

KINEMATIC ANALYSIS OF SYMMETRICAL FLIGHT MANOEUVRES OF ODONATA

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Summary

By analysis of slow-motion films of dragonflies and damselflies in free flight, released in front of a backdrop or startled during flight, the following flight parameters have been quantified for symmetrical manoeuvres: wingbeat frequency, relative durations of up- and downstroke, phase relationships of the beats of fore- and hindwings, stroke amplitude, mean stroke velocity, flight velocity, nondimensional flight velocity, advance ratio, acceleration, angle of attack and stroke plane.

The wingbeat frequencies are higher in the smaller species and in those with relatively large wing loading. As a rule, Zygoptera have a wingbeat frequency only half that of Anisoptera. The stroke amplitude is almost always much larger in Zygoptera than in Anisoptera, which have a greater range of variation in this respect. Stroke velocity is higher in Anisoptera than in Zygoptera; it is also higher in the more elaborate flight manoeuvres than in others. The calculated stroke velocities resemble those actually measured.

Anisoptera fly more rapidly than Zygoptera. With respect to the nondimensional flight velocities, it is notable that although the values for Anisoptera are higher than those for Zygoptera, they are exceeded by the Calopterygidae; the latter can fold their wings back during rapid forward flight and shoot away, as in the 'ballistic' flight of small songbirds. However, the advance ratio is higher in Anisoptera than in Calopterygidae.

Anisoptera also perform better than Zygoptera with respect to acceleration. Three categories of phase relationships between the beats of the fore- and hindwings are established: counterstroking, phase-shifted stroking and parallel stroking. Counterstroking produces uniform flight, whereas the flight produced by phase-shifted and, in particular, parallel stroking is irregular. The angles of attack of the wings are shown to be associated with particular flight manoeuvres, as are the stroke planes. Flight manoeuvres are discussed without drawing detailed aerodynamic conclusions. The flight of Anisoptera is compared with that of Zygoptera.

Introduction

The flight of dragonflies and damselflies is quite obviously superior to that of any

■ Key words: Odonata, kinematics, free flight.

other large insect. They are capable of great acceleration and can execute extremely rapid manoeuvres in a very limited space. Apart from preliminary attempts (Norberg, 1975), no field analysis of Odonata in free flight has previously been conducted. Initial kinematic data derived from laboratory observations (Newman, 1983; Alexander, 1984, 1986; May, 1981*a,b*) coupled with aerodynamic calculations (Azuma *et al.* 1985; Azuma & Watanabe, 1988) present a very incomplete picture of odonatan flight. Moreover, it is debatable whether such laboratory data are applicable to flight under field conditions. The flight of grasshoppers (Baker *et al.* 1981) and Heteroptera (Betts, 1986) in the laboratory is known to differ from that in the field. The present investigation was carried out to check the validity of laboratory data and further elucidate odonatan flight.

Flight variables appear in a variety of forms, all of which must be represented in a comprehensive kinematic analysis. For some of them, such as the changes in shape of the wings, the data obtainable with the photographic method used here are not sufficient. For example, changes in the twisting and profile of the wing (Fig. 1) cannot be taken into account, although they must be significant.

There are two groups of flight parameters required for an adequately precise kinematic description: the temporal and the spatial. The temporal category includes parameters of the whole insect body, such as the flight duration and the distribution of phases of gliding, flapping or turning flight. Analysis of these long-term aspects would have required prolonged recordings – for example, with video

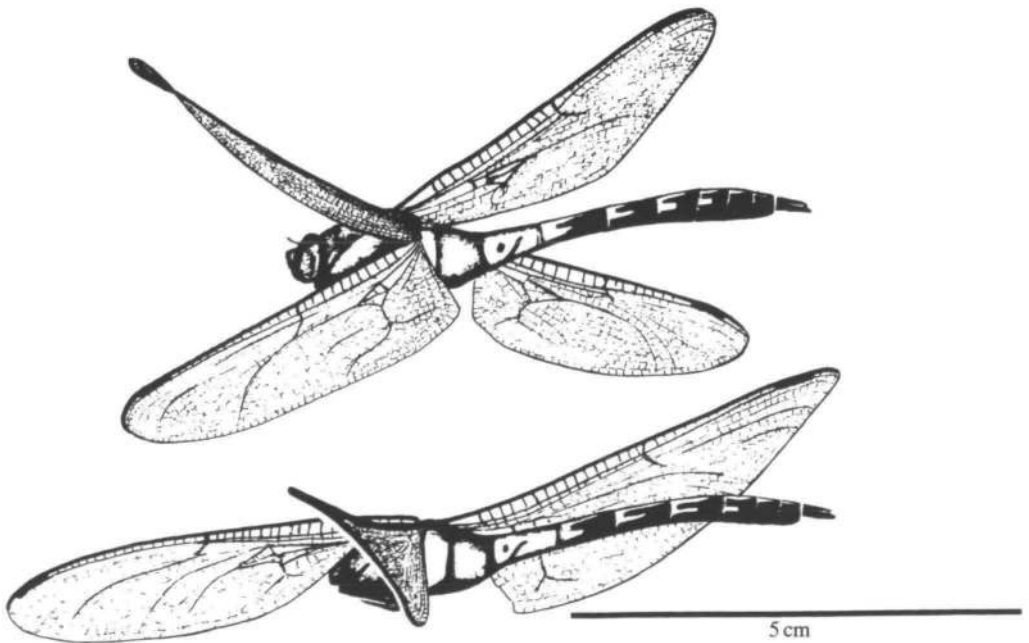


Fig. 1. Twisting of the left forewing (top) and profile of the left hindwing (bottom); each picture shows the downstroke of a hovering male *Anax imperator*.

cameras. With the slow-motion photography employed here, very brief sections of flight behaviour are expanded, to permit analysis of short-term aspects.

The other group in the temporal category is the parameters of wing movement: wingbeat frequency, the ratio of upstroke duration to downstroke duration and the phase relationships of the fore- and hindwings. The latter can be represented precisely for species that beat their wings at a low frequency and approximately for those with a high wingbeat frequency.

The spatial category includes the body parameters, flight path and flight velocity (and, in some cases, the changes in these parameters) as well as the path of the wing stroke and the angle of attack and velocity characteristics of the wings. Only in favourable cases (see Materials and methods) could one or another of these parameters be approximated.

In none of the filmed manoeuvres did the various optimal conditions for measurement of all the flight variables coincide, so that a detailed analysis of even one of the manoeuvres is impossible. In this paper, therefore, no attempt has been made to calculate aerodynamics from kinematic data. Rather, the intention here is to find some preliminary explanations of the mechanisms underlying various flight manoeuvres by comparing the kinematic data from many different manoeuvres in the field. Only manoeuvres in which the wingbeat parameters are the same for the right and left wings (i.e. symmetrical manoeuvres) are considered. Special emphasis is placed on the differences between damselflies and dragonflies of different dimensions.

Materials and methods

Approximately 20 species of Odonata were filmed in slow motion near water in northern Germany (1980–1988), in the rainforests of Panama (January/February 1986 on Barro Colorado Island) and in the grasslands of Texas (September 1986). Species were initially selected on the basis of the ease with which they could be filmed (Calopterygidae, Aeshnidae), but later on other criteria such as size (Pseudostigmatidae) or range of flight manoeuvres (Libellulidae) were given priority. The names of all the filmed species are abbreviated in the text as follows.

Zygoptera

Calopterygidae	<i>Calopteryx splendens</i>	C.s.
	<i>Calopteryx virgo</i>	C.v.
Lestidae	<i>Lestes viridis</i>	L.v.
Platycnemididae	<i>Platycnemis pennipes</i>	P.p.
Coenagrionidae	<i>Ischnura elegans</i>	I.e.
Pseudostigmatidae	<i>Megaloprepus coerulatus</i>	M.c.
	<i>Mecistogaster ornata</i>	M.o.
	<i>Mecistogaster linearis</i>	M.l.

Anisoptera		
Aeshnidae	<i>Aeshna cyanea</i>	<i>A.c.</i>
	<i>Aeshna subarctica</i>	<i>A.s.</i>
	<i>Anax imperator</i>	<i>An.i.</i>
	<i>Anax junius</i>	<i>An.j.</i>
Libellulidae	<i>Orthetrum cancellatum</i>	<i>O.c.</i>
	<i>Perithemis tenera</i>	<i>P.t.</i>
	<i>Tramea lacerata</i>	<i>T.l.</i>
	<i>Sympetrum danae</i>	<i>S.d.</i>
	<i>Sympetrum sanguineum</i>	<i>S.s.</i>
	<i>Sympetrum flaveolum</i>	<i>S.f.</i>
	<i>Sympetrum vulgatum</i>	<i>S.v.</i>
	<i>Leucorrhinia rubicunda</i>	<i>L.r.</i>

A prerequisite for successful filming was detailed knowledge of the whereabouts and behaviour of the insects. Standing near or in the water, I supported a slow-motion camera (LOCAM, model 51) with a telephoto lens (Kern Switar 100 mm, Canon 200, 300 mm) on my shoulder and aimed it towards the flying insects. The camera had to be started at least 2–3 s before a particular behaviour was to occur, to allow time for acceleration to an appropriate film speed.

Some of the close-ups of Calopterygidae and Pseudostigmatidae were provoked with pinned-down conspecifics. It was then possible to film the damselflies flying close to the captive insect and exhibiting various kinds of behaviour.

