Odonatologica 26(4): 477-482 *December 1, 1997*

USE OF FEMALE'S LEGS IN TANDEM-LINKAGE DURING FLIGHT OF LIBELLULID DRAGONFLIES (ANISOPTERA)*

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Received January 9, 1997 / Revised and Accepted March 5, 1997

During tandem flight females of *Zygonyx natalensis*, *Tramea basilaris*, *T. lacerata*, *T. limbata* and *T. transmarina* grasp the male's abdomen with their mid and hind legs. The adaptive and phylogenetic significance of this behaviour is discussed.

INTRODUCTION

Many species of the Libellulidae oviposit in tandem. Tandem flight is particularly well described for species of *Sympetrum*, where contact between the sexes is restricted to the male's grasp of the female's head (e.g. RÜPPELL, 1984a).

In certain species the legs of the female take on an unusual attitude during tandem flight. This behaviour only becomes apparent on closer examination and it has been documented in slow-motion films, photographs, drawings, and written descriptions (RÜPPELL & HADRYS, 1988; MARTENS, 1991; SHIMIZU, 1992). The objectives of this paper are to give a first overview of the occurrence of this special tandem position in relation to tandem-oviposition in libellulids and to discuss the adaptive and phylogenetic significance of this behaviour.

MATERIAL AND METHODS

We evaluated all the film and photographic material of flying libellulid tandems at our disposal, slow-motion films of G. Rüppell (ANDERS & GRABOW, 1992; RÜPPELL, 1984a, 1984b, 1990;

* This paper is dedicated to Peter M i l l e r, whose help and advice is sorely missed now. In memory of the many fruitful discussions with Peter on the topics described here, which will now never be concluded.

RÜPPELL & HADRYS, 1988) and one unpublished film of R. Rudolph. The film on *Tramea lacerata* Hagen (RÜPPELL & HADRYS, 1988) had been taken by up to 500 frames s^{-1} and was analysed by means of a single frame projector (analysis projector nac, model DF-16C). We reanalysed video material and photographs on *Zygonyx natalensis* (Martin) (MARTENS, 1991). Additionally, we observed the reproductive behaviour of some species in the field: *T. basilaris* (Palisot de Beauvois) and *Urothemis assignata* (Selys) in the Comoé National Park, Ivory Coast in 1992-1993 and *T. limbata* (Desjardins) at the Ravine St-Gilles near St-Gilles de Bains at west coast of La Réunion in March and April 1996.

RESULTS

At small savannah ponds in the Comoé National Park, Ivory Coast, in the beginning of the rains pairs of *Tramea basilaris* appeared at water for short egg-laying sequences. They left the sites in tandem, some of them were observed flying to the next water between 5 and 50 m away. At bigger ponds they repeatedly laid eggs, but often disturbed by rival males they cruised above the water. During tandem-flight females grasped their male with their legs. At pools of a rocky river below a waterfall at the west coast of La Réunion pairs of *T. limbata* showed a similar behaviour. The female gripped the male's abdomen near the 6th abdominal segment which is documented in three colour slides. In *Zygonyx natalensis*, the female's mid legs touched the basis of the 7th abdominal segment, the hind legs were put one segment length in front of them (Fig. 1). Females of *Urothemis assignata* did not show this behaviour in tandem.

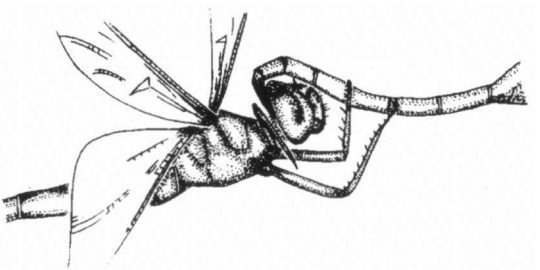

Fig. 1. Tandem linkage in *Zygonyx natalensis*. Redrawn from a slide.

In *T. lacerata*, tandem formation could be described in detail from a film sequence. After the female pulled her abdomen through, the male grasped her in flight. The reconstruction of the tandem can be divided into 4 phases (Fig. 2). In more than 10 other film sequences the grip of the female to the male abdomen was the same. In the same film it is clearly visible that abrupt changes in flight position, viz. after lateral gusts and after turns, never led to twisting of the longitudinal axis of the tandem partners to each other. The tandem flew turns to small circles. Gliding phases of both were often visible in the fast forward flight up to 3.65 m s^{-1}.

