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Laboratory Culture and Flight Development of the Water Beetle *Dytiscus marginalis* L. (Coleoptera, Dytiscidae)

by C.K. Bauer

Abstract: 3 female and one male specimen of *Dytiscus marginalis* L. collected during summer 1980 in the field were kept in aquariums which simulated their natural habitats. In the following May a single female laid eggs in leaves of *Vallisneria*. 30 out of 162 hatched larvae (18.5%) were reared to the adult stage in about 65 days. The most important aspects of the culture method are isolation of larvae to prevent cannibalism, providing living food (esp. chironomid larvae) for the 1st and 2nd instar larvae and control of fungal infections.

Beetles from culture at different ages and mature beetles collected in the field were tested on a flight balance in front of a wind tunnel. Flight posture and wingstroke angle (160°) do not differ with age. Following 10 min of thrust-compensated flight, the mean wingbeat frequency (34 Hz) and the mean “flight speed” (2.4 m/s) of 1 day old beetles are significantly lower than those of fully developed beetles (41 Hz; 3.2 m/s). Variations in wingbeat frequency and body weight during maturation are not correlated. Alterations in the speed of the frontal air current produce changes in wingbeat frequency.

Key words: Coleoptera Dytiscidae – *Dytiscus marginalis* – rearing methods – postlarval development – wingstroke frequency – flight speed – wind tunnel.

I. Introduction

For over 100 years the water beetle *Dytiscus marginalis* L. has been used as an experimental animal. Detailed investigations have been made concerning anatomy (KORSCHOLT, 1923/24), biology (WESENBERG-LUND, 1912, 1943), geographical distribution (KIRBY & SPENCE, 1828; SHARP, 1880–82), reproduction (RÉGIMBART, 1877; LEYDIG, 1895), and metabolism (DU BOIS-REYMOND, 1898; WESENBERG-LUND, 1910–11). More recent researches also include locomotion principally swimming (NACHTIGALL, 1960; GEWECKE, 1895) and flight (SCHNEIDER, 1981; BAUER & GEWECKE, 1985). Previously *Dytiscus* was easily collected in the field. Today the natural environment of the water beetles is limited and their number is decreasing from extensive eradication as pests in fish ponds. Declining natural populations in the face of continued need for these animals for research, led to the culture experiment described here. Furthermore, culturing *Dytiscus* enabled investigations of flight during maturation. Whether flight behaviour changes with age (as shown for

example in Orthoptera; KUTSCH, 1977) is tested by behavioural experiments in tethered flying beetles.

II. Laboratory culture

Materials and methods

Adult beetles (*Dytiscus marginalis* L.) were collected during the summer from small ponds in the area around Düsseldorf. The beetles were maintained in glass aquariums (16–45 l) filled three quarters full with water. Pieces of small tree branches were arranged in each aquarium allowing the beetles to climb out of the water. Broken flower-pots served as hiding-places. Plants in the aquariums, principally *Vallisneria*, were kept in small jars to enable easy replacement. The mean water temperature varied between 17° C in winter to about 20° C in summer. The light-dark photoperiod was adjusted weekly to follow seasonal changes. The light intensity was 600 lx, measured directly above the aquariums with an optometer (United Technology). The beetles were fed small pieces of raw beef twice a week.

In autumn (the time of maximal production of male sex products; KORSCHULT, 1924; WESENBERG-LUND, 1943) three female beetles were successively confined in an aquarium with a single male beetle. Following successful copulation, which could be recognized by a white mark on the abdomen of the females ("Begattungszeichen"; LEYDIG, 1895), the females were isolated in other aquariums to prevent possible suffocation (KORSCHULT, 1924) during subsequent copulation. In the following spring, the aquarium plants were regularly checked for the presence of eggs. During the time of egg laying the females were transferred each week to additional aquariums. Following hatching the larvae of all instars had to be kept in separate containers to prevent cannibalism and to keep records of all individuals. Glass containers with differing diameter and water level were used: 1st instar, 5 cm (diameter), 2 cm (water level); 2nd instar, 7 cm, 4 cm; 3rd instar, 11 cm, 8 cm.

Containers were filled with de-chlorinated water and contained sticks of wood that allowed the larvae to more easily reach the water surface and breath. The water temperature was $19 \pm 1^{\circ}\text{C}$. All larvae were fed and cared for daily. The 1st and 2nd instar larvae were supplied with living food, esp. chironomid larvae. The larvae of the 3rd instar were fed raw beef, and the water was changed daily. Readiness to pu-

pate was noted by cessation of feeding and restless swimming (KORSCHOLT, 1924). The larvae were then transferred to containers (45 × 30 × 30 cm) filled at least 20 cm deep with unfertilized planting soil. In one corner of this "pupation-container" was a small basin full of water, containing suitable stones to allow the larva access to soil. During the pupal stage, the soil was regularly moistened. Adult beetles were isolated in aquariums for the first two weeks. After hardening of the cuticle, male/female pairs were placed in separate aquariums.

The length of eggs and larvae were measured from random samples. The body weight of the imagos was taken following emergence from the soil and consumption of water.

Statistical significance was checked by the distribution-free Wilcoxon-Mann-Whitney Test for independent samples (LIENERT, 1973; SACHS, 1974). By grouping the data into interval classes, the number of classes was objectively defined as the square root of the sample size n . The significance level was 0.05.

Results

Oviposition. Rearing started late in May 1981, when a single female laid its first eggs into leaves of *Vallisneria* (Fig. 2). Parts of the leaves close to the water surface were preferred. Eggs were laid every day until the beginning of July.

Duration of developmental stages. The incubation period varied considerably but was at least seven days. The mean duration of the 1st larval stage was 5.2 days, of the 2nd stage 6.4 days and of the 3rd larval stage 25.6 days. The mean duration of the pupal stage (here defined as the time spent in the soil) was 30.8 days (Fig. 1).

Egg and larval length and adult body weight. Mean length of the eggs was 0.65 cm. The mean body length of the larvae increased during the 1st larval stage from 1 to 2 cm, during the 2nd larval stage from 2.5 to 3.5 cm and during the 3rd larval stage from 4 to 6.5 cm (Figs 2–4). Frequency distributions of adult body weight for males (mean: 13.9 mN) and females (11.9 mN) are statistically different ($p < 0.02$, Fig. 5–6).