About 60 captive insects were released and filmed in front of a grid on a plastic backdrop. In another experiment free-flying dragonflies above the water surface were filmed accelerating in response to a sudden sweeping movement of a butterfly net. Almost all the films were made during periods with no wind and at a temperature above 20°C. Of about 12 000 m of exposed 16-mm film, only 1–3 % was used for flight evaluation. Only when the insect was directly perpendicular to the camera (either sideways or head-on) were the sequences suitable for kinematic analysis. The size of the sample from which various flight parameters were determined is therefore so small that statistical analysis was not attempted. With the help of time markers on the film, chronological sequences could be reconstructed. Films were evaluated using a single-frame analyser (NAC, model DF16B). The surface area of the wings was determined with a digital geometric analysis computer (KONTRON-Videoplan). The dimensions of insects that were not captured were estimated from the values in the literature (mean values from d'Aguilar *et al.* 1985). Some of the body dimensions (*L.v.*, *C.s.*, *A.c.*, *O.c.*, *An.i.*, *L.r.*) were measured by K. Grabow. Where possible, differences in morphology and kinematics of the fore- and hindwings, especially in the Anisoptera, are indicated; otherwise, a mean value is given.

The *wingbeat frequency*, the *upstroke/downstroke ratio* and the *phase relationships* of the fore- and hindwings were found by reference to the time markers. When the transition between up- and downstroke lasted longer than two frames

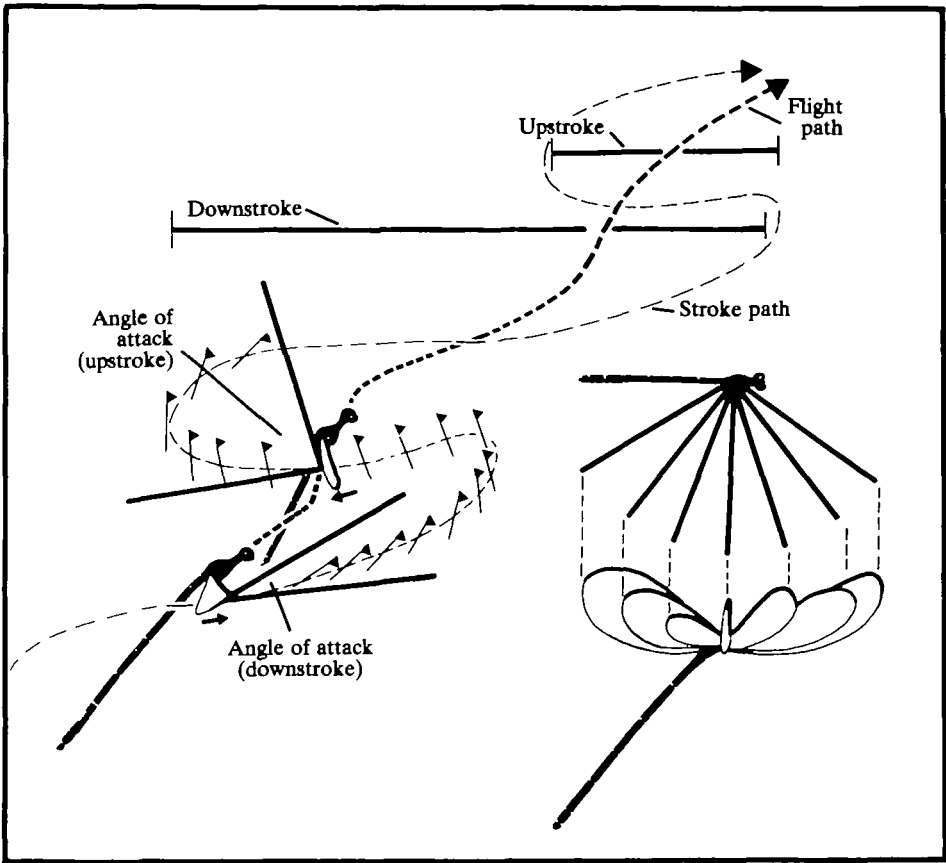


Fig. 2. Left: kinematic parameters of flight (*Megalopterus coeruleus*) in a coordinate system fixed in space; side view of right forewing. The small lines crossing the stroke path indicate the wing positions at those points; the small triangles indicate the underside of the wing. Right: determination of stroke amplitude, in views from above (top) and from the side of *M.c.* with the right wing in various positions.

one frame was assigned to each. The errors in these time measurements varied from 2 to 20 %, depending on film speed and wingbeat frequency. The *stroke amplitude*, the angular distance through which the wings travel, was calculated trigonometrically from wing positions filmed from the side, so that the wings appeared foreshortened (Fig. 2). The actual wing length was known in only a few cases, giving rise to an error of unknown magnitude: the discrepancy between the actual wing length and the mean value found in the literature. An additional error was introduced when the line of sight was not exactly in the stroke plane. The *mean stroke velocity* was calculated from the wingbeat frequency and the stroke amplitude halfway along the wing.

The velocity of the beating wing increases continuously from the base to the tip of the wing. Although the wing joint does not remain at a precisely fixed centre of

rotation, but can shift somewhat (Pfau, 1986), the velocity at the joint is assumed to be zero. The mean stroke velocity (i.e. the velocity halfway along the wing, averaged over the entire wingbeat cycle) can be calculated from the wing length, wingbeat frequency and stroke amplitude. In this paper stroke velocity is always expressed with respect to the body. The true stroke velocity with respect to the air could be calculated from the flight speed and the stroke plane (see Table 2). Stroke velocities were also measured directly on the film, as follows. The displacement of the wingtip (or of the pterostigma) with respect to structures in the background was measured from frame to frame. When the scale of the image had been established by reference to the body dimensions and the elapsed time had been determined, the stroke velocity could be calculated. The *flight velocity* was also calculated by this method; in this case the reference point was a prominent part of the head. Because of the difficulty of evaluating velocity in such rapidly moving insects, perspective distortions in close-up and image size at long range, velocity data are incomplete. At one field site distances were estimated by reference to a rectangular pond, so as to measure time during flights over the pond.

Following Ellington (1984a,b), the *non-dimensional flight velocity* was calculated as the ratio of the distance covered in each wingbeat to the wing length, and the *advance ratio* was obtained by dividing the flight velocity by the mean stroke velocity. *Accelerations* were determined from the films of both free-flying and released insects.

Angle of attack (here always considered to be the angle between the stroke plane and the wing cross-section) was measured only in frames showing the insect from the side, while the wing was roughly perpendicular to the plane of the photograph. In cases of doubt the wing positions in the preceding and following frames were drawn, and the angle of attack in the frame in question was determined by rotating the wing cross-section back and forth until its most probable position had been found. Errors of up to 20 % are realistic; values subject to even larger errors are shown in parentheses in Table 2. The position of the measured attack angle along the wing was not discernible in the side view and hence cannot be specified. The source of error here is the twisting of the wing; since the degree of wing twisting is unknown, the magnitude of the error cannot be estimated. The *stroke plane* was also determined from side views of the dragonfly. A line drawn from the beginning to the end of the wingtip path was considered to represent the mean position of the stroke plane. The values are related to the horizontal, and are negative when the downstroke is inclined below the horizontal.

Films of all species in flight are available from IWF, Nonnensteig 72, D-3400 Göttingen, FRG.

Results

The data do not provide a complete picture of the kinematics of odonatan flight; in particular, the spatial parameters have not yet been adequately quantified. Given the impossibility of a comprehensive flight analysis, the different flight

parameters are treated successively. This presentation is not designed to explain any particular manoeuvre, which would require consideration of all the flight parameters together. Nevertheless, the successive presentation allows easy comparison among species and among manoeuvres.

Wingbeat frequency

More than 20 species were studied, eight of them thoroughly. Comparison revealed that the wingbeat frequency was similar for species of similar size and dimensions (see Table 1). Therefore Fig. 3 shows only typical species, to illustrate the following eight tendencies.

(1) Wingbeat frequency was size-dependent. Small species, which as a rule also have small wings, beat them at a higher frequency than did large species. Within the Libellulidae this trend is shown by the series *Perithemis tenera* (*P.t.*) > *Sympetrum danae* (*S.d.*) > *Leucorrhinia rubicunda* (*L.r.*) > *Tramea lacerata* (*T.l.*).

Even within a species, size differences were associated with changes in frequency (extreme example, *M.c.* males: variation of mass, 156–491 mg; of wing length, 52.2–78 mm; of frequency, 4.7–12.6 Hz).

(2) Of two species with similar wing lengths, the one with the higher wing loading also had the higher wingbeat frequency: *T.l.* (49 mm; 2.45 N m^{-2}) 29 Hz; *An.i.* (47.5 mm; 4.2 N m^{-2}) 36.5 Hz.

(3) Zygoptera normally fly with a much lower wingbeat frequency than Anisoptera, often half that of Anisoptera with similar wing length: *P.t.* (16.5 mm wing length) 73 Hz; *P.p.* (19.8 mm) 32.8 Hz; *S.d.* (23 mm) 43.5 Hz; *L.v.* (22.2 mm) 32.6 Hz; *L.r.* (28.9 mm) 41 Hz; *C.s.* (28.2 mm) 16 Hz.

(4) Whenever great demands were made on flight performance, the wingbeat frequency was increased (the stroke amplitude and phase relationship between the

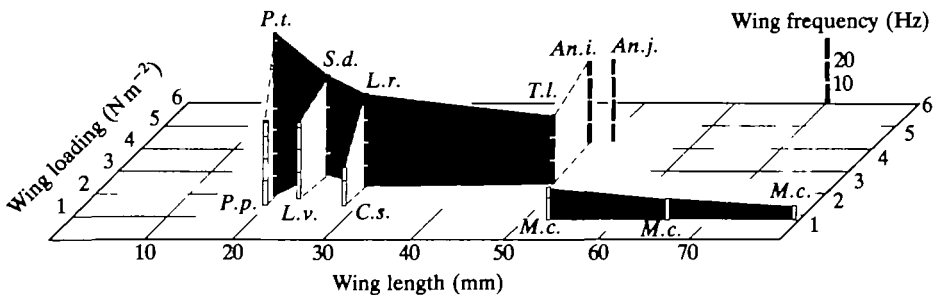


Fig. 3. Examples of mean wingbeat frequencies of representative species, plotted as a function of wing loading and wing length. Abbreviations: *P.t.*, *Perithemis tenera*; *P.p.*, *Platynemesis pennipes*; *S.d.*, *Sympetrum danae*; *L.v.*, *Lestes viridis*; *L.r.*, *Leucorrhinia rubicunda*; *C.s.*, *Calopteryx splendens*; *An.i.*, *Anax imperator*; *An.j.*, *Anax junius*; *T.l.*, *Tramea lacerata*; *M.c.*, *Megalopterus coeruleus*. Each subdivision in the columns corresponds to 10 Hz. The planes connecting the various columns indicate the tendencies discussed in the text. The three columns for *M.c.* represent the smallest male on the left, the largest on the right, and the average of all males in the middle.

