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Development and Swimming Behaviour of the Water Beetle *Acilius sulcatus* L. (Coleoptera, Dytiscidae)

by M. Gewecke & V. Rostock

Abstract: At 18°C *Acilius sulcatus* (L.) requires 8 weeks for development from egg to imago. After the imaginal moult, the median weight is 2 mN, increasing in the following 2 weeks by about 25%. Although the larvae are cannibalistic (depending on availability of food, i.e. *Daphnia* and chironomid larvae), they could be cultured in groups of about 20 individuals of the same stage. To investigate swimming behaviour, imagines were tethered to a strain gauge and stimulated by the current of a water canal. Independent of age, the initial high values (median) of stroke frequency (6–8 Hz) and stroke angle (120–140°) of the hindlegs decrease with swimming duration (3–4 Hz, 90–120°). The “swimming speed” depends in tethered (“thrust-compensated” conditions), as well as in free swimming animals, on the leg-stroke frequency and angle. In free swimming animals the leg-stroke frequency is about 5 Hz, the stroke angle 90°, and the swimming speed 12 cm/s (from high-speed films). The antennal posture is not dependent on the “swimming speed”.

Key words: Coleoptera Dytiscidae – *Acilius sulcatus* – development – culture – strain gauge – water canal – high-speed film – leg-stroke frequency, leg-stroke angle – swimming speed – antennal posture.

Introduction

Generally the study of insect physiology relies on laboratory culture of the experimental animal. This is possible in species of Orthoptera, Coleoptera, Hymenoptera, Lepidoptera and Diptera. In the majority of insects the life cycle and the respective environmental factors are too complicated to be reproduced in the laboratory. In seeking a model animal for our behavioural investigations of insect locomotion, we decided to work with Dytiscidae because these insects are known to be good swimmers and fliers (WESENBERG-LUND, 1912, 1943; KORSCHELT, 1924; NACHTIGALL, 1960, 1964, 1980) and their culture and metamorphosis had already been investigated qualitatively by CZEPA (1907) and BLUNCK (1913).

The laboratory culture and development of flight behaviour of the giant water beetle *Dytiscus marginalis* (L.) is described in a separate article (BAUER, 1986). The present paper aims at analysing the breeding, development and swimming behaviour of *Acilius sulcatus* (L.). Especially the relationships between imaginal age, swimming duration, leg-stroke

frequency and angle, and swimming speed are analysed in tethered as well as in free swimming animals.

Materials and methods

11 males and 8 females of *Acilius sulcatus*, collected in the field, were held for 1–2 years in aquariums at 17–20°C and fed with fresh meat. In 1981 the females layed eggs in moss above the water surface on a piece of slate in the aquarium. The larvae were fed with *Daphnia* and larvae of *Chironomus*. Pupation occurred in containers filled with soil.

Experimental animals (16 imagines) were tethered to the lever arm of a strain gauge, and dipped into the water current of a canal (GEWECKE, 1985). If the thrust of a tethered swimming water beetle compensates its hydrodynamic drag, the speed of the water current equals the "swimming speed" of the animal in relation to the water ("thrust-compensated swimming"). The leg-stroke frequency was recorded from vibration of the strain gauge. The antennal posture and stroke angle of the hindlegs (proximal tarsal joint marked with a white dot) were measured from photographs taken from above (Contarex SE, Zeiss).

10 free swimming females of *Acilius* were photographed (some s after the start) from above by a high-speed camera (Stalex WS-2, 120 frames/s). From the films the stroke frequency and angle of the hindlegs, and the swimming speed were measured by frame-by-frame analysis (Weinberger projector 224 A; BAKER et al., 1981).

