

Effects of male harassment on females' oviposition behaviour in Libellulidae (Odonata)

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ABSTRACT

I investigated whether the level of male harassment affects females' oviposition behaviour, such that females oviposit unguarded under suboptimal conditions and/or vary oviposition duration, dip number, dip frequency or number of oviposition site changes. The study species were the libellulids *Crocothemis erythraea*, *Orthetrum chrysostigma*, *Pantala flavescens*, *Sympetrum fonscolombii*, *Trithemis annulata* and *T. kirbyi ardens*. Only a few ovipositions under suboptimal conditions were observed and females hovered lower under high male harassment. However, in only a few species studied oviposition behaviour differed with the level of harassment. No evidence for a special female strategy to avoid the negative effects of males' harassment was found. Due to the great intraspecific variability females seemed to be able to react flexibly to current conditions, such as changing male density and the level of male harassment.

INTRODUCTION

Density has an important influence on the behaviour of mature male libellulids at reproduction sites (Pezalla 1979). High density intensifies male-male competition so that males have a lower chance to mate and face higher costs due to fights (Corbet 1999: 375). For males, several behavioural parameters are known to change under high densities, for example: (1) a reduction in territorial size (Alcock 1998), (2) a decreasing duration of territorial occupancy (Sherman 1983), (3) shorter courtship (Martens 1996), (4) shorter (Miller 1982) or longer (Rehfeldt 1989) copulation, and (5) increased aggressive behaviour in some species (Pajunen 1966; Wolf & Waltz 1984; Corbet 1999: 657).

As most of the literature on odonate mating patterns has focused on males, while females were often ignored or just considered as passive partners (Fincke et al. 1997), less is known about possible effects of multiple mating and male harassment during oviposition under high male density on females. Multiple mating causes benefits and costs for females. Whereas males can increase their reproductive success

by mating with more females, females cannot produce more offspring than the full complement of their eggs (Thornhill & Alcock 1983; Krebs & Davies 1997). Even in species, in which females can obtain enough sperm for fertilisation from a single mating, females often copulate with more than one male (Rowe 1994; Brown 1997). A benefit to the female might be increased genetic variability of their offspring and sexual selection pressure on the male by arriving at the time of highest male abundance (Walker 1986; Reinhardt 1998). A cost to the female of multiple mating and male harassment during oviposition might be an increased predation risk due to reduced mobility or becoming more conspicuous (Drummond 1984; Siva-Jothy 1988; Rowe 1994; Rehfeldt 1996), loss of energy or foraging time (Clutton-Brock & Langley 1997; Mühlhäuser & Blanckenhorn 2002; Härdling & Kaitala 2004), and increased risk of internal (e.g. genital, Crudgington & Siva-Jothy 2000) or external injuries (e.g. wing, Dunkle 1991).

In my study I investigated whether male harassment increases the probability that a female oviposits (1) unguarded at suboptimal temperatures or light conditions and/or (2) for a shorter time, featuring a higher dip frequency or a higher number of pond changes. The oviposition behaviour of six libellulid species was observed that form the dominant members of a well-studied odonate assemblage at artificial ponds in the semi-desert of Namibia (Padeffke & Suhling 2003; Johansson & Suhling 2004; Schenk et al. 2004; Suhling et al. 2004).

METHODS

Study site

The study was carried out in Namibia at Tsaobis Leopard Nature Park (22°22'S, 15°44'E; 740 m altitude). For this study artificial set up ponds were used that were placed directly in the Swakop River valley. Thereby, eight artificial ponds were newly created each year at the beginning of the study season in 2001 (April - June), 2002 (February - April) and 2003 (March - May). Each pond had an area of 3.0 m x 2.2 m. The water was initially 0.25 m deep but slowly evaporated. The minimal distance between the ponds was 1.0 m and the maximum distance was 9.5 m. The odonates could fly from one pond to another without restriction.

