

FEMALE "REFUSAL DISPLAY" VERSUS MALE "THREAT DISPLAY" IN ZYGOPTERA: IS IT A CASE OF INTRASPECIFIC IMITATION?

C. UTZERI

Dipartimento di Biologia Animale e dell'Uomo, Università di Roma "La Sapienza",
Viale dell'Università 32, I-00185 Roma, Italy

Received March 20, 1987 / Revised and Accepted November 23, 1987

Zygoteran wing display is reviewed, and a distinction is made between threat display of the male and refusal display of the female. The former is suggested to have originated from preliminary movements of attack flight, while the latter from preliminary movements of escape flight. The resemblance of the displays in the 2 sexes is discussed in terms of imitation of the male by the female, through advergent evolution, according to a mimicry system in which the male acts as the model, the female as the mimic, and the approaching male as the signal receiver, which responds the same way to both model and mimic signals.

INTRODUCTION

"Imitation" is reciprocal resemblance of signals unconsciously emitted by different organisms (species, sexes, etc.), which is achieved through evolutionary convergence in situations where the same selective agent operates (cf. WICKLER, 1968). Most cases of imitation are known as "mimicry systems", in which (1) a "model", that is a signal-sender organism, (2) a "mimic", that is an organism that sends signals similar to the model and (3) a "signal receiver", that is an organism that responds to both model and mimic signals by the same reaction, are identified (WICKLER, 1965a). The three components of a mimicry system may belong to three distinct species, to two species or even to the same species, thus representing a great variety of cases either in their reciprocal relations or in function of mimicry systems (cf. PASTEUR, 1982).

Signals often consist in body shape and colour pattern, as for example in Batesian and Mullerian mimicries, yet behaviour often plays an important part in intraspecific imitation as well (e.g. Wickler, 1962, in EIBL-EIBESFELDT, 1967, for *Haplochromis* fishes; Wickler, 1965b, in EIBL-EIBESFELDT, 1967; 1969,

for several Old-World monkeys).

My aim in this paper is to analyze the male and female behaviour of many zygoteran species, usually referred to as the "threat display" (auctorum) and to attempt to identify in the female display a possible case of imitation of the male display.

THE SO-CALLED "THREAT DISPLAY" OF THE ZYGOTERA

It is well known in many zygoteran species that perched males and females, when closely approached by conspecific individuals as well as by similar-sized individuals of other species, open their wings ("Wing-Warning": BICK, 1966) (Fig. 1), and that this causes the approaching individual to retreat (Coenagrionidae: KRIEGER & KRIEGER-LOIBL, 1958; MOORE, 1960; BICK, 1966; BICK & BICK, 1963; 1971; 1972; PAJUNEN, 1963; AOYANAGI, 1973; CRUMPTON, 1975; ROWE, 1978; ARAI, 1979; HILTON, 1983; UTZERI et al., 1983; Calopterygidae: ROBERT, 1958; JOHNSON, 1961; 1962; PAJUNEN, 1966; HEYMER, 1972; KUMAR & PRASAD, 1977; WAAGE, 1973; 1984b; Platynemididae: BUCHHOLTZ, 1956; HEYMER, 1966; AGUESSE, 1968; Lestidae: CORBET, 1962; CRUMPTON, 1975). A more complicated display pattern is observed when additional movements are preformed, namely brief wing vibration (Coenagrionidae), variation of the posture angle of the body (Calopterygidae, Coenagrionidae, Lestidae), flexing of the abdomen tip downwards (Coenagrionidae) or upwards (Platynemididae, Calopterygidae, *Ischnura elegans*) and ventral abdomen curving/curling in the female (Coenagrionidae). The wing display is also performed in tandem, either pre- or post-copula and during copulation (e.g. UTZERI et al., 1983).

Flexing the abdomen tip in the male and in *Ischnura elegans* female and ventral curving/curling of the abdomen in the female are also performed in flight.

The threat display is very effective in eliciting retreat: BICK & BICK (1963) report 84% success in *Enallagma civile*, in which close approach is prevented, and 100% in keeping their perch, and BICK (1966) reports 100% success for 223 displays preformed by females of *Ischnura verticalis* towards conspecific and non-conspecific males and females. I myself recorded 99% success in males of *Coenagrion scitulum* (N = 87) displaying to both conspecific and heterospecific males.

