PREFLIGHT BEHAVIOUR AND THE INITIATION OF FLIGHT IN TETHERED AND UNRESTRAINED DRAGONFLY, *CALOPTERYX SPLENDENS* (HARRIS) (ZYGOPTERA: *CALOPTERYGIDAE*)

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The start of flight in *C. splendens* was investigated using high-speed photography and electrophysiological techniques. Occasional preflight neuromuscular activity and wing vibrations are considered as warm-up behaviour. Flight begins with a downstroke, and typical calopterygoid wing coordination is established in the first wingbeat cycle: the hindwings lead in downstroke, and the forewings lead in upstroke.

INTRODUCTION

In most insects preparing for flight, the wings have to be moved from a folded position to the plane in which they beat during flight. In anisopterous Odonata the wings are not folded but permanently extended, and flight begins either with a downstroke or an upstroke of the wings (POND, 1973). In the zygopterans, on the other hand, the wings are brought to a resting position parallel to the abdomen with their morphological upper sides clapped together, and the forewings enclosed by the hindwings (except *Lestidae*). Thus in Zygoptera fresh flight can be started from only one point in the wingbeat cycle. The aim of this work is to describe the start of flight of a zygopteran in comparison to anisopterans and other insects.

MATERIAL AND METHODS

Experiments were performed on male and female individuals of *Calopteryx splendens*. All experiments were carried out at room temperatures of 27°C ± 2°.

Multiple exposure photographs and stroboscopic films (up to 150 frames/sec) were taken from tethered animals flying in front of a wind tunnel, and from unrestrained animals using the photographic device previously described (RU-DOLPH, 1971), and a modified "Dreitafelprojektion" after NACHTIGALL (1970). Unrestrained animals were placed on a rod and adjusted so that when the completely unstimulated insects started flight, the wings interrupted a system of light beams with phototransistor triggering flashlight or stroboscope, and camera shutters or motors. In addition, 16 mm movies (64 frames/sec) taken from insects at local river banks were analysed. Extracellular electrical activity was recorded with conventional methods. Preflight behaviour and the first two wingbeat cycles are considered as a starting phase; the mechanics of persistent flight will be dealt with elsewhere (Rudolph, in prep.).

RESULTS

In tethered flight as well as in free flight two types of start can be distinguished by the speed of reaction and the kind of coordination between ipsilateral wings. Unstimulated and unrestrained animals perform the "slow" mode of take-off; tethered animals or stimulated free animals generally perform a "quick" start.

PREFLIGHT BEHAVIOUR

Preflight warm-up behaviour has been reported in several anisopterans (MILLER, 1964, 1974; POND, 1973). A similar behaviour could be observed in C. splendens. Even at high room temperatures tethered animals sometimes performed wing vibrations of varying amplitude, but usually only a few millimetres in amplitude, preceding spontaneous flight and still maintaining tarsal contact with a piece of cork. Like in the Aeshnidae (POND, 1973), these whirring movements stopped after a few moments or abruptly turned into complete wing motion. In one individual there was a gradual shift from warm-up to flight (Fig. 1). While in Aeshnidae the frequency of bursts during warm-up may be twice that of flight, in C. splendens the frequency is always similar to that of flight (15-17 beats/sec). In almost all unstimulated starts, when tethered animals gave up tarsal contact spontaneously, electrical activity could be recorded prior to any detectable wing movements (Fig. 1). A varying delay between the appearance of neuromuscular activity and the onset of wing movements has also been observed in the cockroach, Periplaneta, (POND, 1972a), the reason of which is a need for synchronization and summation of several impulses in every muscle unit to produce sufficient muscular tension to raise the wing.
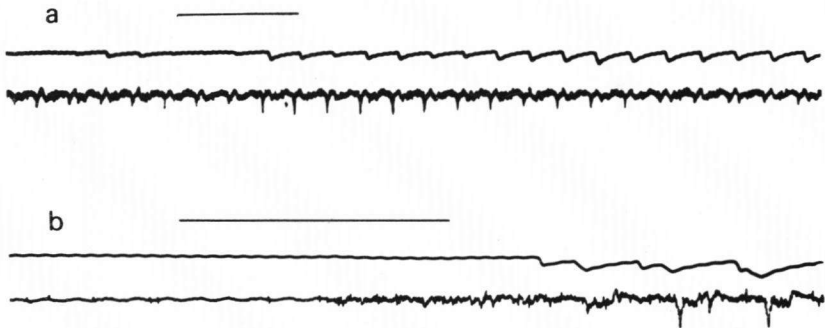
Fig. 1. Onset of tethered flight in two specimens of *Calopteryx splendens*. (a) Preflight warm-up with low amplitude wing movements and gradual shift to full flight. – (b) Electrical activity before the onset of detectable wing movements; large spikes are still absent. – Upper trace: Wing movements recorded by interruption of a lightbeam. Note that in (a) trace amplitude does not correspond directly to stroke amplitude, but to the amount of darkening the lightbeam with 5 mm in diameter, which in (a) was adjusted crossing P_H (cf. Fig. 2). – Lower trace: Neuromuscular activity from metathoracic depressor muscle. Time scale: 200 msec.

SLOW START

In the resting position the forewings are completely enclosed by the hindwings. In consequence, the hindwings begin the downstroke earlier than the forewings, and the forewings follow with some delay in downward motion. The sweep of one hindwing is straight down from its dorsal position, while the forewing is mainly moved forewards before entering definite downwards motion (Fig. 2). The delay of the forewing performing the first downstroke varies to a certain amount in one individual, but it does not depend on headwind air velocity or varied illumination. Generally both wings synchronously arrive at the lower turning point, but the forewing may overtake the hindwing. During upstroke there is a typical phase shift due to increased forewing acceleration. With no exception the forewing will reach the upper turning point earlier than the hindwing (Fig. 2), but it does not return to its resting position (P_F; Fig. 2). The wing tip returns to a point about $10°$ more forward in the sagittal plane. The forewing remains in the dorsal position until the hindwing has arrived and entered the second downstroke. At the end of the upstroke the hindwing returns to its dorsal resting position, so that now the forewings are only partially enclosed. Delay or lead of one wing is clearly shown comparing the stroke amplitudes of ipsilateral wings at certain stages during the wingbeat cycle (Fig. 3).

