REPRODUCTIVE BEHAVIOR OF *PALAEMNEMA DESIDERATA* **SELYS (ODONATA : PLATYSTICTIDAE)**

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Reproductive behavior of *Palaemnema desiderata* Selys was studied in Southeastern Veracruz, México. Sperm translocation, copula, oviposition and certain aspects of aggressive behavior and territoriality are described and a list of the plants used for oviposition is presented.

INTRODUCTION

The genus *Palaemnema* Selys is of interest because it is the only genus of Platystictidae represented in America.

CALVERT (1931) defined the geographic range of the genus and mentioned that in México it is represented by: *P. desiderata* Selys, *P. domina* Calvert, *P. paulicaxa* Calvert, *P. paulicoba* Calvert, *P. paulitaba* Calvert and *P. paulitoyaca* Calvert. Donnelly (pers. comm., 1980) also mentioned the occurrence in México of *P. nathalia* Selys and *P. paulina* (Drury) as well as some other species of *Palaemnema* not yet described.

P. desiderata and *P. paulitoyaca* coexist sympatrically at the stream where the observations were made. Both species are very similar morphologically and sometimes are found at the same reproductive colonies, making their separation during field observations very difficult.

In this paper the sequence of events involved in the reproductive behavior of *Palaemnema desiderata*, whose females oviposit in nonaquatic woody plants, is analysed.

METHODS

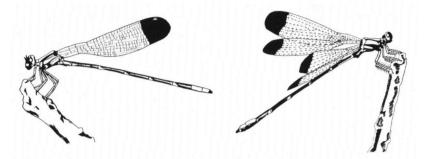
The study was conducted at a stream near Jicacal Beach, 30 km NE of Catemaco in the region of "Los Tuxtlas" in southeastern Veracruz, México $(18^{\circ}34' - 18^{\circ}36' \text{ N}$. Lat. and $95^{\circ}04' - 95^{\circ}09' \text{ W}$. Long.). The rock-bottomed stream runs through part of a rain forest with many species of trees and shrubs bordering it. Other zygopterans found here were: *Heteragrion albifrons* Ris, *H. alienum* Williamson, *Cora marina* Selys, *Argia cuprea* Selys, *A. oenea* Hagen, *Hetaerina macropus* Selys and the very closely related *Palaemnema paulitoyaca* Calvert.

The individuals of *P. desiderata* congregate at small trees bordering the stream. The observations were made at a reproductive colony located on a small *Siparuna nicaraguensis* (Monimiaceae) tree from 2-9 August and from 13-17 September, 1980. Cinematographic records and diapositives of reproductive activity were made and plants where females oviposited were collected for identification. Daily observations were made from 0550 hours to 0930 (corresponding hours for Civil Twilight and Sunrise: 2-9 August: Civil Twilight: 0535-0537, Sunrise: 0558-0600: 13-17 September: Civil Twilight: 0546-0547, Sunrise: 0608-0609; U.S. NAVAL OBSERVATORY, NAUTICAL ALMANAC OFFICE 1946). To make the identification of individual males easier, and to minimize the confusion with the very similar *P. paulitoyaca* 75 males were marked during the August period. During the September period the marking of individuals was unnecessary because of the low reproductive activity.

RESULTS

The first copulations and ovipositions were seen between 0550-0600, with intense reproductive activity until 0930. After 0930 activity declines markedly. However in preliminary observations done in July, 1979 the activity of *P. desiderata* started before 0500, although this was observed at another reproductive colony. This early morning activity is very unusual among Odonata, but MIZUTA (1974) records a similar situation for the coenagrionid *Mortonagrion selenion* Ris in Japan.

Individuals congregated in reproductive colonies at small trees bordering the stream where females oviposited. Males wing-clapped intermittently, separating their wings for very brief periods (N=22, x=1.7 sec, 0.6-2.6 sec), even when no conspecifics were nearby (see Figs 1a and 1b). We believe that this serves both as a territorial decla-



ration and to attract approaching females.

Fig. 1. Palaemnema desiderata d: (a) perching, "normal" position ;- (b) displaying ("wing clapping" of BICK & BICK, 1970).