DISCUSSION

Since approaching individuals react to the threat display by retreating and/or perching some distance from the displayer, it can be assumed that a signal is sent through the wing display, which prevents physical contact and/or safeguards individual space. However, these functions are particularly effective in regulating space relationships among males, whose number is usually much greater than

that of unpaired females at reproductive sites.

On account of sperm precedence (WAAGE, 1979a; 1982; 1984a; MILLER & MILLER, 1981; FINCKE, 1984) and female receptiveness to multiple mating (BICK & BICK, 1963; 1965; 1968; 1972; FINCKE, 1982; 1984; WAAGE, 1979b; 1984a; UTZERI et al., 1983; ROBERTSON, 1985; ALCOCK, 1979; 1982; 1983), males are expected to attempt to seize whichever females they meet, irrespective of whether or not these have been previously inseminated. In my observations of coenagrionid and lestid damselflies, mated females which happen to be recaptured in spite of their attempts to flee or to repel males by the wing display, usually copulate successfully, or at least raise their abdomens to male organs as many times as males stimulate them to do this. This makes me speculate that (1) females cooperate to form the wheel by means of a reflex response to stimulation of the male cerci (also UTZERI et al., 1983; 1987), and (2) females can be forced to copulation, contrary to WAAGE (1984a). Females can take advantage from multiple mating (e.g. KNOWLTON & GREENWELL, 1984), but as far as the *Zygoptera* are concerned, in which both copulation and oviposition are of long duration, remating in the same day may not be advantageous, since repeated copulation(s) would interfere with oviposition. But, besides theoretical considerations, the behaviour of a female gives a good indication as to her "interests". *Zygopteran* females usually mate more than once in their lives but rarely so on the same day. After being taken in tandem on a given day, they display their wings to approaching males, either while in tandem or in copula or during oviposition, irrespective of whether in tandem or alone. Since the wing display prevents close approach, it also prevents seizure and mating, and I conclude that even if the displaying female is physiologically receptive, there is no advantage for her to remate.

Following these considerations, it is worth separating the male "threat display" from the female "refusal display".

Movements of threat and refusal displays appear to be similar within the same taxon, even when additional movements are performed in conjunction with the wing display. Yet, they are slightly different among various taxa (Fig. 1). In my observations, both males and females of *Calopteryx* angle their bodies markedly upwards and flex the distal urites even more upward, while their wings are kept wide open (Fig. 1b); in *Platycnemis pennipes* both males and females open the wings slightly, and slightly bend the abdomen upward (Fig. 1c); in Coenagrionidae commonly only a slight wing display is reported for the male, while abdomen curving/curling is known only in the female. However, in *Coenagrion scitulum* both sexes bring the slightly opened wings forwards, making them describe a wide arch in the sagittal plane (Fig. 1f), and in *Ischnura elegans* both males and females perform a marked wing display, both raise the abdomen and flex the abdomen tip upwards or downwards (Fig. 1c-d). This suggests that either the wing display evolved independently in different taxa or, starting from a

