurements

Noticeable differences in *A. foliaceus* swimming activity in the dark and light observed during the

pilot study suggested variations in the rate of metabolism. To assess this, measurements of the activity of the electron transport system (ETS) were carried out according to the method of Owens & King (1975). In many ways, direct measurement of oxygen consumption rate would have been preferable. However, available methods demanded confinement of an experimental animal within a rather small volume of water which would restrict *A. foliaceus* in its movement. The body length of females pre-starved for 2 days was measured, and pairs were matched to an accuracy of 0.1 mm. Animals from 8 selected pairs were placed individually in 2 l aquaria with black, non-reflective walls; 1 individual in the dark, 1 in the light. They were kept under these conditions for 10 h, after which each parasite was homogenized in a glass tissue grinder with ETS-B and the obtained volume adjusted to 3.5 ml. Samples were incubated for 10 min with an excess of NADH and NADPH, and the reaction was terminated with a mixture of formaldehyde and orthophosphoric acid. Absorbance was measured in 2 replicates of each homogenate at a wavelength of 490 nm with a Shimadzu UV-240 spectrophotometer.

RESULTS

Light-induced variations in Argulus foliaceus activity

There was a pronounced difference between the *A. foliaceus* swimming activity in the dark and light. This was expressed not only in swimming speed which was several times higher in the dark, but also in the overall behavioural pattern. In the light, *A. foliaceus* was most frequently observed 'hovering' in the water column almost without any noticeable movement or slowly 'gliding'. Such a behaviour lasted from several seconds to several minutes, then the parasite would change its position for the next 'hover station'. In the dark, *A. foliaceus* spent most of the time actively swimming, often with long straight moves. Mean swimming speed in the dark was 4.7 times higher than in the light (Wilcoxon matched-pairs test: $n = 8$, $P < 0.01$) (see controls in Fig. 2). Furthermore, it was much less variable than in the light. Coefficient of variation (CV, %) of the swimming speed within trials was, on average, 41 % in the dark and 109 % in the light.

Effects of the stimuli associated with the presence of fish

Both groups of tested stimuli, mechanical and chemical, plus the presence of live fish, resulted in a significant increase in the swimming speed of *A. foliaceus* (Fig. 2). In order to check if there was an effect of the previous trials on *A. foliaceus* behaviour, control trials were repeated for each tested individual

after the end of the experimental series. The 2 controls did not differ (Wilcoxon matched-pairs test: $n = 8$, $P = 0.751$ for dark and $P = 0.657$ for light conditions). The effect of each stimulus on the parasite swimming speed in the dark and light was compared with the controls using Wilcoxon matched-pairs test. Hydromechanical stimulation resulted in an increase in swimming speed by a factor of 0.39 in the dark ($n = 8$, $P = 0.017$) and by a factor of 1.43 in the light ($n = 8$, $P = 0.012$). Both perch and roach odour produced similar effects with slightly higher values for perch. Swimming speed increased by a factor of 0.65 (dark: $n = 8$, $P = 0.049$) and 3.35 (light: $n = 8$, $P = 0.017$) with the perch odour, and by a factor of 0.55 (dark: $n = 8$, $P = 0.012$) and 2.25 (light: $n = 8$, $P = 0.012$) with the roach odour. Although the experiment with roach odour was performed with a different group of 8 parasites, the controls, both light and dark, did not differ significantly from those of the first group of 8 parasites used to test other stimuli (Mann-Whitney *U*-test: $n = 8$, $P = 0.248$ in the dark, and $P = 0.401$ in the light). Pooled values for both controls are presented in Fig. 2. Pouring 60 ml of filtered lake water (without fish odour) did not produce any significant effect on the swimming speed compared to control (Wilcoxon matched-pairs test: dark, $n = 8$, $P = 0.176$; light, $n = 8$, $P = 0.176$). The effect of the presence of a live 0+ perch was in-between those of hydromechanical and chemical stimuli introduced separately (Fig. 2). In the dark, the presence of a fish increased the parasite's swimming speed by a factor of 0.44 (Wilcoxon matched-pairs test: $n = 8$, $P = 0.017$) and by a factor of 1.59 ($n = 8$, $P = 0.025$) in the light.

