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PRECOPULATORY GENITAL CONTACT IN SOME ZYGOPTERA

H.M. ROBERTSON[1] and K.J. TENNESSEN[2]

[1]Department of Zoology, University of Wisconsin, Madison, WI 53706, United States
[2]1949 Hickory Avenue, Florence, AL 35630, United States

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The sequence of mating behavior usually described in the literature (tandem, sperm translocation, copulation) is accurate for species of the zygopteran genera *Lestes, Nehalennia, Calopteryx, Platycypha,* and *Chlorocypha.* Species of the genera *Enallagma, Argia, Amphiagrion, Ischnura, Anomalagrion,* and *Hetaerina* exhibit an additional step between tandem and sperm translocation, here called "genital touching". After tandem formation, the male invites copulation and the female briefly touches her genitalia to his accessory genitalia, whereupon he translocates sperm. Genital touching may allow males to determine female receptivity prior to filling of the sperm vesicle. Data on duration of sperm translocation are also presented.

INTRODUCTION

While working on mate recognition and reproductive isolation with *Enallagma pollutum* and *E. signatum* (TENNESSEN, 1975) and *E. glaucum* (ROBERTSON & PATERSON, 1982), we noticed an aspect of their mating behavior that previously has not been well described. It seems to be referred to by KRIEGER & KRIEGER-LOIBL (1958) for *Ischnura elegans* and by FURTADO (1972) for *Pseudagrion perfuscatum.* Here we describe this behavior afresh, survey its occurrence in most temperate North American genera of Zygoptera, and speculate briefly on its functional significance.

MATERIAL AND METHODS

Enallagma pollutum (Hagen) and *E. signatum* (Hagen) were observed on Hatchet Creek near Gainesville, Florida in 1973-1975. *E. glaucum* Burmeister was observed on the campus of the University of the Witwatersrand, Johannesburg, South Africa in 1979. During 1983 H.M.R.

observed *E. boreale* Selys, *E. civile* (Hagen), *E. ebrium* (Hagen), *E. carunculatum* Morse, *E. aspersum* (Hagen), *E. signatum*, *Ischnura verticalis* (Say), *Lestes eurinus* Say, *L. congener* Hagen, and *Nehalennia irene* (Hagen) at a pond in the University of Wisconsin Arboretum, Madison, Wisconsin; *Argia moesta* (Hagen) at Devil's Lake, Wisconsin; *Hetaerina americana* (Fabricius) in Belleville, Wisconsin; *Calopteryx maculata* (P. de Beauvois) on Otter Creek, Baraboo Hills, Wisconsin; *I. ramburii* (Selys) and *Anomalagrion hastatum* (Say) at Archbold Biological Station, Lake Placid, Florida; *Amphiagrion abbreviatum* (Selys) at Old Faithful, Yellowstone National Park, Wyoming; and *E. anna* Williamson and *L. disjunctus* Selys near Calgary, Alberta, Canada.

In addition to observation of undisturbed pairs, 18 *E. ebrium* pairings and all five *N. irene* pairings were provoked by capturing copulating pairs and carefully releasing the females near single males. If clasped by males, although often initially recalcitrant, these females eventually copulated. Various techniques were also used to present dead females to males so that they could clasp the females and fly away with them in tandem.

RESULTS

The mating sequence in Zygoptera is usually described as follows (e.g. BICK, 1972; CORBET, 1980). A male grasps a perched or flying female with his legs (Fig. 1a) and then clasps her thorax with his anal appendages (Fig. 1b), yielding the tandem position (Fig. 1c). With the male perched and the female hanging free, the male juxtaposes his gonopore (on his 9th abdominal segment) and his accessory genitalia (on his 2nd and 3rd abdominal segments), and translocates sperm from the sperm sac at the former to the sperm vesicle at the latter (Fig. 1f). Thereafter

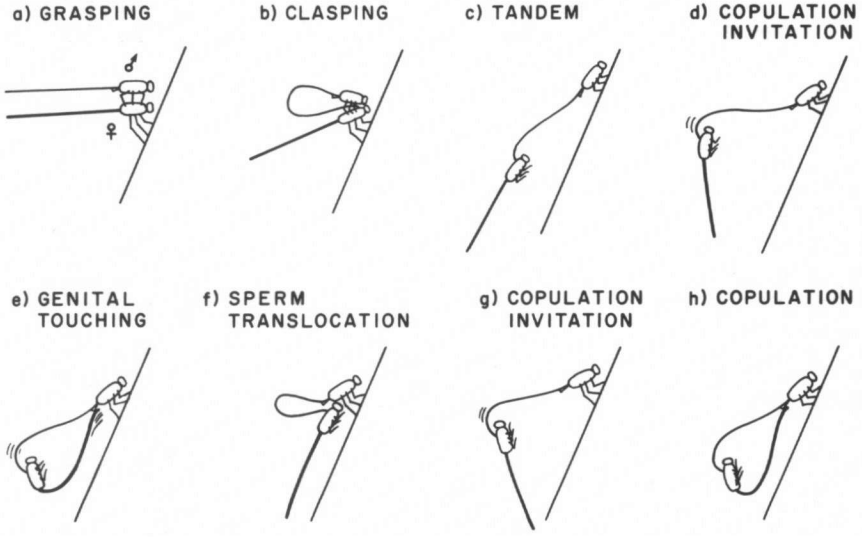

Fig. 1. Sequence of mating behavior in some Zygoptera.

he "invites copulation" by curling his abdomen upward proximally and downward distally, while spreading his wings (Fig. 1g). A receptive female responds by swinging her abdomen forward and upward to achieve genital contact, yielding the copulatory position (Fig. 1h). This account is accurate and complete for the species we observed in the genera *Calopteryx*, *Lestes*, and *Nehalennia* (Tab. I).