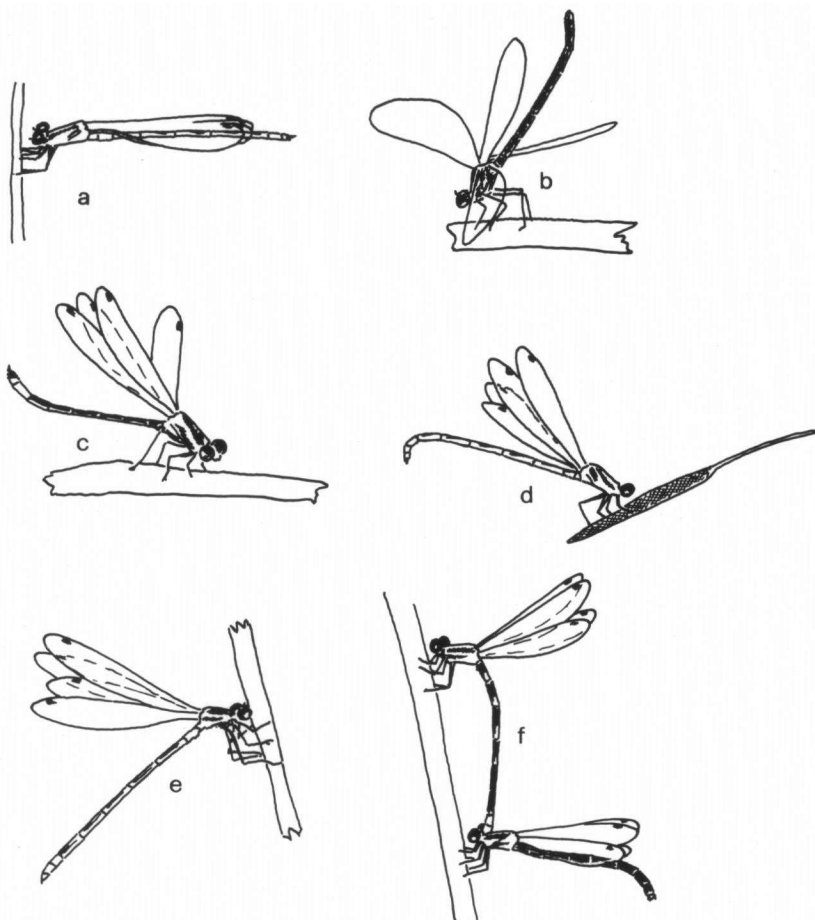


Fig. 1. Patterns of threat and refusal displays in damselflies: (a) perched damselfly (no display); — (b) *Calopterygidae*; — (c) *Ischnura elegans*, *Platynemesis pennipes*; — (d) *Coenagrion lindeni*, *I. elegans*; — (e) *C. puella*; — (f) *C. scitulum*. — [From slides].

common pattern, diverged slightly in different taxa. But since the display functions also in interspecific contexts (e.g. BICK, 1966; UTZERI et al., 1983) probably a selective pressure acts toward convergence or against strong divergence of the display patterns among different taxa.

Displaying the abdomen tip should be particularly effective as a signal in the male where conspicuous coloration does occur, for example, on the ventral surface of *Calopteryx*, on the dorsal surface of *Platynemesis* and of many coenagrionids. This is not so in the female, except in *Ischnura*.

ORIGIN AND EVOLUTION OF THE MALE THREAT DISPLAY

HEYMER (1972) suggested that calopterygid threat display developed from intentional aggressive movements, through a ritualization process. I think this may be valid for all Zygotera. In *Coenagrion lindenii*, the body axis is sometimes raised up to the horizontal while displaying the wings, that is, the flight position is assumed (UTZERI et al., 1983). In *C. puella*, which perches at about 45 degrees downwards, the body is not raised during wing display. But, in crowded conditions of males, I have often observed many males frequently shifting to and from closely situated perches, continually approaching and being approached by other individuals as a consequence of this shifting. In these situations males seemed to be very alarmed, and as soon as they contacted a new perch they rested briefly, keeping the body horizontal and the wings slightly opened (as in the wing display), then they closed the wings and brought the bodies to the normal resting position. Also in this case, the threat position appeared to be intermediate between the flight and resting positions, or rather the position that an individual first takes when taking off (or when first alighting). In less crowded situations, this is never seen, but the alighting damselfly immediately takes up its resting position.

The threat position might have developed through the following evolutionary steps (Fig. 2): (1) At the outset, the male would have directly attacked and driven

