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Responses of *Acilius sulcatus* (Coleoptera: Dytiscidae) to chemical cues from perch (*Perca fluviatilis*)

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Abstract In this study we tested the hypothesis that the presence of chemical stimuli from a hungry predator would initiate anti-predator responses, while stimuli from a satiated predator would not. We used chemical stimuli released from starved perch (*Perca fluviatilis*) and from satiated perch (predator). As prey we used adult *Acilius sulcatus* (Coleoptera: Dytiscidae). The reaction of the beetles to different predator conditions was tested during daytime. We also tested the reaction to starved perch during the night. *A. sulcatus* activity decreased when it was exposed to stimuli released from starved perch during daytime when visibility was poor, due to the presence of artificial vegetation. There was, however, no reaction to satiated perch under the same experimental conditions. These results indicate that *A. sulcatus* can discriminate between chemical cues from hungry and satiated fish predators. When visibility was good and the concentration of chemical cues was constant, the beetles did not react to starved perch in the daytime, but their activity decreased at night in response to stimuli released from starved perch. Visual as well as chemical cues seem to be important for detecting a potential predator. When visibility is good, beetles seem to rely on visual stimuli, while in darkness they seem to use chemical stimuli to detect the presence of predators.

Key words Chemical cues · Predator avoidance · Hunger · Satiation · Day-night

Introduction

During evolution, predators and prey have developed ingenious methods for detecting each other. Predation and avoidance of predation are a matter of life and death to both predators and prey, so it is crucial to use every possible sense in this encounter. Both visual and non-visual communication are important components in predator-prey systems. Most likely a combination of sensory stimuli is used to detect a predator (Peckarsky 1982; Blake and Hart 1993; Ode and Wissinger 1993), with one stimulus being dominant (Peckarsky 1982). Scrimgeour et al. (1994) found that nymphs of the mayfly *Baetis tricaudatus* showed a strong behavioural response to a mixture of predaceous-fish smell and macerated mayfly combined with hydrodynamic stimuli from fish models. Similarly, Crowl and Covich (1994) found that a combination of chemical and tactile cues resulted in very strong movements in the freshwater shrimp *Atya lanpries*, whereas chemical cues alone elicited only a relatively weak response. In aquatic macro-invertebrates, the most common behavioural response among prey in the presence of a predator is reduced activity (Williams and Moore 1985; Andersson et al. 1986; Holomuzki and Short 1988).

The ability to detect a predator by non-visual cues means that the prey has time to initiate escape behaviour before the actual encounter. If the predator is a visual hunter, the prey should use defence mechanisms that make it less visible, for example cryptic coloration (Main 1987). Fish can be “auditory-hunters” (Kalmijn 1988; Rogers and Cox 1988) or they can use their lateral lines when locating prey (Hoekstra and Jansen 1985, 1986). If the predator is far away, fast prey should “run away”, whereas a slow-moving prey should make itself “invisible”, for example by becoming immobile (Williams and Moore 1985; Malmqvist 1992). Reduced activity and shelter seeking can result in reduced foraging, reduced mating activity and less investment in offspring (Holomuzki and Short 1988). Because mediating escape behaviour every time a presumptive predator comes

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along is costly, it should be profitable to identify and characterise an enemy. Chemical signals are more persistent than mechanical ones, and allow species-specific identification of predators (Dodson et al. 1994). According to Appelberg et al. (1993) crayfish can, through chemical stimuli, distinguish between predators and non-predators, and between hungry and satiated predators. Alexander and Covich (1991) and Phillips (1978) found that the snail *Physella virgata* and sea urchin *Strongylocentrotus purpuratus* were able to distinguish between inactive, and active, hungry predators.