Table 1. Means of the body dimensions and of some kinematic values for the species filmed, with standard deviations in parentheses

		Number of bodies	Number of flights	Mass (mg)	Wing length (fore-) (mm)	Wing area (mm ²)	Wing loading (mg mm ⁻²) (N m ⁻²)	Wingbeat frequency (Hz)	Max. speed (cm s ⁻¹)	Acceleration take-off-0.1 s (m s ⁻²)	Acceleration 0.1-0.2 s (m s ⁻²)	
<i>Zygoptera</i>												
<i>Calopterygidae</i>												
<i>Calopteryx splendens</i> (C.s.)	♂	5	>30	118 (8)	28.2 (0.8)	780 (80)	0.15	1.47	16/38 (courting)	190	13	5
<i>Lestidae</i>												
<i>Lestes viridis</i> (L.v.)	♂	3	16	59	22.2	308	0.19	1.86	32.6	230	8.2	6.7
<i>Platycnemididae</i>												
<i>Platycnemis pennipes</i> (P.p.)	♂	2	11	34 (3)	19.8	228 (8)	0.15	1.47	32.8	140	4.8	1.4
<i>Pseudostigmatidae</i>												
<i>Megalopterus coarctatus</i> (M.c.)	♂	13	>20	276 (109)	64.8 (9.3)	2960 (880)	0.091 (0.003)	0.89	7.2	250		
	♀	7	2	280 (33.6)	63.8 (3.1)	2930 (290)	0.095 (0.0001)	0.93	8.8			
<i>Mecistogaster ornata</i> (M.o.)	♂	5		132 (23)	53.7 (3.7)	1360 (170)	0.097 (0.001)	0.95		228		
	♀	14	10	146 (24)	57.2 (2.3)	1620 (140)	0.090 (0.001)		13.5			
<i>Mecistogaster linearis</i> (M.l.)	♂	7	2	147.6 (26.7)	57.6 (1.7)	1530 (148)	0.097 (0.002)		17.8			

fore- and hindwings also change). *M.o.* changed its wingbeat frequency from 15 Hz immediately after take-off to 20 Hz during rapid backward flight, and then to 15 and 13.5 Hz while hovering. In flight, *An.i.* described a steep curve with a wingbeat frequency of 47.5 Hz, and exhibited a frequency of 35–40 Hz for level forward flight on a curved course. *O.c.* increased its wingbeat frequency from 44 to 57 Hz in feeding flight. However, many Anisoptera, in particular many Libellulidae, switched to a gliding phase between wingbeat cycles. This was not included in Fig. 3 and Table 1.

(5) In other cases, such as downward flight (in which less powerful aerodynamic forces may be required), the wingbeat frequency was reduced. For example, a male *L.v.* in tandem position beat its wings at 28.7 Hz during downward flight, compared with up to 35 Hz during straight forward flight and up to 37.5 Hz when flying steeply upwards and backwards. (See also Table 2, manoeuvres 8–12 of *M.c.*)

(6) The variation in wingbeat frequency was less for small Odonata and those with a high wing loading than for large species, especially when their wing loading was low (see Table 1). For example, when deviations from maximum value were compared:

<i>L.v.</i> (small, low wing loading)	25.6 %	28–37.5 Hz
<i>O.c.</i> (large, high wing loading)	36.1 %	38–59.5 Hz
<i>An.i.</i> (large, high wing loading)	38 %	29.2–47.5 Hz
<i>M.c.</i> (large, low wing loading)	62.7 %	4.7–12.6 Hz
<i>M.o.</i> (large, low wing loading)	72 %	6.3–22.5 Hz

(7) In the species that use their wings for communication, the wingbeat frequency could also vary for reasons unrelated to the mechanics of flight. For instance, male *C.s.* executing a sideways threatening flight kept both pairs of wings still, pressed together, after the upstroke (Rüppell, 1985). In a frontal threatening flight, however, movement of the wings of *C.s.* was delayed during the downstroke and in the forward downstroke position. The same occurred in *M.c.*, where a change of as much as 4 Hz was produced, with the downstroke accounting for 64 % of the duration of the wingbeat. Male *C.s.* also changed wingbeat frequency during courting flight: from about 16 Hz during threatening flight, it more than doubled, reaching values around 40 Hz (see Table 2).

(8) Another notable feature was that the hindwings did not always beat at the same frequency as the forewings, owing to phase shifts and changes in stroke duration. Examples are given in Figs 4 and 5. For instance, during the steep curve of *An.i.* in Fig. 5, in five consecutive beats the frequencies of the fore/hindwings changed as follows: 47.5/38, 34.5/38, 31.6/38, 29.2/34.5, 32.6/31.5 Hz.

Stroke amplitude

Although stroke amplitude could be determined in only a few cases, because of perspective distortion, the following tendencies were nevertheless observed.

(1) Zygoptera beat their wings with a greater amplitude than Anisoptera (see

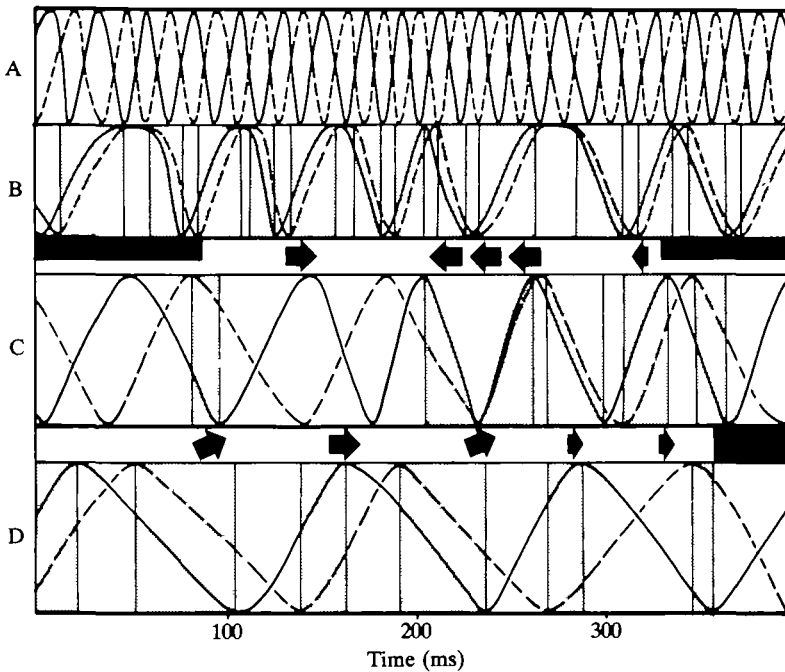


Fig. 4. Phase relationship between the forewings (continuous line) and hindwings (dashed line) of Zygoptera. Rising line, upstroke; falling line, downstroke. Periods of parallel stroking are indicated by shaded areas. (A) *Calopteryx splendens* during courting flight and (B) during threatening flight; sections of the curve running parallel to the upper abscissa indicate pauses in wing beating at the end of the backstroke. (C) *Mecistogaster ornata* during fast forward and backward flight (long arrows) and slow backward flight (short arrows) as well as during hovering flight (black bar). (D) *Megalopterus coeruleatus* in tandem flight just before landing (wide black bar).

Table 2). Apart from the courting flight of *C.s.*, all the values for Zygoptera were very much higher than those for Anisoptera.

(2) During flight manoeuvres involving marked acceleration, Anisoptera could increase their stroke amplitude. *O.c.* changed from approx. $80\text{--}90^\circ$ while hovering to 130° during vertical take-off from the water; in *L.r.*, which also had stroke amplitudes around 90° while hovering or flying slowly forward, there was an increase to 150° during vertical take-off with a female in the mating position (see Fig. 7). As might be expected, *M.c.* (Table 2) exhibited a similar amplitude variation: when carrying a female in the mating position its stroke amplitude was about 130° , and during downward flight in the same position it was only 106° .