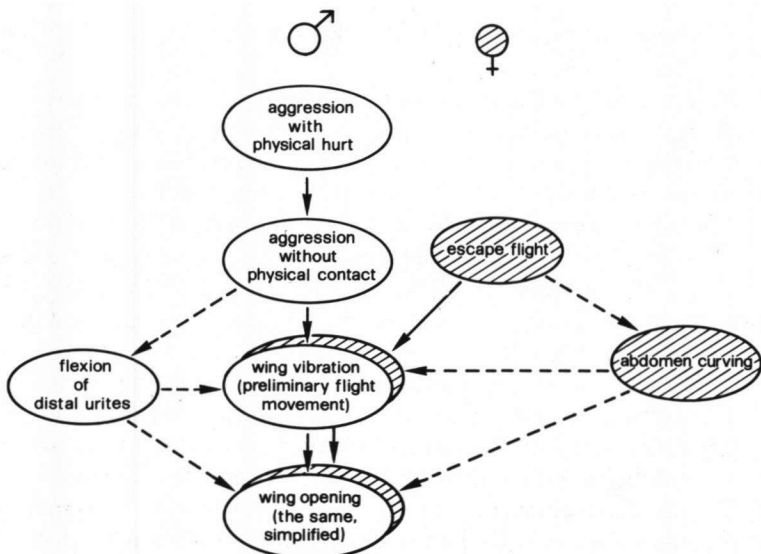


Fig. 2. Advergent evolution of threat (clear) and refusal (hatched) displays. For further explanations see the text.

away approaching individuals. If these attacks ended in physical contact with harmful consequences for the opponents, a strong selective pressure would have worked toward some sort of ritualization, which had the advantage of saving the contenders from injury; in *C. lindeni* and other damselflies, attacks are seldom seen to end in physical contact. — (2) The approaching male developed a fairly rapid retreating response to the incipient take-off of the perching male. By reason of this, actual take-off was lost and wing-fluttering became a signal meaning "warning, I am attacking you", this reducing the risk and time wastage for both individuals. Wing fluttering, reported by UTZERI et al. (1983) for *C. lindeni* and by LOIBL (1958) for *Lestes*, is very likely the only possible kind of wing display the latter could perform, since they perch with open wings. — (3) In those species which perch with folded wings, wing fluttering evolved into the simpler, single opening of the wings. It is worth noting that wing fluttering, which in the above interpretation of the evolutionary process is considered as preceding single wing opening, can in turn be seen as a magnification of the signal in those species where both wing fluttering and wing opening are reported (e.g. *C. lindeni*: UTZERI et al., 1983); in this case, wing fluttering should have developed after wing opening. As abdominal spots, where present, are not always displayed (e.g. *C. lindeni*: UTZERI et al., 1983), the abdominal displays possibly evolved independently from the wing display. However, their functions are possibly to magnify the wing display signal.

ORIGIN AND EVOLUTION OF THE FEMALE REFUSAL DISPLAY

The wing display of the female could be considered as having the same origin as that of the male if it could be shown that females behaved aggressively toward the males originally. However, females are not usually reported in the literature to be aggressive towards conspecific individuals, as is confirmed by my own observations. Ischnuran females seem to be aggressive sometimes (ROBERTSON, 1985), but since these damselflies are known to eat their males occasionally (MÜLLER, 1972; MARTENS, 1978; UTZERI, 1980; ROBERTSON, 1985), caution is needed in order to state whether their attacks are aggressive (sensu LORENZ, 1963) or predatory.

When the female takes flight to escape tandem capture, she performs her first movements in the very same way as the male does when he takes flight to attack an intruder, that is, she flutters her wings and brings her body up to the horizontal position (i.e. the flight position). Assuming that: (1) females unwilling to mate used to flee, (2) the retreating response of the male had developed in the context of male-male interactions and (3) sexual recognition had not yet developed, then the male approaching the female very likely responded to preliminary movements of the female flight in the same way (i.e. by retreating) as to those of the male. As a consequence of this reaction of the male, the female's movements could develop

into the wing display through a ritualization process analogous to that suggested above for the male (Fig. 2). It is a general assumption that sexual dimorphism evolved together with an attraction response of the male to the female pattern. However, even in the sexually dimorphic Zygoptera, the retreating response to the female wing display is apparently stronger than the attraction response.

THE MIMICRY HYPOTHESIS

It is worth emphasizing that while from the intentional standpoint the male wing movements mean "I am attacking you", for the female they mean "I am fleeing from you". However, due to their strict similarity, both signals may be understood as "I am attacking you" by the signal receiver (i.e. the approaching male). If the male understood the female movements in their intentional meaning ("I am fleeing from you"), he would most likely dash to the female instead of retreating from her! In fact, although unwilling to mate, she can be physiologically receptive to copulation (cf. above).