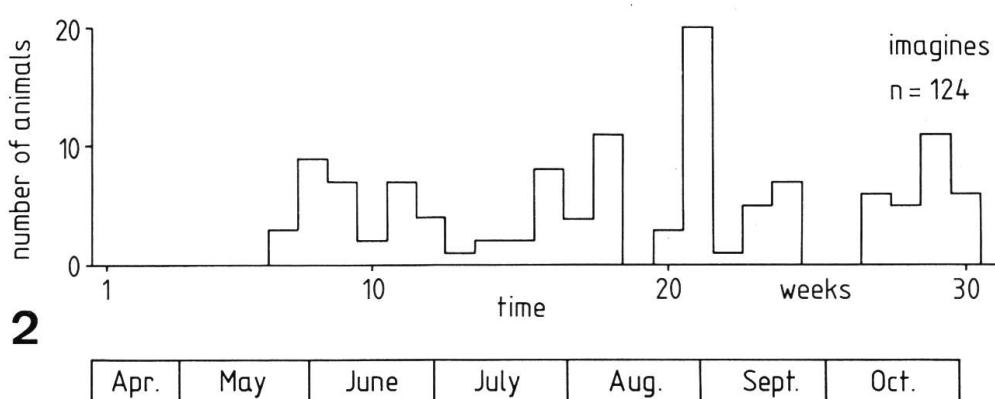
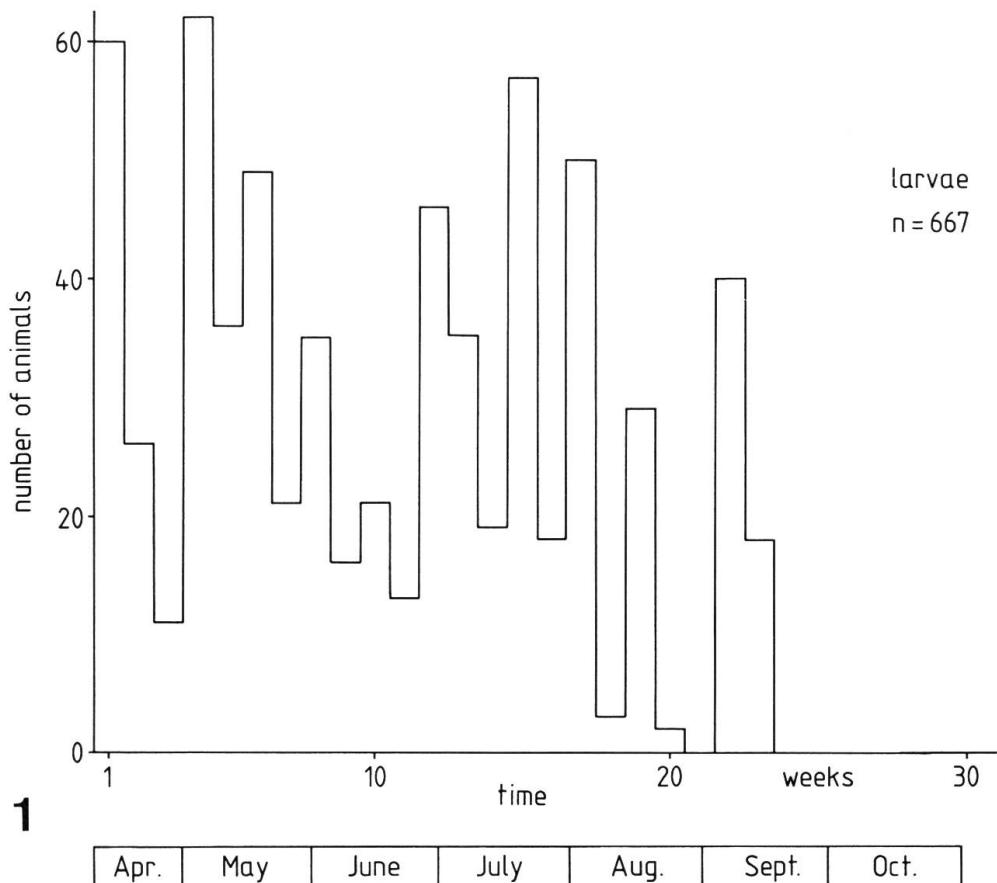
Statistical tests, linear regression and correlation between different parameters were computed after CROXTON (1953) and SACHS (1978).

Results

1. Laboratory culture

667 first instar larvae were collected from breeding aquariums between April and September (Fig. 1). 124 of these larvae (18.6%) reached the imaginal stage (61 ♀, 63 ♂) between May and November (Fig. 2). Although cannibalism occurs in larvae (with shortage of food), the percentage of fully developed beetles was smaller in a group in which individuals were reared separately (13%) than in a second group with about 20 individuals together in each aquarium (25%). The median body weight of the animals directly after the imaginal moult was

about 2 mN, and 2.5 mN two weeks later, i.e. considerably less than that of the fully developed adults collected in the field (3.5 mN).



Figs 1-2: *Acilius sulcatus* (L.), frequency distributions of appearance of: 1, 1st instar larvae (i.e. after the 1st larval moult). 2, imagines from laboratory culture (interval width one week).

The median duration (at $18 \pm 1^\circ\text{C}$) of the different developmental stages was 7 days for the egg, 6 days for the 1st, 7 days for the 2nd, 13 days for the 3rd instar, and 20 days for the pupa (Fig. 3). The total development from 1st instar larva to imago (46 days) is much shorter than in *Dytiscus marginalis* (67 days; GEWECKE & BAUER, 1984). Including the embryonic development (BLUNCK, 1913) the ontogeny of *Acilius* requires about 8 weeks.