Mortality. Out of 162 hatched larvae, 127 made the first moult, 84 the 2nd moult. Thirtyseven 3rd instar larvae entered the soil and 30 imagos were obtained. This represents 18.5% of the hatched larvae. By the time

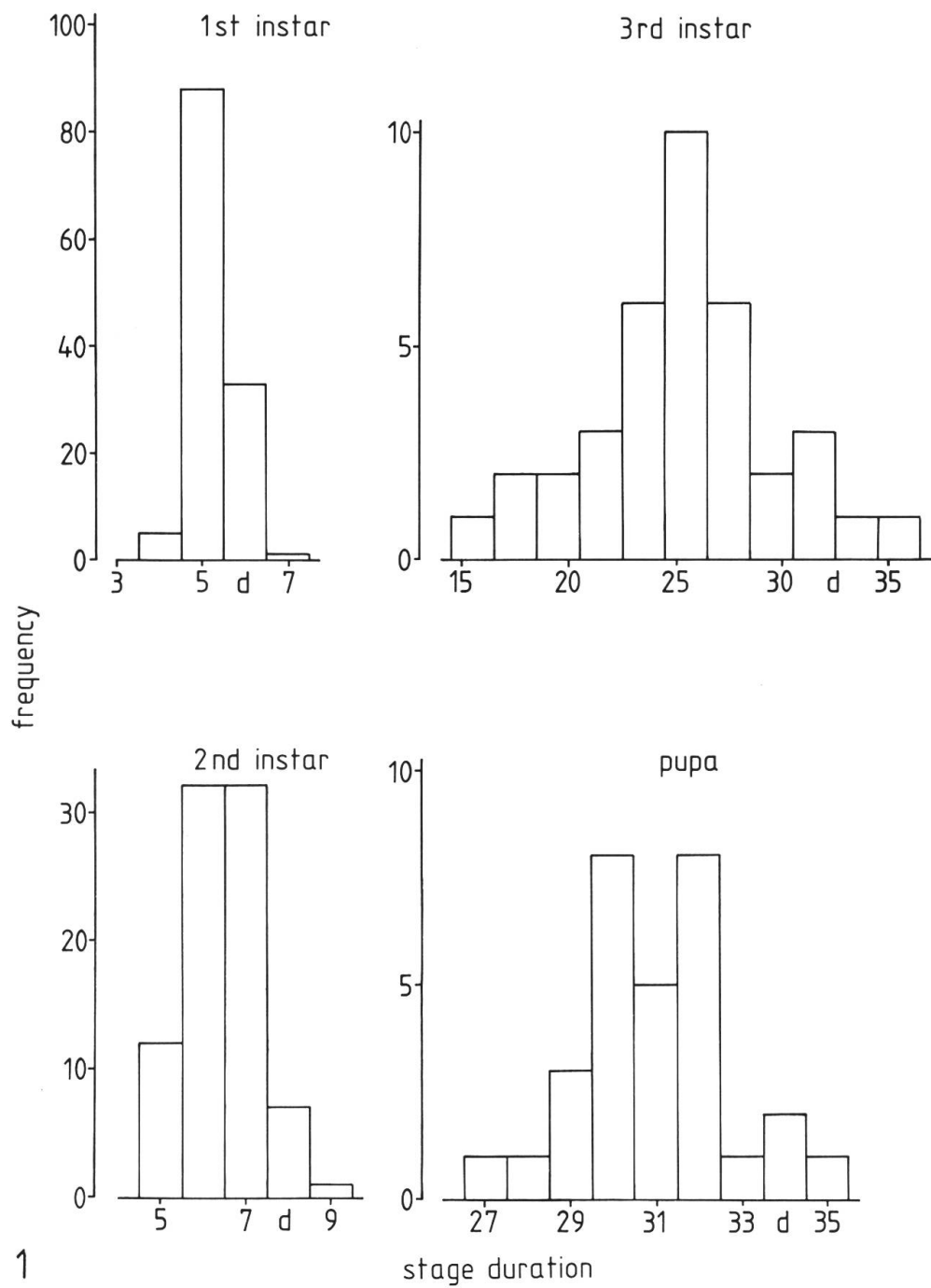
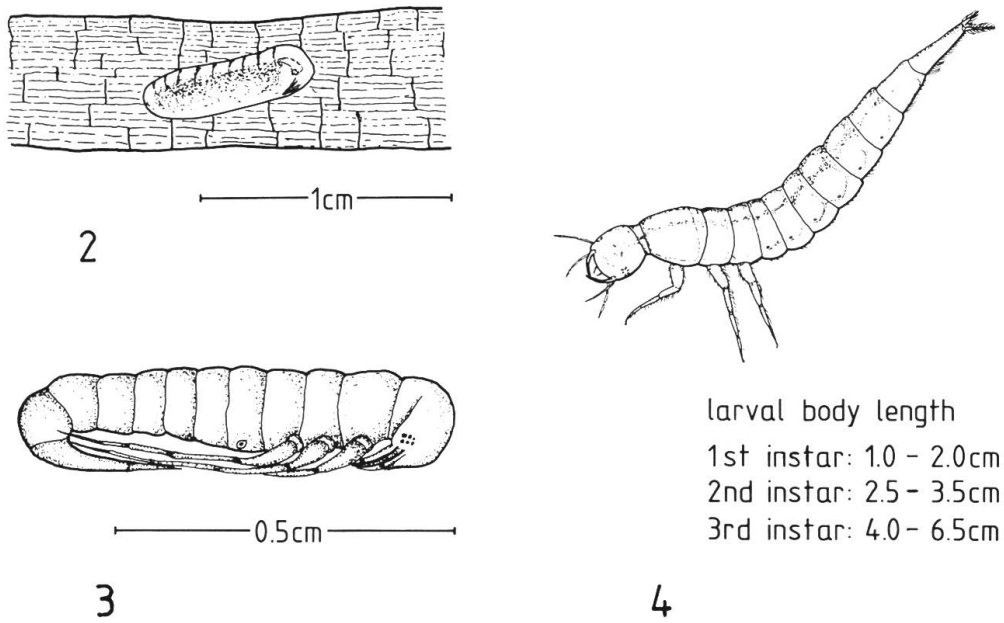
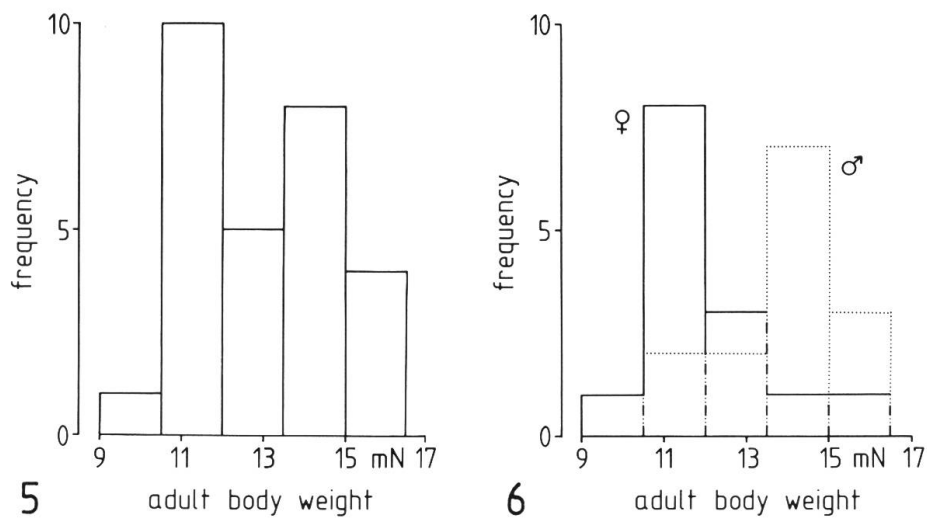