(3) Stroke amplitude could also be changed (often in combination with a frequency change) by species that use their wings for communication (*C.s.*). During the courting flight of *C.s.* the stroke amplitude was almost halved (see Table 2), with a simultaneous increase in frequency. Furthermore, within the threatening flight of *C.s.* or *M.c.* there could be dramatic amplitude reductions;

Table 2. *Kinematic data for special manoeuvres (no. 14 is estimated)*

Species and manoeuvres	Angle of flight path (degrees)	Flight velocity (cm s ⁻¹)	Wingbeat frequency (Hz)	Flight distance per wingbeat (cm)	Non-dimensional flight velocity	Stroke velocity (cm s ⁻¹)
1 <i>C.s.</i> sh f	-14	43.6	14.1/19.2	3.1	1.1	86.7/118
2 <i>C.s.</i> sh b	+155	48	13.5/17.8	3.6	1.3	86.5/114
3 <i>C.s.</i> court, sh b	+180	37.9	37	1.0	0.35	125
4 <i>C.s.</i> fa f		143	11.1/19.2	12.9	4.6	61.3/106
5 <i>C.v.</i> fa f	0	187	107.7/16	17.5	5.7	62.7/93.7
6 <i>L.v.</i> fa f	+15	114	32.8	3.5	1.5	161
7 <i>L.v.</i> fa u	+87	146	32.6	4.5	1.9	161
8 <i>M.c.</i> tandem f	+30	58	7.7	7.5	1	<i>f</i> 134 <i>h</i> 104
9 <i>M.c.</i> cop. f u	+70	99.8	6.9	14.5	1.9	115.5
10 <i>M.c.</i> cop. spot			6.4			111
11 <i>M.c.</i> cop. d	+290	117	6.1	19.2	2.6	84.5
12 <i>M.c.</i> male f	+10	87.5	5.9	14.8	2	93.5
13 <i>A.c.</i> spot			35			<i>f</i> 210 <i>h</i> 240
14 <i>A.c.</i> fa f	(+20)	(1000)	(40)	25	4.7	292
15 <i>An.i.</i> s f	0	190	29	6.2	1.3	<i>f</i> 151 <i>h</i> 207
16 <i>An.j.</i> fa f	0	750	36	20.8	4	294

Letters describing manoeuvres (after abbreviations of species): sh = short, f = forward, b = backward, fa = fast, u = upward, d = downward, s = slow, court = courting flight, tandem = flight in tandem position, cop. = flight in copulation (mating) position, spot = on the spot. Elsewhere in table: *f* = forewings, *h* = hindwings, up = upstroke, down = downstroke.

The flight angle 0° corresponds to a horizontal forward flight direction, 90° to vertical upward, 180° to horizontal backward, and 170° to vertical downward flight. For *C.s.* and *C.v.*, where two values are separated by a slanting line, the first value includes standstill of the wings in the backward position and the second does not.

during frontal threatening the males beat their wings only in the anterior region, over an angle of approximately 80° (estimated) compared with 130° in the normal threatening flight.

(4) The position of the path traced out by the wings could be altered as well as

Table 2. *Continued*

	Advance ratio	Stroke amplitude (degrees)	Angle of stroke plane (degrees)	Angle of attack (all +) (degrees)		Phase shift (degrees)	Parallel stroking (%)	Stroke ratio up:down
				up	down			
1	0.5	<i>f</i> 125	<i>f</i> -8 <i>h</i> -16	60 <i>f</i> 55 <i>h</i>	30	21.8	94	1:1.2
2	0.55	<i>f</i> 130	<i>f</i> 0 <i>h</i> -8	45 <i>f</i> 45 <i>h</i>	85 80	12.4	97	<i>f</i> 1.3:1 <i>h</i> 1.6:1
3	0.3	<i>f</i> 68.5	<i>f</i> +5	20 <i>f</i>	45	180	0	1:1.2
4	2.33/1.34	110	<i>f</i> -30 <i>h</i> -40	<i>f</i> (22) (60) <i>h</i>				1:1.9
5	3/2	(110)				18	94	1:1.7
6	0.7	<i>f</i> 117	<i>f</i> -50 <i>h</i> -60	(>60) <i>h</i>	<i>f</i> (30)	157.5	2	1.5:1
7	0.8	<i>f</i> 118	<i>h</i> +5	30 <i>h</i>	30	180	0	2:1
8	<i>f</i> 0.43 <i>h</i> 0.56	<i>f</i> 133 <i>h</i> 103	<i>f</i> -20 <i>h</i> -27	65 <i>f</i> 65 <i>h</i>	35	21.2	88	1:1.6
9	0.86	<i>f</i> 128	<i>f</i> -5	45 <i>h</i>	25	9	95	1:1.2
10		<i>f</i> 132.4	<i>f</i> -5	25 <i>h</i>	25	8.6	95	1:1
11	1.38	<i>f</i> 106	<i>h</i> -10	30 <i>h</i>	30	8.6	95	1:1
12	0.94	<i>h</i> 121	<i>f</i> -13 <i>h</i> -17	60 <i>f</i>	30	8.6	95	1:1
13		<i>f</i> 73 <i>h</i> 84	<i>f</i> -50 <i>h</i> -60	65 <i>f</i> 55 <i>h</i>	45 50	72	53	<i>f</i> 1:1.3 <i>h</i> 1:1.5
14	3.42	(90)						
15	<i>f</i> 1.2 <i>h</i> 0.87	<i>f</i> 73 <i>h</i> 86	<i>f</i> -60 <i>h</i> -65	(60)	<i>f</i> (50)	90	50	1:1.3
16	2.55	(90)						

Nondimensional flight velocity and advance ratio are defined by Ellington (1984*a,b*).

Stroke velocity is calculated for half the wing length.

Angle of stroke plane, 0° = horizontal; positive angles denote front end of stroke above the horizontal; negative, below the horizontal.

Parallel stroking: percentage of wingbeat cycle, averaged over all relevant beats in the manoeuvre ($N=2-20$). For example, 0, wings never beat in the same direction; 94, on average, fore- and hindwings beat in the same direction for 94% of the cycle duration.

Values in parentheses are subject to an error greater than 20%.

its amplitude. During forward flight *C.s.* moved its wings forward only up to the head and then far backwards, whereas during backward flight the forward wing movement was extended by more than the length of the thorax (see fig. 6 in Rüppell, 1985).

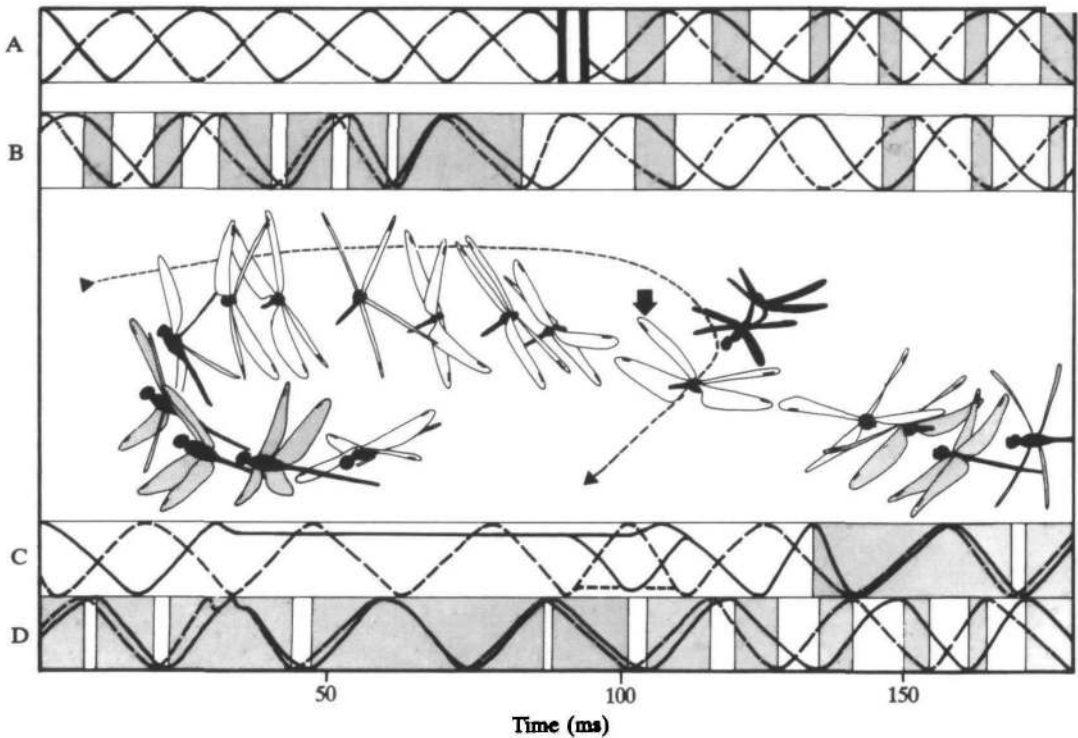


Fig. 5. A male *Anax imperator* pursues a pair of *Orthetrum cancellatum* (dashed line). The time courses of the upstrokes (rising lines) and downstrokes (falling lines) are shown. (A) Two examples of hovering. (B) Flight of the male *An.i.* in the drawing from the beginning until shortly after the steep curve. (C,D) The same flight from the heavy black arrow until the end. Grey regions, wings beat in the same direction; parallel stroking during the flight is indicated in the drawings by grey wings. In C both forewings (continuous line) are held still for some time, and then for one cycle only one is moved. A hindwing (dashed line) is also held still for one cycle in C.

(5) The Anisoptera varied the stroke amplitude over a wider range than the Zygoptera (Table 2, Anisoptera 73–150°, Zygoptera 106–130°, except for the *C.s.* courting flight).

From the wingbeat frequency and the stroke amplitude, angular velocities were derived. These gave various absolute stroke velocities depending on the length of the wings.

Stroke velocity

This parameter, like the frequency and amplitude values, exhibited several tendencies in the various manoeuvres. Stroke velocity was higher in Anisoptera than in Zygoptera, and higher during rapid than during slow flight (*A.c.*, *An.j.*, Table 2). In a phase of accelerating flight the stroke velocities were higher than during steady flight: *C.s.*, 118 or 114 cm s⁻¹ during acceleration vs 106 cm s⁻¹ in unaccelerated straight forward flight; *O.c.*, hovering 208 cm s⁻¹ (44 Hz, stroke

amplitude 90°) vs steep take-off from water 350 cm s^{-1} (42 Hz, 130°); *L.r.*, hovering 165 cm s^{-1} (38 Hz, 86.6°) vs male carrying female in mating position vertically upwards from water 320 cm s^{-1} (42 Hz, 150°). In all cases, the increase was produced primarily by an enhanced stroke amplitude with little change in frequency.

