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WING LOADING IN RELATION TO SIZE AND FLIGHT CHARACTERISTICS OF EUROPEAN ODONATA

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1300 specimens, representing 30 spp. were caught in northern Germany and southern France and measured. The wing areas were determined with a special-purpose computer and the weight was measured with a precision of ± 1 mg. Several weight classes were found, from an average of 45 mg in some Zygoptera to ca 876 mg in some Aeshnidae. The sample also fell into separate groups with respect to wing loading. Certain Anisoptera have relatively large wing loadings. Implications of the data with respect to ecology, ethology and flight biology of the Odonata are discussed. The changes in weight of *Leucorrhinia rubicunda* during the flight season were monitored, particular attention was paid to sex differences.

INTRODUCTION

Flight plays a major role in the life of adult dragonflies and damselflies. Feeding, reproduction, the avoidance of enemies are all aerial activities, and it is by flying that these insects distribute themselves in their habitat. Success in these activities is often determined by an individual's flight skills. In various species, for example, the males that fly most rapidly copulate more frequently than the slower fliers (RÜPPELL & HADRYS, 1987). The ability to fly is just as important in escaping from predators (REHFELDT, 1992) as in travelling from place to place and in finding bodies of water suitable for reproduction. A successful flier must also be able to cope with different wind conditions. Kinematic analyses in the field have demonstrated fundamental differences in the flight performance of damselflies and dragonflies as well as within systematic groups (RÜPPELL, 1989).

However, the existing analyses do not enable the flight performance of a particular type of damselfly or dragonfly to be predicted from the dimensions of its body and wings. MAY (1981) is the only author so far who has attempted to relate parameters of functional morphology to behavioural patterns such as maintained flight or perching. The present paper is a preliminary step toward establishing such behavioural and ecological relationships.

MATERIAL AND METHODS

The Odonata of this study were caught as adults in the vicinity of Braunschweig from May to September 1988, and on two trips to the Crau region of southern France, in the middle of August 1988 and the end of June 1989. 1300 specimens, representing 30 species, were measured. After the insects had been caught and marked (for recapture and to avoid measuring the same individuals twice), they were photographed. The photos were projected by way of a mirror onto the digitizing pad of a digital geometric analysis computer (Kontron Videoplan) and the dimensions of the body were measured, including the wings on the right side only. The total wing area was calculated by adding the area values for the right wings and doubling the result. The insects were weighed with an electronic analytical balance (Mettler, Model PM 100) having a range of 0-150 mg and a precision of ± 1 mg. When used in the field the balance was powered by an automobile battery, via a transistorized inverter.

RESULTS

WEIGHT INCREASE

During the flight phase of their lives, male and female Odonata gradually gain weight. To monitor these changes in weight during one summer, measurements were made in a population of the dragonfly *Leucorrhinia rubicunda*, a species showing synchronised emergence. Because this species has a brief flight period, it does not exhibit the major fluctuations in weight undergone by species with a long

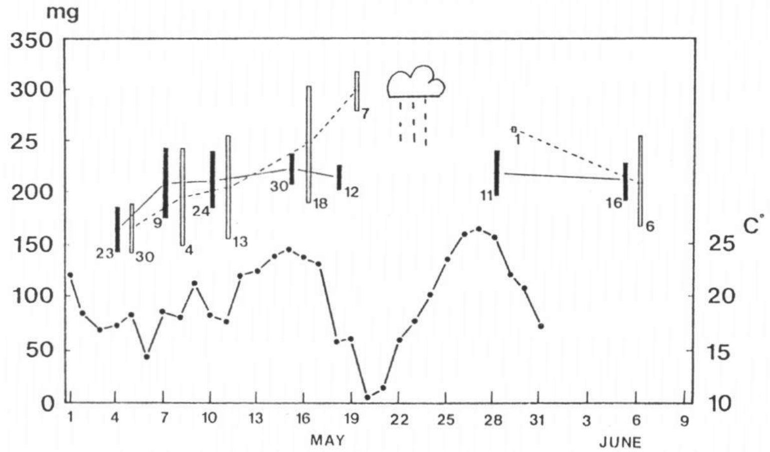

Fig. 1. Ambient temperatures (dots) and mean weights of *Leucorrhinia rubicunda* during May 1988. Males: continuous curve, s.d. [range] shown by black bars; females, dashed curve with white bars. The numbers of individuals weighed on each occasion are indicated. The cloud with rain means rainy weather.

flight phase which are exposed repeatedly to altered environmental conditions.