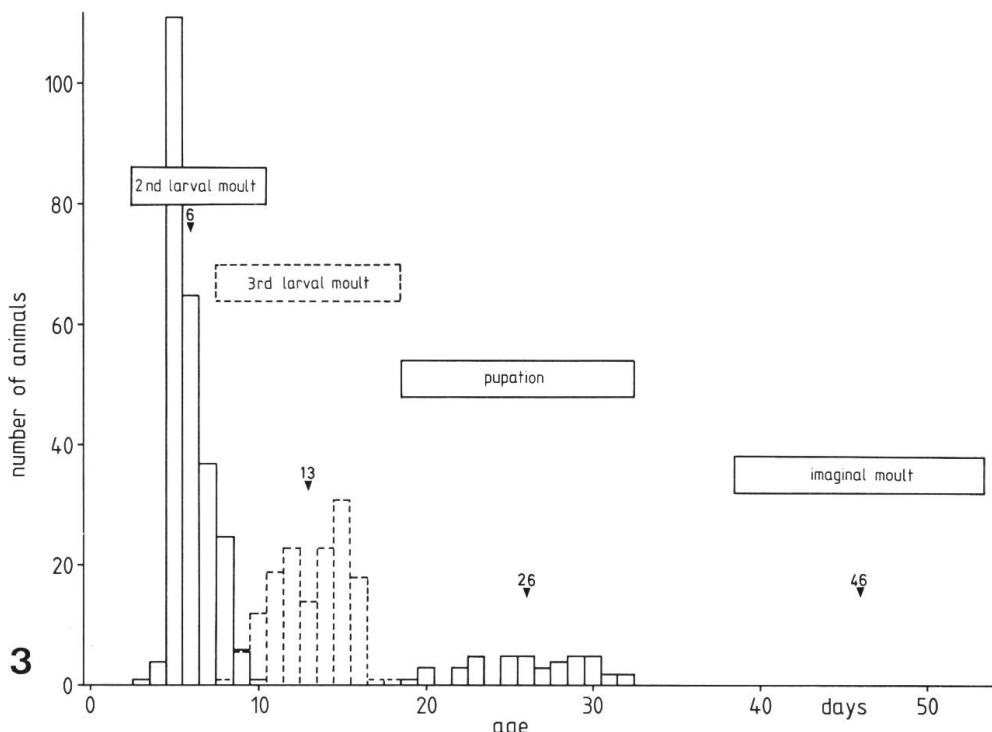


Fig. 3: *Acilius sulcatus* (L.): Frequency distributions of ages at which particular development stages began. 0 days equals the 1st larval moult. Arrows show median values. For imaginal moult only the median can be given.

2. Swimming behaviour

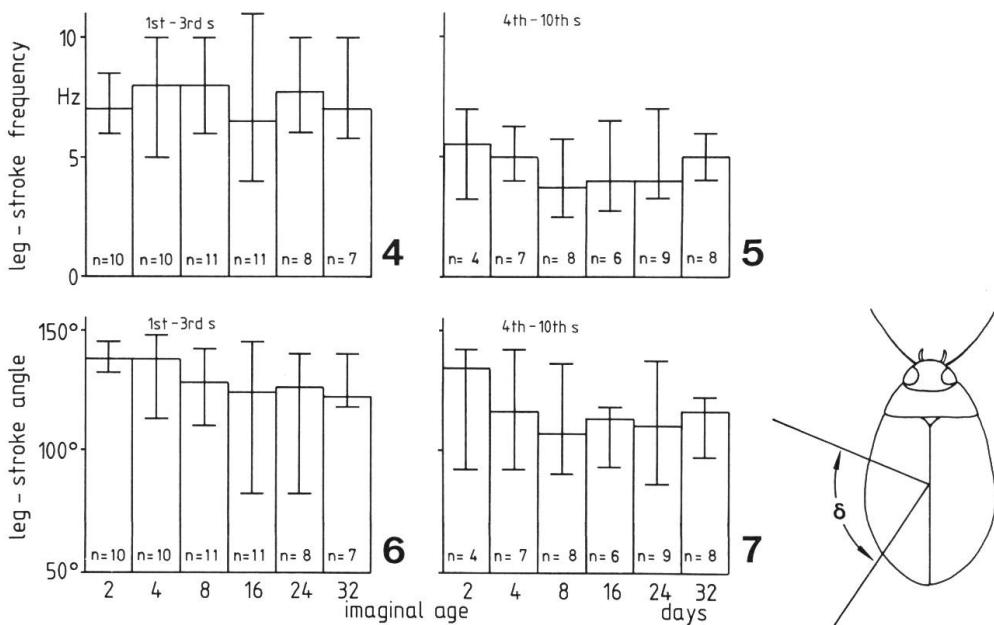
In tethered and in free swimming water beetles the antennae are obliquely stretched forward, the forelegs are held ventral to the prothorax, and the middle and hindlegs are stroked.

2.1 Stroke frequency and angle of the hindlegs

Once lowered into the water current, the tethered animal starts swimming with a high leg-stroke frequency ($f = 11$ Hz maximum), and a large stroke angle of the hindlegs ($\delta = 150^\circ$ maximum).