The calculated values of mean stroke velocity presented here were compared with measured data (see Materials and methods). The measured velocities of the wingtips in forward and backward flight of *C.s.* were $180\text{--}310\text{ cm s}^{-1}$. A point halfway along the wing will move over half the distance and hence will have half that velocity; these values, $90\text{--}155\text{ cm s}^{-1}$, approximated those given in Table 2 for the same manoeuvres. A similar agreement was found for *M.c.* ($95\text{--}185\text{ cm s}^{-1}$ measured, $84.5\text{--}134\text{ cm s}^{-1}$ calculated). The measured values were higher because measurements were taken only during the middle of the stroke, at which time the wing was probably moving at a velocity higher than the average over the entire stroke, which was the value obtained by calculation. In any case, the lowest and highest values of stroke velocity were found for corresponding manoeuvres by both methods; for instance, in *M.c.* the stroke velocity was lowest for downward flight and highest for upward and forward flight.

Flight velocity, nondimensional flight velocity and advance ratio

The flight velocities determined from free-flying, released and startled dragonflies and by estimation with reference to standardized pond dimensions showed that Anisoptera tended to fly at higher velocities than Zygoptera. The data for maximum velocity in Table 1 give a mean of 205 cm s^{-1} for Zygoptera and 563 cm s^{-1} for Anisoptera. The highest value, 1000 cm s^{-1} for *A.c.*, was an estimate. It was somewhat above that calculated for *Anax parthenope julius* by Azuma & Watanabe (1988), but even higher values might be expected to occur.

For special manoeuvres (Table 2) the values of non-dimensional flight velocity ranged from 0.35 [which, according to Ellington (1984*a,b*), is equivalent to hovering] to 5.7. The only manoeuvres with similar nondimensional flight velocities were those marked 'fa' (fast), since these were performed in similar situations: males chasing rivals. The exceptionally high value of 5.7 for the Calopterygidae is noteworthy; these dragonflies can fold their wings together over the abdomen after every wingbeat (or several beats) and hold them still, gliding like songbirds in ballistic flight (Csicsáky, 1977). In this way, they travel relatively large distances per wingbeat. *L.v.*, a typical representative of the Zygoptera, can only achieve values of about 2, whereas typical Anisoptera such as *An.j.* or *A.c.* reach values around 4.

The advance ratio (Ellington, 1984*a,b*) is informative with respect to the effectiveness of the wingbeat. The smaller the advance ratio, the less effective is the wing movement in driving the dragonfly forward. Here again, the (first) value for *C.v.* was remarkably high, exceeded only by the data for rapidly flying Anisoptera. *L.v.* exhibited a low value in the sequence analysed, which seemed to be typical of other Zygoptera.

Phase relationships between fore- and hindwings

Phase relationships between the fore- and hindwings differ in nature, depending upon the size and identity of the specimen as well as upon the flight manoeuvres. Among the Zygoptera (e.g. in the genera *Lestes*, *Ishnura* or *Platycnemis*), as well as among small Anisoptera such as *Perithemis*, the wings remained in relatively constant phase. Here the hind- and forewings beat in opposition; the downstroke of one pair of wings coincided with the upstroke of the other (counterstroking). In this case the phase shift with reference to a complete wingbeat cycle would be 180° (as in *C.s.* courting flight, Fig. 4, *L.v.*, Table 2, and *An.i.*, Fig. 5). However, such large species as the Pseudostigmatidae, *M.o.* from Panama and the large European Anisoptera observed (*An.i.*, *A.c.*, *O.c.*) varied the phase relationship of the fore- and hindwing movements considerably, to phase shifts up to $90-70^\circ$ and finally to synchronous movement in the same direction (with only a very small shift, about $18-9^\circ$). The time during which the wings beat in the same direction varied accordingly, from 0% in *L.v.*, *C.s.* in courting flight (Table 2) and others to over 90% during parallel stroking in *C.s.*, *M.c.* (Fig. 4) and even Anisoptera in extreme situations (Figs 5, 7, *An.i.* and *L.r.*).

The various phase relationships were associated with particular manoeuvres in the different groups, as follows (the symbols < and > indicate species smaller/larger than).

Counterstroking (phase shifted by 180°)

Zygoptera < <i>L.v.</i> (included)	: in almost all manoeuvres
Calopterygidae	: <i>C.s.</i> in courting flight
Pseudostigmatidae	: hovering
Anisoptera < <i>P.t.</i> (included)	: in almost all manoeuvres
Anisoptera > <i>An.i.</i> ; <i>A.c.</i>	: hovering

Phase shifted by less than 120°

<i>M.o.</i> , Anisoptera > <i>P.t.</i>	: in almost all manoeuvres
----------------------------------------	----------------------------

Parallel stroking (phase shifted by no more than 30°)

Zygoptera < <i>L.v.</i> (included)	: rare (seen only in <i>L.v.</i> while pulling up a female clinging to the substratum)
Calopterygidae	: almost always (except in courting flight)
Pseudostigmatidae	: <i>M.o.</i> , rapid backward flight <i>M.c.</i> , almost always
Anisoptera	: during flight requiring great force (rapid acceleration or carrying a female) in the range from straight up to horizontally backward flight

Phase relationships and flight acceleration

Odonatan flight was characterized by pronounced changes in velocity. Mean flight accelerations in a temporal range of fractions of a second to seconds were

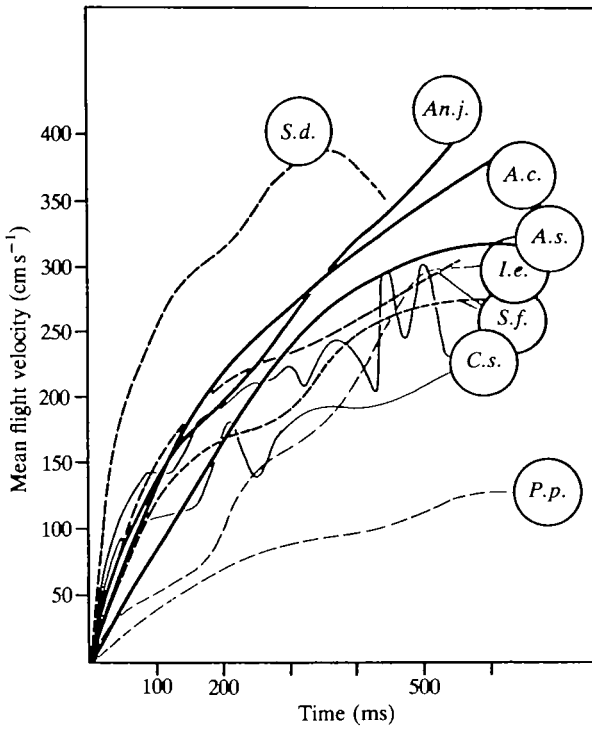


Fig. 6. Mean flight velocities from the releasing experiments. Flight direction was horizontal or not more than 45° inclined forward-upward. For species identification see Materials and methods.

varied by striking short-term velocity changes lasting less than 0.1 s. At take-off, higher mean accelerations were found for the Anisoptera than for the Zygoptera (apart from the Calopterygidae) (releasing experiments, Table 1, Fig. 6). A male *Lestes viridis* pursuing another male, as shown by slow-motion analysis, reached accelerations in the first 100 ms similar to those of *Ischnura elegans* or *Calopteryx splendens* in the releasing experiments. The mean acceleration varied widely in all the species studied, except for small Zygoptera such as *L.v.* or *P.p.* and the Calopterygidae (males in courting flight). At present, therefore, it is not yet clear which flight parameters are the most important. Even during straight forward flight both the mean and the short-term acceleration varied markedly (*An.i.*, Fig. 7).

The short-term variations seemed to depend upon the phase relationships between the fore- and hindwings. When the fore- and hindwings were beating in opposite directions, the flight velocity remained relatively constant. This counter-stroking was observed in the flight of *L.v.* and in the courting flight of *C.s.* (Table 2), in which there was no measurable change in velocity. With phase shifts, such that the wings beat in parallel for a considerable part of the cycle, large variations of flight acceleration occurred simultaneously with the parallel stroking.

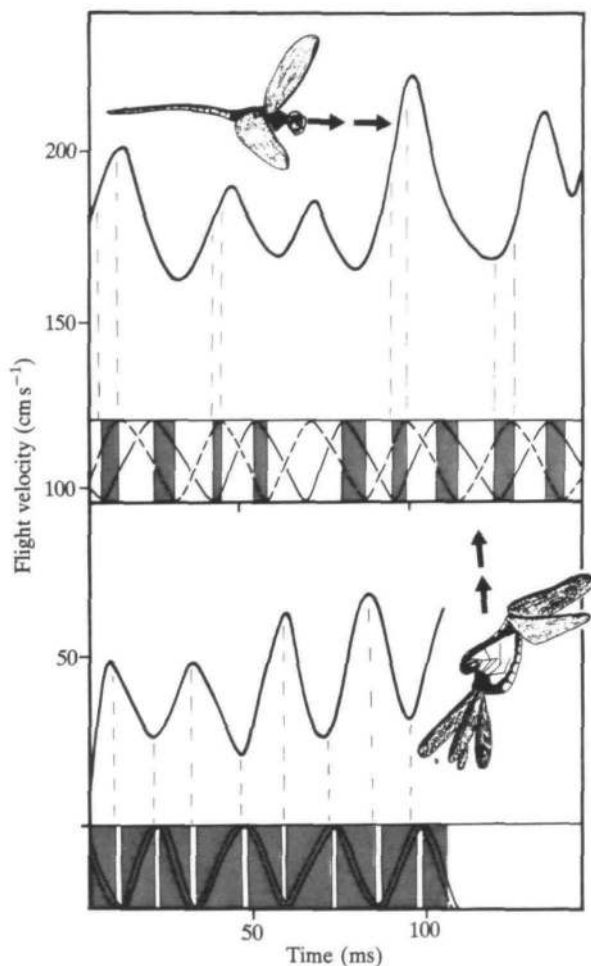


Fig. 7. Flight velocity of *Anax imperator* (above) in forward flight (arrows) and of *Leucorrhinia rubicunda* (below) in vertical upward flight (arrows). Below each curve is a diagram showing the associated stroke phases of the fore- (continuous line) and hindwings (dashed line). Rising line, upstroke; falling line, downstroke. In the grey regions the wings beat in the same direction (parallel stroking). The dashed vertical lines are to aid comparison of the curves.

