

Zeitschrift: Entomologica Basiliensia
Herausgeber: Naturhistorisches Museum Basel, Entomologische Sammlungen
Band: 11 (1986)

Artikel: Studies about flight of *Dytiscus marginalis* L. (Coleoptera, Dytiscidae)
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DOI: <https://doi.org/10.5169/seals-980563>

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Entomologica Basiliensia	11	451–460	1986	ISSN 0253-2484
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Studies About the Flight of *Dytiscus marginalis* L. (Coleoptera, Dytiscidae)

by P. Schneider

Abstract: The waterbeetle *Dytiscus marginalis* was investigated in regard to flight behaviour, kinematics of the alae and flight control. All adephagous waterbeetles fly like terrestrial *Adephaga* (*Cicindela*-type) with the elytra completely stretched out to side, and supported by the front and middle legs. They are held like airfoils, do not oscillate and support the lift.

Once airborne *Dytiscus* is a permanent flyer. In a wind tunnel, I measured a maximum flight duration of 195 minutes, e.g. ca. 25 km.

In a roundabout the flight distance and the flight willingness are less. The ability for long distance flight indicates that these beetles consume fat. The total loss of body weight after sustained flights can amount to 15 percent and up to 5.3 percent of the loss in weight is fat. The regeneration of body tissue requires more than two weeks after total exhaustion.

Flight speed varies from 2.20–2.60 m/s and wingbeat frequency from 34–46 c/s. An increase of the velocity of airstream causes a passive increase of the wing beat frequency. The increase of the wing stroke amplitude in the downstroke part is probably an active control reaction of the beetle.

Key words: Coleoptera Dytiscidae – *Dytiscus* – flight behaviour – wing-beat frequency – flight control – metabolism

Introduction

Flight types of beetles are differentiated by flight technique and position and function of the elytra. The original type, found in *Adephaga*, was named *Cicindela*-type (SCHNEIDER, 1975, 1978).

As with the different flight-types and wing folding-types (SCHNEIDER, 1975, 1981), various kinds of start preparations are observed. In waterbeetles spontaneous starts can not be expected because tarsal reflex and start for escape are not usual. In tethered flight in front of a wind tunnel *Rhantus* sp. starts very fast and *Acilius* sp. has a complicate even audible activation of the flight muscles (LESTON & PRINGLE, 1965; NACHTIGALL, 1961). Once airborne waterbeetles should have the ability for long distance flights because of finding new water places.

In this study comparative data about flight behaviour, wing kinematics and flight control will be presented.

Material and methods

Waterbeetles were collected in free water and kept with sufficient food (meat, fish and earthworm) in laboratory. The flight behaviour of the diving beetle *Dytiscus* is compared with *Rhantus* sp. and *Acilius* sp. The wing beat frequency was measured by 4 infra red light barriers (SCHNEIDER, 1982). This method made it possible to record also the progress of the wing beat amplitude with defined up- and downstroke phases. High speed film was made with Stalex MS 16A, 3.000 f/s, illumination 6 hallogen lamps (15 V, 150 W), Kodak high speed film 2475, development for 37 DIN with Microphen. For permanent recording we used video-systems. The analysis was made per frame (1/25 s). Flight speed and flight performance were measured in roundabout or in front of a wind tunnel with laminar air stream (SCHNEIDER, 1981). Lift in relation to body angle was recorded by an aerodynamical balance (SCHNEIDER & HERMES, 1977).