The two pairs of wings come close together in a distinct dorsal clap at the end of every upstroke. This typical calopterygoid dorsal clap is an exception in
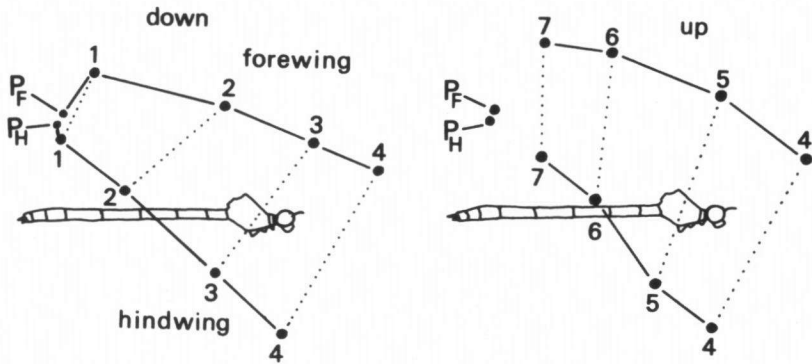
Fig. 2. An example of the path of the right wing tips during the first wingbeat cycle at slow start of *Calopteryx splendens* compared to their position when closed (P_F, P_H). The numbers indicate consecutive wing positions, separated by 8 msec.
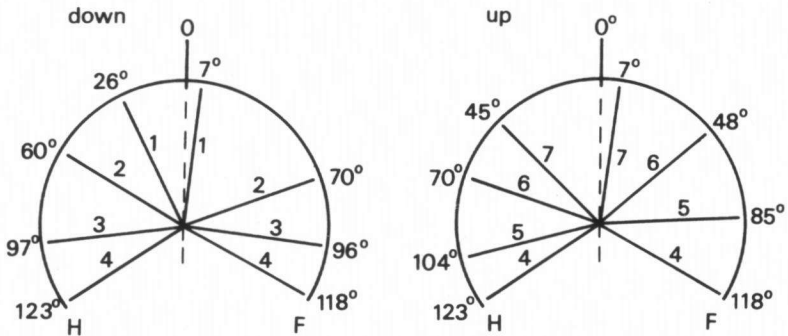

Fig. 3. The correlation between stroke amplitudes of right wings during the first wingbeat cycle. The numbered radii correspond to the wing positions of Figure 2. Note that position 4 of the forewing does not represent maximum amplitude, but has been photographed shortly after supination and beginning upstroke. Consecutive positions are separated by 8 msec. H: hindwing, F: forewing.

Odonata, but occurs in other insects as well, e.g. in butterflies, in *Drosophila* (VOGEL, 1966), and might be typical of minute insects (WEIS-FOGH, 1973).

The second wingbeat cycle is entered by the hindwing with no time-lag, and it is much the same as the first with very little changes in wing coordination. With no exception the first two downstrokes are of full amplitude in both fore- and hindwing, while in most other insects there is an initial phase of increasing amplitude, e.g. in beetles (PRASSE, 1960), dipteran flies (NACHTIGALL, 1968), locusts and cockroaches (POND, 1972a, 1972b). There are no differences between tethered and unrestrained animals performing slow start. It is very

remarkable that take-off is never achieved by the first downstroke, but exceptionally within the last third of the first upstroke or generally only within the second downstroke. Evidently all insects not provided with an extra catapulting mechanism like that found in locusts (POND, 1972b, dipteran flies (NACHTIGALL, 1968), or in some beetles (SCHNEIDER, 1974), give up tarsal contact only after having performed several wingbeat cycles.

QUICK START

During quick start the ipsilateral wings form one aerofoil, the forewing's posterior margin overlapping the hindwing's costa. The initial overlapping is continuously reduced during the sweep due to the lesser stroke plane inclination in the forewings. From their dorsal position the wings are flung apart like the opening of a book, every wing being pronated, with the posterior margin of the hindwings remaining in apposition at first. So there is less or no forward motion in the forewing prior to entering the downward motion. The wing movements in quick start of *C. splendens* are identical with those termed "fling" in the minute chalcid wasp, *Encarsia formosa* by WEIS-FOGH (1973).

After the initial opening with greater acceleration in the forewing both wings move downwards with almost equal velocity, but the forewing may outdistance the hindwing. In the first upstroke the forewing is accelerated and arrives at the dorsal position earlier than the hindwing, but generally there is less lead than in slow start. So in quick start only the temporal coordination between ipsilateral wings is altered, but the typical pattern with forewings leading in the upstroke remains unchanged. The second wingbeat cycle is much the same as the first. Take-off in unrestrained animals is never achieved within the first downstroke. During flight of *C. splendens* the wings keep a characteristic and persistent coordination, which is already established in the first wingbeat cycle. This coordination is unique; other insects flying on four morphologically similar but functionally separate wings, e.g. Neuroptera, perform a significantly different wing coordination (MILLER, 1975). The calopterygoid wing coordination might originate in that wings are clapped together dorsally at the end of every upstroke and in the resting posture. However, in other Zygoptera clapping wings together while resting, there is another coordination already during the first downstroke: while initiating flight, the forewings are moved downward prior to the hindwings (BULL, 1909), and there is no dorsal clap at the end of an upstroke.

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