The weights were found to change dramatically during the season (Fig. 1). After the imaginal molt, at which time both sexes of *L. rubicunda* weigh about 170 mg, the feeding period begins. The males gain 55 mg (= 32,4%), reaching 225 mg, and the females gain 130 mg (= 76,5%) to reach about 300 mg. The rate of weight gain in the short term depends very much on the weather, because both the dragonflies and their prey, flying insects, are active only when conditions are suitable. Perhaps the delayed weight gain of the females in Figure 1 can be explained in this way, because from the 6th to the 11th of May, 1988, the weather was unfavorable. Similarly, the females had actually lost weight after the period of bad weather from the 19th to the 26th of May.

WEIGHT COMPARISON AMONG SPECIES

The weights of the 30 species (all mature individuals) examined were between 33 mg (*Ischnura elegans*, ♂) and 1098 mg (*Aeshna cyanea*, ♀). Apart from certain Libellulidae, the males were always about 20% lighter than the females (Tab. I).

In the Zygoptera the Lestidae, Platycnemididae and Coenagrionidae constitute one weight class (mg):

Means	male	45	sd	12.05	n	30
	female	57.6	sd	18.9	n	35

and the Calopterygidae form another:

Means	male	112.5	sd	20.7	n	160
	female	142.5	sd	31.4	n	148

Among the Anisoptera three weight classes can be distinguished:

(I) the Aeshnidae and Cordulegastridae

Means	male	725.4	sd	126.3	n	74
	female	876.8	sd	136.7	n	20

(II) the Gomphidae

Means	male	378	sd	45	n	21
	female	513	sd	152	n	6

(III) the Libellulidae

Means	male	192.6	sd	93.6	n	429
	female	204	sd	93.6	n	296

the last having the largest relative variation.

WING-AREA COMPARISON

The wing areas (Tab. I) fall into similar groups (Fig. 2). Again the Calopterygidae are distinguished from the other damselflies by their large wings. And here again, the greatest variation is found in the family Libellulidae.

One measure of wing shape is the aspect ratio (the ratio of the square of the wing-span here less the distance between the wingbases; the aspect ratio is so about 10% lower than normally). The higher the aspect ratio, the more elongate is the

Table I

Morphometric data of the species measured – [n = number of measured insects; – ma = mass (mg); – a = area (cm^2); – wl = wing loading ($mg \cdot cm^{-2}$); – l = length of right forewing (cm); – ar = aspect ratio (span without body spread); – first line of values for males, second for females. – Mean values with standard deviation in brackets]