Study species

Six species of Libellulidae were observed: *Crocothemis erythraea* (Brullé) ($n = 13$), *Orthetrum chrysostigma* (Burmeister) ($n = 24$), *Pantala flavescens* (Fabricius) ($n = 44$), *Sympetrum fonscolombii* (Selys) ($n = 30$), *Trithemis annulata* (Palisot de Beauvois) ($n = 19$), and *T. kirbyi ardens* (Gerstäcker) ($n = 83$). These species made up the majority of the odonate assemblage of the artificial ponds at Tsaobis but also at several natural habitats in Namibia (own observation). All species oviposit exophytically in open water during flight. *P. flavescens* (Sakagami et al. 1974; Schenk et al. 2004) and *S. fonscolombii* (Schenk et al. 2004) oviposit usually in tandem guarded, and males are not territorial. The other species perform usually non-contact guarding (Schenk et al. 2004), and males are territorial. Thereby, all territorial males took one single pond as their territory respectively.

Oviposition behaviour

All observations within this study were conducted on unmarked individuals. I declared each female seen at a given time at the artificial ponds to be unique. Throughout the day the following aspects were recorded: (1) males' guarding behaviour, (2) frequency of contact of the females' abdomen with the water surface (dip frequency) by counting all contacts (dip number) and dividing them by the total oviposition duration, measured with a stop-watch, and (3) the number of pond changes during an oviposition. The latter was used as a measure for the strength of microhabitat selection during an oviposition (Schenk et al. 2004). To investigate whether oviposition behaviour varied between species, a MANOVA was conducted with species as independent variable and oviposition duration, dip number, dip frequency, and number of pond changes as response variables. MANOVA allows more than one variable to be analysed at once, hence is a multivariate test (Dytham 2003: 210). Additionally, the mean height of the females hovering above the water surface during oviposition and direct behaviour reactions of females to male harassment were recorded.

To characterise the libellulid assemblage at the artificial ponds and to give an impression of the probability of females getting in contact to males and/or getting disturbed by them, I measured the density of both sexes and sex ratio. Therefore, every day at 12:00 h, which was 12:10 h solar time on 1 February and 12:01 h solar time on 30 June, the number of males and females per species and per pond was counted. To examine whether there exists a correlation between males density and the number of males, who harassed ovipositing females, regression analyses were done with the number of males per pond as the independent variable and the number of conspecific or heterospecific males, who harass ovipositing females as response variables. In this way, harassment by males was registered during oviposition and was classified into three arbitrary levels: (1) no harassment, (2) low harassment, namely brief harassment by one male, and (3) high harassment, namely repeated harassment by one or more males. To determine, whether there was a correlation between the number of males who harassed females per unit of time and the level of harassment, data were analysed using a correlation analysis. To examine, whether harassment had a significant influence on oviposition behaviour, MANOVAs were carried out for each species using harassment level as an independent variable and oviposition duration, dip number, dip frequency, and number of pond changes as response variables.

RESULTS

Most ovipositions were observed during daytime under favourable temperature conditions. The number of unguarded females in all species was low (Fig. 1). No differences in time of day between guarded and unguarded females could be discerned (Fig. 1). Only a few unguarded females of *Crocothemis erythraea* were observed, which oviposited before or after the guarded females in the early and relatively cold morning or during the evening (Fig. 1). Additionally, a few times females of *C. erythraea* and *Pantala flavescens* were seen to oviposit unguarded just before or after rain or thunderstorms.