This was illustrated in detail by the upward flight of *L.r.* shown in Figs 7 and 8. During a simultaneous downstroke of both pairs of wings the flight velocity increased sharply by as much as 40% (second downstroke, Fig. 8). When only the hindwings were beginning a downstroke, the increase in flight velocity was very much smaller. Parallel wingbeats were evidently extremely effective; correspondingly, the short-term acceleration was greater, the larger the part of the cycle in which the wings beat in parallel (Table 3). Given that flight velocity was increased during the downstroke in some manoeuvres and during the upstroke in others, it

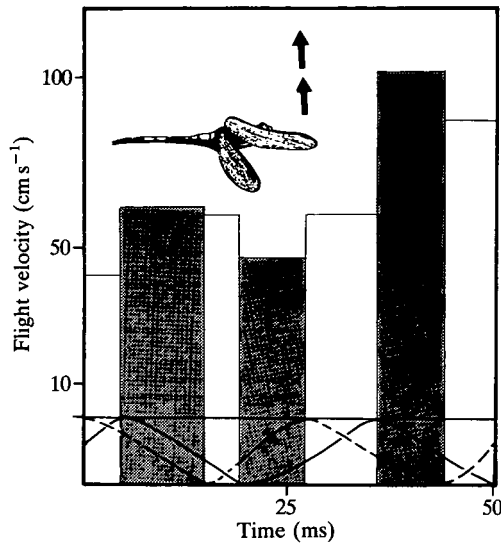


Fig. 8. Male *Leucorrhinia rubicunda* in vertical flight (arrows). Changes in flight velocity during slightly phase-shifted stroking; the bottom curves show the phase relationship of the fore- (continuous line) and hindwings (dashed line). At the times indicated by the grey areas, the wings are beating in the same direction.

follows that the wing kinematics must have changed in these two phases of the wingbeat.

Phase-related changes in angle of attack

The angles of attack changed greatly during a wingbeat cycle (Fig. 2). Within the middle part of a stroke, where measurements were made with species having a low wingbeat frequency, such as *M.c.*, *M.o.*, *C.s.* and *A.c.*, there seemed to be little variation in angle of attack. However, the angle of attack in the upstroke may be quite different from that in the downstroke, with correlated changes in flight velocity. During the backward start of *M.c.* (Fig. 9), the first forward stroke was executed with the wings at a steep angle (measured in the midregion of the downstroke), whereas in the first backward stroke the angle of attack was small. During the subsequent transition to straight forward flight, the wings were inclined at small angles in the middle of the forward stroke and at large angles during the backward stroke. In forward flight of *M.c.* (Fig. 10) the effects of the different phases of the wingbeat can be expressed in terms of the vertical and horizontal distances covered, as follows. During the upstroke, with a large angle of attack, the wings generated mainly thrust (gain in horizontal distance); the less steeply angled wings during the downstroke generated mainly lift (gain in vertical distance). In five different flight manoeuvres of giant damselflies (*Pseudostigmatidae*) the angle of attack was always found to be large, $57\text{--}75^\circ$, during a stroke away

from the flight direction and small, 10–35°, during a stroke in the flight direction. Similar angles and effects have also been observed in *C.s.* (Rüppell, 1985).

In Anisoptera, too, such relationships probably applied to extreme upward and backward flight manoeuvres; for example, during upward flight of *O.c.* and *L.r.*,

Table 3. *Short-term and mean flight accelerations of Odonata beating the wings with different phase shifts*

	Phase shift (degrees)	Velocity (cm s ⁻¹)	Maximal acceleration (m s ⁻²)	Mean acceleration (m s ⁻²)	Velocity variation (%)
<i>L.v.</i> fast forward (Table 2)	180	230	0	0	0
<i>An.i.</i> slow forward (Fig. 7; Table 2)	90	170–210	29.4	1.5	25 in u
<i>O.c.</i> forward downward	90	20–140	36.5	15.4	30–40 in u
<i>O.c.</i> backward upward, mating position	<18	40–120	33.2	7	52 in d
<i>L.r.</i> upward, mating position (Fig. 7)	<18	30–50	34.4	2.1	65 in d
<i>M.o.</i> forward upward	36	30–60	11.5	1.6	60 vertical component u
		50–70	16.7	1.5	85 horizontal component d

Phase shift of fore- and hindwings; flight velocity in the analysed period (maximum 0.1 s); maximal short-term flight acceleration; mean flight acceleration; variation of velocity per upstroke (u) or downstroke (d), as a percentage of maximum velocity.

Orthetrum cancellatum backward upward flight, male carrying a female up from hot sandy ground; *Leucorrhinia rubicunda*, male carrying a female nearly vertically up from the water surface.

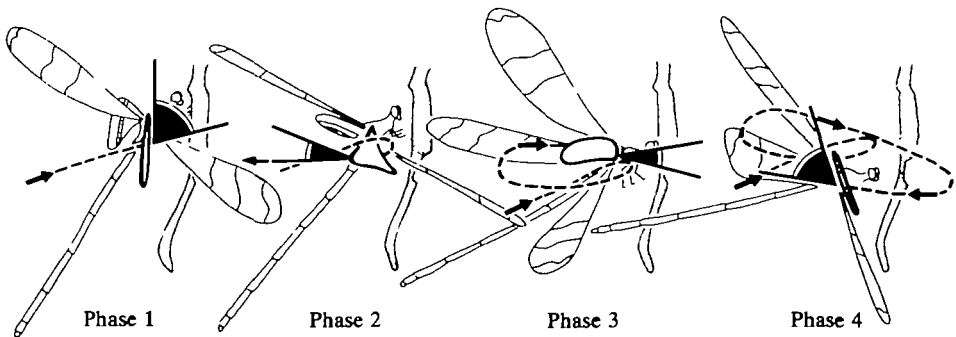


Fig. 9. When taking off backwards *Megalopterus coeruleus* beats its wings forwards with a large angle of attack (phase 1), and then reduces the angle of attack for the backstroke (phase 2). In forward flight, which begins immediately thereafter, the situation is reversed (phases 3 and 4). The angles of the right forewing are shown. The dashed line is the stroke plane, and the direction of the stroke is shown by the arrows. A twig is shown in grey.

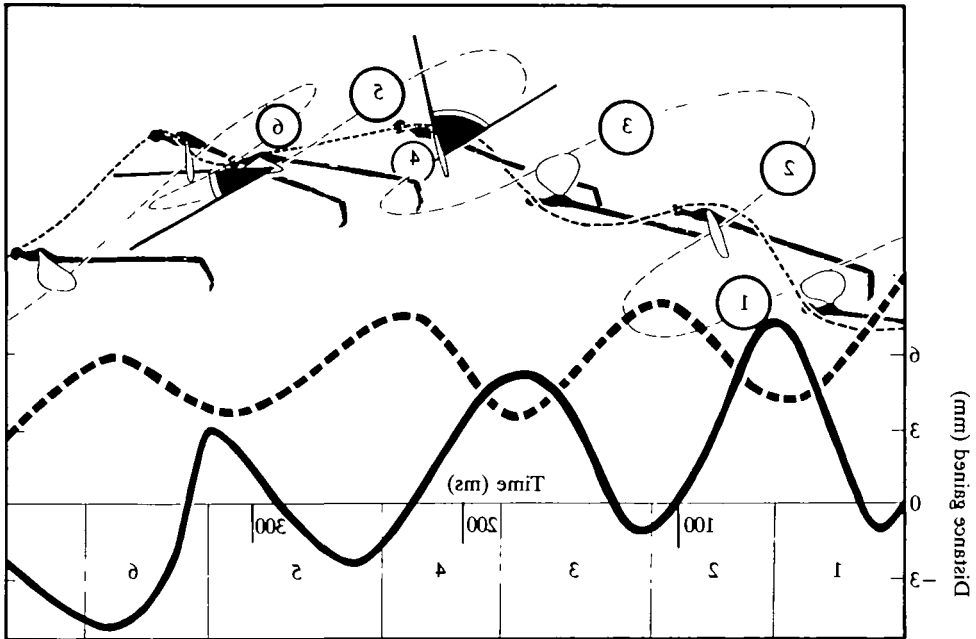


Fig. 10. Forward flight of a tandem male (*Megalopterus coeruleus*). Top: flight path (thick dashed line) and stroke plane (thin dashed line) of the right forewing of a male *M.c.* in the tandem position. The two superimposed graphs of angles (heavy lines) show the angle of attack during the upstroke on the left and during the downstroke on the right. The phases of the wingbeat are numbered to facilitate comparison with the curves below. These curves represent the distance gained in the horizontal (dashed line) and vertical (continuous line) directions in every second successive frame of the film; in the minus range the damselfly loses height.

which employed parallel stroking (Table 3; Figs 7, 8). That is, the downstroke away from the flight direction was carried out with large angles of attack, whereas the angles of attack in the upstroke were very much smaller. Furthermore, this asymmetry in the up- and downstroke was also observed in phase-shifted flight or counterstroking – for instance, in the slow forward flight of *An.i.*, the courting flight of *C.s.* (Table 2) and the prey-seizing flight of *M.o.* Similarities between Zygoptera and Anisoptera were found not only with respect to these relationships between angle of attack and velocity change, but also with respect to the relative durations of the up- and downstroke.