Species	n	ma	a	wl	l	ar
Calopteryx virgo	9	143 (±22)	12.1 (±0.74)	11.8 (±1.32)	3.41 (±0.18)	3.84
	4	186 (±18)	12.2 (±1.09)	15.2 (±0.24)	3.62 (±0.13)	4.30
C. splendens	55	120 (±11)	8.7 (±0.46)	13.7 (±1.30)	3.07 (±0.13)	4.33
	56	156 (±19)	9.8 (±0.58)	15.9 (±2.02)	3.37 (±0.12)	4.64
C. xanthostoma	29	95 (±10)	8.3 (±0.40)	11.5 (±1.16)	3.05 (±0.08)	4.48
	30	125 (±16)	9.7 (±0.63)	13.0 (±1.60)	3.43 (±0.11)	4.85
C. haemorrhoidalis	67	92 (±12)	8.6 (±0.49)	10.6 (±1.16)	3.04 (±0.09)	4.30
	68	103 (±21)	9.2 (±0.48)	11.2 (±2.09)	3.20 (±0.08)	4.45
Lestes sponsa	10	43 (±4)	3.3 (±0.28)	13.3 (±1.45)	2.22 (±0.08)	5.97
	16	49 (±7)	3.5 (±0.30)	13.7 (±1.37)	2.34 (±0.07)	6.26
L. virens	2	49 (±1)	2.8 (±0.06)	17.5 (±0.15)	2.20 (±0.00)	6.91
	2	56 (±5)	2.7 (±0.28)	21.5 (±4.14)	2.05 (±0.07)	6.23
L. viridis	6	66 (±4)	3.8 (±0.18)	17.1 (±0.63)	2.57 (±0.05)	6.95
	2	94 (±10)	4.2 (±0.37)	22.3 (±0.41)	2.70 (±0.14)	6.94
Platycnemis pennipes	12	34 (±3)	2.8 (±0.26)	12.2 (±1.10)	2.20 (±0.10)	6.91
	9	49 (±6)	3.5 (±0.28)	14.9 (±0.39)	2.45 (±0.07)	6.86
Ischnura elegans	17	33 (±3)	1.9 (±0.15)	17.7 (±1.41)	1.82 (±0.09)	6.97
	13	40 (±5)	2.3 (±0.15)	17.8 (±2.17)	2.02 (±0.07)	7.10
Brachytron pratense	9	555 (±25)	11.1 (±0.53)	49.8 (±2.36)	3.54 (±0.11)	4.50
	1	701	12.0	58.5	3.80	4.80
Aeshna juncea	10	753 (±32)	19.9 (±1.18)	37.9 (±2.53)	4.65 (±0.14)	4.30
	8	836 (±77)	21.6 (±1.30)	38.7 (±2.77)	4.73 (±0.14)	4.14
A. grandis	4	798 (±63)	23.0 (±1.25)	34.8 (±1.21)	4.82 (±0.25)	4.04
	1	1045	23.0	44.2	5.00	4.35
A. cyanea	28	729 (±41)	18.7 (±1.20)	39.0 (±2.39)	4.49 (±0.14)	4.31
	2	1098 (±52)	19.2 (±1.02)	57.2 (±0.31)	4.55 (±0.21)	4.31
A. mixta	1	528	16.1	32.8	4.10	4.12
	1	832	17.1	48.7	4.20	4.13
Anax parthenope	16	821 (±71)	22.3 (±0.97)	36.9 (±2.94)	4.89 (±0.14)	4.29
	7	779 (±170)	22.6 (±1.55)	34.2 (±6.23)	4.89 (±0.20)	4.23
Ophiogomphus cecilia	16	423 (±20)	10.1 (±0.45)	42.1 (±2.00)	3.30 (±0.09)	4.36
	3	665 (±68)	12.5 (±0.14)	56.1 (±2.10)	3.65 (±0.07)	4.26
Onychogomphus uncatus	5	333 (±20)	9.5 (±0.71)	35.2 (±3.68)	3.18 (±0.11)	4.26
	3	361 (±71)	9.8 (±0.80)	36.5 (±4.74)	3.30 (±0.17)	4.40
Cordulegaster boltonii	8	894 (±68)	16.5 (±0.91)	54.1 (±4.29)	4.40 (±0.11)	4.69
Cordulia aenea	73	375 (±27)	10.6 (±0.68)	35.2 (±2.90)	3.42 (±0.11)	4.41
	4	429 (±45)	10.8 (±1.12)	39.9 (±5.57)	3.43 (±0.10)	4.36
Libellula quadrimaculata	20	382 (±35)	12.5 (±0.57)	30.6 (±2.78)	3.73 (±0.10)	4.45
	3	350 (±130)	12.5 (±1.07)	28.1 (±10.54)	3.60 (±0.10)	4.15
Orthetrum coerulescens	20	199 (±45)	9.7 (±0.54)	20.3 (±4.64)	3.18 (±0.10)	4.17

Table I (continued)