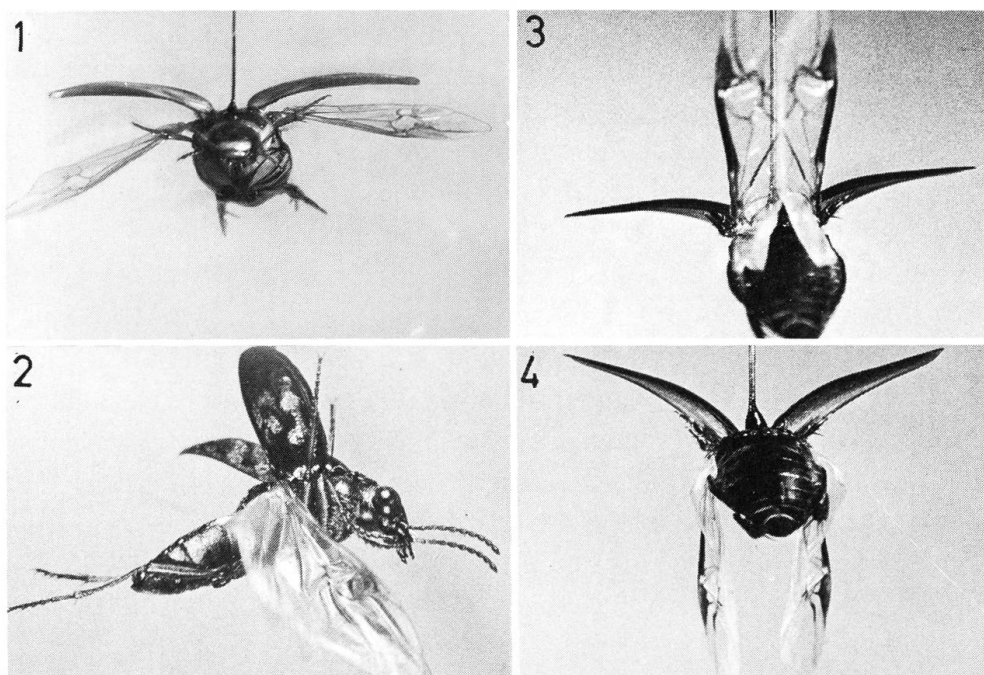
Results and discussion

1. Flight behaviour

Initiation of flight of a tethered diving beetle can not be released directly by tarsal reflex, turning around or blowing. Without tarsal contact the beetles first make swimming movements, then the elytra are opened and aligned in flight position. After some seconds or minutes, the alae are put in downstroke position but still folded. When the alae are completely stretched, flight begins. Once started a new start can easily be released by turning the beetle in the airstream or blowing.

Figures 1–4 show the *Cicindela*-flight-type: 1. flight attitude of *Dytiscus*. 2. *Elaphrus* sp. representative of terrestrial Adephaga. 3–4. upstroke and downstroke position of the alae in *Rhantus* sp.

In *Rhantus* the wing beat amplitude is very large, sometimes more than 180 degrees on each side. The same could be observed in *Acilius* and often in *Dytiscus*. Diving beetles swinging freely around the yaw axis show a quiet flight attitude when the air stream reaches 3–3.5 m/s. The typical flight position of *Dytiscus* is: elytra completely stretched out to side, 11–14 degrees relative to the airstream, front and middle legs trying to support the elytra like airfoils and produce additional lift. With an airstream velocity of 3.5 m/s the elytra produce 12.4 and 21.4 percent of the total lift for body angles of 20 or 30 degrees respectively.



Figs 1–4: 1. Tethered flight of *Dytiscus marginalis*. 2. *Elaphrus* sp. 3–4. *Rhantus* sp. up- and downstroke position of the alae. All adephagous beetles belong to the “Cicindela-type”, here represented by the terrestrial *Elaphrus*: the elytra are held like airfoils, do not oscillate and support the lift passively. The front and middle legs try to support the elytra, but usually they are too short.

