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Part I

THE SIGNIFICANCE OF WING CLAPPING IN ZYGOPTERA

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Wing clapping is recorded for 14 species of Zygoptera and is illustrated and described for 8 of these, all Nearctic species. It is hypothesized that the inconspicuous clappings observed in ♂♂ of Coenagrionidae and Lestidae serve as generalized territorial declarations to competitors, but that the more conspicuous clappings in both sexes of *Calopteryx* serve an additional, more specialized function, that of communication between members of a pair declaring their presence to each other.

INTRODUCTION

Wing clapping (BICK & BICK, 1965) consists of the separation of right and left wings and a return to the resting position (Fig. 1). Meso- and metathoracic wings on each side remain together, acting in unison. The clap occurs in the presence or absence of nearby odonates, most often after a return to the perch following a patrol flight. Wing clapping should not be confused with wing warning, which is always a response to another odonate and consists of elevating and separating the four wings, as we (BICK & BICK, 1963) illustrate for *Enallagma civile* (Hagen). Wing clapping, although not always designated as such, has been recorded by: WALKER (1953), ROBERT (1958), JOHNSON (1962), BICK & BICK (1965, 1971), LOGAN (1971), HEYMER (1972, 1973).

In the course of 12 years, cinematographic records of wing clapping were obtained for these 8 Nearctic species: *Argia apicalis* (Say), *A. immunda* (Hagen), *A. moesta* (Hagen), *A. plana* Calvert, *Archilestes grandis* Rambur, *Lestes unguiculatus* Hagen, *Calopteryx aquabilis* Say, *C. maculata* (P. de Beauvois). This paper describes and diagrams wing clapping in representatives of three families of Zygoptera (Coenagrionidae, Lestidae, Calopterygidae) and presents a hypo-

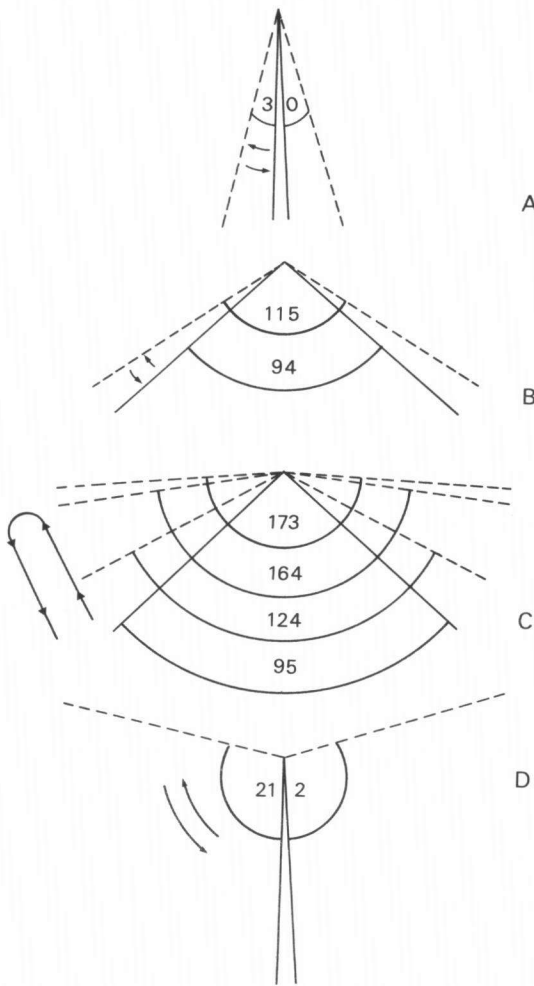


Fig. 1. Wing clapping in: *Argia immunda* (A), *Lestes unguiculatus* (B), *Archilestes grandis* (C), *Calopteryx maculata* (D). Solid lines represent the anterior margins of the fore wings at rest; dashed lines, the extensions of the anterior margins of the fore wings during a clap. The numbers are the sizes of the angles between the anterior wing margins. In *A. grandis* the clap consists of three stepwise forward movements of right and left wings, followed by two backward ones to the resting position; in the other species the clap consists of one such forward and one backward movement.

thesis concerning its significance.

VARIATION

Coenagrionidae.

In the above coenagrionids, a wing clap consists of one small forward and outward, then one backward wing movement to the resting position (Fig. 1A). In these species the clap is very brief: the mean duration in *A. apicalis* is 0.7 sec (N=2), in *A. immunda*, 0.8 sec (N=1), in *A. moesta*, 0.5 sec (N=4), and in *A. plana*, 0.5 sec (N=9). Also, the angles formed by the anterior margins of the fore wings are small: 28° and 30° in two individuals of *A. apicalis*, 30° in *A. immunda*. (No measurements for *A. moesta* and *A. plana* were possible because only side views were available for study). For these reasons a wing clap can be easily overlooked. Although we have not observed wing clapping in any species of *Enallagma*, LOGAN (1971) records it for *E. boreale* Selys and *E. carunculatum* Morse.