Species	n	ma	a	wl	l	ar
	9	251 (±78)	9.6 (±0.71)	25.5 (±7.75)	3.09 (±0.16)	3.98
O. cancellatum	26	373 (±37)	14.3 (±1.02)	26.4 (±2.54)	3.96 (±0.16)	4.39
	22	439 (±74)	13.5 (±0.75)	32.5 (±5.19)	3.84 (±0.14)	4.37
Crocothemis erythraea	30	172 (±54)	8.6 (±0.79)	20.0 (±6.32)	3.02 (±0.14)	4.24
	16	151 (±72)	8.9 (±0.92)	16.9 (±7.19)	2.98 (±0.15)	3.99
Sympetrum fonscolombii	46	175 (±18)	9.7 (±0.82)	18.1 (±1.17)	3.17 (±0.13)	4.14
	21	205 (±28)	10.2 (±0.74)	20.1 (±2.14)	3.20 (±0.13)	4.02
S. flaveolum	16	127 (±12)	8.5 (±0.47)	15.0 (±1.12)	2.86 (±0.10)	4.23
	8	158 (±24)	8.6 (±0.50)	18.3 (±2.94)	2.91 (±0.10)	3.94
S. danae	38	90 (±24)	6.9 (±0.79)	13.1 (±2.63)	2.56 (±0.15)	3.80
	46	82 (±29)	6.8 (±0.86)	11.8 (±3.54)	2.52 (±0.16)	3.74
S. depressiusculum	30	113 (±19)	9.1 (±0.73)	12.5 (±2.04)	2.95 (±0.11)	3.83
	32	90 (±18)	9.3 (±0.64)	9.7 (±1.88)	2.97 (±0.11)	3.92
S. sanguineum	20	127 (±19)	8.1 (±0.68)	15.6 (±1.85)	2.85 (±0.12)	4.01
	5	164 (±18)	8.5 (±0.22)	19.3 (±2.01)	2.90 (±0.00)	3.96
Leucorrhinia dubia	37	153 (±54)	7.6 (±0.46)	20.1 (±7.23)	2.78 (±0.12)	4.07
	39	150 (±33)	7.4 (±0.38)	20.3 (±4.23)	2.73 (±0.09)	4.03
L. rubicunda	146	208 (±31)	9.0 (±0.59)	23.1 (±3.48)	3.06 (±0.11)	4.16
	93	212 (±57)	8.9 (±0.65)	23.7 (±6.53)	3.00 (±0.12)	4.04

shape of the wing. By far the largest aspect ratios are found among the damselflies (Zygoptera), except for the Calopterygidae (Tab. I). The libellulids especially the *Sympetrum* species have the relatively broadest wings of all measured odonates.

Another characteristic parameter is the distribution of area over the length of the wing. As shown in Table II, among the Zygoptera (apart from the Calopterygidae) the outer half of the wing is considerably broader than the inner half, so that the outer half accounts, on average, for 67% of the total area; the corresponding figure for the Calopterygidae is $\bar{x}$=60%, while for the forewings of Anisoptera $\bar{x}$=52.8% only. In the case of Anisoptera hindwings, the proportions are reversed, the outer half accounting for only 45.3% of the total area. In this parameter, again, the damselflies (apart from the Calopterygidae) occupy a special position.

MASS AND WING AREA

Wing area was positively correlated with weight in all species (Fig. 2), both among the dragonflies (r=0.90) and among the damselflies (r=0.94). In the latter group the wing size increases considerably more rapidly with increasing mass than in the dragonflies (Tab. I). When the Calopterygidae are set apart, however, the increase found for the remaining three species is not as high.

There are 4 groups which have relatively small wing areas. They are marked in

Figure 2 by shaded areas:

(I) the Zygoptera (*Ischnura elegans, Platycnemis pennipes*, Lestidae)
(II) the Gomphidae (*Onychogomphus uncatus, Ophiogomphus cecilia*)
(III) *Brachytron pratense*
(IV) *Cordulegaster boltonii.*

Consequently, the wing loading of these four groups is very high. Among the Libellulidae the small species are exceptional, in that they exhibit no enlargement of the wing surfaces with increasing mass (*Sympetrum depressiusculum, S. flaveolum, Crocothemis erythraea, Orthetrum coerulescens*). That is, the wing loading is greater in the heavier species.

MASS AND WING LOADING

On geometric principles for animals as a whole, the mass per unit surface area increases with increasing size, because area changes by a power of 2 while the volume of the body is changing by a power of 3. Wing loading, however, does not necessarily follow such a rule. In the Odonata size was positively correlated with wing loading only among the Anisoptera (r=0.86; Fig. 2).