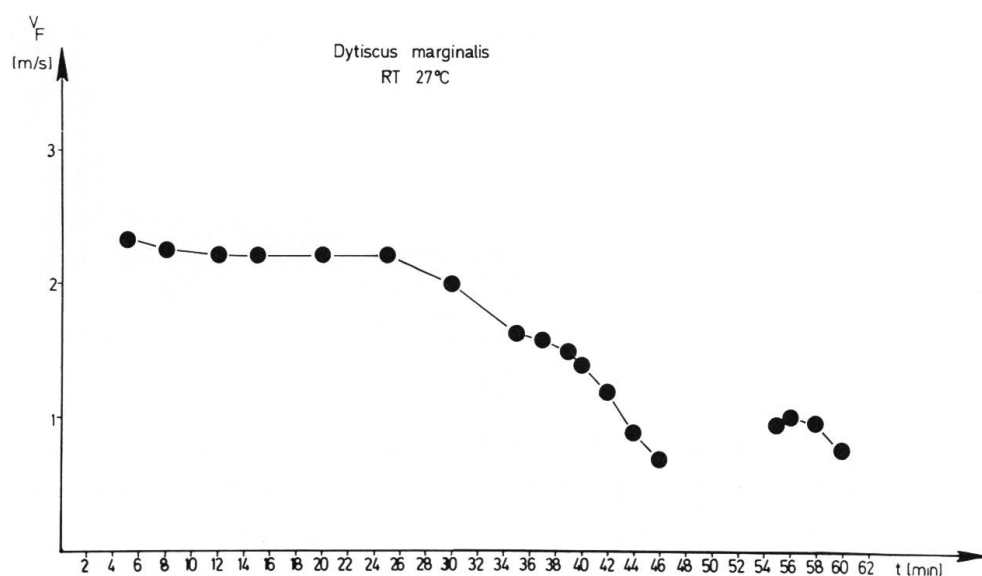


Fig 5: Flight of a diving beetle at the flight mill. First stop after 46 minutes, 8 minutes later a new voluntary start. After the first 26 minutes the wing beat frequency (w.b.f.) begins to decrease (beginning exhaustion).

2. Flight performance

Tethered with an angle of 20 degrees *Dytiscus* has a maximum speed of 2.6 m/s in the flight mill. Flight on a thread 3 m/s are possible. Figure 5 shows an experiment, where after 26 minutes (nearly 4 km) the flight speed decreased. After 46 minutes the flight was stopped. 8 minutes later the beetle started again for a flight of 6 minutes, but with an initial speed of 1 m/s. This speed decreased rapidly. Three other beetles showed indications of exhaustions already after 3, 3.4 and 3.6 km.

SCHNEIDER, (1981) showed that a female who flew 1 h and 20 minutes showed signs of exhaustion after 34 minutes one week later. Though the wing movements seems to indicate a good flight, measurements at the aerodynamical balance proved, that in such a case the lift is less than the body weight. Such an apparent good flight has no physiological importance, because amplitudes lower than 160 degrees produced not sufficient lift in free flight, also when the wing beat frequency is optimal.

In the steady air stream of a wind tunnel, flight is more sustained. The maximum flight time we measured in *Dytiscus* was 3 hours and 15 minutes (wing beat frequency 37–38 Hz, wing stroke amplitude 170–190 degrees). With a flight speed of 2.2 m/s distance flown would be 25 km. After these 195 minutes the first stop occurs. By a new start the flight time could be elongated for 25 minutes. During this time exhaustion, represented by the decreasing wing beat frequency and wing beat amplitude, appeared clearly: 1.–5. min 37 Hz (normal flight), 15. min 32 Hz, 20. min 22 Hz, 22. min 16 Hz. In the last ten minutes the amplitude was less than 100 degrees (initial amplitude more than 160 degrees). This beetle was unable to start again, even two weeks later.

Data about the loss of weight may explain these exhausting flights. A male (1637 mg) flew 137 minutes until total exhaustion losing 246 mg body weight. When returned into water (but without food) the weight returned to 1548 mg after nearly 4 hours, e.g. 89 mg less than original weight (consumed fat?). The next day it flew 56 minutes with a loss of 136 mg, e.g. 2.4 mg/min. Over four days we offered food in sufficient amounts and the body weight returned to 1594 mg, but flight not observed again.