The median leg-stroke frequency (measured in the first three seconds after the start) with a current speed (v) of 10 cm/s is 6–8 Hz, inde-

pendent of the imaginal age of the experimental animals (Fig. 4). The median leg-stroke frequency is reduced, however, in the following seconds (4th–10ths s, Fig. 5). The initial decrease of leg-stroke frequency with increasing swimming duration is shown in Figs. 8–9. After about half a minute a plateau of 3–4 Hz is reached. In addition, Fig. 9 demonstrates that the speed of the water current (5–20 cm/s) has no effect on leg-stroke frequency. In free swimming animals the mean initial leg-stroke frequency ranges between 3 and 8 Hz (Fig. 14).

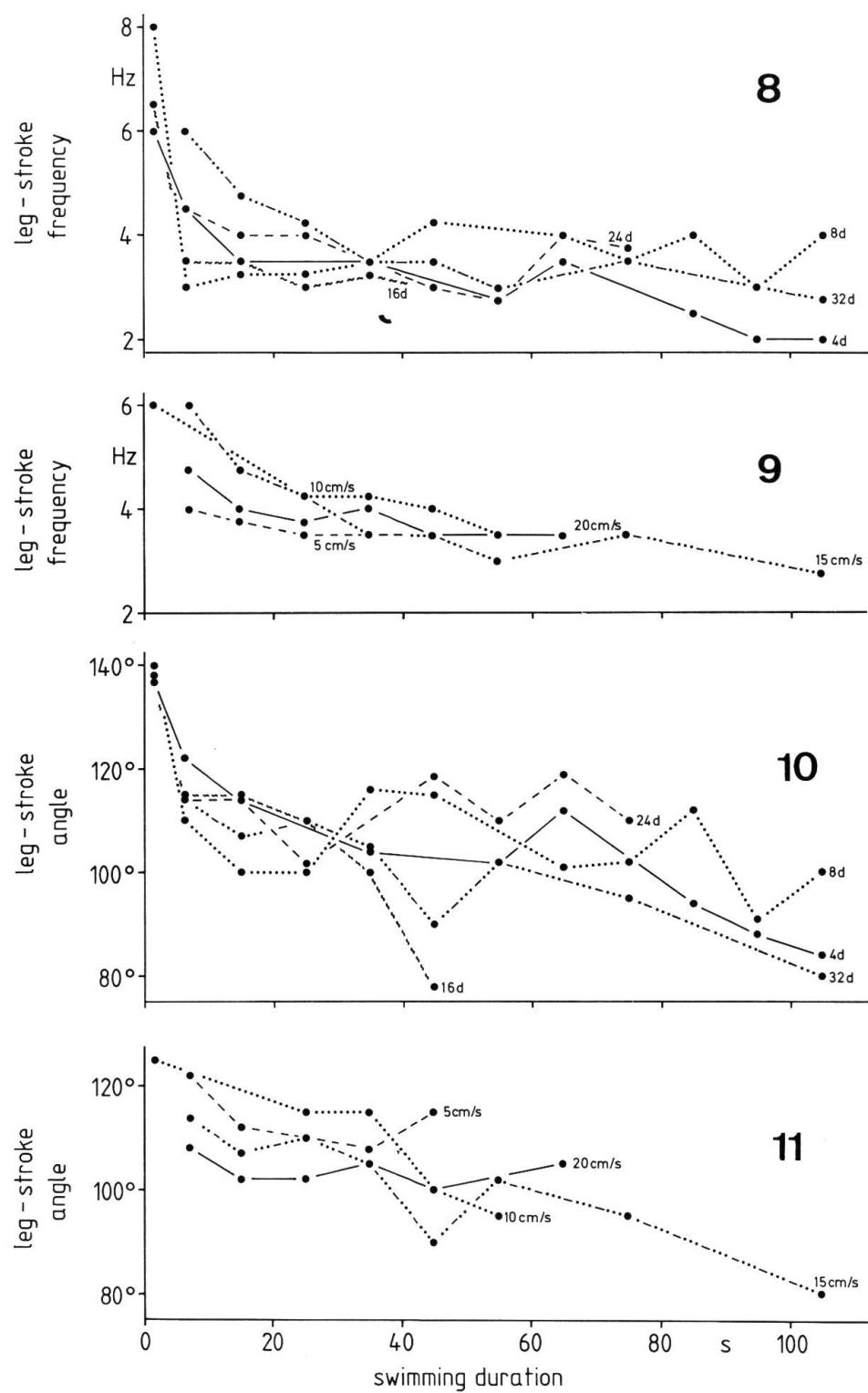


Figs 4–7: leg-stroke frequency and leg-stroke angle (hindleg; δ , inset) of 11 tethered swimming beetles (5 ♀, 6 ♂) at different imaginal ages. 1st–3rd s (4th–10th s), data from measurements in the first 3 s (4th–10th s) after the start of swimming movements. n, sample size. Vertical bars, range. Speed of water current, 10 cm/s.