Among the damselflies there was no systematic change in wing loading associated with increasing mass, because the heavier Calopterygidae disproportionately have a large wing area (Fig. 2).

The wing loading in damselflies is very much lower than that in dragonflies. Two groups of damselflies can be distinguished: the Calopterygidae (southern C. (sC) + northern C(nC)), with very low wing loadings averaging

Table II

The percentual relation between the area of the inner half (proximal) and the outer half (distal) of both wings of Zygoptera and fore- and hindwings of Anisoptera. – [n = number of measurements]

Species	n	wing area (%) distal	proximal
Calopteryx virgo	1	60.9	39.1
C. splendens	3	59.4	40.6
C. haemorrhoidalis	7	58.1	41.9
Lestes sponsa	17	73.0	27.0
L. virens	13	62.7	37.3
Platycnemis pennipes	22	69.5	39.5
Ischnura elegans	68	66.1	33.9

	n	forewings distal	forewings proximal	hindwings distal	hindwings proximal
Aeshna juncea	82	51.1	8.1	48.4	51.6
A. cyanea	92	53.3	46.7	44.5	55.5
A. grandis	95	54.2	5.8	48.5	51.5
Gomphus pulchellus	114	55.5	4.5	47.4	54.3
Cordulegaster boltonii	129	52.7	47.3	45.7	54.3
Orthetrum coerulescens	170	50.8	49.2	45.5	54.5
Libellula quadrimaculata	153	52.2	47.8	44.3	55.7

only 12.0 mg cm-2, sd=1.8, n=318, and the group (*Ischnura elegans, Platycnemis pennipes*, Lestidae) with somewhat higher wing loadings averaging 16.8 mg cm-2, sd=3.2, n=82.

Because of their availability and the great differences between the sexes, only the males are considered in comparing different dragonfly species. The Libellulidae have the lowest wing loading, which tends to increase in the larger (heavier) species (ranging from the smallest to the largest: *Sympetrum danae, S. depressiusculum, S. fonscolombii, Crocothemis erythraea, Orthetrum coerulescens, O. cancellatum, Libellula quadrimaculata*). This tendency continues for some of the Aeshnidae (*Aeshna mixta, A. cyanea, A. juncea*) but appears not to apply to the heavy species (*A. grandis, Anax parthenope*). There are a few exceptional species with very high wing loadings – the Gomphidae (*Onychogomphus uncatus, Ophiogomphus cecilia*), *Brachytron pratense* and *Cordulegaster boltonii* (Fig. 2).