Oviposition duration, dip number, dip frequency, and the number of pond changed during oviposition varied between species (Table 2). The more conspecific males (Regression analysis: $F_{1, 346} = 693.42$; slope = 1.06; $R^2 = 0.07$; $p < 0.001$) or even hetero-specific males (Regression analysis: $F_{1, 346} = 178.75$; slope = 1.13; $R^2 = 0.33$; $p < 0.001$) were present at a pond at the same time, the more males harassed arriving females. Additionally, the more males that harassed a female the higher were the level (see Methods) of male harassment (Correlation analysis: $F_{1, 346} = 169.94$; $p < 0.001$). The level of harassment had a significant influence on oviposition duration of *Orthetrum chrysostigma* and *Trithemis kirbyi*, on dip number of *O. chrysostigma*, *T. annulata*, and *T. kirbyi*, on dip frequency of *Sympetrum fonscolombii*, and on number of pond changes by *O. chrysostigma* (Table 3). In *O. chrysostigma*, *T. annulata*, and *T. kirbyi* no pond changes were observed during oviposition without harassment (Fig. 2). Under a low level of harassment, all species showed some pond changes; under a high level of harassment these increased in *S. fonscolombii*, and *T. annulata* and decreased in all other species (Fig. 2).

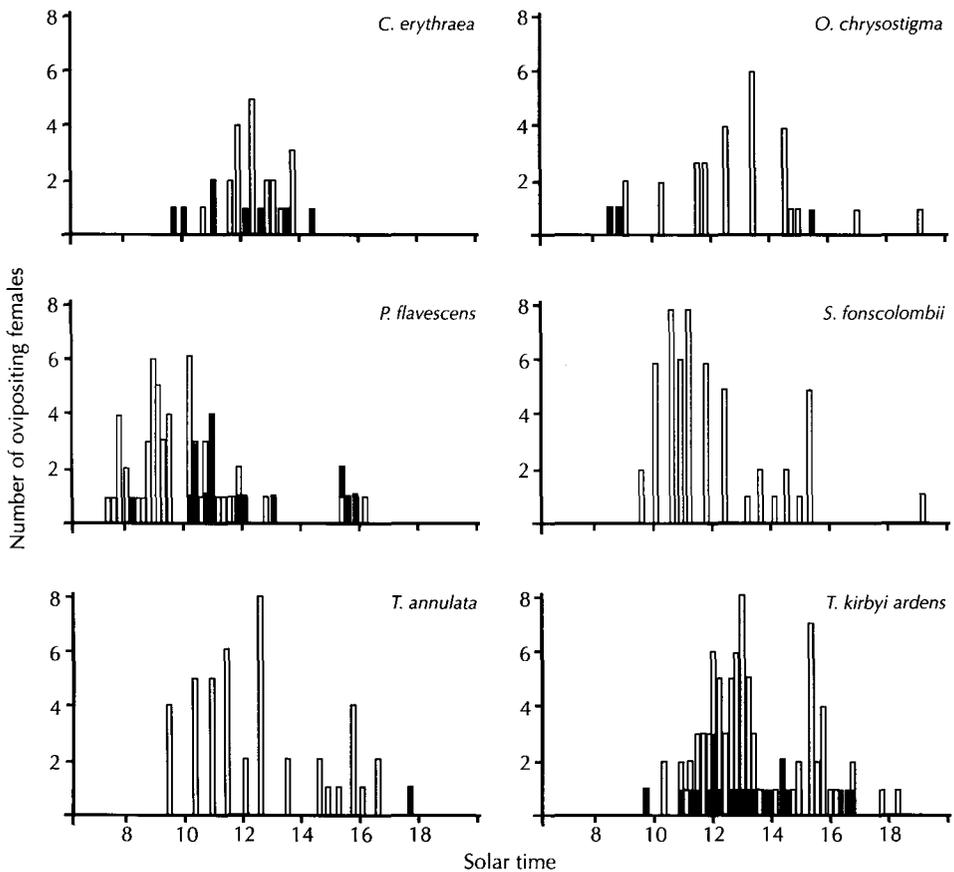


Figure 1: Number of ovipositing females at artificial ponds in Tsaobis during the course of the day — gray bars: guarded ovipositions, black bars: unguarded ovipositions.