Fig. 1: *Dytiscus marginalis* L., frequency distribution of durations of developmental stages: 1st instar, 2nd instar, 3rd instar and pupa at 19° C



Figs 2-4: *Dytiscus marginalis* L.: 2, Embryo short before hatching in a leaf of *Vallisneria*. 3, Embryo dissected out of the egg. 4, Larva with body length data.



Figs 5-6: *Dytiscus marginalis* L.: 5, Frequency distribution of adult body weight. 6, Data of fig. 5 separated for males and females.

the eggs developed the plants in which they were laid were often dead. These eggs rarely hatched. The 3rd instar larvae often suffered from fungal infections and mortality was greatest during this stage. In general, the larvae usually died on the date of their expected moult.

Discussion

Oviposition. In nature, oviposition of the females of *Dytiscus* takes place in the months of March, April, and May, and each female lays up to 1000 eggs (KORSCHOLT, 1924). In this culture experiment, only one out of three impregnated females deposited about 250 eggs. Nevertheless, this is regarded as successful since *Dytiscus* females rarely oviposit during prolonged captivity (KORSCHOLT, 1924). Apparently simulating the natural habitat of the beetles is important for oviposition to occur in culture.

Development. The durations of developmental stages observed here at 19°C are similar to previous laboratory data determined at 20°C (JESSEN, 1903; KORSCHOLT, 1924) with the exception of the 3rd larval stage. Korscholt found the mean duration of this stage to be 10.5 days as compared with 25.6 days in this experiment. A possible reason for this deviation might be the use of raw beef for food; a dependence of the stage duration on the amount of food has already been shown (KORSCHOLT, 1924). Observed larval body length and body weight of the young imagos are not significantly different from literature data (KORSCHOLT, 1924) although sex-specific differences in body weight are not mentioned.

Mortality. The percentage of animals reared from hatched egg to adult was 18.5%; this is a greater percentage than in nature, but not yet satisfactory for laboratory purposes. Prior rearings of *Dytiscus* (BLUNCK, 1909; JESSEN, 1903; KORSCHOLT, 1924) were carried out to examine aspects of development and not to determine effective culture methods suitable for the laboratory. The methods described here represent a compromise between imitating the natural living conditions of the animals and simplifying culture maintenance.

Methods. *Iris*, *Alisma plantago-aquatica* and *Scirpus lacustris* are mentioned as preferred plants for oviposition (KORSCHOLT, 1924). These

aquatic plants are too tall for aquariums or difficult to obtain or keep. *Vallisneria*, on the other hand, is uncomplicated and once rooted grows quickly. Females of *Dytiscus* accept the leaves of *Vallisneria* for oviposition. Limiting the number of eggs deposited in a given amount of *Vallisneria* probably helps prevent the plants from dying before the eggs hatch. Natural food of the 1st and 2nd instar larvae are *Asellus* and larvae of other water beetles, ephemerids, trichopterans and mosquitos (WESENBERG-LUND, 1943). Living chironomid larvae are relatively easy to obtain (in pet stores as fish food) or to culture (NEEDHAM, 1959) and were fed with good results. A few 1st and 2nd instar larvae took small pieces of raw beef, but the larvae died before the next moult. The 3rd instar larvae require relatively large amounts of food, and the fact that they accept raw beef eliminates the need for extensive food cultures (a single larva requires up to 30 tadpoles of 2 cm length daily; KORSCHOLT, 1924). The main disadvantages of feeding raw beef are the increase in fungal infections and the necessity for frequent water changes. Perhaps keeping the larvae in containers with flowing water, irradiated by UV-lamps, could solve these problems.

III. Flight development

Materials and methods

Males and females of the water beetle *Dytiscus marginalis* L. were used as experimental animals. Both, fully developed beetles, collected in the field, and beetles obtained from laboratory culture (age: 1, 4, 7, 14, 21, and 70 days) were tested. *Dytiscus* belongs to the group of beetles which do not fly spontaneously (FRAENKEL, 1932; WESENBERG-LUND, 1943; NACHTIGALL, 1961). Extensive active preparations (e.g. body weight reduction and increase of body temperature) are necessary for flight. To elicit flight, the beetles were allowed to dry in a light-tight box containing absorbent material at least one hour before a flight experiment. After "drying", the pronotum of the beetles was glued with a rosin-wax mixture (3:1) to a needle, parallel to the longitudinal axis of the body. Using this needle the beetle was rotated rapidly around the longitudinal axis, until an opening of the elytra and some wingstrokes were released (BURTON, 1970). This stimulus was repeated, combined with air current stimulation, to obtain stable flight. The needle was then fixed to the end of the lever arm of a flight balance (Fig. 7), similar to that used in locust