Hunger state and activity of A. foliaceus

The swimming speed of *A. foliaceus* changed during a week of being away from the host, both in the dark and light (Fig. 3). Throughout the whole period, activity in the dark was higher than in the light, but the means significantly differed on the 1st (24 h of food deprivation), 2nd, 3rd and 4th days (Wilcoxon matched-pairs test: $n = 6$, $P < 0.05$). Freshly detached parasites (day 0), and those starved for 5 and 6 days, differed, but not significantly, in the dark and light (Wilcoxon matched-pairs test: $n = 6$ (5 on the 6th day), $P = 0.345$, 0.249, 0.345 on the days 0, 5 and 6, respectively).

Light-induced variations in the activity of the fish hosts

Fish swimming activity was tested in the same experimental situation as in our experiments on the infection rate (Mikheev *et al.* 1998). The swimming speed of juvenile perch was significantly lower in the

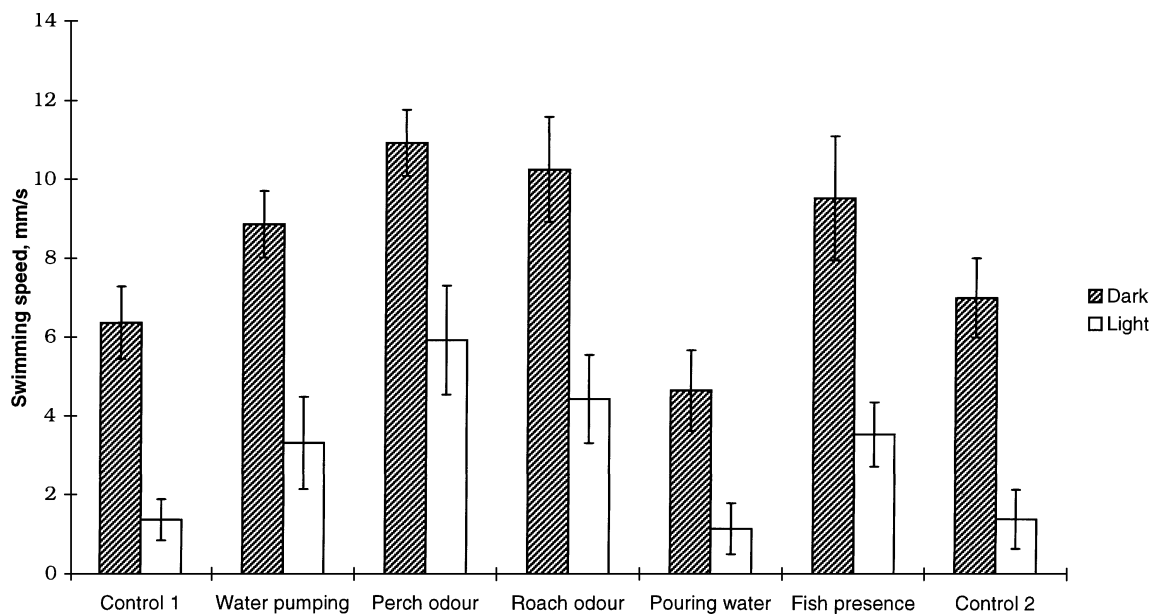


Fig. 2. Effects of external stimuli on *Argulus foliaceus* swimming activity. Mean and s.e. bars are shown. $n = 8$.