Lestidae. In *L. unguiculatus* (Fig. 1B), as in the Coenagrionidae, a wing clap can be easily

overlooked. Lasting 1.7 sec, it consists of one small (an increase of 21°) forward and one small backward movement to the resting position with wings outspread. In contrast, a wing clap in *A. grandis* (Fig. 1C) lasts 3.2 to 4.3 sec and consists of stepwise movements, three small forward ones (increases of 29° , 40° and 90°) and two small backward ones to the resting position.

Calopterygidae. A wing clap in *C. maculata*, although brief (1 sec), is obvious because the angle formed by the anterior margins of the fore wings is very large (212° , Fig. 1D) and because the black wings are so conspicuous. A similar activity, although not designated as wing clapping, has been recorded for a perching ♂ and ♀ *C. maculata* (WALKER, 1953) and for a ♂ and ♀ of that species during oviposition (JOHNSON, 1962, "wing flaps"). In other species of *Calopteryx*, the activity appears to be essentially as in *C. maculata*. This was so for the episode we filmed of a perching ♂ of *C. aequabilis* in Indiana. In Europe, ROBERT (1958) records it for a perching ♂ of *C. virgo* (L.), HEYMER (1972, 1973) for guarding ♂♂ of four *Calopteryx* species and for a ♂ *C. splendens* (Harris) ("Flügelklappen") showing the oviposition site to a ♀.

DISCUSSION

JOHNSON (1962) states that the function of wing clapping is unknown, but LOGAN (1971) maintains that, whereas its function is unclear, it may be either some sort of declaration or a mechanical separation of the wings. Although wing clapping may be merely a comfort movement, we believe that, particularly in *A. grandis*, it is too stereotyped to serve this function. Instead, we hypothesize that wing clapping is a kind of territorial declaration whereby a clapping individual demonstrates to possible competitors, present or not, that he is present here on his perch. BICK & BICK (1971) state that there seems to be a direct relationship between territorial activity and wing clapping: species of Coenagrionidae and Lestidae without elaborate, ritualized, territorial activity do not have pronounced wing claps, whereas members of the genus *Calopteryx* show both complex territorial activity and pronounced wing claps.

We observed wing clapping only in ♂ coenagrionids and lestids. If clapping occurs in ♀♀ of these species, we have never seen it in spite of many years of observation. In contrast, *C. maculata* ♀♀ frequently wing clap in the same manner as the ♂♂ whether or not other odonates are nearby. Females clap most frequently during oviposition.

WALKER (1953) states that the wing clap in the ♀ *C. maculata* seemed to be a response to the ♂'s clap. In both Indiana and Oklahoma we frequently watched and photographed pairs at the oviposition site, the ♀ on vegetation at the surface, the perched ♂ guarding nearby. When one member of the pair clapped, the other seemed to respond with a clap, as though the sexes were communicating their presence to each other (Fig. 2). This figure shows that there is always a

time interval, sometimes very brief, between initiation of a clap by one sex and the response by the other. At times the ♀ clapped slightly before the ♂, at other times the reverse was true. For this reason, and because of uncertainty that in each case we had seen the beginning of a clapping sequence, it is unclear which sex, if either, routinely initiates the clapping.

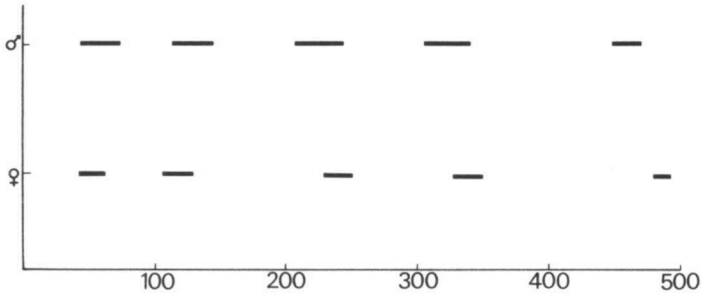


Fig. 2. A continuous cinematographic record of wing claps during an oviposition sequence in one *Calopteryx maculata* pair. The ♀ was ovipositing in *Nasturtium*, the ♂ was guarding at the creek's edge not more than 30 cm from her. Each horizontal line represents the duration of a single wing clap. The numbers to a 500 frame sequence taken at 32 frames per sec.

It seems that, in species having generalized behavior patterns, wing clapping serves a single generalized function, namely, a declaration of territory to all competitors in the vicinity. On the other hand, in species with specialized territorial and reproductive behavior, wing clapping could serve both as a declaration of territory to competitors and as a communication between members of a pair declaring their presence to each other.

HEYMER (1972, 1973) states that abdominal bobbing (Abdomenschwingen", "Balancement de l'abdomen") serves a grooming function in Lestidae, a group with simple, generalized behavior patterns, but in Calopterygidae, with vividly colored ventral ♂ abdomen tips, and with specialized and elaborate reproductive behavior, abdominal bobbing has become a ♂ signal to the ♀. Similarly, we hypothesize that the inconspicuous wing claps which we observed in ♂♂ of Lestidae and Coenagrionidae are generalized territorial declarations, but that the clappings in both sexes of *Calopteryx* serve as an additional, more specialized signal between the sexes, that of communicating the presence of one member of a pair to the other.

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