Table 1. Presence of all Odonata observed at artificial ponds in Tsaobis, Namibia — numbers of males and females per pond and the mean operational sex ratio. All species were monitored at noon; see Methods.

	Mean	± s.d.	Maximum	Mean	± s.d.	Maximum	Sex ratio
		♂		♀	♀		♂ : ♀
<i>Crocothemis erythraea</i>	0.21	0.44	2	0.01	0.07	1	1 : 0.02
<i>Orthetrum chrysostigma</i>	0.57	0.54	2	0.03	0.17	1	1 : 0.05
<i>Pantala flavescens</i>	0.52	0.71	2	0.07	0.25	1	1 : 0.13
<i>Sympetrum fonscolombii</i>	1.21	1.12	6	0.09	0.29	2	1 : 0.07
<i>Trithemis annulata</i>	0.88	0.62	3	0.03	0.16	1	1 : 0.03
<i>Trithemis kirbyi ardens</i>	2.05	1.55	10	0.14	0.36	3	1 : 0.07

The greatest number of females present at one pond at one time was one in *C. erythraea*, *O. chrysostigma*, *P. flavescens* and *T. annulata*, two in *S. fonscolombii*, and three in *T. kirbyi* (Table 1). Mean and maximal female abundance was much lower than male abundance; so the operational sex ratio at the artificial ponds of all species studied was strongly biased towards males (Table 1). Normally females of all species hovered ca 0.2-0.3 m above the water surface, but the higher the level of harassment, the lower the females hovered. At a high level of harassment females sometimes hovered only 0.05 m above the water surface. For three times it was observed that at high male densities (9-10 conspecific males per pond), females of *T. kirbyi* were not able to lay their eggs, because males copulated with them repeatedly. Under these conditions, unusual oviposition behaviour was observed. After copulation, females settled on the ground next to the water and waited until a big drop of eggs had formed at the tip of the abdomen. Then, they quickly flew to the water, dipped the abdomen with the eggs into the water and settled again on the ground until the next drop of eggs had formed.

DISCUSSION

All behaviour parameters were generally species-specific, but exhibited high variability. The data of this study confirm the results of Corbet (1999: 303-313) that libellulids usually concentrate their activity at the breeding site around noon, when most territories are established (Watanabe & Higashi 1989) and males are most aggressive (Campanella 1975). One possible reaction of females to male harassment might be ovipositing unguarded under suboptimal conditions (Hilfert & Rüppell 1997). Flying unguarded under less optimal light conditions, strong wind or lower temperatures, should result in additional costs for the females. In general, in the species studied, unguarded oviposition was infrequent and unguarded oviposition under suboptimal conditions even highly seldom. Therefore, it is not clear for the studied species whether these few ovipositions under suboptimal conditions might be seen as a strategy to avoid male harassment under high male density.

Females might also react with variable oviposition duration, dip number, dip frequency, or number of pond changes on male harassment. Oviposition duration and dip number increased under low harassment and decreased under a high level of harassment. Under a low level of harassment, oviposition was often interrupted for

Table 2. Influence of male harassment on oviposition behaviour — results from a MANOVA with species as independent variable and oviposition duration, dip number, dip frequency, and number of pond changes as response variables; see Methods. The Pillai's trace was used for calculating the p -values because the design of these analyses was not balanced (Scheiner & Gurevitch 2001: 105).

	<i>n</i>	d.f.	Pillai's trace	<i>F</i>	<i>p</i>
MANOVA		908	1.08	16.75	< 0.001
ANOVAs					
oviposition duration [s]	233	5, 227		19.77	< 0.001
dip number	233	5, 227		14.92	< 0.001
dip frequency [# s ⁻¹]	233	5, 227		48.95	< 0.001
pond changes	233	5, 227		22.97	< 0.001

a short time and couples or females searched for another oviposition microhabitat within the same pond or another pond. This behaviour extended the duration of oviposition. Under a high level of harassment, couples or females often stopped oviposition and left the reproduction site. Hence, the total oviposition duration was shorter and the dip number lower as under low harassment.