This is a mimicry system in which the threatening male (model) is mimicked by the fleeing female (mimic), the latter duping the approaching male (signal receiver). By this mimicking the displaying female is protected from disturbance.

My reasoning suggests that the similarity of the male and female displays resulted from evolution of the female display pattern toward the male one, which is named "advergent evolution" by BROUWER & BROUWER (1972). This is distinct from similarity obtained through either "convergent evolution" (evolution toward a communal pattern) or "parallel evolution" (similarity preserved through evolution). Advergent evolution characterizes Batesian mimicry (BROUWER & BROUWER, 1972), in which it is the mimic's "interest" to resemble the model, but not the reverse. The same seems to be valid for the threat/refusal displays of the Zygoptera.

Since the female display functions also in interspecific contexts, this type of mimicry can be classified as a "bipolar open mimicry system" (Vane-Wright, 1966, in PASTEUR, 1982), where bipolar means that two species are involved and open means that the dupe can belong to various species. It is also similar to the "conjunct automimicry" (all members belong to the same species; Vane-Wright, 1966, in PASTEUR, 1982), firstly described by WICKLER (1965b) in the hamadryas baboons, where the high-ranked male is "deceived" (as a signal receiver) by the low-ranked male mimicking both shape and colour of the female back as well as her behaviour ("Wicklerian mimicry" sensu PASTEUR, 1982). In Zygoptera, behavioural imitation is chiefly involved, but in some species (e.g. of genus *Ischnura*) several females (homochromic or andromorph) show a colour pattern similar to the male. ROBERTSON (1985) suggests that automimicry can be identified in the latter, even though the threat/refusal displays are

not involved in his reasoning. Field research could indicate whether or not the refusal display has an even stronger effect when performed by a homochromic female.

REFERENCES

- AGUESSE, P., 1968. *Les Odonates de l'Europe Occidentale, du Nord de l'Afrique et des Iles Atlantiques*. Masson & Cie, Paris.
- ALCOCK, J., 1979. Multiple mating in *Calopteryx maculata* (Odonata: Calopterygidae) and the advantage of non-contact guarding by males. *J. nat. Hist.* 13: 439-446.
- ALCOCK, J., 1982. Post-copulatory mate guarding by males of the damselfly *Hetaerina vulnerata* Selys (Odonata: Calopterygidae). *Anim. Behav.* 30: 99-107.
- ALCOCK, J., 1983. Mate guarding and the acquisition of new mates in *Calopteryx maculata* (P. De Beauvois) (Zygoptera: Calopterygidae). *Odonatologica* 12: 153-159.
- AOYANAGI, M., 1973. Observations of actions and postures of the adult damselfly *Ceriagrion melanurum* Selys (Odonata: Agrionidae). Studies on adult behaviour of the damselfly *Ceriagrion melanurum* Selys, I. *Kontyû* 41: 241-253. (Jap.)
- ARAI, Y., 1979. (Copulation and refusing behaviour of mature *Ischnura asiatica* females). *Nature & Insects* 14: 38-40. (Jap.)
- BICK, G.H., 1966. Threat display in unaccompanied females of the damselfly, *Ischnura verticalis*. *Proc. ent. Soc. Wash.* 68: 271.
- BICK, G.H. & J.C. BICK, 1963. Behaviour and population structure of the damselfly *Enallagma civile* (Hagen). *S.-West. Nat.* 8: 57-84.
- BICK, G.H. & J.C. BICK, 1965. Demography and behaviour of the damselfly, *Argia apicalis* (Say) (Odonata: Coenagriidae). *Ecology* 46: 461-472.
- BICK, G.H. & J.C. BICK, 1968. Demography of the damselfly, *Argia plana* Calvert (Odonata: Coenagriidae). *Proc. ent. Soc. Wash.* 70: 197-203.
- BICK, G.H. & J.C. BICK, 1971. Localization, behavior and spacing of unpaired males of the damselfly, *Argia plana* Calvert (Odonata: Coenagrionidae). *Proc. ent. Soc. Wash.* 73: 146-152.
- BICK, G.H. & J.C. BICK, 1972. Substrate utilization during reproduction by *Argia plana* Calvert and *A. moesta* (Hagen) (Odonata: Coenagrionidae). *Odonatologica* 1: 3-9.
- BROUWER, L.P. & J.V.Z. BROUWER, 1972. Parallelism, convergence, divergence, and the new concept of advergence in the evolution of mimicry. In: E.S. Deevey, [Ed.]. *Growth by intussusception*, Vol. 44, pp. 59-67.
- BUCHHOLTZ, C., 1956. Eine Analyse des Paarungsverhaltens und der dabei wirkenden Auslöser bei den Libellen *Platynemis pennipes* Pall. und *P. dealbata* Klug. *Z. Tierpsychol.* 13: 13-25.
- CORBET, P.S., 1962. *A biology of dragonflies*. Witherby, London.
- CRUMPTON, W.J., 1975. Adult behaviour of *Xanthocnemis zealandica* McLachlan and *Austrolestes colsonis* White at selected South Island (New Zealand) habitats (Zygoptera: Coenagrionidae, Lestidae). *Odonatologica* 4: 149-168.
- EIBL-EIBESFELDT, I., 1967. *Grundriss der vergleichenden Verhaltensforschung*. Ethologie. Piper & Co., München.
- FINCKE, O.M., 1982. Lifetime mating success in a natural population of the damselfly, *Enallagma hageni* (Walsh) (Odonata: Coenagrionidae). *Behav. Ecol. Sociobiol.* 10: 293-302.
- FINCKE, O.M., 1984. Sperm competition in the damselfly, *Enallagma hageni* Walsh (Odonata: Coenagrionidae): benefits of multiple mating to males and females. *Behav. Ecol. Sociobiol.* 14: 235-240.
- HEYMER, A., 1966. Etudes comparées du comportement inné de *Platynemis acutipennis* Selys