flight experiments (GEWECKE, 1975). Head wind of free flying animals was simulated with a wind tunnel. The average aerodynamic horizontal force, produced by a tethered flying beetle and the opposing air current, was measured by means of a mechanoelectric transducer (Hugo Sachs Elektronik). The speed of the air current was changed stepwise of manually adjusted so that the drag of the flying beetle was compensated by its thrust (i.e. horizontal force = thrust – drag = 0). In this case, the speed of the air current (v_a , measured by thermistor anemometers, Lamprecht 641bN and Fenwal 32BC L1) is a measure of the “flight speed” (v_f) of the beetle in relation to the surrounding air (thrust-compensated flight). The wingbeat frequency was measured with a photodiode and two lamps (10000 lx), left and right in front of the wings. The wingstroke angle (ϕ = angle between maximal elevated and depressed positions of the hindwings) was recorded by a camera (Canon F1, exposure time 1s), positioned perpendicular to the wingstroke plane of the beetle, and the kinematics of the beating wings by a high-speed camera (Stalex WS-2, 1000 frames/s). Air speed and wingbeat frequency were recorded simultaneously. During an experiment, the laboratory was darkened and the temperature was 24°C.

Statistical significance of the results was checked by using a nonparametric procedure for two independent samples of response curves (KRAUTH, 1980) and the distribution-free Wilcoxon-Man-Whitney Test for two independent samples (Sachs, 1974, $P < 0.05$ significant).

Results

Flight performance. Stable flights were induced in all animals tested for the first time. Beetles used in several experiments during the first three weeks of imaginal life often could not be motivated to fly. In spite of the higher body weight of male beetles, no significant differences in wingbeat frequency or “flight speed” exist between the sexes. Therefore in all results, male and female data were combined. Flight posture and performance are identical for beetles of all ages (Figs 8–9): the elytra are held in a fixed posture during flight. The hindwings move between dorsal posterior and ventral anterior positions during each wingstroke; the wingstroke angle is about 160°. The forelegs are held close to the body, the midlegs under the elytra and the hindlegs stretched posteriorly.

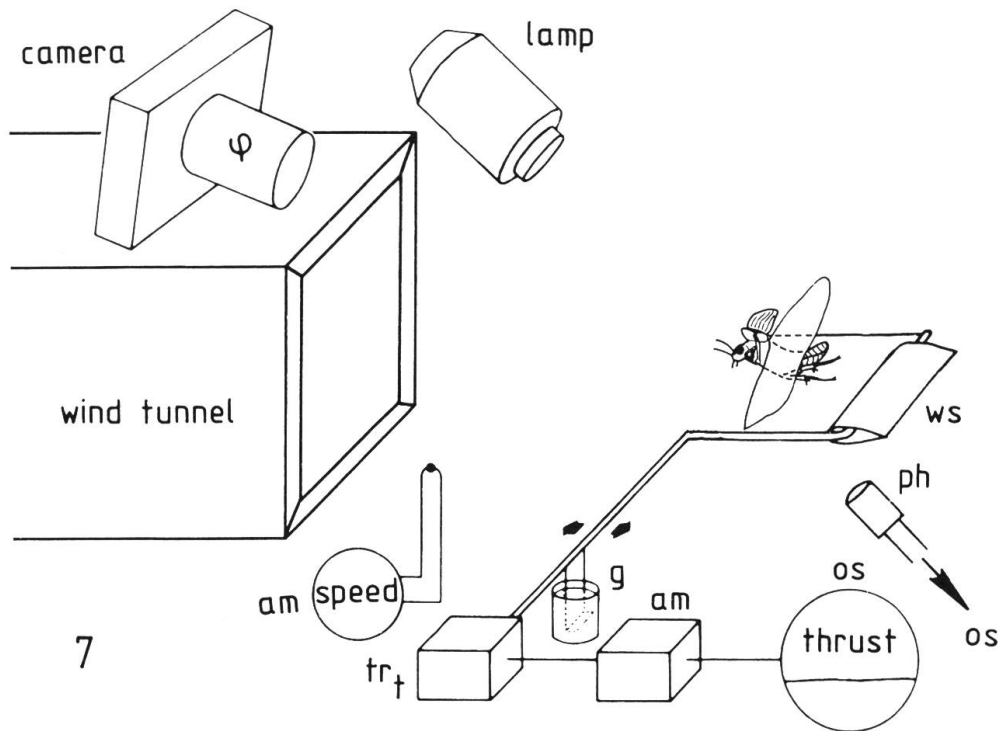
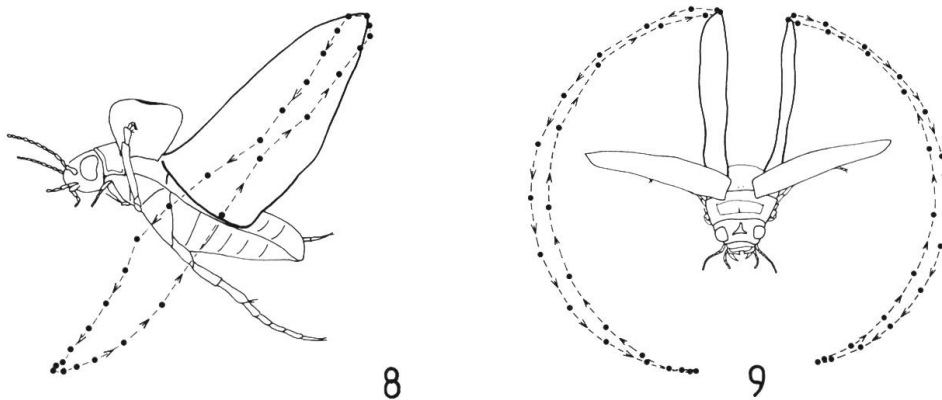


Fig. 7: Experimental setup for simultaneous measurement of wingbeat frequency by a photodiode (ph), the wingstroke angle ϕ by a camera, the horizontal force by a transducer (tr_t) and the air speed by an anemometer (am); a: amplifier; g: vane-in-glycerine dash pot; os: oscilloscope; ws: windshield.



Figs 8–9: 8, Drawing of a tethered flying beetle (lateral view) from high-speed film; the dots (1 ms interval) mark the path of the tip of the hindwings during a single stroke. 9, Same as figure 8. View perpendicular to the wingstroke plane.