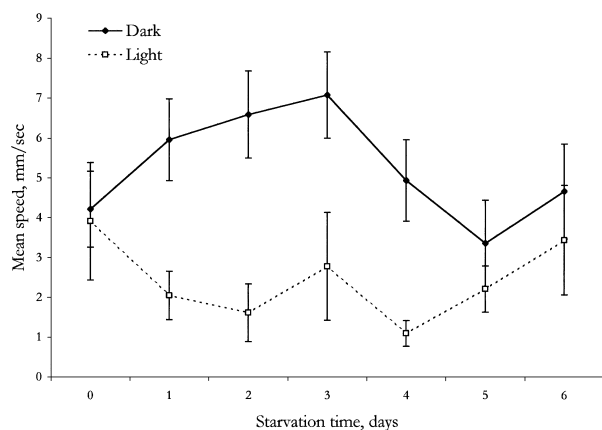


Fig. 3. Changes of *Argulus foliaceus* swimming activity during the period of food deprivation. Mean and s.e. bars are shown. $n = 6$.

dark than in the light (Mann–Whitney U -test: $n = 9$, $P = 0.019$) (Fig. 4). In juvenile roach no significant differences were observed between light and dark trials ($n = 9$, $P = 0.63$). Moreover, perch swimming pattern differed in the dark and light, being more intermittent in the dark, i.e. the stop-and-move was more pronounced. The coefficient of variation of swimming speed within a trial was significantly higher in the dark (Mann–Whitney U -test: $n = 9$, $P = 0.007$). No significant differences in variability of swimming speed were obtained for roach ($n = 9$, $P = 0.45$).

Metabolic costs of *A. foliaceus* activity in the dark and light

A. foliaceus kept for 10 h in the dark showed 25% higher ETS-activity than those kept in the light (Wilcoxon matched-pairs test: $n = 7$, $P < 0.05$). The

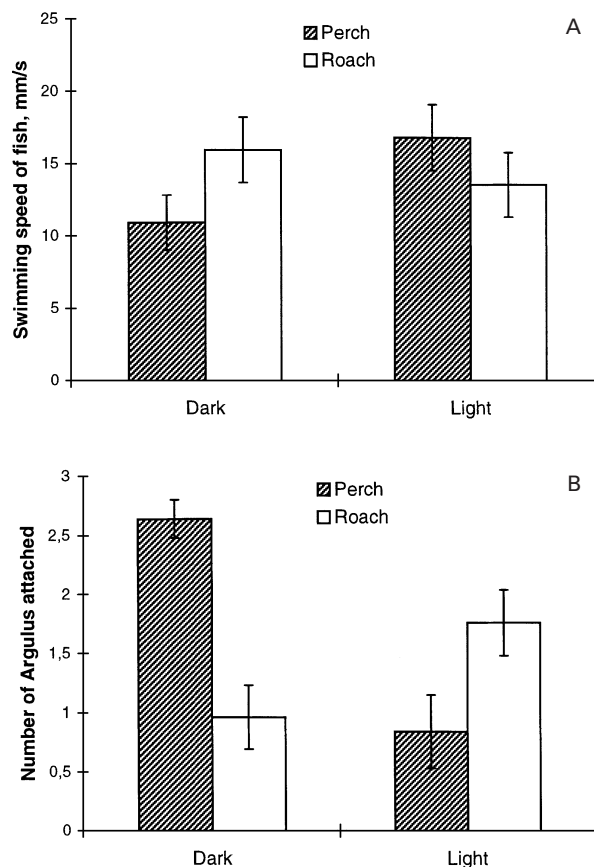


Fig. 4. *Argulus*–fish behavioural interplay. (A) Activity of 0+ perch and roach under experimental conditions. (B) Infection rate of *A. foliaceus* on 0+ perch and roach under similar experimental conditions (from Mikheev, Valtonen & Rintamäki-Kinnunen, 1998 with minor changes). Mean and s.e. bars are shown. $n = 9$.

difference in actual oxygen consumption could be even greater, as ETS is known to be a more conservative measure (Bamsted, 1980).