- 1841 et de *P. latipes* Rambur 1842 (Odonata: Zygotera). *Annls Soc. ent. Fr.* (N.S.) 2: 39-73.
- HEYMER, A., 1972. Comportement social et territorial des Calopterygidae (Odonata, Zygotera). *Annls Soc. ent. Fr.* (N.S.) 8: 3-53.
- HILTON, D.F.J., 1983. Mating isolation in two species of *Nehalennia* (Zygotera: Coenagrionidae). *Odonatologica* 12: 375-379.
- JOHNSON, C., 1961. Breeding behavior and oviposition in *Hetaerina americana* (Fabricius) and *H. titia* (Drury) (Odonata: Agriidae). *Can. Ent.* 93: 260-266.
- JOHNSON, C., 1962. Breeding behavior and oviposition in *Calopteryx maculatum* (Beauvais) (Odonata: Calopterygidae). *Am. Midl. Nat.* 68: 242-247.
- KNOWLTON, N. & S.R. GREENWELL, 1984. Male sperm competition avoidance mechanisms: the influence of female interests. In: R.L. Smith, [Ed.], *Sperm competition and the evolution of animal mating systems*, pp. 62-84. Academic Press, New York.
- KRIEGER, F. & E. KRIEGER-LOIBL, 1958. Beiträge zum Verhalten von *Ischnura elegans* und *I. pumilio* (Odonata). *Z. Tierpsychol.* 15: 82-93.
- KUMAR, A. & M. PRASAD, 1977. Reproductive behaviour in *Neurobasis chinensis chinensis* (Linnaeus) (Zygotera: Calopterygidae). *Odonatologica* 6: 163-171.
- LOIBL, E., 1958. Zur Ethologie und Biologie der deutschen Lestiden (Odonata). *Z. Tierpsychol.* 15: 54-81.
- LORENZ, K.Z., 1963. *Das sogenannte Böse. Zur Naturgeschichte der Aggression*. Borotha-Schoeler, Wien.
- MARTENS, K., 1978. Libellen in de Camargue. *Phegea* 6: 1-8.
- MILLER, P.L. & C.A. MILLER, 1981. Field observations on copulatory behaviour in Zygotera, with an examination of the structure and activity of male genitalia. *Odonatologica* 10: 201-218.
- MOORE, N.W., 1960. The behaviour of the adult dragonfly. In: P.S. Corbet, C. Longfield & N.W. Moore. *Dragonflies*, pp. 106-126. Collins, London.
- MÜLLER, K., 1972. Kannibalismus bei *Ischnura elegans* (Vander Linden) während der Paarung (Zygotera: Coenagrionidae). *Odonatologica* 1: 51-52.
- PAJUNEN, V.I., 1963. On the threat display of resting dragonflies (Odonata). *Ann. ent. fenn.* 29: 236-239.
- PAJUNEN, V.I., 1966. Aggressive behaviour and territoriality in a population of *Calopteryx virgo* (L.) (Odonata: Calopterygidae). *Ann. zool. fenn.* 3: 201-214.
- PASTEUR, G., 1982. A classificatory review of mimicry systems. *A. Rev. Ecol. Syst.* 13: 169-199.
- ROBERT, P.A., 1958. *Les libellules* (Odonates). Delachaux & Niestlé, Neuchâtel.
- ROBERTSON, H.M., 1985. Female dimorphism and mating behaviour in a damselfly, *Ischnura ramburi*: females mimicking males. *Anim. Behav.* 33: 805-809.
- ROWE, R.J., 1978. *Ischnura aurora* (Brauner), a dragonfly with unusual mating behaviour (Zygotera: Coenagrionidae). *Odonatologica* 7: 375-383.
- UTZERI, C., 1980. Considerations on cannibalism in Zygotera. *Notul. odonatol.* 1: 100-102.
- UTZERI, C., E. FALCHETTI & G. CARCHINI, 1983. The reproductive behaviour in *Coenagrion lindenii* (Selys) in central Italy (Zygotera: Coenagrionidae). *Odonatologica* 12: 259-278.
- UTZERI, C., E. FALCHETTI & R. RAFFI, 1987. Adult behaviour of *Lestes barbarus* (Fabricius) and *L. virens* (Charpentier) Zygotera: Lestidae. *Fragm. entomol.* 20(1): 1-22.
- VANE-WRIGHT, R.I., 1976. A unified classification of mimetic resemblances. *Biol. J. Linn. Soc.* 8: 25-56.
- WAAGE, J.K., 1973. Reproductive behaviour and its relation to territoriality in *Calopteryx maculata* (Beauvois). *Behaviour* 47: 240-256.
- WAAGE, J.K., 1979a. Dual function of damselfly penis: sperm removal and transfer. *Science* 203: 916-918.