We are now investigating whether the fat content in the tracheoblast of the flight muscles is consumed (shown in *Melolontha melolontha* L. by SCHNEIDER, HOESE & JANSSEN, 1984), or if a degeneration of the mitochondria or histolysis of the flight muscles takes places (observed in the flight muscles of *Oryctes boas* unpubl.).

3. Kinematics of the alae

As mentioned above the amplitude of the alae of flying adepagous waterbeetles is very large (SCHNEIDER, 1975, 1982). The path way of the wing tip of *Dytiscus* differs slightly from that of other beetles (SCHNEIDER, 1980). Figure 6 shows the path of the wing tip (dotted line, comp. GEWECKE & BAUER, 1984). Sometimes a loop in the lower part of the downstroke can be found (directional change?, SCHNEIDER, 1980).

Dytiscus marginalis

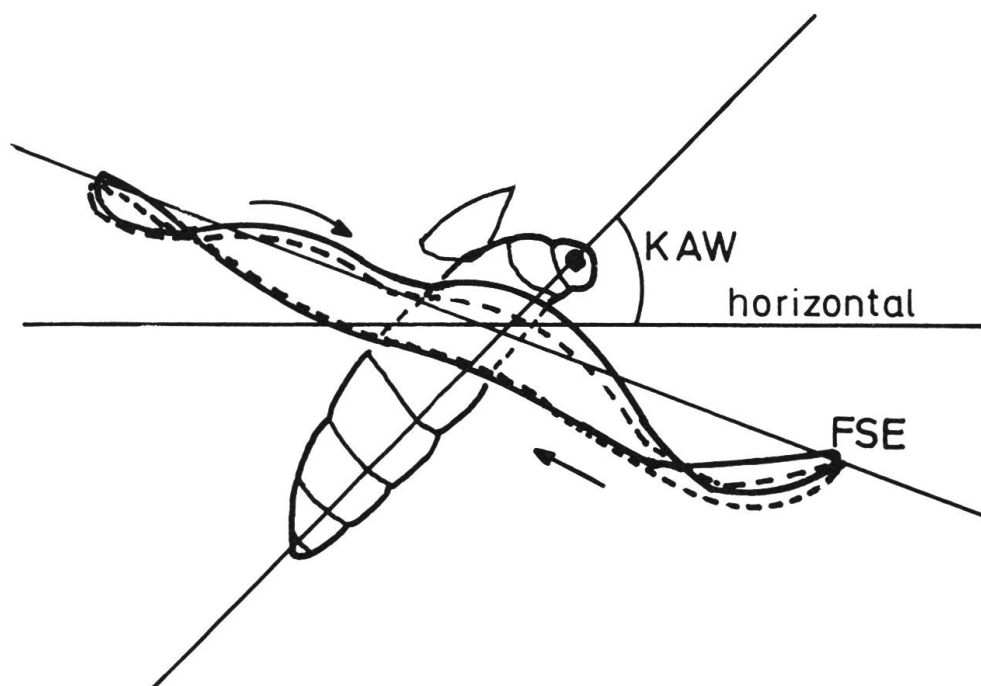


Fig 6: Path way of the wing tip of *Dytiscus*. Dotted line: normal progress, continuous line: additional loop in the lower part of the downstroke. KAW = body angle relative to the horizontal plane, FSE = wing beat plane relative to the body length axis.

Figure 7 and 8 show the progress of the wing tip drawn from high speed film. The downstroke runs faster than the upstroke, although the path is longer because of the wave like path way. The highest acceleration appears in the middle of the stroke. On the other hand figure 8 shows that the optimal speed of the angular velocity is already reached shortly after the turnings, e.g. acceleration and braking of the alae occur in extreme short time. In both turns real twistings of the wing are visible.