TERRITORIALITY

Males become established in trees used by the females to oviposit and agressively defend their positions against other conspecific males. They regularly return to a fixed area defending vertical territories in a manner similar to that reported by DREYER(1978) for *Lestes viridis* V.d.Lind.

The interactions between the males begin when a male invades another's territory or tries to mate with a protected ovipositing female. During the interactions the males face each other, fly in a stationary position and bend their 3 posterior segments slightly upward and forward displaying the blue on the dorsum of segments VIII and IX. One male may fly upward in a movement resembling a small "jump" as he seemingly tries to gain a higher position than his adversary. The interactions end when one of the males leaves.

SPERM TRANSLOCATION

BICK & BICK (1965) record that this event always occurs in tandem throughout the Suborder. In *P. desiderata* the translocation was always in tandem after the male had grasped the female with his abdominal appendages. We observed a very characteristic movement before sperm translocation: once the male had taken the female in tandem, he swung her forward several times with the female's head approaching his external genitalia. Generally, after the third balancing movement, the sperm translocation occurs. In this species, the event averaged only 1.3 sec (N=58, 0.7-2.3 sec) whereas BICK & BICK (1965) report 7-32 sec for five different species. Each translocation was followed by copula in a 1:1 ratio, indicating that it precedes each copulation.

COPULA

Copulation occurs without any preliminary courtship and takes place under two situations: (1) when a female arrives at the reproductive site for the first time that day, (2) when the female is interrupted during oviposition and is taken again by the same or a different male. During copula the male separates his wings and the female remains with her legs folded against her thorax (Fig. 2a). Later, in copula, the male pushes the female's head forward until it contacts her abdomen, whereupon the pair separates (Fig. 2b).

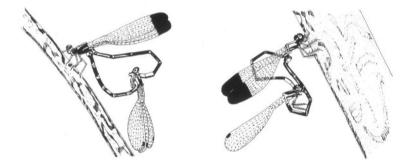


Fig. 2. Palaemnema desiderata: (a) copula; - (b) end of copula, male pushes female's head until it touches her abdomen.

Copula averaged only 59.6 sec (N=57, 33-121). CORBET (1963) records 1.5 min for *Calopteryx splendens* Harris and 2-5 min for *C. virgo* L. and WAAGE (1973), a mean of 101 sec for *C. maculata* Beauvois. We know of no record for any member of Coenagrionidea which closely approaches the very brief time in copula for *P. desiderata*.

OVIPOSITION

A female oviposits immediately after copula and usually at the same site. The male remains a few cm from the female and guards her from other conspecific males that approach. This active protection contrasts with many other zygopterans where the male maintains the control of the female by remaining in the classical tandem position.

If a female is ovipositing and it starts raining, she does not inter-

rupt this activity. That is, if the female was originally ovipositing on the upperside of a horizontal branch, she changes her position and oviposits on the underside in such a way that the branch prevents the raindrops from hitting her. If a male is protecting the ovipositing female, he changes to a vertical position with his head facing directly upwards so that the least surface possible of the body is exposed to the raindrops.

Females lay their eggs on twigs, branches and leaf petioles of various non-aquatic woody plants hanging over the water. If a tree has only a few of its branches hanging over the water, the individuals tend to congregate on them. Four species used by these aggregations for oviposition are: Siparuna nicaraguensis (Monimiaceae), Licaria peckii (Lauraceae), Amphitecna tuxtlensis (Bignoniaceae) and Cymbopetalum bailloni (Annonaceae); however we do not discard the possibility that P. desiderata uses a greater variety of species of plants to oviposit. Before inserting eggs, the female briefly probes the site with her ovipositor. During oviposition, she bends her abdomen so as to form two 90° angles (one between segments III and IV, the other between IV and V) and holds her wings slightly separated (Fig. 3) resembling

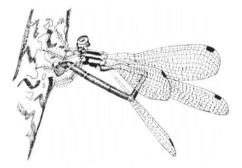


Fig. 3. Palaemnema desiderata, oviposition.