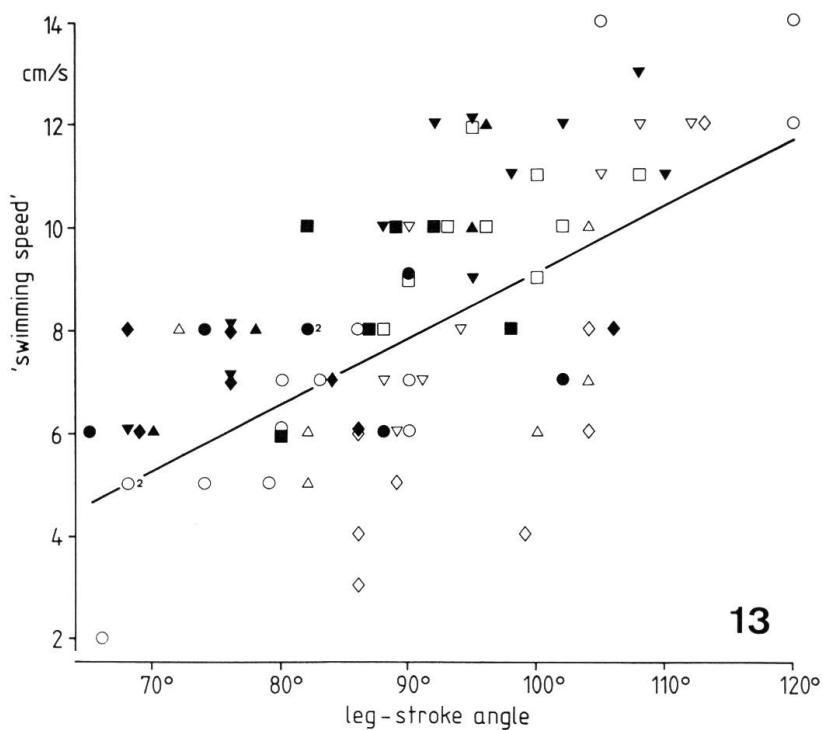
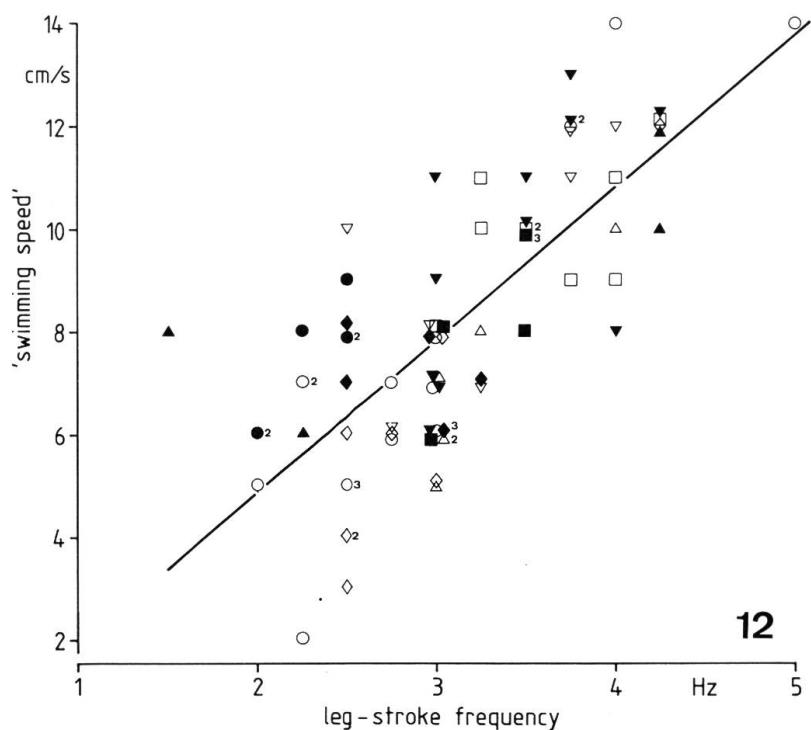
The median leg-stroke angle after the start ($v = 10$ cm/s) is about 120–140° in tethered animals, and does not depend on imaginal age (Fig. 6). During the swimming period from the 4th to the 10th second after the start, the median leg-stroke angle was reduced in all age groups (Fig. 7). The decrease of the leg-stroke angle of a single female with increasing swimming duration is observed both with changes in age (4 to 32 days, Fig. 10), and in the speed of the water current (5 to 20 cm/s, Fig. 11). Both variables have no influence on the leg-stroke angle.

