International Journal of Odonatology 2 (1): 123-131, 1999.

PREY CAPTURE FLIGHT OF CALOPTERYX HAEMORRHOIDALIS (VANDER LINDEN) (ZYGOPTERA: CALOPTERYGIDAE)

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This paper is dedicated to Philip S. Corbet on the occasion of his 70th birthday.

Key words: Odonata, functional morphology, kinematic, foraging, acceleration

Abstract

Calopteryx haemorrhoidalis females (mainly) and males were filmed with a slow-motion camera to analyse, frame by frame, manoeuvres during prey capture flight. Acceleration immediately after take-off was very high, although no high maximum speed resulted. The legs did not assist acceleration but at take-off were already spread in a capture position and remained so until landing. Most successful approaches were frontal but prey often escaped by rapid flight. Approach flights were short and often several odonates pursued the same prey individual. The kinematics of prey capture flight are discussed in relation to calopterygid evolution.

Introduction

Calopterygids feed mainly in mid air, on flying insects. Published descriptions of general performance show differences in flight mode between feeding flight and all other flight types in all species so far investigated, e.g. *Calopteryx splendens* (Zahner, 1960), *Epiophlebia superstes* (Selys, 1889) (Asahina, 1950; Rüppell & Hilfert, 1993), *Epitheca cynosura* (Say, 1839)(Kormondy, 1959) and several other Anisoptera (Williamson, 1923; Williamson & Williamson, 1930). All odonates capture prey by using their legs which are highly specialised to form a prey-catching apparatus (Fig. 1), particularly with regard to position, relative length, articulation and complement of spines (St. Quentin, 1953; Corbet, 1962). How this apparatus functions has not hitherto been investigated: the process operates too rapidly to be detected with the unaided eye.

A first step towards understanding prey capture flight is to consider the spectrum of prey taken by *C. haemorrhoidalis* (Vander Linden, 1825). Nora Weinheber (pers. comm.) listed prey taken at a channel in southern France: small insects including Diptera (Chironomidae and Culicidae) and Ephemeroptera (Baetidae and Caenidae), and a large cicada, introduced from North America (*Metcalpha proinosa* (Selys), Hemiptera, Flatidae; live weight 7.2 mg). Flying ants (Hymenoptera, Formicidae) were also captured. During May and June prey included aphids (Hemiptera, Aphididae) and during July through October Ephemeroptera.

Calopterygids themselves are often captured in flight by Anisoptera such as *Orthetrum cancellatum* (Rehfeldt et al., 1993) and *Anax imperator* (Hilfert, pers. comm.). Such records and earlier descriptions of flight of calopterygids (Schiemenz, 1953; Robert, 1959) could convey the impression that calopterygids have a weak flight, but until now no detailed study of their prey capture flight has been made. On the other hand kinematic analyses of calopterygid flight reveal high acceleration and good manoeuvrability (Rüppell, 1985, 1989). Furthermore, calopterygids often occur at high density, a condition that would require prey capture flight to be efficient.