Dytiscid beetles have superposition eyes, the most effective of invertebrates eyes. However, they are not very useful in environments with low visibility because then, only large objects can be detected and the image-forming ability is low (D.E. Nilsson, personal communication). Underwater, scattering by suspended particles, such as sand and plankton, often reduces horizontal visibility from 50 m or so in clear water to small fractions of a metre when it is turbid (Lythgoe 1979). Chemoreception (in both aqueous and gas phases) is very well developed in many adult dytiscids (Hodgson 1953 and references therein). Some studies on the distributions of fish and invertebrates have shown that dytiscid beetles occur sparsely in lakes with fish, possibly because they are preyed upon. Another possibility is that dytiscid beetles prefer fish-free lakes, or avoid habitats where fish are abundant (Eriksson 1979; Stenson 1979; Larson 1990; B.M.A. Wagner 1997; B.M.A. Wagner and L.-A. Hansson, unpublished data). As many adult dytiscids can fly and choose their habitat, it is possible that they use chemical senses to detect the presence of fish, as has been suggested for some other invertebrates (e.g. Dodson et al. 1994)

Our aim was to study whether the dytiscid beetle *Acilius sulcatus* uses chemoreception to detect fish, and if it changes its activity in response to predator cues. Our studies were performed in aquaria and in a fluvium where the beetles were exposed to water scented by fish. We examined if *A. sulcatus* could distinguish between hungry and satiated predators (perch, *Perca fluviatilis*). Further, we investigated whether the beetle reaction to hungry perch differed between day and night. We hypothesised that *A. sulcatus* should be able to detect fish through chemical stimuli and to discriminate between hungry and satiated predators and, if so, it should show a stronger reaction to chemical cues from hungry perch at night due to poor visibility.

Materials and methods

A. sulcatus (Leach) belongs to the Dytiscidae, and is common in ponds and small lakes in Sweden (personal observations). The adult beetles can fly and can search for new oviposition sites (Galewski 1971). Perch is one of the most common fish species in ponds and small lakes in Sweden. Perch go through ontogenetic niche shifts in diet, feeding first on zooplankton, then switching to benthic macroinvertebrates and finally becoming piscivorous (Johansson and Persson 1986). When about 15 cm long, perch may

include both macroinvertebrates and fish in their diet. Because of its wide distribution, *A. sulcatus* should often be exposed to perch, and therefore might be expected to have developed anti-predator behaviour decreasing the risk of predation.

Aquarium experiments

Our aim was to determine the response of adult *A. sulcatus* to chemical substances released by hungry and satiated perch during daytime. The experiment was conducted in the laboratory in May 1993. There were two treatments, each replicated nine times: (1) satiated perch; (2) hungry perch. We used nine individual *A. sulcatus* as prey, each beetle being used in both treatments. The experiments were recorded on video. One replicate with hungry perch was excluded due to technical problems.

All animals were collected in Scania, southern Sweden in May 1993. The animals were kept in aerated tap water for 2–7 days before the start of the experiments (water temperature 16–20°C, light:dark regime 12:12 h). *A. sulcatus* was fed frozen chironomid larvae. To satiate perch predators, they were fed roach (*Rutilus rutilus*) and frozen chironomid larvae. The hungry perch were not fed at all.

The experiments were performed in three aerated aquaria (volume 100 l, water depth 35 cm), each with artificial vegetation (plastic threads knotted at 3/dm²). The bottom was covered with a 1-cm-thick layer of gravel. The front of each aquarium was divided into 30 quadrats (9.2 × 9.2 cm) for analysis of *A. sulcatus* movements. Tap water was pumped from two separate aquaria, one containing fish (either hungry or satiated perch) and one without fish, to the experimental aquaria through plastic tubes at a flow rate of 1 l/min.

All aquaria were filled with water 18 h before the start of an experiment. The fish (perch; two–four individuals with a total weight of 400–500 g) were placed in separate aquaria (volume 100 l) 18 h before the start of an experiment (the fish were not fed during this time). *A. sulcatus* (one individual/aquarium) was stocked 90 min before the start of an experiment. The water temperature was 16–20°C.