DISCUSSION

Switching between two strategies in the searching behaviour of A. foliaceus

Two alternative host searching strategies were used by *A. foliaceus*. The first one, observed in the light, is similar to the sit-and-wait (ambush) strategy described in many vertebrate and invertebrate predators, both aquatic and terrestrial (Pianka, 1966; Bell, 1991). In fact, *A. foliaceus* did not sit attached to the substrate but hovered over a very limited area, maintaining an almost vertical stationary (or slowly gliding) position in the water. The second strategy, observed mainly in the dark, is a typical widely foraging (cruising) strategy employed by predators which acquire their prey by extensive searching (Pianka, 1966). Compared to free-living aquatic predators, studies on foraging (host searching) behaviour in parasites are scarce (Poulin, Curtis & Rau, 1990; Lewis *et al.* 1995).

When a foraging strategy fails, animals may alter their behaviour in order to enhance their chances of encountering food or host (Akre & Johnson, 1979; Formanowicz & Bradley, 1987). These switches are often based on extrinsic information, such as prey size and encounter rate (e.g. Davies, 1977; Nakamura, 1985), and intrinsic factors caused by food deprivation (e.g. Crowley, 1979; Inoue & Matura, 1983). The extrinsic information associated with the fish hosts and available to *A. foliaceus* is limited; this is mainly due to the scarcity and unpredictability of their resources. In such a situation, switching between ambush and cruising search strategies induced by changed illumination seems quite an adequate response. Its adequacy is primarily related to diurnal changes in the activity of many freshwater fishes, such as cyprinids, percids and salmonids, which are commonly hosts of *A. foliaceus*. The swimming activity of both the parasites and the hosts complement each other on a diurnal basis; that is, when the host is active, the parasite chooses hide-and-peek strategy, and *vice versa*. Moreover, the lower swimming activity of *A. foliaceus* in the light could be helpful to the parasite in preventing its early detection by the fish host.

As is the case for most small aquatic animals, *A. foliaceus* should be vulnerable to predators while free swimming in the open water. They seem to use neither physical refuges nor shoaling as anti-predatory mechanisms (Kollatsch, 1959; Stammer, 1959; our observations). However, fish, as the most likely potential predators of argulids, usually avoid preying upon them. Some cyprinid fishes were reported to be able to eat *A. foliaceus* (Herter, 1927), but normally this is considered an exception (Bauer, 1970). Our observations on *A. foliaceus* and fish kept together in the laboratory tanks showed that both juvenile perch and roach usually avoided free-swimming parasites, attempting to attack them only

after a rather long period of starvation. In cases where a parasite was caught, it usually was spat out (rejected) immediately. The most obvious reason of such apparent unpalatability appears to be the presence of numerous spines and setae on both the ventral and dorsal surfaces of the body and on the appendages (Rushton-Mellor & Boxshall, 1994). Moreover, it was shown that fish tend to avoid microhabitats with a high abundance of argulids (Poulin & FitzGerald, 1989a); increased shoaling in the presence of parasites was considered as an anti-ectoparasite mechanism (Poulin & FitzGerald, 1989b). Therefore, the risk of predation appears not to be a serious problem for *A. foliaceus* (but see Poulin & FitzGerald, 1989b), allowing it to allocate most of its energy and time to host searching.

The two distinct host searching strategies differ greatly in swimming speed and, consequently, metabolic cost. A reduction in the rate of metabolism in the light enables *A. foliaceus* to save energy reserves during the period when the potential hosts are most active and might more successfully avoid parasite attacks. In the dark, *A. foliaceus* has to risk high energy losses, as this is the most favourable time for host finding.

External and internal control of A. foliaceus searching activity

A. foliaceus considerably increased their swimming activity when exposed to stimuli associated with fish presence, both in the dark and light. The effect was even more pronounced in the light; this clearly indicates that parasites remained highly motivated with respect to host searching. Reduced swimming activity in light conditions may be a component of the *A. foliaceus* anti-predator behaviour. However, if this were the case, parasites would not be so markedly activated by olfactory and hydromechanical stimuli.