Upstroke/downstroke ratio

There was relatively large variation in the upstroke/downstroke ratio. Reasons for this variation could be found in the Calopterygidae. When their wings are beating in the direction of the flight (i.e. forward = downstroke in forward flight), the total air flow over the wing is produced by vectorial addition of the airstream associated with wing movement to that associated with the body's movement

forward. But when the stroke is away from the flight direction (backward = upstroke in forward flight), the total air flow is less, because the airstream due to wing movement is subtracted from that due to forward movement. Consequently, the upstrokes were shortened in forward flight; in *C.s.*, during slow forward flight, the up/down ratio was 1:1.2. From the upstroke/downstroke ratio, the wingbeat frequency, the stroke amplitude and half the wing length, the velocity of each stroke could be calculated. The mean stroke velocity (over the entire cycle) for the slow forward flight of *C.s.* was 118 cm s^{-1} ; the calculation gave a downstroke velocity of 108.2 cm s^{-1} and an upstroke velocity of 127.9 cm s^{-1} . During rapid forward flight, the upstroke became still shorter, as predicted, giving an upstroke/downstroke ratio of 1:1.9 (the wingbeat frequency remaining the same as in slow forward flight). In a male *M.c.* that first descended and then carried a female in the mating position up in forward flight, the upstroke/downstroke ratio reached 1:3 due to extreme shortening of the upstroke. *L.v.* is exceptional in having relatively large upstroke durations, even in forward flight (Table 2). The upstroke/downstroke ratio was not always the same for the fore- and hindwings. In *A.c.* and *An.i.* during hovering and slow forward flight, the upstroke of the hindwing was about 10% shorter than that of the forewing (Table 2), as it was in *C.s.* (Table 2); in *L.v.* the upstroke of the hindwing was 35% shorter.

Stroke plane

The stroke plane cannot be represented exactly, because of the distortion produced by even slight changes in orientation of the insect's body. Furthermore, according to Ellington (1984*a,b*) the exact form of the wing path within the stroke plane can be neglected, because its details are probably not very important for flight. The mean orientation of the stroke plane (averaged over fore- and hindwings), however, did seem to make an important contribution to the manoeuvres.

Although the stroke plane was extremely variable, three tendencies were evident.

(1) The more the stroke plane was inclined forward, the more the flight path was shifted towards forward-down. Conversely, if the stroke plane was tilted towards forward-up, the flight direction was also shifted upwards, or even upwards and backwards (Figs 11, 12, 13).

(2) The higher the velocity of flight in a given direction, the more the stroke plane was tilted towards forward-down (Fig. 11). This effect was been observed only in *L.v.*

(3) For a given flight direction, the inclination of the stroke plane with respect to the flight path can vary widely (Figs 11, 13). In *L.v.*, for example, the angle between the vector of forward flight and the stroke plane ranged from 0° to 100° (Fig. 11). When this range of angles was divided into 10° classes, and the angles observed were assigned to these classes, the distribution was clearly non-uniform. An angle between 0° and 10° was found in 30% of the cases, and 50% were in the range 40° – 70° ; the remaining 20% were in other classes. This relationship was

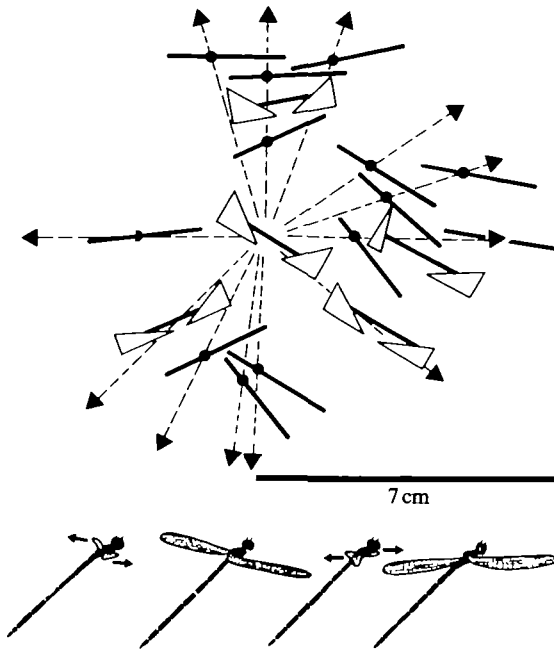


Fig. 11. Symmetrical flight manoeuvres of a male *Lestes viridis* flying in the counter-stroking mode (drawings at the bottom illustrate vertical flight). Flight directions shown by dashed lines with arrowheads; the associated stroke planes (thick lines) are averages of the fore- and hindwings. In the centre: hovering. The hypotenuses of the triangles indicate the estimated angles of attack during the downstroke (triangles on the right) and upstroke (triangles on the left).

also clear in the Anisoptera (Fig. 13), in which stroke planes at a small angle to the flight direction were usually observed during parallel stroking. It is very likely that in this situation the angles of attack during the downstroke were large. Parallel stroking in a plane at a small angle to the flight direction and with a large angle of attack was associated with upward or backward flight at large accelerations.

Coupling of the same parameters was also found in the flight of *M.c.* (Fig. 12) and *C.s.* (Rüppell, 1985). Nevertheless, when an anisopteran had sufficient time it employed the alternative mode of flying, with stroke plane at a large angle, phase-shifted stroking and, probably, smaller angles of attack.

Discussion

Variation of the wingbeat parameters – especially changes in the phase relationships of the hind- and forewings, in the angles of attack of the wings, in stroke amplitude and plane, and in wingbeat frequency – determine how rapidly an insect accelerates and brakes, the direction in which it flies, and the loads (prey, conspecifics) it can carry.

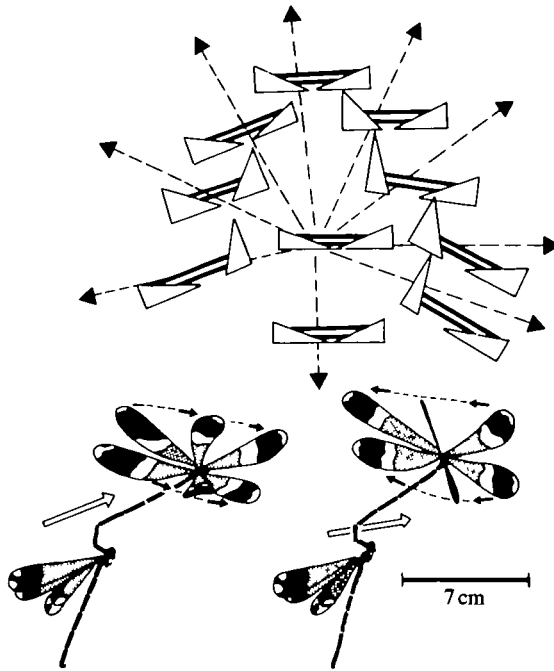


Fig. 12. Symmetrical flight manoeuvres of a male *Megaloprepus coerulatus*. Flight directions (averaged, dashed lines with arrowheads) in parallel-stroking mode with associated stroke planes (thick double lines). Hypotenuses of the triangles indicate the angles of attack during the upstroke (left) and downstroke (right). The drawings below show an *M.c.* pair in forward-upward flight (about 40°) as the male executes a downstroke (left) and an upstroke (right). The open arrows indicate the flight directions. In each drawing the right wings are shown at the beginning, in the middle and at the end of the stroke.

Characterization

Counterstroking, with a half-cycle phase shift between fore- and hindwings, produces the most uniform flight, because inequalities in the aerodynamic actions of the upstroke and downstroke can be compensated to some extent by changing the angle of attack. For example, although an upstroke with a very steep angle of attack generates strong thrust, a pair of wings simultaneously beating downwards with a small angle of attack mainly generates lift. In the next wingbeat phase the situation is reversed, giving relatively constant thrust and lift production. This uniformity is evident in almost all flight manoeuvres of the small Zygoptera, as well as in the courting flight of the Calopterygidae, and in the hovering and slow forward flight of *M.o.* and the Anisoptera. A transition from counterstroking to phase-shifted stroking, in which the stroke of the fore- or hindwing is delayed by one-third to one-eighth of a cycle, can occur even during hovering in the large Zygoptera and the Anisoptera, and phase-shifted stroking is the rule during fast forward flight in these groups. The smaller the phase shift, the larger the part of

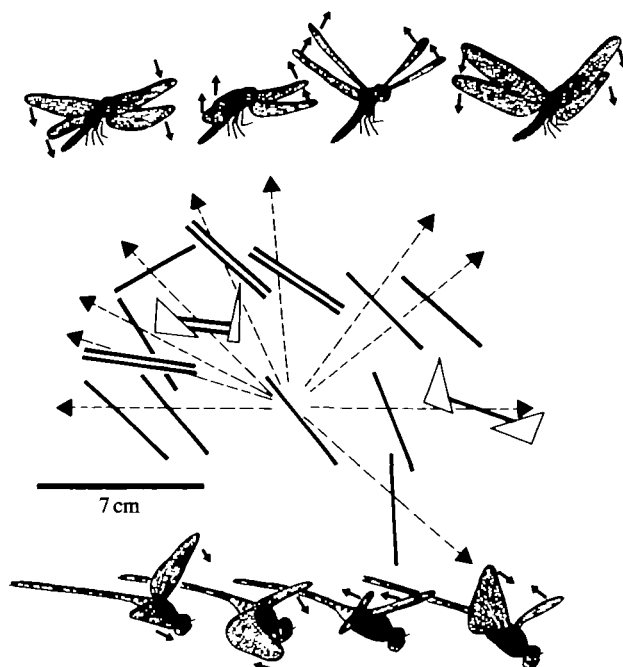


Fig. 13. Symmetrical flight manoeuvres of Anisoptera (conventions as in Figs 11, 12). Counterstroking and phase-shifted stroking are represented by single lines, parallel stroking by double lines. The bottom drawings show an *Anax imperator* in slow forward flight with phase-shifted beats of the fore- and hindwings (arrows show direction of stroke). Those at the top show an *Orthetrum cancellatum* during a vertical backward take-off (flight direction approx. 100°) in parallel-stroking mode.

the cycle during which the two pairs of wings beat in parallel. Flight in which parallel stroking is emphasized appears to generate more aerodynamic force than does counterstroking, because parallel stroking is always employed in forceful manoeuvres such as a sudden vertical take-off.