Thrust-compensated flight. Wingbeat frequency and “flight speed” have a maximum during the first minutes of thrust-compensated flight (Fig. 10). Following 10 min of flight the level of wingbeat frequency of 1 day old beetles (mean: 33.9 Hz, range: 30.6–36.7 Hz) is significantly ($p = 0.001$) lower than that of fully developed beetles (40.9 Hz, 34.0–49.8 Hz). The level of “flight speed”, too, is significantly lower for the young beetles (mean: 2.4 m/s, range: 1.4–2.8 m/s) than for the fully developed ones (3.2 m/s, 2.3–4.1 m/s). All beetles were weighed after the flight experiment. Mature beetles are significantly heavier (mean: 18.2 mN) than 1 day old beetles (9.6 mN).

Out of ten beetles tested at ages of 1, 4, 7, 14 and 21 days, stable flight could never be induced on more than four test days. Figure 11 shows the data of a male beetle at four different ages: at the age of 1, 4 and 14 days the “flight speed” is stable at about 2.6 m/s and the wingbeat frequency varies between 32 Hz (4d) and 36 Hz (14d). At the age of 21 days both wingbeat frequency and “flight speed” increased dramatically; the level of wingbeat frequency is 47 Hz and the level of “flight speed” is 3.6 m/s.

Given the incomplete results obtained with 21 days old animals, an additional four beetles from culture were also tested at the age of 70 days. Their levels of wingbeat frequency (42–45 Hz) and of “flight speed” (3.9–4.0 m/s) are in good agreement with the results from fully developed beetles collected in the field.

Figure 12 shows the level of wingbeat frequency as a function of body weight, considering all data of beetles between ages of 1 and 21 days. Variations of wingbeat frequency and body weight during the first three weeks of imaginal maturation are not significantly correlated ($r = 0.04$).

Flight without compensation. Step changes in air speed reveal an influence on the wingbeat frequency. Figure 13 shows changes in wingbeat frequency of four beetles (aged 1 day) to altered air speed. The onset, magnitude and, in some cases, the direction of the reactions differ considerably. Nevertheless a tendency for higher wingbeat frequencies to occur with higher air speeds is apparent, with the exception of flight without air current ($v_a = 0$ m/s). In this case the flight is sporadic and of short duration, and high frequencies similar to the beginning of flight frequently recur. The wingbeat frequency of 10 beetles was averaged over the period from 10 to 20 s after altering the speed of the air current from the “compensated” air speed to 4 and then to 2 m/s. Correlation

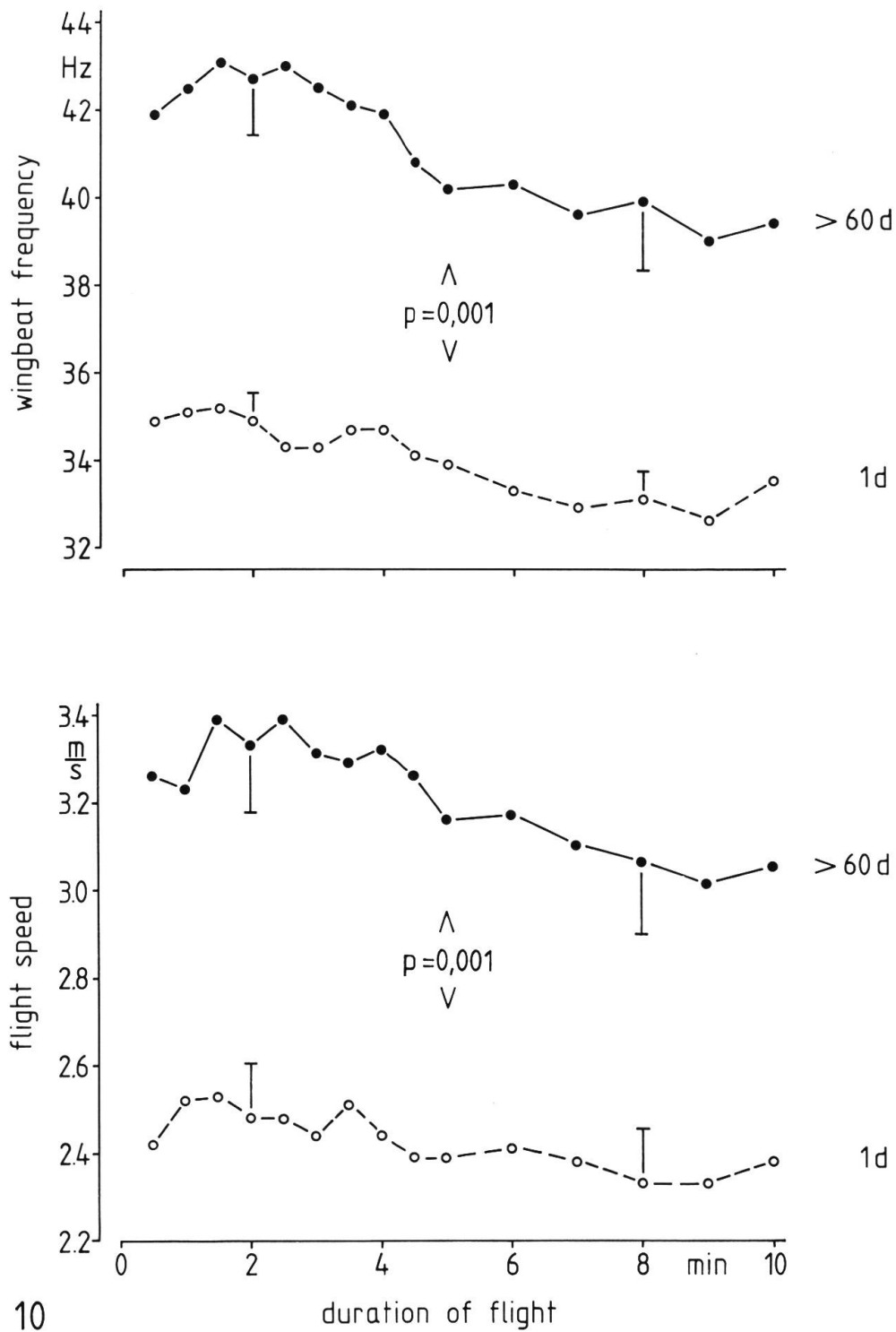


Fig. 10: Mean wingbeat frequency and "flight speed" of beetles aged 1d (n=10) and fully developed beetles (n=15) as functions of flight duration; S.E. indicated.