2.2 Swimming speed

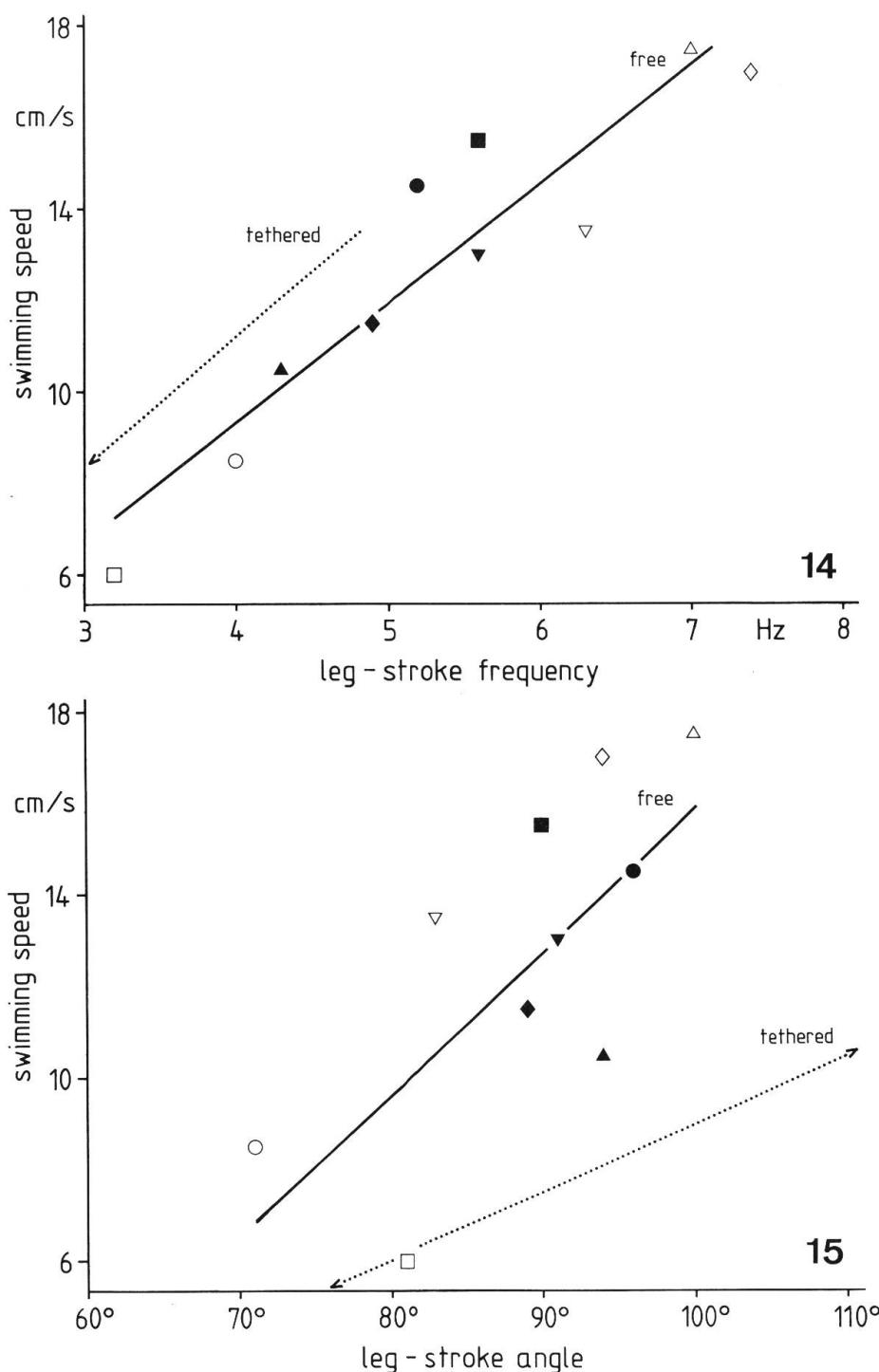
The middle and hindlegs, stroking with a specific frequency and angle, produce a thrust which normally moves the water beetle forward with



Figs 8–11: Leg-stroke frequency and leg-stroke angle of a female in dependence on swimming duration: 8 and 10, at different imaginal ages (d), water speed 15 cm/s. 9 and 11, at the imaginal age of 32 d, different water speeds (cm/s).



Figs 12–13: “Swimming speed” (in “thrust-compensated” conditions) of 10 tethered *Acilius sulcatus*(L.) females as a function of leg-stroke frequency and leg-stroke angle. Numbers indicate multiple data. $n = 80$. 12, $r = 0.751$, $p < 0.001$. 13, $r = 0.665$, $p < 0.001$.



Figs 14–15: Swimming speed of 10 untethered females (same as in figures 12–13) as a function of leg-stroke frequency and leg-stroke angle. Data points are means from individual animals. Regression lines from these data (free) and from those of tethered swimming animals (Fig. 12–13; dashed lines) are also shown. 14, $r = 0.934$, $p < 0.001$. 15, $r = 0.724$, $p < 0.01$.

an adequate speed. The relationships among these parameters were investigated quantitatively in 10 *Acilius* females (age > 32 d) under tethered as well as under free swimming conditions.