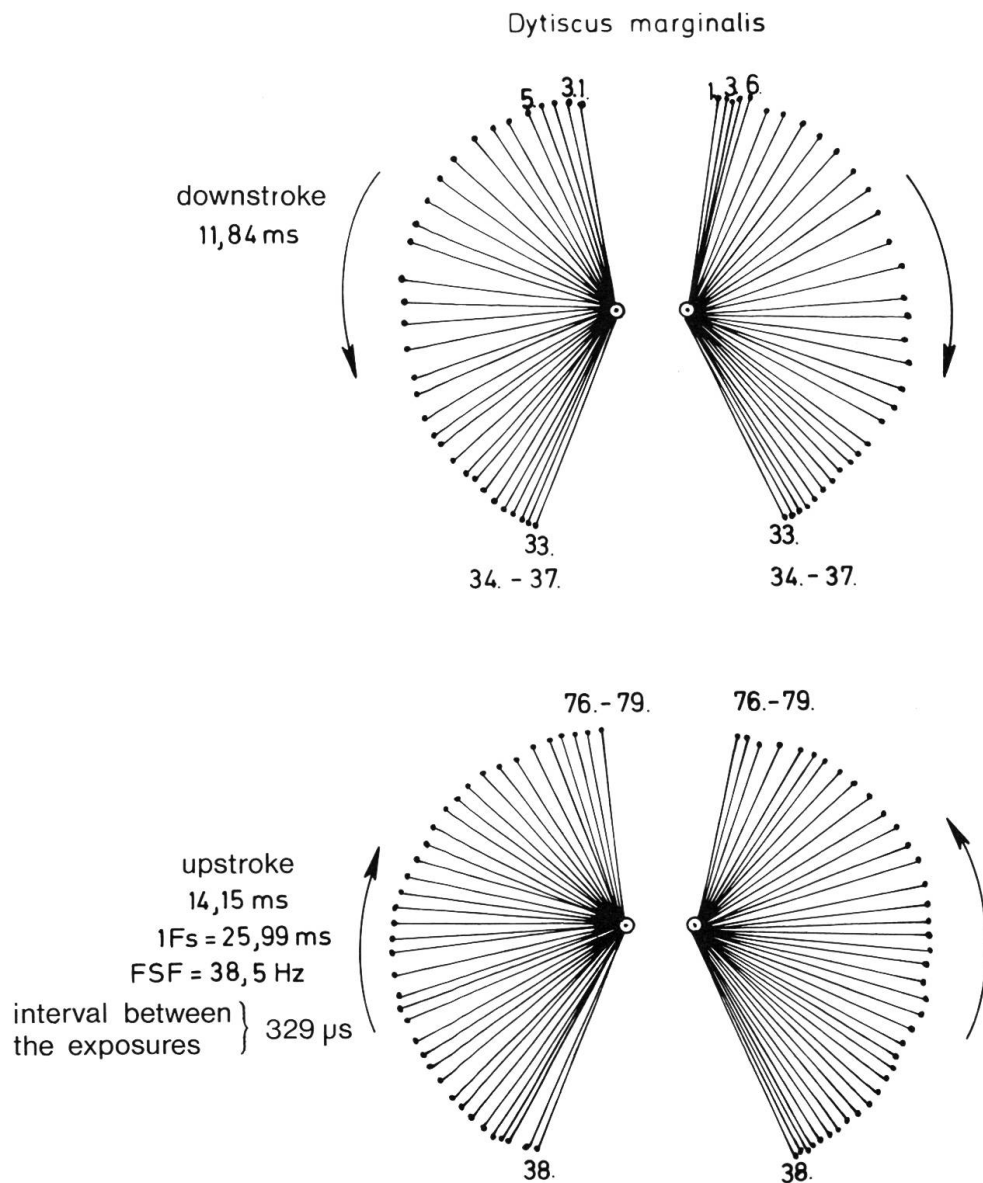


Fig 7: Path way of the alae from vertical view on the wing beat plane (comp. Fig 6, FSE, high speed film, > 3000 b/s, time distance of the points 329 μ m). The turn of the wings at up- and downstroke happens in 1.5 ms. Above downstroke (11.84 ms), below upstroke (14.15 ms), FSF = wing beat frequency, FS = wing stroke.