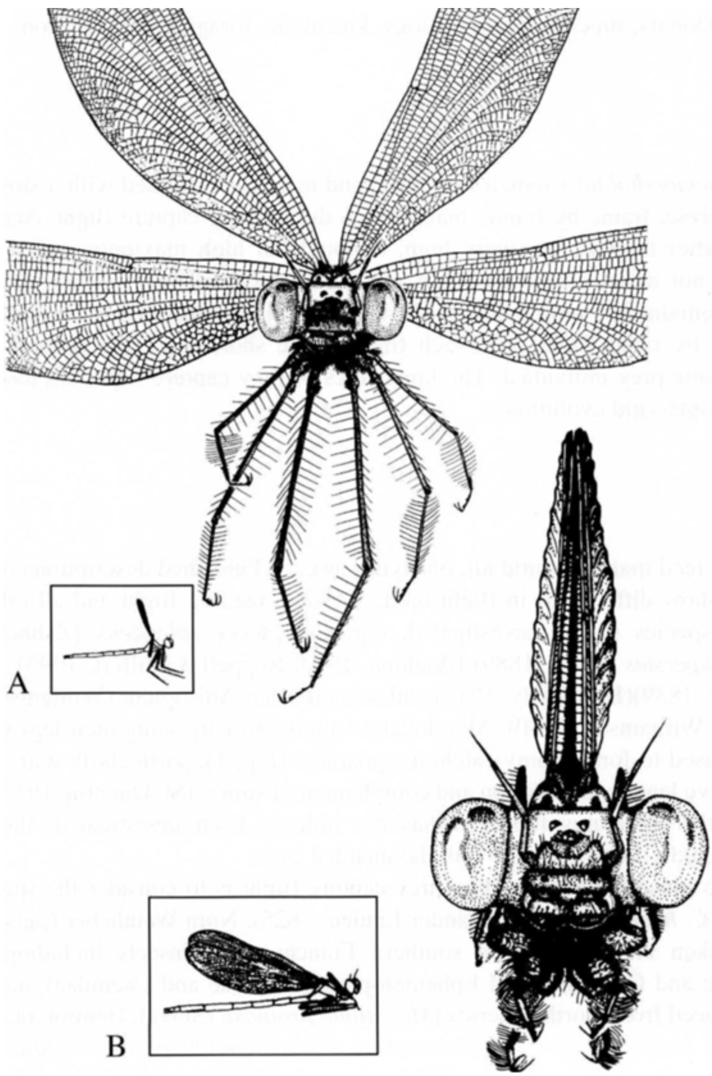

Figure 1. Capture flight of *C. haemorrhoidalis* (A). Constructed after slow motion films, still photographs and dead damselflies. The wings are drawn in a forward position. For comparison a phase from a normal forward flight is depicted (B). The legs are then folded against the body.

Table 1. Number of prey capture flights (by 62 females and 5 males) and success of *C. haemorrhoidalis* with prey insects (mostly Diptera of 1-2 (small), 2-3 (medium) and 3-5 mm (large) body length). Successful were only frontal approaches with small prey. (sim. means simultaneous flights)

Flights			approach		success		prey		
number	sim.	mean participants	frontal	behind	yes	no	small	medium	large
67	55	3,15 (2-6)	17	6	3	24	5	12	6

Methods

Observations were conducted in late May 1996 beside a forest rivulet in hilly country south of the Alpilles near St. Remy de la Provence in southern France (43¡42'; 4¡55'). The rivulet, *ca* 1-2 m wide, flows through a valley with a dense growth of trees and shrubs, *ca* 6 m high, so that its course resembles a tunnel through forest punctuated by small sunny spots. In an open area beside a road, where the rivulet entered dense tree cover, I observed and filmed aggregated calopterygids, mainly females foraging there in the morning until noon, when the sun illuminated this part of the rivulet. The distance between observer and odonates was 2-6 m. Each time prey appeared, illuminated by the sun and thus contrasting well against the dark background of the trees, the slow-motion camera was started at 250-400 frames per s. (LOCAM camera with 70-210 mm objective, 500 ASA Kodak-Negativfilm). Only flights nearly at a right angle to the lens were analysed. Conditions acceptable for filming were sunshine without wind and an ambient temperature (in the shade) of 22-26°C.

The course and velocity of the body of the calopterygids and the prey, and the wings and legs of the calopterygids, were analysed using a single frame projector (NAC). *Wing-beat frequency* denotes the number of up- and downward beats per second, and *wing amplitude* denotes the angle between the hind and frontal turning points of the wings. The *phase relationship* between the pairs of forewings and hindwings was 0 only when both pairs of wings were beaten together at the same time in the same direction. In all other cases the phase relationship departed from 0.

The acceleration of flight (a) is the difference in speed divided by the time interval within which the difference occurred.

The length of the abdomen and hindwing of 41 individuals and the live weight of 15 individuals was measured.