Each trial lasted 30 min. During the first 15 min, untreated tap water was added to the experimental aquarium. Water from the aquarium with fish was added during the remaining 15 min. We added fluorescent dye, after the experiment, to see the diffusion of the scented water in the aquaria. Although it took 4 min for the water to disperse through the whole aquarium, we assumed that there was a gradient of odour from the side where the water was pumped in to the opposite side of the aquarium during the whole experiment.

Analysis

Twenty minutes per replicate were used for analysis. 10 min before and 10 min after the switch from ‘pure’ water to water with fish (including the 4 min when the odour was dispersing). The activity of beetles was measured as the number of quadrats passed per minute. The Wilcoxon signed-rank test (two-tailed Siegel 1956) was used to test the difference in activity of *A. sulcatus* before and after the addition of scented water.

Fluvium experiments

The aim of the fluvium experiments was to determine the reaction of *A. sulcatus* to chemical substances released by hungry perch during day and night. The experiment was conducted in August 1993. We tested the reaction of *A. sulcatus* to odour and visibility, each factor with two levels (odour: water scented by perch, or ‘pure’ water; visibility: day or night); each treatment level was replicated eight times. Piscivorous perch were collected from southern Sweden near Uppsala and *A. sulcatus* from the same pond as for the aquarium experiments. All animals were collected in

August. The animals were kept in aerated tap water (temperature 8–11°C, light:dark regime 13:11h). The beetles were fed frozen chironomid larvae. Perch were starved for 3–5 days before the experiments.

The fluvium in which the tests were performed (Fig. 1) was an artificial stream with laminar flow (Olsén and Höglund 1985; Olsén 1986). Equal amounts of water (350 ml/min) from each of two aquaria (with and without fish) were pumped into opposite halves of the fluvium, to create two longitudinal halves with different water quality without any gradual gradient between them. Every 30 min, the water supply was switched automatically from one side to the other. A video camera was installed above the experimental area, and connected to a computer which registered the position of the beetle in the experimental area every second and calculated the locomotory movement (m) and time spent in each longitudinal section (cf. Winberg et al. 1993; Bjerselius et al. 1995). The total experimental area of the fluvium, which measured 23.3 cm × 33 cm × 9 cm (length × width × depth), was limited upstream and downstream by two fine-mesh plastic nets, and covered by a glass plate. During daytime experiments, the experimental area was illuminated with 2.1 lx. Two 20-W halogen lamps equipped with red glass filters, which allowed transmission of wavelengths longer than 750 nm, were used as light sources for the video camera. We assumed that the beetles could not perceive red light. There was also a filter in front of the video camera that did not allow any wavelengths shorter than 670 nm. One *A. sulcatus* was placed in the experimental area 5 min before the start of an experiment, and the fish was acclimatised for about 1 h in the donor aquarium, which was supplied with a continuous flow of water. For daytime experiments, a beetle was used only once, while individuals that had participated in one former daytime experiment were randomly chosen and used during the night, giving a total of 16 beetles used in the experiments. The total biomass of perch was 200–300 g (three–four fish).

Each trial lasted 2 h and the computer made one registration of the position of the beetle every second, giving a total of 7200 registrations/replicate. The water from the donor aquaria (with fish/without fish) switched side every 30 min and a test with dye added

to the water current showed that it took 14–15 min before all the “old” water was eliminated from the experimental area. The water was switched to eliminate any disturbances in the room affecting the beetles choice of side.

Analysis

We calculated reaction values (Rv), a measure of the choice of water quality by *A. sulcatus*, and locomotory activity (m/2 h). Rv was calculated as $(NA - NB) / (NA + NB) \times 100$ where NA is the number of times the beetle was recorded in water quality A and NB the number of times in water quality B (Olsén 1986, 1989). Rv calculations were made during the last 15 min of each 30-min period. Student's *t*-test was used to compare mean Rvs (MRv) obtained during each type of testing with the theoretical MRv for an indifferent reaction equal to zero (Olsén 1985). The effects of odour (two levels: “pure” water or water scented by perch) and visibility (two levels: day time or night) on *A. sulcatus* locomotory activity were examined in a two-factor analysis of variance (Zar 1984).