For many libellulid species it is known that the mean dip frequency is species-specific, although there is relatively large intraspecific variation (Miller 1983; Rehfeldt 1996; Schenk et al. 2004). Females seem to be able to change their dip frequency in short term (Miller & Miller 1985). Indeed, in some species dip frequency increased with the level of harassment, but there was no significant correlation due to the high level of variance. In all species a clear relation was seen: the higher the male density was, the nearer females hovered to the water surface. Therefore, under high harassment the distance females had to fly during oviposition became shorter and so the time from one dip to another and the dip frequency were reduced.

At high male density I observed that females of *Trithemis kirbyi* settled on the ground next to the water after copulation until a big drop of eggs had formed at the tip of the abdomen. The benefit for females from hovering lower (see above) or settling on the ground might have been that they were less easily seen and caught by males. Another way to reduce visibility might be to oviposit amongst vegetation (Pajunen 1966). As vegetation at the artificial ponds was lacking, females had no chance to do so. However, females' risk of injury and predation might be increased in both cases – to hover lower should increase the risk of predation by fish and frog, and to settle on the ground should entail the risk of predation by terrestrial animals.

Pond changes were never observed under oviposition without harassment in *Orthetrum chrysostigma*, *T. annulata*, and *T. kirbyi*. The number of pond changes increased under harassment. Therefore, pond changing seems to be one reaction females use to avoid male harassment. Nevertheless, the level of harassment had no significant influence on the number of pond changes because of the high degree of variability within the number of pond changes. Beside this, tandem guarded species performed a high number of pond changes even during oviposition with no harassment. In tandem species the number of pond changes primarily seems not to be a tactic to avoid male harassment, but a strategy for spatial risk spreading for their offspring (Schenk et al. 2004).

Female abundance at the reproductive site was typically low. Therefore, as expected (Campanella 1975; Corbet 1999: 538), the operational sex ratio at the reproductive site was biased towards males and no group oviposition was observed. The number of males present per pond correlated positively with the number of males that harassed arriving females.

In conclusion, oviposition behaviour varied between the species, but was highly variable within the species studied. No evidence for a special female mechanism or strategy to avoid harassment by males under high male density could be found. Instead, the observed general variability in oviposition behaviour may allow females to react flexibly to current situations, such as changing weather conditions, changing male density, male harassment or the arrival of predators.