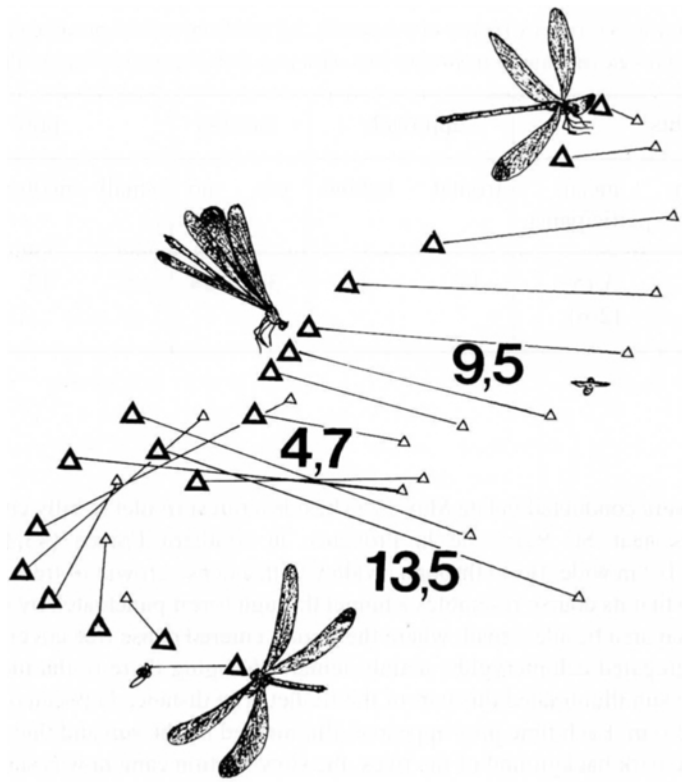

Figure 2. Success with assistance of the environment. A small dipteran (successive positions marked by small triangles) approaches the hunting *Calopteryx* (adjacent positions marked by large triangles and connected by lines). Twice the dipteran returned from leaves to be caught. The numbers give the distances of the lines touched by them in cm.

Results

Behavioural observations

In 28 of the 67 prey capture flights filmed, encounter with the prey could be recognised and analysed, and in 4 (14%) of such flights the prey was captured (Table 1).

Perches near the open sunny space above the flowing water were favoured and defended by a threat display. Individuals spread all four wings and raised the abdomen nearly to the vertical position. When a potential prey animal appeared, calopterygids started from the normal perching position and returned often to the same perch.

Diptera flying fast (at 3.3-5.4 m·s-1) were never pursued. The calopterygids flew only after slower prey, a flight lasting only a few seconds (maximum 6 s). Often several individuals at once chased the same prey (up to 6 filmed [Table 1]; up to 10 observed) .

Take-off was effected only by the wings, the legs not even being flexed, but immediately after take-off the legs were stretched, thus forming the catching apparatus (Fig. 1);

and they remained in that position throughout the flight. At the moment of prey capture in flight, the legs were positioned within 0.003 s 30-35° towards the prey.

The calopterygids mainly chased prey that flew towards them, and did so rarely by pursuing prey flying in the same direction (Table 1).

Kinematics

The phase relationship during prey capture flight was always 0, the wings beating synchronously. Only shortly before landing could the forewings and hindwings be out of phase by 1-2 beats.

Wing-beat frequency and wing-beat amplitude varied in a consistent manner during prey capture flights.

Wing-beat frequency was always higher before than after the encounter: values before exceeded 20 Hz (maximum 24 Hz) whereas those after were about half pre-encounter values. For example, in one instance the last three wing-beats before the encounter were 19.3, 20.7 and 22.3 Hz and the next three wing-beats were 11.0, 12.6 and 10.0 Hz.

Wing-beat amplitude changed concurrently with wing-beat changes. Before an encounter wing-beat amplitude was shortened in the backward-beating plane by about 30-40°, from 110-120° (characteristic of normal flight) to 70-90°. These shortened wing-beats numbered about 3-5 but there could be up to 16 when an encounter was protracted. Wing 'standstills' in the backward position, as in forward flight of both sexes and threatening flight of males, never occurred before encounters with prey, but did so afterwards. In general, whether successful or not, the calopterygids showed gliding phases with wings folded in the backward position after each capture attempt. In one such case a female held the wings stationary for 0.16 s, a period equivalent to 3 wing beats.