Results

Aquarium experiments

A decline in locomotory activity was found when *A. sulcatus* was exposed to water scented by hungry perch (Wilcoxon's signed-rank test, $P = 0.01$). However, the beetles did not react to chemical substances from satiated perch (Fig. 2).

Fluvium experiments

Odour or visibility alone did not affect the activity of *A. sulcatus* (ANOVA, $P = 0.1614$ and $P = 0.2949$, respectively). However, a significant interaction occurred when the two factors were combined (ANOVA, $P = 0.0087$, Table 1). The lowest activity was found

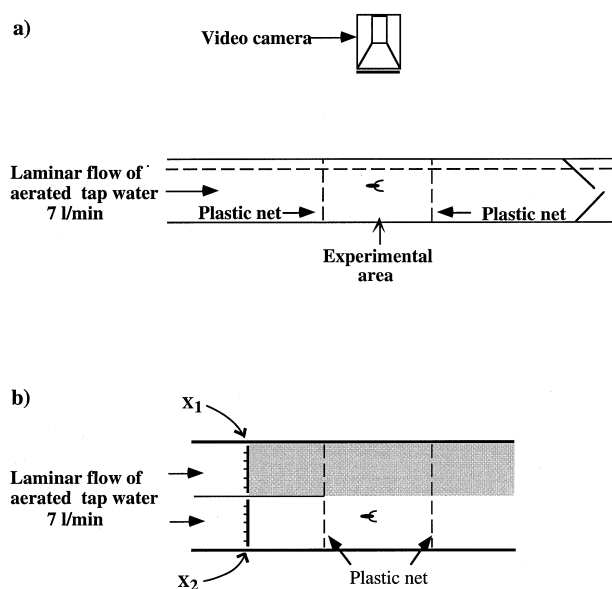


Fig. 1 The fluvium seen from the side (a) and above (b). Modified from Winberg et al. (1993). The experimental area is limited upstream and downstream by two nets. The water (7 l/min) runs upstream through the experimental area; “fish water” or “pure water” (0.35 l/min) was added at alternately X1 and X2. In the experimental area, *A. sulcatus* is able to move freely and can thereby choose a side (water quality)

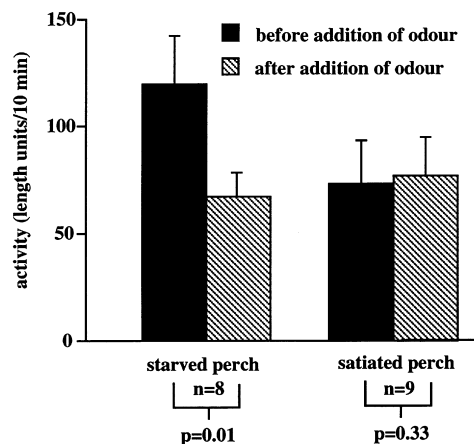


Fig. 2 Activity (mean + SE) of *Acilius sulcatus*, counted as the number of quadrats passed during 10 min before and after adding “fish water” in the aquarium experiment. The *P* values show the result of the Wilcoxon signed-rank test of the difference in activity before and after adding “fish water”

Table 1 Two-way ANOVA table of the locomotory activity of *Acilius sulcatus* in relation to odour (water scented by perch, or “pure” water) and visibility (daytime or night)

Source	df	MS	F	P
Odour (A)	1	7 022.90	2.07	0.1614
Visibility (B)	1	3 868.04	1.14	0.2949
A × B	1	26 977.00	7.95	0.0087
Error	28	3 394.95		