Additional changes in the intensity of the stroke produce altered flight performance, such as acceleration. The ways in which such intensification can be achieved seem to differ in the various odonatan groups that have been filmed. Therefore, it is useful to divide them into categories as follows: small Zygoptera (smaller than *L.v.*) with little capacity for variation of the wingbeat parameters, large Zygoptera (*C.s.*, *M.c.*, *M.o.*) with intermediate capacity, and Anisoptera (larger than *S.d.*) with the greatest capacity.

Small Zygoptera

Even during unaccelerated manoeuvres, such as hovering or steady forward flight, the small Zygoptera beat their wings with large amplitude and high frequency (Table 2). Evidently, they do not have much performance in reserve, for they are far less capable of enhancing their wingbeat parameters than are the

Anisoptera. That they usually operate near the performance limit is also indicated by the fact that they fly by counterstroking, which saves energy not only because of the balanced aerodynamic force generation but probably also because it causes reduced or self-compensating wake vorticity (H. Oehme, personal communication). In spite of their limited performance reserves, their small mass allows them to achieve sudden turns and linear acceleration to some extent by changing the stroke plane or the angle of attack.

Although the larger *Lestes* species are more manoeuvrable than the Coenagrionidae, which can readily be caught, even their flight appears relatively slow and uniform. This might be a consequence of the large drag encountered by all small insects because of the relatively high surface friction.

Large Zygoptera

Although the large Zygoptera can also fly with large stroke amplitude, they do not always do so. For example, in the frontal threatening flight of *C.s.* and *M.c.* the wings oscillate over only a small angle (estimated as one-half to two-thirds of the usual angle). Indeed, large damselflies generally seem to be more capable of modifying their flight parameters. For instance, *M.c.* and male Calopterygidae fly with parallel stroking, undeterred by the irregularity of the movement so produced – or even putting it to use in their territorial flights. That this parallel stroking enhances the aerodynamic action of the wingbeat is demonstrated by many cases of rapid transition from counterstroking to a synchronous wingbeat. After plunging into a spider's web to seize prey, for example, an *M.o.* switched to parallel stroking while backing away, thereby considerably accelerating its flight. A male *C.s.* that had been slowly approaching a female in a counterstroking courting flight, advancing at a rate of 12.4 mm per wingbeat, was propelled 46.5 mm backwards by a single parallel beat. These damselflies gain a large distance with each beat of their wings, having a favourable advance ratio (Table 2). They can also 'coast downhill' by gliding. The giant damselfly *M.c.* can glide without any impulse from the wings for more than 20 m at an angle of 10° and a velocity of more than 74 cm s⁻¹, corresponding to a gliding ratio of 1:6 – which is similar to that of some birds (e.g. fulmar 1:8, gliding angle 7.1°; Pennycuik, 1960).

Large Anisoptera, especially the Libellulidae (German name *Segellibellen* = gliding dragonflies), can also glide, but probably not at such a favourable angle as *M.c.*

Anisoptera

The (large) Anisoptera are the flyers with the greatest capacity for varying their flight parameters. They can change the frequency, amplitude and phase relationship of their wingbeats over the widest range, producing a broad spectrum of flight velocities, accelerations and manoeuvres.

In counterstroking or strongly phase-shifted flight, they hover or proceed only a short distance with each wingbeat. The change in phase relationships of the forel

and hindwings seems to be an important factor in acceleration. During phase-shifted stroking, the aerodynamic action increases when the two pairs of wings are moving in the same direction, as revealed by the concomitant acceleration. In other situations an enhancing interaction of the two wing pairs seems to be possible. Whether these effects occur during the upstroke or during the downstroke depends entirely on the nature of the manoeuvre and on the stroke variables.

Azuma *et al.* (1985) found that even in slow, regular, rising flight of a dragonfly (*Sympetrum frequens*) in a laboratory, lift was increased during the downstroke and drag was increased during the upstroke in phases of parallel stroking. These results agree with velocity measurements based on the films presented here.

The greatest accelerations are reached by Anisoptera using nearly total parallel stroking. Because during backward and upward flight the wings are beating at a large angle away from the flight direction (Fig. 13), this can be regarded as an instance of 'flight by drag' (D. Hummel & H. Oehme, personal communications). Backward flight of Anisoptera, or of large Zygoptera with parallel stroking, bears some kinematic resemblance to the backward flight of the redstart (Rüppell, 1971). In this process, air is probably accelerated away from the wings in a direction opposite to the flight direction. The reaction force would then propel the dragonfly. This principle of flight by drag was inferred by von Holst almost 50 years ago (von Holst & Küchemann, 1941). But there is some doubt as to whether the air movement actually occurs. First, it must be made clear how large the aerodynamically more effective angles of attack are – that is, the angles between the theoretical airstream and the wing cross-section. The airstream can be found from the stroke plane (more precisely: the air flow generated by wing movement) and the flight velocity (more precisely: the air flow generated by propulsion). In most of the flight manoeuvres discussed here in which the flight velocity is low (low advance ratio) nonstationary effects probably contribute in unknown ways (Weis-Fogh, 1973; Savage *et al.* 1979; Ellington, 1984*a,b*). Because of its complexity, discussion of aerodynamic events in general will be omitted here; for the time being, it would appear too speculative.

Questions

Many other kinematic details cannot yet be elucidated. The wingbeat cycle of parallel stroking is initiated by the forewings in the Zygoptera and by the hindwings in the Anisoptera, but it remains unclear what, if any, aerodynamic advantages are involved.

In *C.s.* and the Anisoptera the hindwings appear more important for flight, because in these groups the forewings are often held still while the hindwings beat alone. Viewing an approaching dragonfly from the front, one sees that the hindwings have a larger angle of attack than the forewings (see also Table 2). Can they manage this without stalling because the forewings deflect the air flowing from the flight direction downwards, so that it strikes the hindwing in such a way that the effective (aerodynamic) angle of attack is not so large? What kinds of

interactions are there between the fore- and hindwings in the various phase-shifted stroking modes?

We can only speculate on the detailed interaction of both pairs of wings. Using various methods for visualizing air currents on sequentially positioned wings, Schwieger (1988) gathered data suggested that even with greater angles of attack more favourable air circulation is obtained with two wings, one behind the other, than with a single wing.

Further differences between Zygotera and Anisoptera derive from the morphology of the wing joint. According to Pfau (1986), the Anisoptera cannot beat their hindwings over as great an arc as their forewings. Although Zygotera can move their wings horizontally forwards, achieving a very large stroke amplitude (Figs 11, 12), the Anisoptera as a rule cannot (Fig. 13). Their stroke is directed predominantly forwards and down. This difference in the range of movement of the wings is also evident in the anterior minimal angle between the long axis of the body and the stroke plane. In Zygotera this angle could be as small as 10° , whereas in Anisoptera 40° was the minimum.

For the Zygotera, therefore, there are more flight situations in which a choice of methods is available: in a given stroke phase, either steeply inclined stroke plane (with reference to the long axis of the body) with the wings at a small angle of attack, or stroke-plane angle small and angle of attack large (Fig. 11). The Anisoptera appear to have this choice only when they are flying upwards and backwards, because they are unable to tilt the stroke plane so far forwards and up. Another indication that they cannot do so is that in most flight manoeuvres the Anisoptera point the long axis of the body in the flight direction; in Zygotera this is only rarely the case. For instance, in four of nine cases observed *L.v.* had a very large angle between the body axis and the flight direction (40° , 63° , 75° , 95°), in four cases an intermediate angle (12° , 12° , 13° , 21°) and in only one case was the body axis parallel to the flight direction. Similar observations were made of *M.c.* In contrast, in the Anisoptera it is only during parallel stroking that there is a major disparity between the body axis and the flight direction. The increase in resistance of the body when its long axis is not parallel to the flight direction appears to play no role; probably so much effort must be invested in flight in any case that this factor is negligible. The large stroke amplitude, the large angles of attack and the pulsatile force production in parallel stroking demand the generation of large forces. As a result, this powerful flight method is employed only briefly: a female *T.l.* flying vertically up from the male after their joint egg-laying, with the flight direction at about 80° to the body axis, carried out three parallel wingbeats and then switched to phase-shifted stroking (which brought the body axis into line with the flight direction).

Both Zygotera and Anisoptera are adapted to the circumstances of their lives by their flight abilities. As the circumstances vary, so does the flight performance. Anisopteran flight is technically superior to that of the Zygotera, which serve them as prey. Anisoptera have more ways to vary their flight. They fly more powerfully over larger ranges of velocity, are less sensitive to wind and gusts, and

can also fly much further than the Zygoptera (only Anisoptera can migrate over thousands of kilometres). However, the flight of the Zygoptera is smoother and very agile in the low-velocity range, because of the great adjustability of the wings. Furthermore, the Zygoptera fly in cloudy weather and at low temperatures (around 14–16°C) (personal communications from H. Grunert, A. Martens, L. Müller & P. Schridde, and my own observations).

Anisoptera fly primarily in the open air, whereas Zygoptera tend to stay in the dense vegetation near water. It should be possible to examine these preferences, and even species-specific niche preferences, in the context of flight capabilities.

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