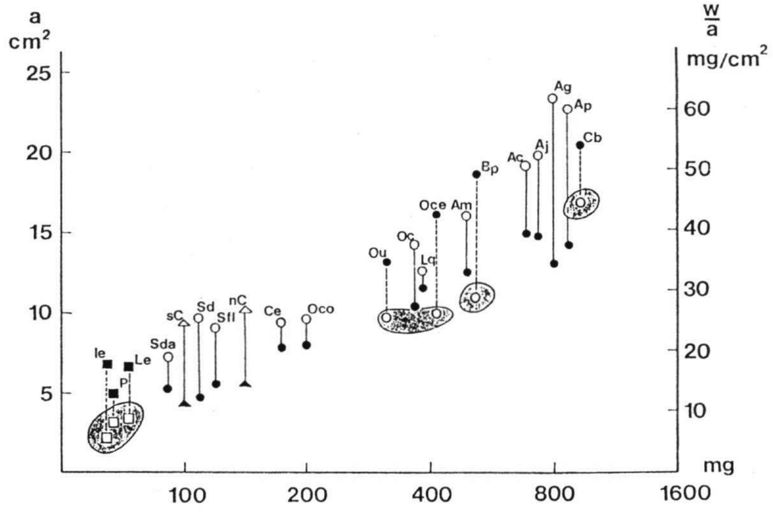

Fig. 2. Wing area (a; open symbols, left ordinate) and wing loading (w/a; black symbols, right ordinate) of species of different masses (mg; abscissa). Squares: Z y g o p t e r a: *Ischnura elegans* (Ie), *Platycnemis pennipes* (p) and Lestidae (Le). – Triangles, Calopterygidae: nC = northern species, sC = southern species. – Circles, A n i s o p t e r a: Sda = *Sympetrum danae*, – Sd = *S. depressiusculum*, – Sfl = *S. flaveolum*, – Ce = *Crocothemis erythraea*, – Oco = *Orthetrum coerulescens*, – Ou = *Onychogomphus uncatus*, – Oc = *Orthetrum cancellatum*, – Lq = *Libellula quadrimaculata*, – Oce = *Ophiogomphus cecilia*, – Am = *Aeshna mixta*, – Bp = *Brachytron pratense*, – Ac = *Aeshna cyanea*, – Aj = *A. juncea*, – Ag = *A. grandis*, – Ap = *Anax parthenope*, – Cb = *Cordulegaster boltonii*. – [Figure is constructed in the way that the open symbols are under the black ones, in cases where the area is relatively small; – alternatively, the wing loading is high when black symbols appear above the open ones (marked by shaded areas)]

DIFFERENCES OF WING LOADING BETWEEN MALES AND FEMALES

As would be expected from the weight differences, males and females also differ from one another in wing loading. The values for males are generally lower than those for females, by an average of 14% in the Calopterygidae and by 15% in the other damselflies (Fig. 3). In the group characterized by the aeshnids, the male wing loadings are lower by 18%. The measurements for the Libellulidae do not reveal such clear-cut relationships (Fig. 4).

DISCUSSION

The data previously available on odonate weight and wing area leave much to be desired. The samples were often small and not separated according to sex. For instance, the value given by GREENWALT (1962) for *Calopteryx virgo* is lower than that for *C. splendens* and amounts to only 63% of the value found here. *Cordulia aenea* weighs only half as much in Greenwalt's study as in our data. The findings of other authors (MÜLLENHOFF, 1885) are also drawn only from individual specimens. The sole detailed analysis is that of MARDEN (1988), for the libellulid *Plathemis lydia*. The fact that most of the values in the older literature are distinctly lower may be due to a longer period in captivity and to differences in the condition of the animals. However, other factors can also contribute to measurement variation. MICHIELS & DHONDT (1988) found that *Sympetrum danae* caught at different sites and at different times during the flight phase varied in body size. In our own experience, the weight of *Calopteryx haemorrhoidalis* fluctuates considerably from year to year (1988 average 83 mg, n=30; 1989 average 99 mg, n=36). N. Weinheber & G.E. Rehfeldt (pers. comm.) documented a seasonal change in weight of *C. haemorrhoidalis* (based on regression analysis of forewing length and weight), which was a consequence of starvation caused by great heat.

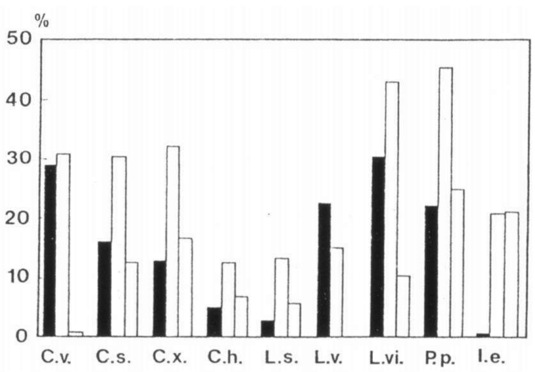

Fig. 3. In Zygoptera, wing loading (black bars), weight (grey bars) and wing area (white bars) are much greater in the females than in the males of all species examined (ordinate: percentage by which females exceed males): C.v. = *Calopteryx virgo*; – C.s. = *C. splendens*; – C.x. = *C. xanthostoma*; – C.h. = *C. haemorrhoidalis*; – L.s. = *Lestes sponsa*; – L.v. = *L. virens*; – L.vi. = *L. viridis*; – P.p. = Platycnemis pennipes; – I.e. = *Ischnura elegans*.