- WAAGE, J.K., 1979b. Adaptive significance of postcopulatory guarding of mates and nonmates by male *Calopteryx maculata* (Odonata). *Behav. Ecol. Sociobiol.* 6: 147-154.
- WAAGE, J.K., 1982. Sperm displacement by male *Lestes vigilax* Hagen (Zygoptera: Lestidae). *Odonatologica* 11: 201-209.
- WAAGE, J.K., 1984a. Sperm competition and the evolution of odonate mating systems. In: R.L. Smith, [Ed.], *Sperm competition and the evolution of animal mating systems*, pp. 251-290. Academic Press, New York.
- WAAGE, J.K., 1984b. Female and male interactions during courtship in *Calopteryx maculata* and *C. dimidiata* (Odonata: Calopterygidae): influence of oviposition behavior. *Anim. Behav.* 32: 400-404.
- WICKLER, W., 1962. Ei-Attrappen und Maulbrüten bei afrikanischen Cichliden. *Z. Tierpsychol.* 18: 129-164.
- WICKLER, W., 1965a. Mimicry and the evolution of animal communication. *Nature, Lond.* 208: 519-521.
- WICKLER, W., 1965b. Die äusseren Genitalien als soziale Signale bei einigen Primaten. *Naturwissenschaften* 52: 269-270.
- WICKLER, W., 1968. *Mimikry*. Kindler Verlag München.
- WICKLER, W., 1969. Socio-sexual signals and their intra-specific imitation among Primates. In: D. Morris [Ed.], *Primate ethology*, pp. 89-189. Anchor Books, Doubleday, New York.