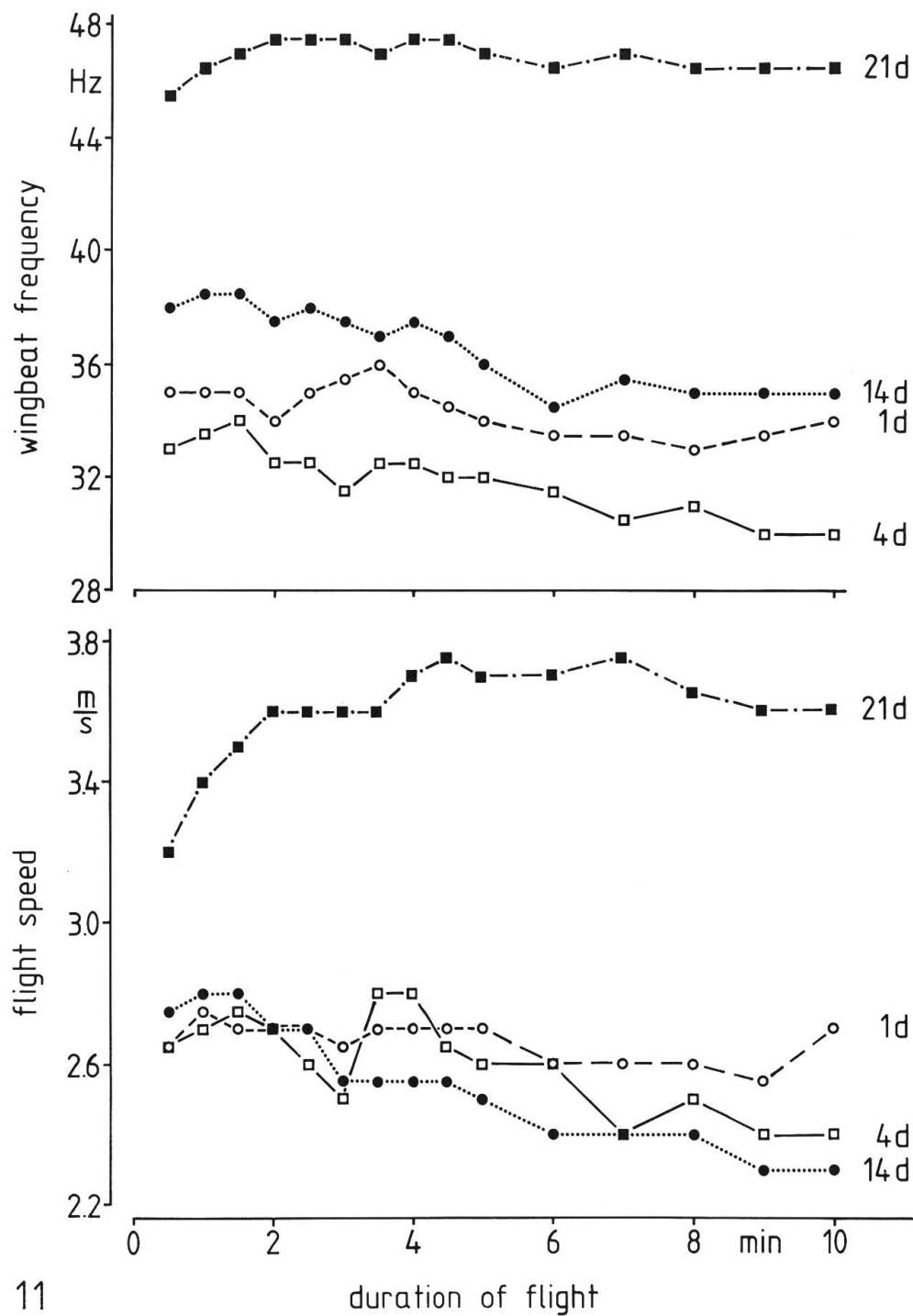
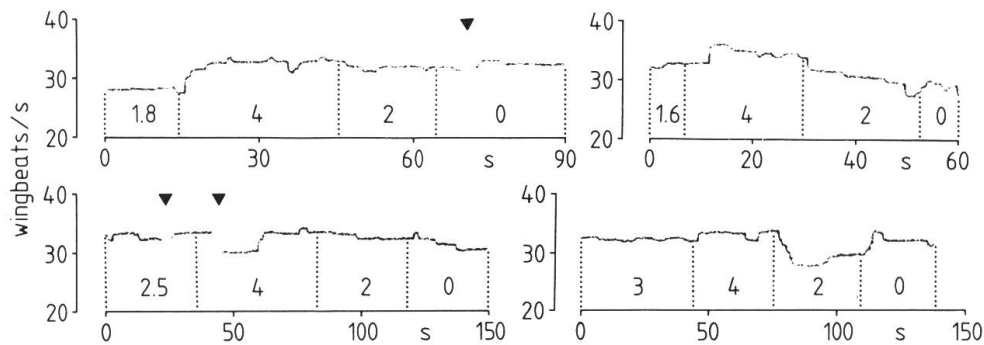
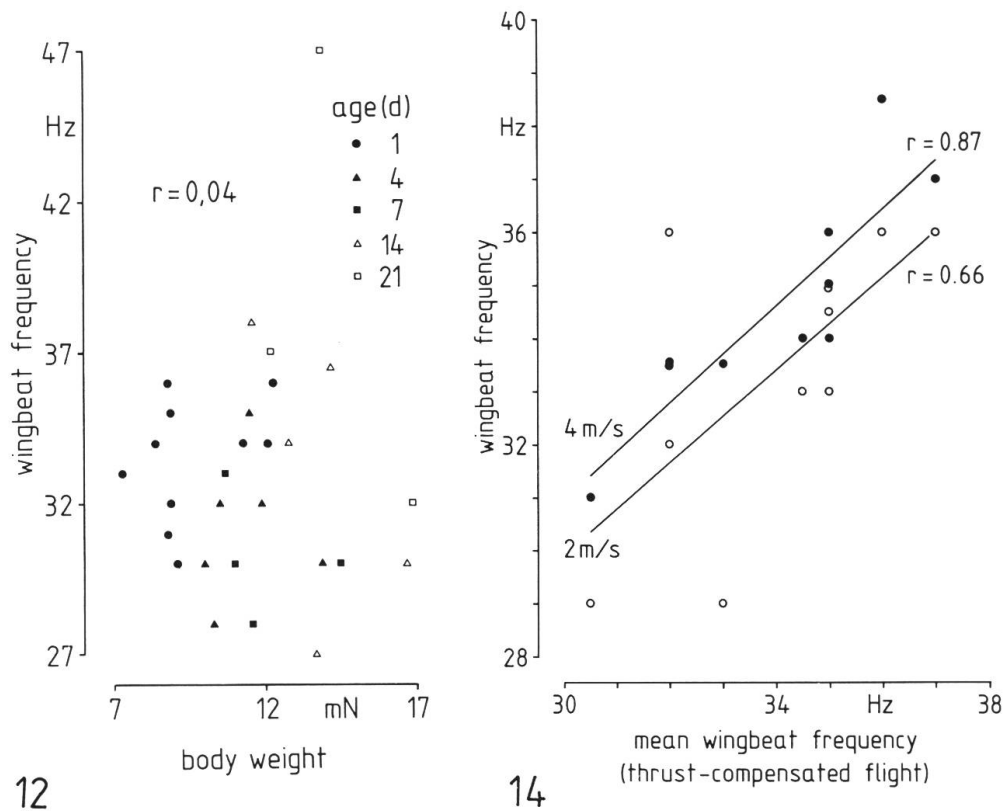