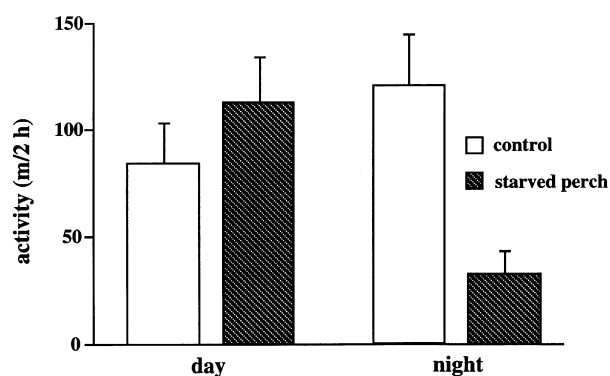


Fig. 3 Activity (metres moved/2 h) for *A. sulcatus* in the different treatments in the fluvium experiment (mean + SE)

Table 2 Reaction values by choice of water quality (mean ± SE) in the fluvium experiments. A positive mean reaction value (MRv) means that *A. sulcatus* spent more than half of the experimental time in the water without fish odour. MRvs are compared with the theoretical MRv for an indifferent reaction (MRv = 0) by Student's *t* test

Treatment	n	MRv ± SE	P
Daytime, control	8	-5.9 ± 8.4	>0.05
Daytime, hungry perch	8	+1.5 ± 5.4	>0.05
Night, control	8	+0.9 ± 10.9	>0.05
Night, hungry perch	8	+8.5 ± 13.0	>0.05

when *A. sulcatus* was exposed to water scented by perch at night (Fig. 3). The beetles did not avoid the side of the experimental area with water scented by perch but were randomly distributed in the experimental area (Table 2).

Discussion

The importance of chemical cues in aquatic predator-prey systems is well known (e.g. Dodson et al. 1994). However, there is no study to our knowledge revealing anti-predator responses by adult dytiscid beetles responding to chemical cues from predatory fish. The present results suggest that *Acilius sulcatus* uses chemoreception when detecting predators. Using chemical signals should allow species-specific identification of predators to ensure that escape behaviour is not initiated unnecessarily, and thus to costs in terms of decreased opportunities for foraging.

The activity of *A. sulcatus* decreased significantly when exposed to water from hungry perch during daytime in the aquarium experiment, and at night in the fluvium experiment. The results support our hypothesis that *A. sulcatus* reacts to chemical substances from fish. The observed drop in activity is a common response among aquatic invertebrates upon detection of a predator (Peckarsky 1982; Holomuzki and Short 1988; Malmqvist 1992).

There may be several reasons for the differences in daytime results between the aquarium and the fluvium experiments. The design of the experimental areas may have had an influence on activity. In the aquarium experiments, we tried to mimic the “natural” environment, with sediment and artificial macrophytes which functioned as refuges. In the fluvium, the surroundings were as “clean” as possible, so as not to disturb the laminar flow. The lightly scored bottom plate was the only place to which diving beetles could attach. In the aquaria, they seemed to prefer the bottom substrate to moving freely. When visibility was poor, as in the aquarium experiments, the beetles seemed to prefer to use chemical rather than visual stimuli. The beetles in the daytime fluvium experiments had a full view over the experimental area and may therefore have mostly relied on visual cues.

Prey responses may also vary with the concentration of chemicals emitted (Stein 1979). Concentrations of behaviour-modifying chemicals may depend on the size of the predator and the distance from the prey (Phillips 1978). The concentration of chemical substances in the water was probably higher in the aquarium experiments than in the fluvium experiments, since the biomass of fish was higher and the fish spent more time in the “donor aquaria” than they did in the fluvium experiments. Furthermore, in the aquaria, the concentrations of chemical substances probably increased during experiments, and may have been interpreted by the beetle as an approaching predator. The predator should therefore have been experienced as more threatening and closer than in the fluvium, leading to a greater change in activity in the aquarium experiments.

There was a decrease in locomotion in response to chemical substances from hungry perch during the night but not during the daytime in the fluvium experiments. Appelberg et al. (1993) found similar results in an experiment with the noble crayfish (*Astacus astacus*) exposed to both chemical and visual stimuli from predatory fish (perch). At night, *A. sulcatus* probably relies completely on chemical senses to detect predators. Many fish active at night locate their prey by hydrodynamic stimuli (Hoekstra and Janssen 1985, 1986), and thus a decrease in activity then is a good anti-predator strategy.