LIEFTINCK's (1939) figure for Orolestes wallacei Kirby. The average time of a single period of oviposition is 50.9 min (N=54, 4-147 min).

SPECIAL BEHAVIOR

Wingwarning. – Males often separated their wings and elevated their abdomens when conspecific males approached, causing the intruder to leave. PAJUNEN (1966) states that this behavior in Calopteryx virgo announces occupancy to another individual trying to occupy the site.

Female unreceptivity. – Some females show signs of unreceptivity when they are ovipositing and a male tries to take them in tandem. This is done only by females that have mated more than twice during one day. The females open their wings and lift their abdomens, similar to the wing-warning movement described for the males, or they loosen their abdomen and bring their bodies unusually close to the branch where they were ovipositing. If the male leaves, the female resumes oviposition.

On some occasions the male, trying for a tandem position, alights on the female, in which case the female holds on with her legs to the branch, until the male ceases his attempt. In other cases, after the females have finished ovipositing, they fly to the roosting sites and are sometimes intercepted by males which take them in tandem. By quickly falling to the ground such a female can cause a quick break in the tandem grip, whereupon both sexes fly away.

Grooming.— Some perched males cleaned their heads and abdomens using pro- and metathoracic legs respectively. Some individuals bobbed their abdomens up and down between their wings. This activity is more commonly observed after it has rained, and seems to remove excess water from the wings. HEYMER (1973) considers that abdominal bobbing functions as grooming in Lestidae but attracts females in Calopterygidae.

Thanatosis.— On some occasions when Palaemnema males were captured for marking, they remained immobile and rigid. If we placed them on the palm of our hands, they remained there for a few seconds after which they flew away. This "acting dead" is similar to that reported for other insects such as: beetles, bugs, grasshoppers, stick insects and mantids (EDMUNDS, 1974).

Predation.— Because individuals of P. desiderata remain perched for most of the day on branches where the reproductive colony has gathered, they are easy prey for reduviid bugs, web-spinning spiders, wolf spiders and jumping spiders. Wings and other body parts of P. desiderata were found daily trapped in spider webs or under leaves. We also observed actual predation but did not take quantitative data.

DISCUSSION AND CONCLUSION

Most information on sexual behavior of Zygoptera has been for temperate zone species, there being few data on tropical (especially neotropical) ones. The calopterygid genera, *Calopteryx* (BUCH-HOLTZ, 1951; JOHNSON, 1962b; WAAGE, 1973; ZAHNER, 1960) and *Hetaerina* (JOHNSON, 1961, 1962a; BICK & SULZBACH, 1966), have been extensively studied and have proved to be excellent subjects for basic investigation on territoriality and reproductive behavior. We consider that with further study *Palaemnema* could yield equally significant information. Their congregation at limited reproductive sites, sedentary nature and high degree of localization are attributes which combined are conducive to behavioral work.

The ovipositing behavior of *Palaemnema desiderata* is probably shared by the rest of the Palaemnemas. At "Los Tuxtlas", we observed *P. paulitoyaca* ovipositing in the same way and occasionally using the same plants as *P. desiderata*. Donnelly (pers. comm., 1980) mentioned that he observed a species of *Palaemnema* in Guatemala: "a female placed eggs in a thin, woody stem about five feet above a tiny stream".

P. desiderata resembles calopterygids rather than coenagrionids or lestids in its vigorous defense of territory, high degree of localization and in the brevity of sperm translocation and copula. In its oviposition in non-aquatic woody plants, it resembles the lestids: *Archilestes* grandis Rambur (BICK & BICK, 1970), *A. californica* MacLachlan (KENNEDY, 1915), *Lestes viridis* V.d. Lind., *L. barbarus* Charpentier, (NIELSEN, 1954), *Sympecma paedisca* Brauer (ROBERT, 1958), *Orolestes wallacei* Kirby (LIEFTINCK, 1939) and the protoneurid, *Selysioneura cornelia* Lieftinck (LIEFTINCK, 1953). In its early morning activity, it resembles the coenagrionid, *Mortonagrion selenion* Ris (MIZUTA, 1974).