Fig. 11: Wingbeat frequency and "flight speed" of a male beetle at different ages as functions of flight duration.



Figs 12–14: 12, Relationship between wingbeat frequency and body weight; data of 10 beetles tested at different ages. 13, Four examples of histograms of wingbeat frequency with altered air speed, indicated by the numbers between the dotted lines (m/s). 14, Relationship between the wingbeat frequency of individual beetles at air speeds of 2 m/s (○) and 4 m/s (●) and their level of wingbeat frequency in thrust-compensated flight.

analysis (Fig. 14) shows a linear relationship ($v_a = 4 \text{ m/s} : r = 0.87$; $v_a = 2 \text{ m/s} : r = 0.66$) between the wingbeat frequency at particular air speeds and the individual level of wingbeat frequency during thrust-compensated flight. In general, the wingbeat frequency at 4 m/s air speed is increased by about 1 Hz to corresponding values at $v_a = 2 \text{ m/s}$.

Discussion

One day old beetles of *Dytiscus* are easily motivated to fly. Flight ability is probably very important for survival of even young beetles. In hot summers, many of the small ponds in which the larvae of *Dytiscus* are found, are dried up during the month of pupation. Emerging beetles are forced to reach new habitats by flight. In *Acilius sulcatus*, another dytiscine, if young beetles, emerging from the soil after the imaginal moult, are not allowed to enter water, they often attempt to fly away (unpublished observations). Other probable reasons for flight are scarcity of food and high density of population.

During maturation, wingbeat frequency and "flight speed" are the only parameters examined that change. Flight position and wingstroke angle remain unaltered as in locusts (GEWECKE & KUTSCH, 1979; KUTSCH & GEWECKE, 1979). Also in mature *Dytiscus*, individual wingbeat frequency and wingstroke angle are not significantly correlated, even though both parameters change simultaneously during flight (BAUER & GEWECKE, 1985). "Flight speed" depends mainly on the wingbeat frequency and the wingstroke angle (BAUER & GEWECKE, 1985). Since the wingstroke angle isn't altered during maturation, the increase in "flight speed" can be explained by an increase in wingbeat frequency.

The data here are insufficient to relate changes in wingbeat frequency with particular periods during maturation. Nevertheless, the increase in wingbeat frequency seems to occur stepwise about three weeks after the imaginal moult. This differs from the continuous increase in wingbeat frequency found in locusts (KUTSCH & GEWECKE, 1979). Although the higher wingbeat frequency in mature beetles might compensate for increased body weight, individual changes in wingbeat frequency and body weight are not correlated during the first three weeks of imaginal life. In mature beetles too, body weight and flight parameters such as wingbeat frequency, wingstroke angle and "flight speed" show no linear relationship (BAUER & GEWECKE, 1985). Identical results have been found in locusts; flight parameters are independent of

body weight and they all increase with maturation (KUTSCH & GEWECKE, 1979).

Several factors might account for the increase in wingbeat frequency during maturation of *Dytiscus*. The hardening of the cuticle can influence the "oscillating properties" of the thorax, an important component of an asynchronous flight motor system (HEIDE, 1982). Further, the frequency of power muscle contraction, generating the wingstroke, is dependent on the supply of energy (GOLDSWORTHY, & COUPLAND, 1974). Most energy reserves of the 3rd instar larvae have been consumed during the pupal stage, and the young beetles need several weeks after the imaginal moult to restore them (KORSCHOLT, 1924). The increase of the wingbeat frequency might also result from an inherent increase in the frequency of the flight motor center. It has already been shown, that changes of the wingbeat frequency are coincident with changes in the frequency of actionpotentials in power muscles (BAUER & GEWECKE, 1985). Also the wingbeat frequency can be manipulated by altering the speed of frontal air current, suggesting a possible sensory influence on the flight motor center be similar to that found in flies (SPÜLER et al., 1981). The increase of wingbeat frequency at increasing air speeds is contrary to the scheme of "negative feedback" found in other insects (locusts: GEWECKE, 1972b; flies: GEWECKE, 1974; dragonflies: GEWECKE, et al., 1974). Schneider (1981) considered this effect of the air speed on the wingbeat frequency to be passive, but an entirely passive mechanism cannot explain the variability in wingbeat frequency of individual animals that we observed. The response of beetles to altered air speed implies the existence of air current sense organs. The antennae are not likely to be involved in this reaction. Prior investigations have shown that removing the flagella doesn't influence wingbeat frequency (SCHNEIDER, 1974), but only the vector resulting from "flight speed" and lift (BAUER & GEWECKE, 1985). Organs that might be responsible for the perception of air current are proprioceptors of the elytra and hindwings, as well as campaniform sensilla on the 1st and 2nd maxilla, the coxae and trochanters (KORSCHOLT, 1923).