Chemical substances from satiated perch did not produce any change in activity, supporting the hypothesis that *A. sulcatus* can distinguish between hungry and satiated predators. A satiated predator constitutes no threat to a presumptive prey. Similarly, Appelberg et al. (1993) found that crayfish exposed to chemical sub-

stances could distinguish between hungry and satiated perch. The mechanism behind these responses is not known, but it may be due to a substance liberated in conjunction with the digestive process, excreted in both urine and faeces, that gives the prey information about whether or not the predator is hungry.

In the fluvium experiments, *A. sulcatus* did not avoid the water scented with fish. The beetles may have had difficulty distinguishing between the different water qualities maybe because there was no chemical gradient. Williams and Moore (1985) suggested that a prey organism exposed to predator odour at a fixed concentration for a long time does not need to take precautions, because the predator is not approaching. According to this theory, in the daytime fluvium experiments, *A. sulcatus* should calm down after a while and consider the danger "not impending", especially as it had a good view and did not see the perch anywhere. At night, however, it has to be more cautious, as discussed above.

Many studies have shown that fish may affect dytiscid populations. Larson (1990) found that, among macro-invertebrates, dytiscids had the lowest frequency of co-occurrence with fish. The introduction of fish to a pond can lead directly to the total disappearance of diving beetles, probably through predation on larvae (Macan 1966). Many studies have shown that the abundance of diving beetles increases in the absence of fish (Eriksson 1979; Healey 1984; B.M.A. Wagner 1997). Some adult diving beetles seem to be protected against predation by their size, cuticle and defence secretion (Pritchard 1964; Griffiths 1973), but Wilson (1923) and Eriksson (1979) claimed that adult diving beetles are easily eaten by fish. Hartley (1948) and Macan (1966) found larvae of *A. sulcatus* in perch stomachs. The fact that perch eat dytiscid larvae indicates that natural selection for an appropriate behaviour in *A. sulcatus* should be pronounced.

A possible reaction that we could not observe would be the secretion of chemical defence substances by the beetles. Many adult dytiscids produce toxic substances making them unpalatable to fish (Schildknecht 1971; Schildknecht and Tacheci 1971; Gerhart et al. 1991). There is a great variety of these toxic substances ranging from steroids to sesquiterpenes, alkaloids and nucleoproteids (from prothoracic glands) up to aromatic and aliphatic compounds (from pygidial glands) (Dettner 1987). One contribution to the difference between the results in the aquarium and fluvium experiments could have been seasonal variation in the amount of chemical defence substances. Newhart and Mumma (1978) studied the seasonal variation of defence substances in *A. semisulcatus*, a species closely related to *A. sulcatus*, and found that all steroids were at much higher concentrations in August than in May. Therefore, because the concentration of defence substances produced by *A. sulcatus* may have been higher during the fluvium experiments, the beetle may not have had to be as cautious as in the aquarium experiments. Some *A. sulcatus* fly to temporary ponds during spring and

early summer (Wiggins et al. 1980). They must, however, spend winter in permanent waters, often with fish, possibly explaining the high concentration of defence substances in the autumn. The seasonal fluctuations in the titres of defensive chemicals is mainly due to adult age differences and a seasonally varying age structure of adult dytiscid populations (Dettner 1987). However, both predation pressure (Newhart and Mumma 1978) and food supply (Miller and Mumma 1974) have been discussed as factors influencing seasonal variation in defence substances.

In conclusion, the results of our study indicate that *A. sulcatus* uses chemoreception to detect predators. The beetles can distinguish between satiated and hungry fish predators by means of chemical substances. Our results suggest that during daytime, *A. sulcatus* dytiscids use a combination of visual and chemical cues to detect danger, while chemical cues are most important during the night.

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