Acceleration after take-off can be extremely high. One female reached a speed of 1.6 $m{\cdot}s^{-1}$ after only 0.013 s (a = 121.3 $m{\cdot}s^{-2}$). Subsequently the speed did not increase much. Another female started more slowly, attaining a maximum speed of 1.8 m after 0.12 s (Fig. 2). Two females chasing the same prey and flying together wing to wing reached a speed of 2.5-3.0 m, which was maintained at least while they remained in view over a distance of 35 cm. The maximum flight velocity of the dipteran prey was, depending on their size, often up to 5 $m{\cdot}s^{-1}$, somewhat higher than that of the calopterygids. Most Diptera escaped. A fly about 5 mm body length flew vertically upwards at a speed of 0.87 $m{\cdot}s^{-1}$ pursued by a female *Calopteryx* flying at 0.76 $m{\cdot}s^{-1}$; the distance between them (8.2 cm) increased and the fly escaped. Another fly similar in size flew at 2.80 $m{\cdot}s^{-1}$ directly towards a female flying at 0.8 $m.s^{-1}$. The female decreased its speed to 0.5 $m{\cdot}s^{-1}$, 15 cm before the encounter. The fly passed close by the female which at that moment almost stopped, reducing its speed to only 0.15 $m{\cdot}s^{-1}$, making no attempt to capture the prey and then accelerating to 0.6 $m{\cdot}s^{-1}$ in its original direction. Another instance of a *Calopteryx* decreasing its flight velocity during a frontal encounter resulted in a capture (Fig. 3).

Sometimes habitat features, such as leaves, facilitated prey capture. The flying prey might be forced to change direction and so could be captured (Fig. 4).

Occasionally *C. haemorrhoidalis* gleaned prey from the surface of leaves. Then the approach was slower than to flying prey.

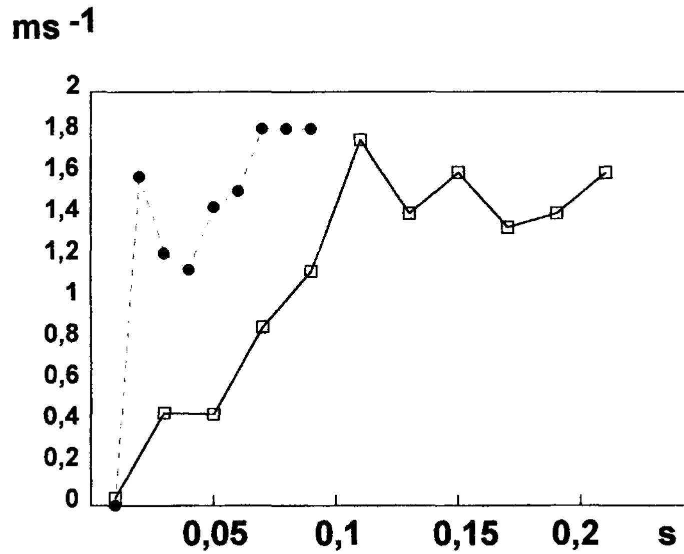

Figure 3. Two females *C. haemorrhoidalis* when starting the approach flight reached different accelerations, one of it the highest ever measured. The dots mark equal time periods from measurements.

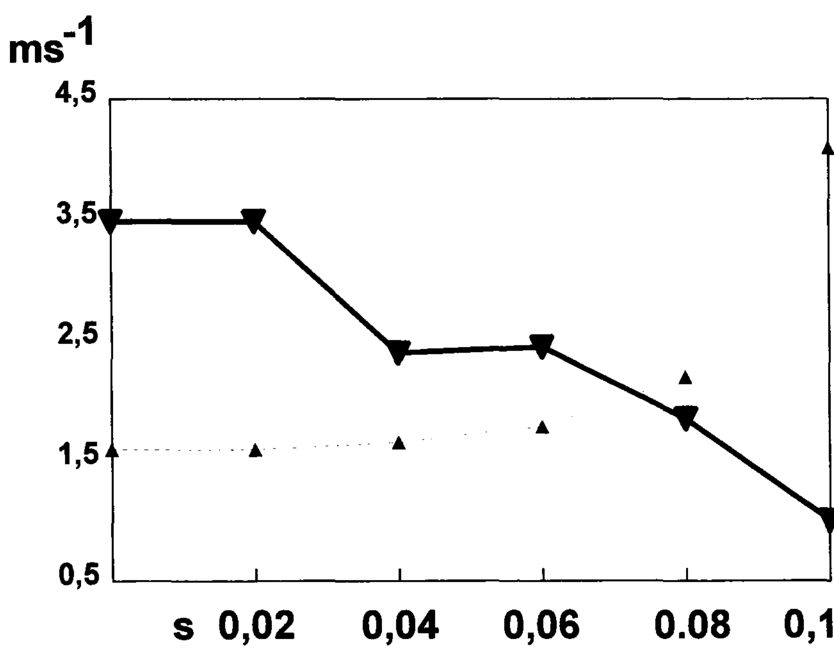

Figure 4. A female *C. haemorrhoidalis* (solid line) approaching a prey, Diptera (broken line) were successful (at the right end of the graph), decelerating before the encounter.