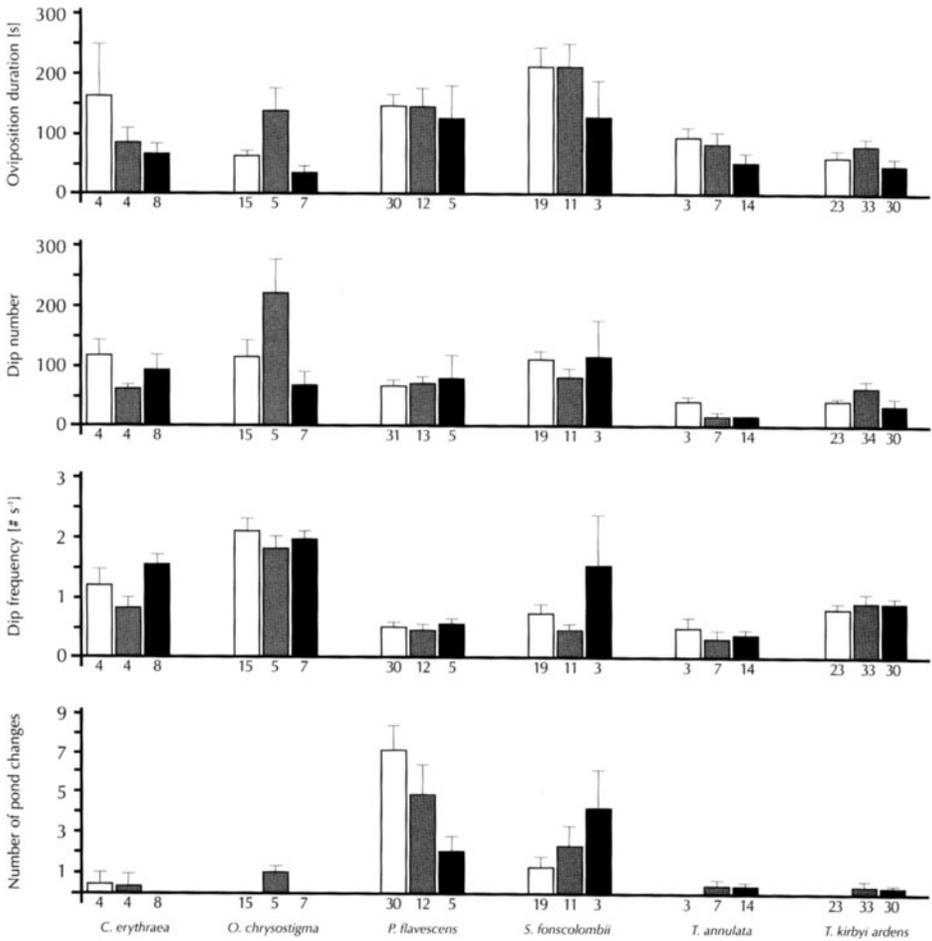


Figure 2: Oviposition behaviour at different levels of harassment — mean (\pm s.d.) oviposition duration, dip number, dip frequency, and number of pond changes. White bars: no harassment; gray bars: low level of harassment; black bars: high level of harassment. The numbers below bars refer to sample sizes. Estimates are given \pm standard deviation.

Table 3. Influence of male harassment on oviposition behaviour — results from MANOVAs for all study species with level of harassment as independent variable and oviposition duration, dip number, dip frequency, and number of pond changes as response variables; see Methods.

Source	Species	d.f.	Pillai's trace	F	p
MANOVA	<i>Crocothemis erythraea</i>	22	0.75	1.66	n.s.
	<i>Orthetrum chrysostigma</i>	44	0.75	3.27	0.005
	<i>Pantala flavescens</i>	84	0.18	1.09	n.s.
	<i>Sympetrum fonscolombii</i>	56	0.54	2.62	0.017
	<i>Trithemis annulata</i>	38	0.51	1.62	n.s.
	<i>Trithemis kirbyi ardens</i>	162	0.15	1.79	n.s.
ANOVAs	oviposition duration [s]	<i>Crocothemis erythraea</i>	2, 13	1.40	n.s.
		<i>Orthetrum chrysostigma</i>	2, 24	4.88	0.002
		<i>Pantala flavescens</i>	2, 44	0.04	n.s.
		<i>Sympetrum fonscolombii</i>	2, 30	0.54	n.s.
		<i>Trithemis annulata</i>	2, 21	1.96	n.s.
		<i>Trithemis kirbyi ardens</i>	2, 83	3.72	0.028
	dip number	<i>Crocothemis erythraea</i>	2, 13	1.22	n.s.
		<i>Orthetrum chrysostigma</i>	2, 24	3.17	n.s.
		<i>Pantala flavescens</i>	2, 44	0.53	n.s.
		<i>Sympetrum fonscolombii</i>	2, 30	0.96	n.s.
		<i>Trithemis annulata</i>	2, 21	5.25	0.014
		<i>Trithemis kirbyi ardens</i>	2, 83	4.73	0.011
	dip frequency [# s ⁻¹]	<i>Crocothemis erythraea</i>	2, 13	3.03	n.s.
		<i>Orthetrum chrysostigma</i>	2, 24	0.64	n.s.
		<i>Pantala flavescens</i>	2, 44	0.76	n.s.
		<i>Sympetrum fonscolombii</i>	2, 30	3.66	0.038
		<i>Trithemis annulata</i>	2, 21	0.36	n.s.
		<i>Trithemis kirbyi ardens</i>	2, 83	0.49	n.s.
	pond changes	<i>Crocothemis erythraea</i>	2, 13	1.07	n.s.
		<i>Orthetrum chrysostigma</i>	2, 24	13.73	<0.001
		<i>Pantala flavescens</i>	2, 44	1.58	n.s.
		<i>Sympetrum fonscolombii</i>	2, 30	2.08	n.s.
		<i>Trithemis annulata</i>	2, 21	0.25	n.s.
		<i>Trithemis kirbyi ardens</i>	2, 83	2.11	n.s.