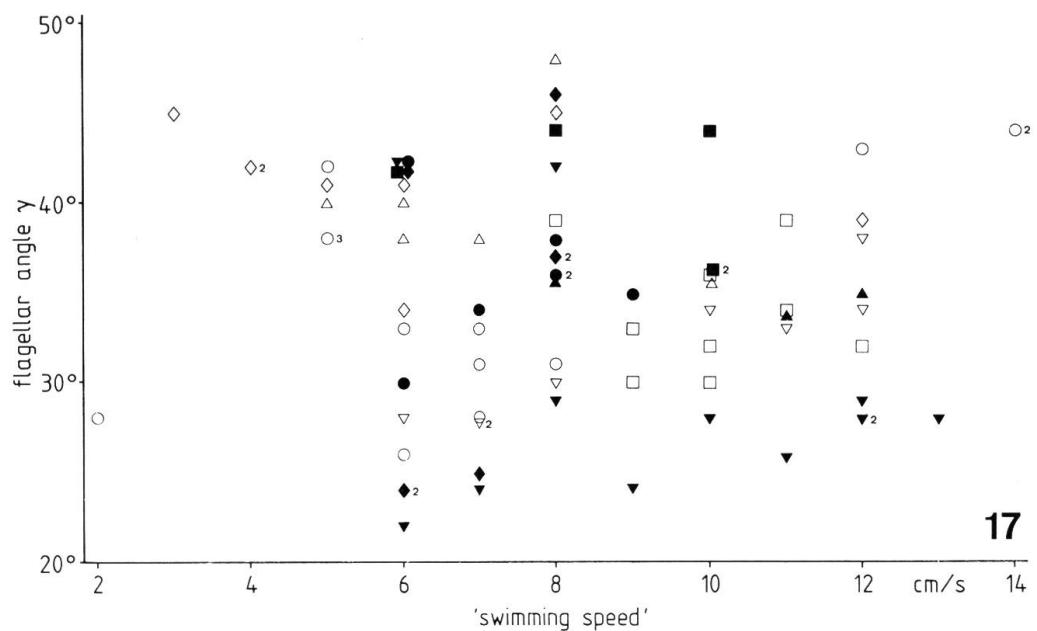
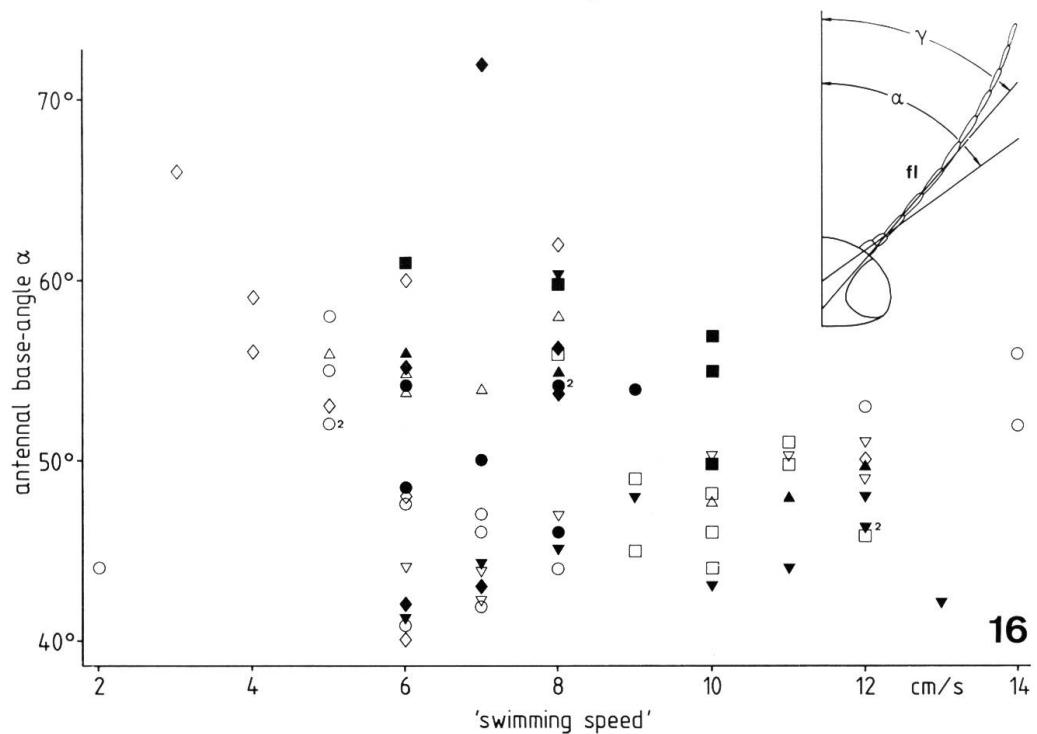
In tethered animals the "swimming speed" was determined from the speed of the water current during thrust-compensation (see materials and methods). Figure 12 shows a significant positive correlation between leg-stroke frequency and "swimming speed". The correlation of the leg-stroke angle with "swimming speed" is also significant (Fig. 13). From this a positive correlation between leg-stroke frequency and angle results ($r = 0.547$, $p < 0.001$).