DISCUSSION

The list of genera which deposit eggs in tandem (Tab. I) is surely incomplete, the behaviour of many tropical forms is still unknown. Instances of prolonged post-

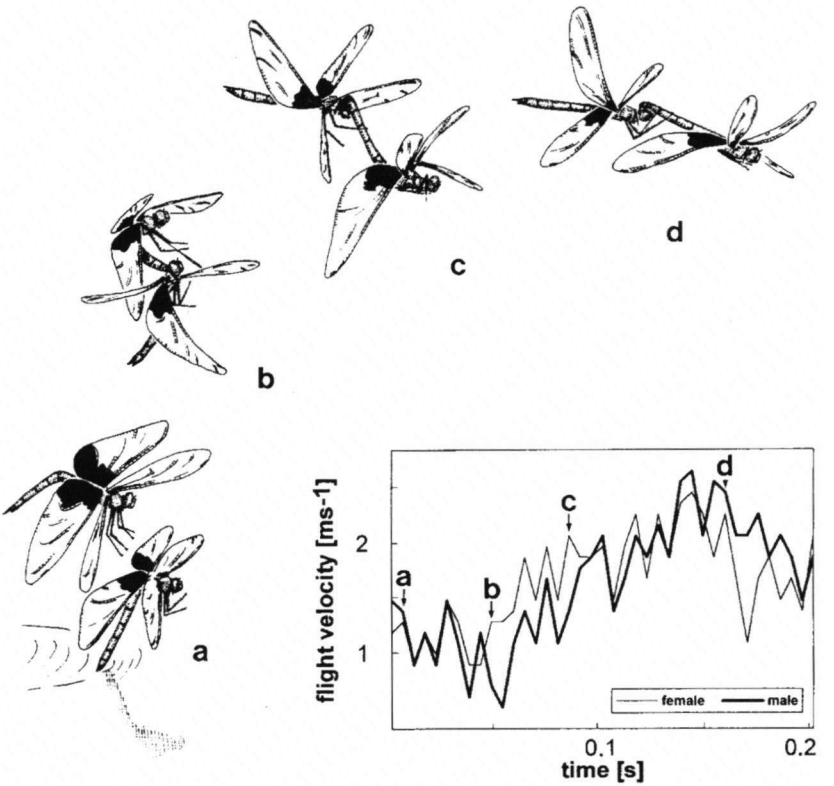

Fig. 2. Reconstruction of the tandem linkage during oviposition in *Tramea lacerata*; redrawn from a sequence of a slow motion film of G. Rüppell (RÜPPELL & HADRYS, 1988). – (a) The male landed on the female's thorax. (b) While the female ascended the male coupled with his claspers. (c) The male stretched his abdomen, while the female accelerated furthermore the male declines. The female grasped the male's abdomen with the mid legs, followed by the hind legs. (d) The male accelerated and stretched his abdomen. – Diagram below: flight velocity of both partners during that sequence, film speed at 350 frames s^{-1} and each second frame analysed.

-mating flight in tandem are also described, but only during exploration activity; the oviposition itself is performed without mate-contact, e.g. in *Aethriamanta* or *Leucorrhinia* (HASSAN, 1981; RÜPPELL, 1989).

While it is typical in Anisoptera for the female to grasp the male's abdomen during copulation (CORBET, 1962), such behaviour following copulation is exceptional. It is only known from *Tramea transmarina* Brauer (SHIMIZU, 1992), *T. basilaris*, *T. lacerata*, *T. limbata* and *Zygonyx natalensis*; species of the two subfamilies Trameinae and Zygonychinae (Tab. I), both of which are characterised by advanced wing venation (DAVIES & TOBIN, 1985). Should further instances of post-copulatory female leg use in tandem in these two subfamilies become known,

Table I

Tandem oviposition in the Libellulidae. – [The subfamily classification follows DAVIES & TOBIN, 1985]