Discussion

Because most of the body dimensions and the behavioural elements of prey capture are very similar in the European species of *Calopteryx*, the results for *C. haemorrhoidalis* can be discussed in the context of the genus.

Potential prey flying within the range of possible capture often releases prey capture flight in several individual *Calopteryx* simultaneously. Aggregated foraging behaviour has been described for many odonate species (Corbet, 1962). In contrast to Anisoptera, some of which may engage in long-lasting, aggregate foraging flights at places where prey is at high density, collective foraging flights of calopterygids are extremely brief. Such flights may represent races between participating individuals. At the same time, the winner may benefit from the decreasing escape area available to the prey.

Several attributes facilitate prey capture by calopterygids.

High manoeuvrability is achieved by the wings being large relative to body mass, and by the unique mode of wing beating.

Large wings can accelerate a relatively low body mass very effectively: wing loading in calopterygids is very low (Rüppell, 1985; Grabow & Rüppell, 1995).

The nondimensional flight velocity, as the ratio of the distance covered in each wing beat to wing length (Ellington, 1984), is higher in calopterygids than in any other odonates (Rüppell, 1989). This must be true especially at take-off, when the effective wing strokes produce the highest accelerations ever measured in odonates (Rüppell, 1989, this study). From this we can conclude that calopterygids are highly manoeuvrable. Were the wings to beat on right and left sides in a counteracting way, changes of flight direction would be accomplished on the spot, by only one or two wing beats. Such a manoeuvre was performed by a male *C. virgo* (Linnaeus, 1758) direction by 180° during one and a half wing strokes (Rüppell, unpubl.).

The approach to, and capture of prey is presumably energetically costly. Normally Zygoptera are able to take advantage of the clap-and-fling mechanism (Weis-Fogh, 1973; Rudolph, 1976, Wakeling, 1997), which saves energy but is possible only by clapping the wings together at the conclusion of each backstroke. After that calopterygids often hold the wings stationary in this position, thus further saving energy (Rüppell, 1985). Long wing 'standstills' that follow attempts at prey capture probably help the flight muscles to recover. No wing 'standstills' were witnessed just before encounters with prey, probably to improve manoeuvrability and prey capture, for which the higher wing-beat frequency and the shortening of wing-beat angles shortly before prey capture are further aids.

When beaten all together , facing the prey and only in the front area of the wing-stroke plane, the wings may present an impenetrable screen to the prey, which therefore has reduced opportunities for escape. The prey may be led by the screen into the area of the highly specialised legs which might be less of an optical obstruction than the wings. The legs of *Calopteryx*, unlike those of raptorial birds which manoeuvre their legs during a strike, resemble flying spider webs, a resemblance enhanced by the inconspicuousness of the leg spines.

Capture success depends not only on the capture technique but also on the prey spectrum. In this study fast-flying Diptera comprised the main food resource, but capture success was very low (16%, n = 28), and not energetically profitable because each prey item was small. In other habitats, far from forest, a wider range of aquatic insects is available. As Weinheber (pers. comm.) observed, capture success for Diptera (Nematocera), Ephemeroptera and Trichoptera, all of which are poor fliers, can be 40-70%. Such values resemble those found for the calopterygid *Mnais pruinosa* (Selys, 1853) (44%, Higashi, 1979) and for the anisopterans *Pachydiplax longipennis* (Burmeister, 1839) (62%, May, 1984) and *Sympetrum frequens* (Selys, 1883) (52%, Higashi, 1978). Perhaps the poor prey availability and the associated low capture success contributed to the low densities of *C. haemorrhoidalis* at the study site.

As judged by the fossil record, the morphology of the capture apparatus is of great antiquity, from which one may infer that Odonata have been specialised to forage in mid air while in flight from an early stage in their evolution (Corbet, 1962).

The mode of beating the wings simultaneously and just before a frontal capture, may also be of great antiquity. It could have facilitated territorial behaviour because this capture flight closely resembles frontal threat, which is one of the basic elements of male territorial behaviour of calopterygids.

Acknowledgements

I am grateful to Dagmar Hilfert-Rüppell who helped me to analyse and draw and to Philip Corbet for correcting my English.

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