Large differences in weight and hence in wing loading develop between males and females in the course of reproductive activity (ANHOLT, et al., 1991). Although the life--cycle stage of an animal caught in the field could never be accurately established, major differences between the sexes were found. Female Zygoptera were always heavier and had a higher wing loading than the males. In the Anisoptera this relationship was not so clear (Figs 3, 4). The difference may be related to the sampling times, most of the Zygoptera having been caught during mating or egg--laying, whereas the Anisoptera were also caught after egg-laying (*Sympetrum depressiusculum, Ophiogom-phus cecilia*).

Despite this variability, the present data suffice to establish certain aspects of flight biology and of the ecological relationships.

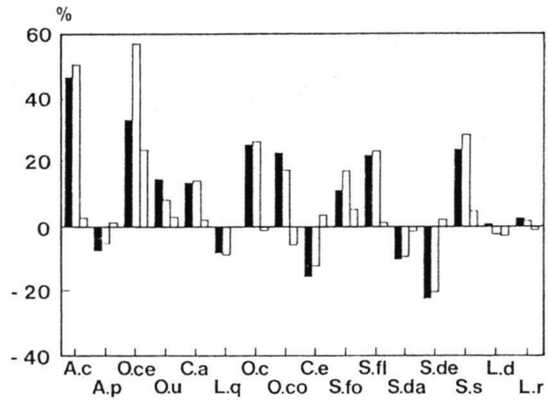

Fig. 4. The values of wing loading (black), weight (grey) and wing area (white) are higher for females than for males of most anisopteran species (bars in positive region of ordinate). In some cases, however, the values for males are higher (as indicated by the negative-going bars): A.c = *Aeshna cyanea*; – A.p = *Anax parthenope*; – O.ce = *Ophiogomphus cecilia*; – O.u = *Onychogomphus uncatus*; – C.a = *Cordulia aenea*; – L.q = *Libellula quadrimaculata*; – O.c = *Orthetrum cancellatum*; – O.co = *O. coerulescens*; – C.e = *Crocothemis erythraea*; – S.fo = *Sympetrum fonscolombii*; – S.fl = *S. flaveolum*; – S.da = *S. danae*; – S.de = *S. depressiusculum*; – S.s = *S. sanguineum*; – L.d = *Leucorrhinia dubia*; – L.r = *L. rubicunda*.

FLIGHT BIOLOGY

Mass, body dimensions and structure, as well as wing loading provide information about the lift a flying animal must generate. For small animals with little mass and a relatively large drag-generating surface, such as the damselflies, the downward force is relatively weak. Hence, the small Zygoptera (*Ischnura elegans, Platycnemis pennipes*, Lestidae) can fly even with a relatively high wing loading compared with that of dragonflies even with high weights and small wing areas (Fig. 2). Their flight performance differs considerably from that of the dragonflies.

As a spotlight, parameters of fast forward flight of the representatives of the three groups considered separately here are shown in Table III.

It can be seen from these data that the small Zygoptera fly with maximal effort; their wing pairs beat in opposite phase, with large amplitude and at a relatively high frequency. Their wings are relatively narrow, with an aspect ratio that is exceptionally high (Tab. I).

In contrast, the Calopterygidae have large relative wing areas and can fly with a

Table III

Flight parameters in fast forward flight of *Lestes viridis, Calopteryx splendens* and *Aeshna cyanea*. Non dimensional flight velocity means the ratio of the distance covered in each wingbeat to the wing length. – [Data from RÜPPELL, 1989]

Features	*viridis*	*splendens*	*cyanea*
Max. velocity (m/s) n: 1 each	2.30	2.00	>10
Propulsion distance of body wingbeat (cm) n: 1 each	3.5	17.5	25
Nondimensional flight velocity	1.5	4.6	4.7
Mean wingbeat frequency (Hz) n: each >10	32	19*	40
Mean velocity of wingtip (cm/s) n: 2 each	161	107	232
Mean stroke amplitude (°) n: 2 each	117	120	82
Phase relation of fore and hindwings (°)	150-180	10-20	70-90