Subfamily	Genus	Reference
Leucorrhiniinae	*Celithemis*	MILLER (1982), WAAGE (1976)
Sympetrinae	*Diplacodes*	SAKAGAMI et al. (1974), ROWE (1987)
	Erythrodiplax	DUNKLE (1989)
	Indothemis	MILLER (1992)
	Sympetrum	well described by many authors
Urothemistinae	*Macrodiplax*	DUNKLE (1989)
	Selysiothemis	ASKEW (1988)
	Urothemis	HASSAN (1981)
Trameinae	*Hydrobasileus*	FRASER (1952)
	Idiataphe	DUNKLE (1989)
	Miathyria	DUNKLE (1989)
	Pantala	BUSKIRK & SHERMAN (1985)
	Tramea	SAKAGAMI et al. (1974), RÜPPELL & HADRYS (1988)
Zygonychinae	*Zygonyx*	FRASER (1952), MARTENS (1991)

as we expect, this will be a further indication of the close relationship between them. The classification of the Libellulidae is still in progress. Between the systems published by FRASER (1957) and DAVIES & TOBIN (1985) are remarkable differences. At present the libellulid classification is strongly based on wing characters. MILLER (1988) compared genitalia and reproductive behaviour of different libellulid species and concluded that similarities in the genitalia and the reproductive behaviour suggest a new classification may be needed.

Having long legs may be a requirement of a female's grip, but other forms with long legs such as *Urothemis* did not show this behaviour. Apart from a supposed phylogenetic significance of this type of tandem-linkage there might be an adaptive significance as well. The grip of the female has a stabilising effect on the tandem, which might be expected to be of considerable adaptive importance. The following hypotheses are put forward as tentative explanations for this behaviour.

(1) There may be a great distance between the mating and oviposition sites which is covered in tandem flight. Flying tandems of *T. lacerata* in Texas were observed far away of any body of water crossing dry grassland (G. Rüppell, pers. comm.). Because of male competition (MARTENS, 1991; RÜPPELL & HADRYS, 1988) pairs may be forced to search for alternative oviposition sites. In addition, there may be a trend for widely dispersed oviposition, from few eggs per site at one water, to the distribution of the eggs into several waters (BUSKIRK & SHERMAN, 1985).

(2) All the 5 species listed above have broad wings and colonise open habitats. They have larger wind attack areas to gusts of wind than many other species. During post-copulatory behaviour a pair never land in tandem position. They

are able to use their legs in other ways.

(3) Male appendages of libellulids with rapid and sustained flight when actually in tandem like *Tramea* and *Pantala* show no remarkable differences. The structure of contact points was essentially similar (PINHEY, 1969). In relation to most Anisoptera the anal appendages are quite simple and uniform in the Libellulidae (PINHEY, 1969). The trend to simple and uniform appendages in the Libellulidae may lead to a disadvantage in the stabilisation of the tandem linkage which can be compensated by the additional use of the female's legs.

(4) This stable type of tandem linkage may reduce the risk of tandem splitting by rival males.

(5) In the tandem linkage described here, the female has a remarkably active part, which leads one to the question of female's interests. It is in the female's interest to avoid damages of their compound eyes resulting from the grip of male's claspers. Head damages are common in female Aeshnidae and Gomphidae (RIS, 1910; DUNKLE, 1979, 1991). In *Anax junius* (Drury) this damage is already discussed in the context of tandem oviposition (DUNKLE, 1979).

(6) Predation pressure and interspecific male competition should evolve a fast flight with high manoeuvrability. The grasping of the female to the male's abdomen increases the stability of the longitudinal axis of the pair. As the film and observations show, in *Tramea* both partners beat their wings during flight. So both are producing lift and thrust. Turns are much more efficient and quicker if both partners exhibit beating at the same instant. In tandems of *Sympetrum*, where this feature is not present, the female's body is shaking as it follows the new flight direction of the male (RÜPPELL, 1984a).

But before one attempts a definitive evaluation of the various hypotheses, further observations of libellulid reproductive behaviour are needed on the use or non-use of the female's legs during tandem-linkage.

ACKNOWLEDGEMENTS

We are very grateful to RAINER RUDOLPH who showed us his unpublished film on *Zygonyx natalensis*, and GEORG RÜPPELL for the opportunity to reanalyze his film on *Tramea lacerata*. We would like to thank JENS ROLFF, Georg Rüppell and FRANK SUHLING for helpful comments and critical reading of the manuscript.

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