We originally noticed, however, that in species of the genus *Enallagma*, after the tandem pair had perched (Fig. 1c) but before sperm translocation, the male repeatedly invited copulation (Fig. 1d). A receptive female would respond to each invitation by swinging her abdomen toward the male's accessory genitalia. Usually a number of attempts were required before their genitalia briefly touched (Fig. 1e). Only then did the male translocate sperm (Fig. 1f). Thereafter the male again invited copulation (Fig. 1g) and the pair usually attained the copulatory position after a few attempts (Fig. 1 h). This additional behavioral step, which we call "genital touching", has now been noted by us in every full mating sequence observed for ten species of *Enallagma* (Tab. I). It has also been recorded independently for *E. hageni* by Ola Fincke (personal communication).

We have also observed genital touching for species of the genera *Amphiagrion*, *Anomalagrion*, *Argia*, *Hetaerina*, and *Ischnura* (Tab. I), with some differences in

Table I

Presence or absence of genital touching and duration of sperm translocation in various Zygoptera

Species	Genital touching	No. of matings observed	Duration (sec) of sperm translocation (mean ± S.D.)
Lestes eurinus	Absent	6	17 ± 4
L. congener	„	1	10
L. disjunctus	„	6	37 ± 14
Nehalennia irene	„	5	76 ± 44
Calopteryx maculata	„	45	—
Enallagma signatum	Present	10	—
E. pollutum	„	18	—
E. glaucum	„	14	—
E. ebrium	„	31	11 ± 2
E. boreale	„	3	11 ± 4
E. civile	„	1	34
E. aspersum	„	2	13; 15
E. carunculatum	„	3	11 ± 4
E. anna	„	1	15
E. signatum	„	2	8; 11
Argia moesta	„	5	13 ± 4
Amphiagrion abbreviatum	„	2	6; 7
Anomalagrion hastatum	„	1	~ 1
Ischnura ramburii	„	11	~ 1
Hetaerina americana	„	4	6 ± 2

execution. *Amphiagrion abbreviatum* was similar to the *Enallagma* species. *Argia moesta* females responded to each copulation invitation by edging their abdomens progressively closer to the males' accessory genitalia rather than swinging them repeatedly. *Hetaerina americana* females usually touched genitalia in response to the first invitation, and in *Ischnura ramburii* and *Anomalagrion hastatum* the entire process including sperm translocation was extremely swift, lasting only 3-5 sec. Duration of sperm translocation for most species is also presented in Table I (cf. also BICK & BICK, 1965). Although the Anisoptera have not been examined specifically, genital touching was not observed by H.M.R. in three libellulids: *Pachydiplax longipennis* (no. of matings observed = 27), *Erythrodiplax minuscula* (N = 12), and *Perithemis tenera* (N = 7).

Three lines of evidence indicate that genital touching is the releaser for sperm translocation in some species. First, males that were not immediately successful in translocating sperm after genital touching (because of mechanical problems, or another individual interfered, or wind blew the pair around), would reinvite copulation until the female again touched genitalia before reattempting sperm translocation. Second, *Enallagma* males that had clasped non-conspecific females (N = 13) or unreceptive conspecific females (N = 22), which would not respond to their copulation invitations, were not observed to translocate sperm before eventually releasing the females. Third, *Enallagma* males that clasped dead females seldom translocated sperm (3 of 12 *E. boreale* and 1 of 24 *E. pollutum*) before dropping the female, and then only because the male eventually curled his abdomen so far that the female's legs touched his accessory genitalia. Similarly, five of seven *Ischnura verticalis* males that clasped dead females quickly dropped them after briefly and vigorously inviting copulation. The other two very swiftly translocated sperm and then dropped the female.

DISCUSSION

A possible function of genital touching is to allow males to determine female receptivity before they fill their accessory genitalia with sperm. If a male translocated sperm immediately after clasping an unreceptive female, it is possible that the sperm would die and coagulate in the sperm vesicle. This might prevent subsequent translocation of sperm and so preclude the male from ever mating successfully again. Because of their courtship behavior, *Calopteryx maculata* males never clasp unreceptive females and so have no need for genital touching. Similarly, three chlorocyphids (*Platycypha caligata, P. fitzsimonsi* and *Chlorocypha consueta*) have courtship behavior, do not clasp unreceptive females, and do not exhibit genital touching (ROBERTSON, 1982). Why *Lestes* and *Nehalennia* males should not require genital touching is not clear in this scenario, and they are being examined further. Clearly, many more species from

other genera and families should be examined by carefully observing full mating sequences.

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