Wing beat frequencies of individual *Dytiscus* vary from 34 to 46 Hz. As with other insects (SCHNEIDER & HOESE, 1982), beetles with the same body size have different wing beat frequencies measured under the same physical conditions. In the above mentioned flight of 195 minutes the wing beat frequency was nearly constant for 134 minutes (37–38 Hz).

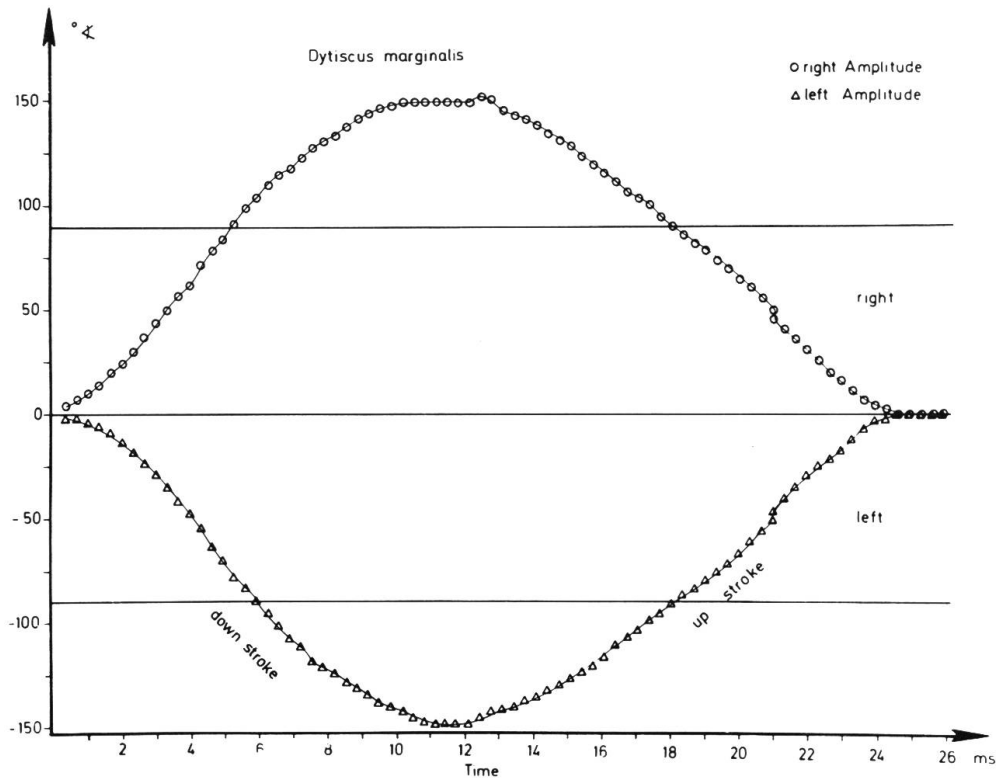


Fig 8: Angle change of one stroke during down- and upstroke of the right and left alae (high speed film, see Fig 7).

SCHNEIDER (1981, Abb. 14) has shown that the wing beat frequency increases with increasing velocity of the air stream. This was confirmed by GEWECKE & BAUER (1984). Since such an increase of the wing beat frequency was always observed in beetles which were not able to control the flight speed. This phenomenon is caused passively by the air stream (SCHNEIDER, 1981). Cetoniid beetles which are able to control the flight speed by the antennae do not show this effect. Control of wing receptors or by Johnston's organ in *Dytiscus* (GEWECKE & BAUER, 1984) must be studied with special interest.

Figure 9 shows the effect of varying airstream on the position of the elytra and the amplitude of the wing beat. Up to 3.00 m/s the elytra were raised up passively. The amplitude also increases with increasing speed of the air stream (Figure 9). This reaction can be interpreted as a control reaction, e.g. a feedback from mechanoreceptors on the wings or on the articulations (PFAU & HONMICH, 1979) to the direct flight muscles.