The paramount role of visual cues for *A. foliaceus* host searching in the light has already been demonstrated (Mikheev *et al.* 1998). Among the external stimuli tested in the present study, chemical cues were found to be more efficient than hydromechanical ones, both in the dark and light. Chemical signals were shown to be more persistent than mechanical ones and to allow species-specific identification (Dodson *et al.* 1994). The presence of live perch influenced *A. foliaceus* activity less than perch odour, especially in the light, although the differences were not statistically significant. Most likely a combination of sensory stimuli is used to detect a target animal (Peckarsky, 1982; Blake & Hart, 1993). However, we have not observed such an effect with fish as a source of combined stimulation. One of the reasons for this might be related to non-quantified levels of stimulation, as the concentration of chemicals is known to influence the responses of stimulated animals (Stein, 1979).

In this study a hierarchical organization of *A. foliaceus* host searching behaviour could be deduced. Firstly, parasite activity is controlled by light–dark changes which result in the switching between sit-and-wait and cruising strategies. Secondly, superimposed upon the illumination rhythm that determines the search strategy are external cues associated with host presence that modify local activity. High activity levels are adaptive only if the expected probability of making contact with a host is high (Poulin *et al.* 1990).

An animal's physiological state can modify its response to external cues. *A. foliaceus*, freshly detached (engorged) from the fish host, demonstrated no distinct light and dark search strategies. However, the described sit-and-wait and cruising strategies soon established. They were most pronounced when the parasites were moderately starved; when exhausted, *A. foliaceus* tended to abandon the two distinct strategies and showed no difference between light and dark activities. Such an impaired behaviour was observed shortly before the free-swimming parasites started to die of starvation. Contrary to many predators, which switch between ambush and active searching modes depending on their state of hunger (Bell, 1991), *A. foliaceus* employs the two light-induced search strategies permanently, with the exception of complete satiation and extreme starvation.

Behavioural interplay between hosts and parasites

Selectivity as an ecological phenomenon is determined not only by the predator's (parasite's) preference, but also by the behaviour of their prey (hosts) which influences their vulnerability (e.g. Smith & Mead, 1974; Hassell & Anderson, 1984). In our recent paper (Mikheev *et al.* 1998), considerably different infection rates of *A. foliaceus* on perch and roach were reported for dark and light conditions. We postulated that fish swimming behaviour in the dark could be responsible for the observed host preference. Our present results showed that perch markedly reduced its swimming speed and swam more intermittently in the dark, which made it more susceptible to actively searching parasites. The swimming behaviour of roach in the dark was much the same as in the light. Its faster and continuous swimming in the dark reduced the parasite's search success. However, due to their brightness (higher reflectivity), roach became more heavily infected in the light (Mikheev *et al.* 1998). The overall infection rate on perch was found to exceed that on roach, which is in agreement with field data (Valtonen, Holmes & Koskivaara, 1997). Thus, no additional mechanisms, such as innate preference for a host species, are needed to explain the higher infection level on perch. In the field, other factors (water temperature and dissolved oxygen concentration)

can influence fish distribution and, thus, their spatial overlap with parasites, and infection levels (Poulin & FitzGerald, 1988).

The availability of resources in time and space constitutes the major environmental constraint in terms of searching success and is an important selective pressure in relation to the efficiency of searching behaviour (Bell, 1991). The higher activity of *A. foliaceus* in the dark can be explained in adaptive terms, whereby animals search when it is most profitable to do so (Daan, 1981). Our results on the behaviour of *A. foliaceus* and its potential fish hosts illustrate that not only variations in search strategy induced by light but also an interplay between host and parasite behaviour determine the host searching success and, consequently, the observed selectivity patterns.

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