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REFERENCES

- Alcock, J., 1998. Annual variation in the mating system of the dragonfly *Platthemis lineatipes* (Anisoptera: Libellulidae). *Journal of the Zoological Society of London* 218: 597-602.
- Brown, J.L., 1997. A theory of mate choice based on heterozygosity. *Behavioral Ecology* 8: 60-65.
- Campanella, P.J., 1975. The evolution of mating systems in temperate zone dragonflies (Odonata: Anisoptera) II: *Libellula luctuosa* (Burmeister). *Behaviour* 51: 278-310.
- Clutton-Brock, T.H. & P. Langley, 1997. Persistent courtship reduces male and female longevity in captive tsetse flies *Glossina morsitans morsitans* Westwood (Diptera: Glossinidae). *Behavioral Ecology* 8: 392-395.
- Corbet, P.S., 1999. Dragonflies: behaviour and ecology of Odonata. Harley Books, Colchester.
- Crudgington, H.S. & M.T. Siva-Jothy, 2000. Genital damage, kicking and early death. *Nature* 407: 855.
- Drummond, B.C., 1984. Multiple mating and sperm competition in the Lepidoptera. In: Smith, R.L. (ed.) "Sperm competition and the evolution of animal mating systems", Academic Press, New York, pp. 291-370.
- Dunkle, S., 1991. Head damage from mating attempts in dragonflies (Odonata: Anisoptera). *Entomological News* 102: 37-41.
- Dytham, C., 2003. Choosing and using statistics. Blackwell Publishing, Oxford.
- Fincke, O.M., J.K. Waage & W. Koenig, 1997. Natural and sexual selection components of odonate mating patterns. In: Choe, J.C. & B. Crespi (eds) "Mating systems in insects and arachnids", Press Syndicate of the University of Cambridge, Cambridge, pp. 58-74.
- Härdling, R. & A. Kaitala, 2004. The evolution of repeated mating under sexual conflict. *Journal of Evolutionary Biology* 18: 106-115.
- Hilfert, D. & G. Rüppest, 1997. Early morning oviposition of dragonflies with low temperatures for male-avoidance (Odonata: Aeshnidae, Libellulidae). *Entomologia Generalis* 21: 177-188.
- Johansson, F. & F. Suhling, 2004. Behaviour and growth of dragonfly larvae along a permanent to temporary water habitat gradient. *Ecological Entomology* 29: 196-202.
- Krebs, J.R. & N.B. Davies, 1997. Behavioural ecology: an evolutionary approach. Blackwell, Oxford.
- Martens, A., 1996. Die Federlibellen Europas. Platycnemididae. Westarp, Magdeburg & Spektrum, Heidelberg.
- Miller, P.L., 1982. Temporal partitioning and other aspects of prereproductive behaviour in two African libellulid dragonflies. *Entomologist's Monthly Magazine* 118: 177-188.
- Miller, P.L., 1983. The duration of copulation correlates with other aspects of mating behaviour in *Orthetrum chrysostigma* (Burmeister) (Anisoptera: Libellulidae). *Odonatologica* 12: 227-238.
- Miller, P.L.M. & A.K. Miller, 1985. Rates of oviposition and some other aspects of reproductive behaviour in *Tholymis tillarga* (Fabricius) in Kenya (Anisoptera: Libellulidae). *Odonatologica* 14: 287-299.
- Mühlhäuser, C. & W.U. Blanckenhorn, 2002. The costs of avoiding mating in the dung fly *Sepsis cynipsea*. *Behavioral Ecology* 13: 359-365.
- Padeffke, T. & F. Suhling, 2003. Temporal priority and intra-guild predation in temporary waters: an experimental study using Namibian desert dragonflies. *Ecological Entomology* 28: 340-347.
- Pajunen, V.I., 1966. The influence of population density on the territorial behaviour of *Leucorrhinia rubicunda* L. (Odon., Libellulidae). *Annales Zoologici Fennici* 3: 40-52.