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REFERENCES

BICK, G.H. & J.C. BICK. 1965. Sperm transfer in damselflies (Odonata : Zygoptera). - Ann. ent. Soc. Am. 58: 592.

BICK, G.H. & J.C. BICK. 1970. Oviposition in Archilestes grandis (Ramb.) in Ohio (Odonata : Agrionidae). - Ent. News 81: 157-163.

BICK, G.H. & J.C. BICK. 1978. The significance of wing clapping in Zygoptera. -Odonatologica 7(1): 5-9.

BICK, G.H. & D. SULZBACH. 1966. Reproductive behavior of the damselfly, Hetaerina americana (Fabricius) (Odonata : Calopterygidae). - Anim. Behav.14: 156-158.

BUCHHOLTZ, C. 1951. Untersuchungen an der Libellen-Gattung Calopteryx Leach, unter besonderer Berücksichtigung ethologischer Fragen. -Z. Tierpsychol. 8: 273-293.

CALVERT, P.P. 1931. The generic characters and species of Palaemnema. - Trans. Am. ent. Soc. 57: 1-111. CORBET, P.S. 1963. A biology of dragonflies. -Quadrangle Books, Chicago, 247pp.

- DREYER, W. 1978. Etho-ökologische Untersuchungen an Lestes viridis (Vander Linden). -Odonatologica 7: 309-322.
- EDMIINDS. M. 1974. Defense in animals. -Longman, New York: 357pp.
- HEYMER, A. 1973. Étude du comportement réproducteur et analyse des mécanismes déclencheurs innés (MDI) optiques chez les Calopterygidae (Odon., Zygoptera). —Ann. Soc. ent. Fr. (N.S.) 9(1): 219-254.
- JOHNSON, C. 1961. Breeding behavior in Hetaerina americana (Fabricius) and H. titia (Drury) (Odonata : Agriidae). - Can. Ent. 93: 260-266.
- JOHNSON, C. 1962a. A description of territorial behavior and a quantitative study of its function in males of Hetaerina americana (Fabricius) (Odonata : Agriidae). -Can. Ent. 94: 178-190.
- JOHNSON, C. 1962b. Breeding behavior and oviposition in Calopteryx maculatum (Beauvois) (Odonata : Calopterygidae). - Am. Midl. Nat. 68: 242-247.
- KENNEDY, C.H. 1915. Notes on the life history and ecology of the dragonflies (Odonata) of Washington and Oregon. -Proc. U.S. natn. Mus. 49: 259-345.
- LIEFTINCK, M.A. 1939. On the true position of the genus Orolestes MacLach., with notes on O. wallacei (Kirby), its habits and life history (Odon., Lestid.) -Treubia 17: 45-61.
- LIEFTINCK, M.A. 1953. The larval characters of the Protoneuridae (Odon.). with special reference to the genus Selysioneura Förster and with notes on other Indo-Australian genera. -Treubia 21: 641-684.
- MIZUTA, K. 1974. Ecological and behavioral isolation among Mortonagrion selenion Ris, Ceriagrion melanurum Selys, and Copera annulata (Selys) (Zygoptera : Coenagrionidae, Platycnemididae). -Odonatologica 3(4): 231-239.
- NIELSEN, C. 1954. Notule odonatologiche II. Notizie sul Gen. Lestes Leach. -Boll. Ist. Ent. Univ. Bologna 20: 65-80.
- PAJUNEN, V.I. 1966. Aggressive behavior and territoriality in a population of Calopteryx virgo L. (Odonata : Calopterygidae). Annls zool. Fenn. 3: 201-214.
- ROBERT, P.A. 1958. Les libellules (Odonates). Delachaux and Niestlé, Neuchâtel; 364pp.
- U.S. NAVAL OBSERVATORY, NAUTICAL ALMANAC OFFICE. 1946. Tables of sunrise, sunset and twilight. Supplement of the American Ephemeris 1946. -U.S. Government Printing Office Washington U.S.A.
- WAAGE, J.K. 1947. Reproductive behavior and its relation to territoriality in Calopteryx maculata (Beauvois) (Odonata : Calopterygidae). -Behaviour 47: 240-256.