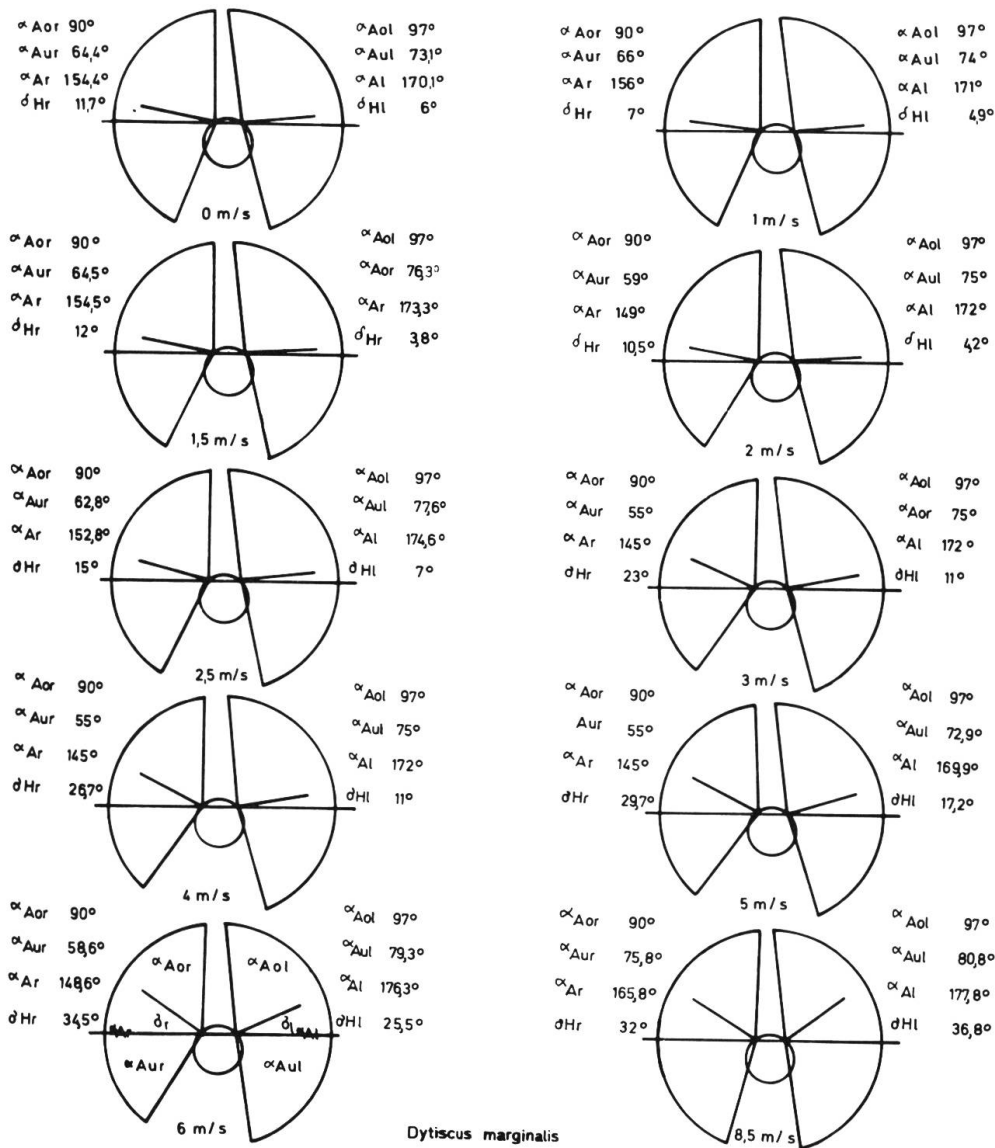


Fig 9: Position of the elytra and amplitude of the alae dependent on the velocity of the air stream. Aor(1) = upper part of the right (left) amplitude, Aur(1) = lower part of the right (left) amplitude, Ar(1) = total amplitude right (left), Hr(1) = angle between the horizontal plane and the right (left) elytron.