- Pezalla, V.M., 1979. Behavioral ecology of the dragonfly *Libellula pulchella* Drury (Odonata: Anisoptera). *American Midland Naturalist* 102: 1-22.
- Rehfeldt, G.E., 1989. Female arrival at the oviposition site in *Platycypha caligata* (Sélys): temporal patterns and relation to male activity (Zygoptera: Chlorocyphidae). *Advances in Odonatology* 4: 89-93.
- Rehfeldt, G.E., 1996. Copulation, oviposition site selection and predation risk in the dragonfly species *Crocothemis erythraea* (Odonata: Libellulidae). *Entomologia Generalis* 20: 263-270.
- Reinhardt, K., 1998. Reproductive behaviour of *Leucorrhinia albifrons* (Burmeister) in a non-territorial situation (Anisoptera: Libellulidae). *Odonatologica* 27: 201-211.
- Rowe, L., 1994. The costs of mating and mate choice in water striders. *Animal Behaviour* 48: 1049-1056.
- Sakagami, S.F., H. Ubukata, M. Iga & M. Toda, 1974. Observation on the behaviour of some Odonata in the Bonin islands, with considerations on the evolution of reproductive behaviour in Libellulidae. *Journal of the Faculty of Science, Hokkaido University* 19: 722-757.
- Scheiner, S.M. & J. Gurevitch, 2001. Design and analysis of ecological experiments. Oxford University Press, Oxford.
- Schenk, K., F. Suhling & A. Martens, 2004. Relation between egg distribution, mate-guarding intensity, and offspring characteristics in dragonflies (Odonata). *Animal Behaviour* 68: 599-606.
- Sherman, K.J., 1983. The adaptive significance of postcopulatory mate guarding in a dragonfly, *Pachydiplax longipennis*. *Animal Behaviour* 31: 1107-1115.
- Siva-Jothy, M.T., 1988. Sperm "repositioning" in *Crocothemis erythraea*, a libellulid dragonfly with a brief copulation. *Journal of Insect Behaviour* 1: 235-245.
- Suhling, F., K. Schenk, T. Padeffke & A. Martens, 2004. Field data on larval development patterns in a dragonfly assemblage of African desert ponds. *Hydrobiologia* 528: 75-85.
- Thornhill, R. & J. Alcock, 1983. The evolution of insect mating systems. Harvard University Press, Cambridge.
- Walker, J.K., 1986. Sperm utilization in non-social insects. *American Naturalist* 115: 780-799.
- Watanabe, M. & K. Higashi, 1989. Sexual difference of lifetime movement in adults of the Japanese skimmer, *Orthetrum japonicum* (Odonata: Libellulidae), in a forest-paddy field complex. *Ecological Research* 4: 85-97.
- Wolf, L.L. & E.C. Waltz, 1984. Dominions and site-fixed aggressive behaviour in breeding male *Leucorrhinia intacta* (Odonata: Libellulidae). *Behavioural Ecology and Sociobiology* 14: 107-115.