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V. References

- BAUER, C.K., GEWECKE, M. (1985): *Flight Behaviour of the Water Beetle Dytiscus marginalis L. (Dytiscidae, Coleoptera)*. In: *Insect locomotion* (GEWECKE, M. & WENDLER, G. eds) Paul Parey, Hamburg, Berlin pp. 205–214.
- BLUNCK, H. (1909): *Regenerationsversuche an Dytiscus marginalis L.* Zool. Anz. 34: 172–180.
- BURTON, A.J. (1971): *Directional change in a flying beetle.* J. Exp. Biol. 54: 575–585.
- DU BOIS-REYMOND, R. (1898): *Über die Atmung von Dytiscus marginalis.* Arch. Anat. Physiol. Abt. Physiol.: 378–381.
- FRAENKEL, G. (1932): *Untersuchungen über die Koordination von Reflexen und automatisch-nervösen Rhythmen bei Insekten. I. Die Flugreflexe der Insekten und ihre Koordination.* Z. Vergl. Physiol. 16: 371–393.
- GEWECKE, M. (1972b): *Antennen und Stirnscheitelhaare von Locusta migratoria L. als Luftströmungssinnesorgane bei der Flugsteuerung.* J. comp. Physiol. 80: 57–94.
- GEWECKE, M. (1974): *The antennae of insects as air-current sense organs and their relationship to the control of flight.* In: *Experimental analysis of insect behaviour* (BARTON BROWNE, L., ed.). Berlin, Heidelberg, New York, Springer. pp. 100–113.
- GEWECKE, M. (1975): *The influence of the air-current sense organs on the flight behaviour of Locusta migratoria.* J. comp. Physiol. 103: 79–95.
- GEWECKE, M. (1985): *Swimming Behaviour of the Water Beetle Dytiscus marginalis L. (Dytiscidae, Coleoptera)*. In: *Insect locomotion* (GEWECKE, M. & WENDLER, G., eds) Paul Parey, Hamburg, Berlin pp. 111–120.
- GEWECKE, M., HEINZEL, HG. and PHILIPPEN, J. (1974): *Role of antennae of the dragonfly Orthetrum cancellatum in flight control.* Nature 249: 584–585.
- GEWECKE, M. and W. KUTSCH (1979): *Development of flight behaviour in maturing adults of Locusta migratoria: I. Flight performance and wing-stroke parameters.* J. Insect Physiol. 25: 249–253.
- GOLDWORTHY, G.J. and COUPLAND, A.J. (1974): *The influence of the corpora cardiaca and substrate availability on flight speed and wingbeat frequency in Locusta.* J. comp. Physiol. 89: 359–368.
- HEIDE, G. (1982): *Neural mechanisms of flight control in Diptera.* In: *BIONA, report 2* (NACHTIGALL, W., ed.). Akad. Wiss. Mainz: G. Fischer, Stuttgart, New York, pp. 21–34.
- JESSEN, K. (1903): *Die Entwicklung des Gelbrands (Dytiscus marginalis) bis zur fertigen Imago im Schulaquarium.* Illustrierte Wochenschrift für Tier- und Pflanzenfreunde 5: 283–285.
- KIRBY, W. and SPENCE, W. (1828): *An introduction to Entomology.* 5 ed., London.
- KORSCHULT, E. (Hg.) (1923/1924): *Der Gelbrand Dytiscus marginalis L.* 1. und 2. Band. Bearbeitung einheimischer Tiere. Wilhelm Engelmann, Leipzig.
- KRAUTH, J. (1980): *Nonparametric analysis of response curves.* J. of Neuroscience Methods 2: 239–252.
- KUTSCH, W. (1977): *Ontogeny of rhythmic behavioural patterns in Orthoptera.* J. Physiol. Paris 73: 593–616.
- KUTSCH, W. & GEWECKE, M. (1979): *Development of flight behaviour in maturing adults of Locusta migratoria. II. Aerodynamic parameters.* J. Insect Physiol. 25: 299–304.
- LEYDIG, F. (1895): *Zu den Begattungszeichen der Insekten.* Arbeiten zool.-zootom. Institut Würzburg 10: 37–55.

- LIENERT, G. A. (1973): *Verteilungsfreie Methoden in der Biostatistik*. A. Hain, Meisenheim.
- NACHTIGALL, W. (1960): *Über Kinematik, Dynamik und Energetik des Schwimmens einheimischer Dytisciden*. Z. vergl. Physiol. 43: 48–118.
- NACHTIGALL, W. (1961): *Einige Beobachtungen über die Fortbewegung der Dytisciden ausserhalb des Wassers*. Zool. Anzeiger 166: 105–108.
- NEEDHAM, J. G. (1959): *Culture methods for invertebrate animals*. Dover Publications, Inc. New York, New York.
- RÉGIMBART, M. (1876–1877): *Caractères spécifiques des Dytiscides d'Europe*. Feuille jeunes Natural. 7: 113–115.
- SACHS, L. (1978): *Angewandte Statistik*, 5. Auflage; J. Springer Berlin, Heidelberg, New York.
- SCHNEIDER, P. (1981): *Beiträge zur Flugbiologie der Käfer. 1. Einstellung der Flügelschlagfrequenz im fixierten und freien Flug*. Zool. Jb. Physiol. 85: 126–145.
- SHARP, D. (1880–1882): *On aquatic carnivorous Coleoptera of Dytiscidae*. Sc. Trans. Roy. Dublin Soc. 2: 179–1003.
- SPÜLER, M., HEIDE, G. & GÖTZ, K. G. (1981): *Der Einfluss der Bewegungsrichtung von Streifenmustern auf die Aktivität der Flugsteuermuskeln von Fliegen*. Kolloquium des DFG-Schwerpunktprogramms "Neurale Mechanismen des Verhaltens" vom 23.–26.2.1981 in Tutzing.
- WESENBERG-LUND, C. (1910–1911): *Über die Respirationsverhältnisse bei unter dem Eise überwinternden, luftatmenden Wasserinsekten, besonders der Wasserkäfer und Wasserwanzen*. Intern. Rev. Hydrobiol. 3: 467–486.
- WESENBERG-LUND, C. (1912): *Biologische Studien über Dytisciden*. Internat. Rev. Hydrobiol. 5: 1–129.
- WESENBERG-LUND, C. (1943): *Biologie der Süsswasserinsekten*. J. Springer, Berlin.

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