Such an increase in the amplitude was also found for each stroke. Figure 10 gives an example for photoelectric measurements of each wing beat at start and stop of the wind tunnel (3 m/s or 4 m/s). Except the data for each stroke an average of 3 or 5 strokes before or after the external stimulus (dotted line, open symbols) and an average of 10 strokes (filled symbols) was drawn. In these experiments we found:

- an increase of the time in the lower turn, e.g. the stroke must run lower.
- the time for the upper turn does not change.
- t_1 as representative for the time of the downstroke increases when the wind stops, probably caused by the diminished wing beat frequency.

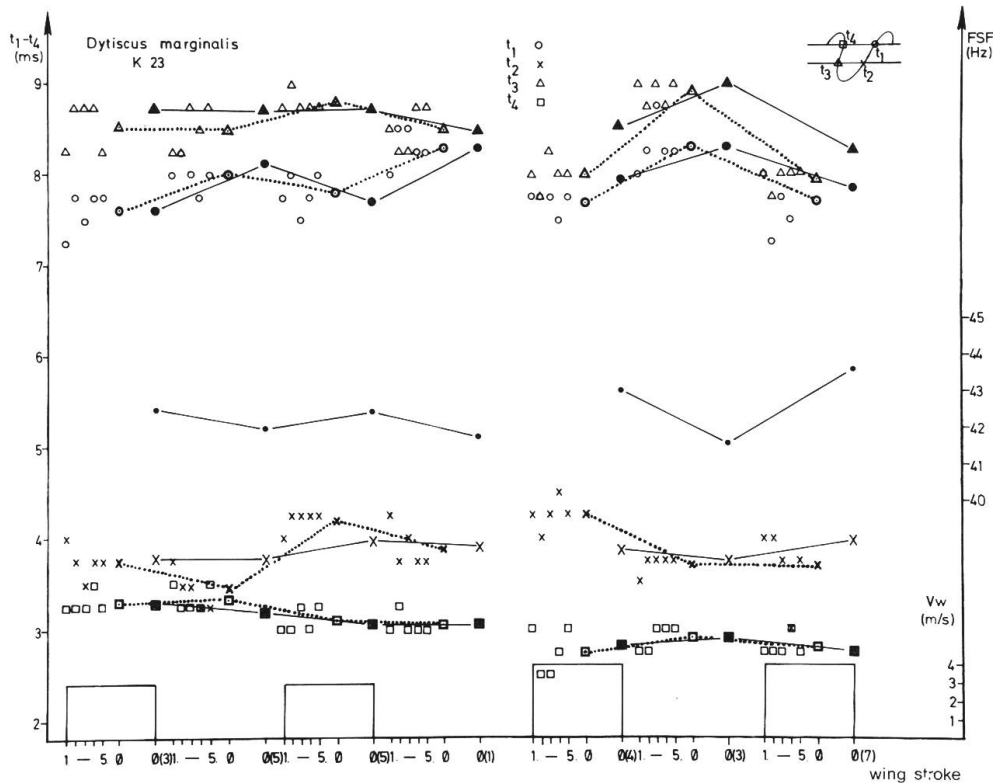


Fig 10: Photoelectric control of the wing beat at wind on and wind off (3.0 m/s or 4.0 m/s). Data of 5 strokes were plotted, open symbols and pointed line = average of 3 or 5 strokes, filled symbols and continuous line = average of 10 wing beats before or after the change of wind speed. o = wing beat frequency, t_1 () = time of the downstroke (comp. small insert picture in the right corner), t_2 () = time for the lower turn, t_3 () = time for the upstroke, t_4 () = time of the upper turn. FSF = wing beat frequency (Hz), Vw = wind velocity (m/s).

On the other hand we can see, that the wing beat is not exactly running machine, sometimes it changes from stroke to stroke, and the summary of the reactions presents the effect. This is not the case in experiments about orientation to light (SCHNEIDER, in prep.).

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