To prove if the relationships found in tethered swimming animals also apply under free swimming conditions, the high-speed films of free swimming in the same 10 individuals were evaluated. Some beetles stroke their legs with high frequency (c. 7 Hz), and reach high swimming speeds (c. 18 cm/s, Fig. 14). The correlation of swimming speed with leg-stroke frequency is also significant in free swimming animals. Their leg-stroke angles are similar (Fig. 15) to those in "thrust-compensated swimming" (Fig. 13). With a specific angle (e.g. 90°), however, the free animals reach higher values of swimming speed (c. 13 cm/s) than if they are tethered (c. 8 cm/s). This results from the fact that the average leg-stroke frequency in free animals is higher ($f = 5.3$ Hz) than in tethered ones ($f = 3$ Hz).

2.3 Antennal posture

Simultaneously with the leg-stroke variables the antennal posture was recorded in the 10 *Acilius* females during "thrust-compensated swimming". For analysis of the active antennal movements the antennal base-angle (α = angle between the longitudinal axis of scape and pedicel, and the longitudinal head axis; figure 16, inset) was measured. In addition, the flagellar angle (γ = angle between the longitudinal axis of the proximal flagellar joints, projected onto the horizontal plane, and the longitudinal head axis; figure 16, inset) was evaluated as a measure for passive antennal deflection.

The antennal base-angle (α) ranges from 40° to 70° (mean 51°, Fig. 16), but it is neither significantly correlated with the leg-stroke frequency or angle nor with the "swimming speed" of the animals ($p > 0.05$). Similarly, no significant correlations with the leg-stroke frequency, angle or "swimming speed" were found ($p > 0.05$) for the flagellar angle (γ), ranging between 20° and 50° (mean 35°, Fig. 17).



Figs 16–17: Antennal base-angle (α) and flagellar angle (γ) at different "swimming speeds" in 10 tethered females (same as in figures 12–15) under "thrust-compensated" conditions. Both angles are not correlated with "swimming speed" ($p > 0.05$). Inset: dorsal view of the head of an *Acilius* female showing the antennal base-angle (α) and the flagellar angle (γ). fl, flagellum.

Discussion

A successful rearing of *Acilius sulcatus* in the laboratory is dependent on the availability of living food for the larvae. If *Daphnia* or chironomid larvae are available, the breeding of a large number of experimental animals for about six months a year (Figs 1, 2) is possible with a relatively small amount of work. Other advantages for *Acilius* as a model animal are a rapid development (c. 8 weeks, Fig. 3), the easy maintenance of imagines, and their long life span (1–2 years or more). The body weight depends on the age of the imagines and on environmental conditions during ontogenesis. It is not clear if the final weight depends on culture temperature (e.g. Lepidoptera, NIEHAUS, 1982), population density or food.

Investigations on the swimming behaviour of *Acilius* demonstrate that neither the imaginal age (as in flying locusts, GEWECKE & KUTSCH, 1979) nor the water-current speed influence the leg-stroke frequency and angle significantly. These parameters are mainly dependent on swimming duration (Figs 4–11). Swimming speed was found (multiple correlation analysis) to depend on leg-stroke frequency and angle. These relationships are influenced, however, by external conditions, e.g. by tethering the experimental animals (Figs 12–15).

From maximal values found in tethered animals for stroke frequency (11 Hz) and angle of the hindlegs (150°), and from the regression between these parameters and the "swimming speed" (Fig. 12), the highest possible speed for the escape reaction can be calculated as 30 cm/s. However, values greater than 18 cm/s have not been observed. NACHTIGALL (1960) supposed that swimming speeds of 10–30 cm/s are produced in *Acilius sulcatus* only for a short time during prey capture or escape. The dependence of the maximal swimming speed on the body length of water beetles is discussed by NACHTIGALL (1977).

Among Dytiscidae, the antennae are normally held in a fixed posture during swimming, i.e. they are directed anteriorly against the frontal water current (Fig. 16, inset). In *Colymbetes fuscus* (L.) (GEWECKE, 1980) and *Dytiscus marginalis* L. (GEWECKE, 1985) it has been shown that the antennae measure the frontal water current. This information is necessary for the maintenance of swimming movements. As in the two species mentioned above in *Acilius* the antennal base-angle and the flagellar angle are independent of the "swimming speed" (Figs 16, 17), i.e. they are actively controlled. Expected passive deflections of the

proximal flagellar segments by hydrodynamic drag could not be measured from the photographs.

It is shown that behavioural parameters in tethered swimming water beetles differ in some respects from those of free swimming animals. However, the method used in tethered swimming experiments allows analyses of sensory and neuronal mechanisms underlying the control of swimming behaviour in water beetles. The validity of these mechanisms can be tested in free swimming beetles.

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