* calculated without wingstandstills

low wingbeat frequency. This is also possible by the fact that the hind pair of wings move nearly in phase with the forewings; that is, they beat in the same direction at the same time: This mode of flight is evidently effective, because the Calopterygidae are able to fly with very large angles of attack and much drag (RÜPPELL, 1985). Furthermore, these species fold their wings back during forward flight, reducing drag. This posture, together with the large propulsive strokes of the wings, enables extremely effective flight to occure, which is very conspicuous and allows the animals to fly at high speed and with great endurance. The shape of the wing in the damselflies (including the Calopterygidae) is different from that in the dragonflies. The surface area is largest in the distal region of both pairs of wings of damselflies, so that during the wingbeat the bearing surface moves over a long distance, toward the outer end of relatively long wings. Therefore the efficacy of the stroke is relatively great. Another effect of the petiolate wings is to minimise the parasite drag at the body, because the generated vortex wakes do not hit the damselflies body (WOOTTON, 1991).

In the Anisoptera the hindwings are broadest in the proximal region (Tab. II), so that their main bearing surface moves over a shorter distance and may serve mainly to produce lift. The distal parts of the wing probably generate predominantly propulsive forces. Dragonflies can fly 3-4 times as fast as damselflies (RÜPPELL, 1989), and they can glide for long distances and actually soar without wingbeats. Their muscle mass, which may be up to 60% of the total mass in *Plathemis lydia*, consists mainly of flight musculature (MARDEN, 1988); this large mass and the dimensional effects of these relatively large insects together with their wingbeat characteristics make such rapid flight possible. But dragonflies flying at these high speeds are subject to large inertial forces, so that they need considerable room to slow down or fly in a curve.

ECOLOGICAL ASPECTS

Anisoptera have been classified as "fliers" and "perchers" (CORBET, 1962), on the basis of their behaviour. Fliers are usually airborne during their daily activity period, and their flight style is characterized by frequent gliding. The perchers, in contrast, continually alternate between periods of flight and perching.

MAY (1981) distinguishes fliers and perchers by taxonomic families, except that he assigns the libellulid subfamily Trameinae to the fliers most other libellulids being perchers. According to May, they are also morphologically distinct, fliers having narrower and longer wings than perchers of the same body size. This distinction does not apply to the European Anisoptera. The Gomphidae, as perchers, have narrower wings than the fliers of the Aeshnidae or *Cordulegaster boltonii* (Tab. I).

However, the classification of fliers vs perchers is consistent with a grouping by weight classes. Among the species examined here, those that lie in wait for prey always weighed less than 500 mg whereas species characterized by maintained flight always weighed more than 400 mg (Fig. 2). Because their energetics (see above), the larger Anisoptera are well suited for prolonged flight. Large Anisoptera do not reach such high population densities as smaller species (such as *Leucorrhinia rubicunda*, RÜPPELL, 1989, or *Sympetrum depressiusculum*, MILLER, et al., 1984; REHFELDT, 1993). For a sparsely distributed population, greater endurance and the ability to fly over longer distances increases the probability of encountering a female.

Another factor, apart from behaviour, is the nature of the space through which an insect flies. This is usually determined by the density of the vegetation. The denser the vegetation, the more of an advantage it is to be small and agile. Larger species usually prefer a more open flight space, where they can make use of their high flight speeds and gliding abilities.

REPRODUCTIVE ASPECTS

In the context of reproduction the relatively low wing loading of the Calopterygidae is of interest. In comparison with Anisoptera of equal weight, the Calopterygidae have much larger wings. The coloured wings of the males also serve for communication – as a threat signal during territorial disputes and as a courtship signal in the presence of a female.

The signalling function of the wings, probably related to reproductive success, has contributed along with the locomotor function to the direction wing development has taken during evolution.

This influence is emphasized by the fact that during threat flights the wing pairs of the male beat in synchrony at a very low frequency (ca 16 Hz) – that is, very conspicuously. Such a flight mode is possible only because this synchronous beating is probably more effective aerodynamically than counter-stroking or phase-shifted wing strokes (RÜPPELL, 1985, 1989).

A striking feature of the Calopterygidae is the lighter weight and lower wing loading of the southern species (Fig. 2). A similar relationship has also been suggested for other species of warm regions. It would be of interest, therefore, to undertake more extensive series of measurements at different geographical latitudes.

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