Residence advantage in heterospecific territorial disputes of *Erythrodiplax* Brauer species (Odonata, Libellulidae)

Daniela Chaves Resende[1]

[1]Laboratório de Bioinformática e Evolução, Departamento de Biologia Geral, Universidade Federal de Viçosa, 36570-000, Viçosa-MG, Brasil. dcresende@ig.com.br

ABSTRACT. Residence advantage in heterospecific territorial disputes of *Erythrodiplax* Brauer species (Odonata, Libellulidae). Territories are the outcome of interactions determining where and how long individuals settle. To odonate species, aggressive disputes are not so common since the outcome can be predetermined by advantages such as residency, age, and body size. However, it is possible to predict that at heterospecific disputes, larger body-sized or more aggressive species have some profits overcoming these individual advantages, generating patterns of species hierarchy. Here, I studied the aggressiveness of five *Erythrodiplax* species (Odonata, Libellulidae) during territorial disputes and verified if larger body-sized species are more aggressive than smaller ones or if the residence advantage prevails on the heterospecific disputes. Larger species were not more aggressive than smaller ones and winners of intra- and interspecific territorial disputes were defined mainly by the residence. So, the residence advantage between heterospecific opponents appears to prevail over any other asymmetry among these species. This pattern may occur because, despite the territorial behaviour in dragonfly males, heterospecific disputes may not increment male reproductive success because it may not increase their access to females.

KEYWORDS. Asymmetry; hierarchy; interspecific competition; territoriality.

RESUMO. Vantagem do residente nas disputas territoriais interespecíficas entre espécies de *Erythrodiplax* (Odonata, Libellulidae). Territórios resultam de interações comportamentais que determinam onde e por quanto tempo um indivíduo consegue se estabelecer. Para espécies de Odonata, as disputas agressivas entre machos são raras, pois, vantagens pré-existentes como idade, tamanho corporal ou residência definem o vencedor. Entretanto, é possível esperar que nas interações interespecíficas, espécies de maior tamanho corporal ou mais agressivas possam ter vantagens nas disputas, sobrepujando as vantagens individuais pré-existentes e gerando um padrão hierárquico entre as espécies. Neste trabalho, eu estudei a agressividade exibida por espécies de *Erythrodiplax* (Odonata, Libellulidae) e verifiquei se espécies maiores são mais agressivas ou se a vantagem do residente prevalece também nas disputas interespecíficas. Espécies maiores não são mais agressivas e os vencedores das disputas territoriais intra- e inter-específicas foram machos residentes. Logo, a vantagem do residente parece prevalecer sobre qualquer assimetria existente entre as espécies estudadas, o que pode ocorrer porque, apesar do comportamento territorial exibido por elas, o recurso defendido pelos machos é o acesso às fêmeas e vencer disputas interespecíficas pode não afetar positivamente o sucesso reprodutivo dos mesmos.

PALAVRAS-CHAVE. Assimetria; competição inter-específica; hierarquia; territorialidade.

Territories are not fixed areas, but the outcome of complex behavioural interactions determining where and how long individuals settle (Gordon 1997). Territorial disputes among odonate males comprise behaviours or conventions that determine some kind of asymmetry between opponents, such as body size differences (Marden & Cobb 2004), previous experiences (Hsu *et al.* 2006) or simply residence (Waage 1988; Kemp & Wiklund 2004). The residence status appears to be an important source of asymmetry between opponents and frequently residents win territorial disputes (Alcock 1982; Van Buskirk 1986; Alcock 1987; Waage 1988). Intense disputes between intruders and residents are expected only if the intruder is strong enough to overcome the residence advantage or when both individuals consider themselves territorial residents (Waage 1988).

Odonate females do not present any form of parental care (Corbet 1962, 1999), so choice of a suitable oviposition site may be determinant to their reproductive success (Michiels & Dhondt 1990; Fincke 1992; Osborn & Samways 1996), mainly because odonate larvae present morphological and behavioural specializations that increase their survival in some specific microhabitats (Pritchard & Kortello 1997; Mikolajewski & Johansson 2003; McCauley 2007). In consequence, males defending territories with this suitable microhabitat must access more females, also increasing their reproductive success.

Costs associated to species co-occurrence into territorial sites may derive from (Singer 1990; Tynkkinen *et al.* 2004): i) heterospecific aggressiveness, ii) heterospecific mates or yet iii) female guard against heterospecific males, when the oviposition site is near to the territory. It is also possible that heterospecific competition for resources occurs during the larval phase (Johnson & Crowley 1980). So, it is reasonable to propose a selection of heterospecific aggressiveness mainly among related species sharing an ecological space, due to their high morphological similarities.

Territorial activity of odonate males can be affected by thermoregulatory abilities (De Marco & Resende 2002), since disputes involve rapid flies with intense muscle activity, increasing the thoracic temperature (May 1977; Marden 1989). Small sized species have a high convection heating, depending strongly from environmental temperature to be

active, while larger species may be more able to control body temperature by exposition to solar radiation (May 1991). If body size affects thermoregulatory abilities of species, it may also affect male activity patterns (May 1991; De Marco & Resende 2002). Indeed, competitive asymmetry is often associated with individual size differences (Aikio 2004). Larger species may be more aggressive than smaller ones due to their thermoregulatory abilities and fight advantages, so we could expect some pattern of hierarchy on the spatial distribution or on resource utilization.

Erythrodiplax Brauer, 1868 is highly diversified tropical Libellulidae (Odonata) genus, comprising about 58 species (International Dragonfly Fund 2003). In general, males of *Erythrodiplax fusca* (Rambur, 1842), *E. famula* (Erichson, 1848), *E. latimaculata* Ris, 1911, *E. pallida* (Needham, 1904) and *E. media* Borror, 1942 defend mating territories around lakes or river shorelines and swamps. Males of these species perch on branches, grasses, macrophytes or directly on the soil and the females lay their eggs after soon copulation, directly on water with some kind of submerged vegetation, along the shoreline of the pond (De Marco *et al.* 2005; Resende & De Marco 2008).

In this paper, I studied the aggressiveness exhibited by five *Erythrodiplax* species (Libellulidae, Odonata): *E. fusca*, *E. famula*, *E. latimaculata*, *E. pallida* and *E. media*, during territorial disputes. I emphasized heterospecific interactions, verifying if larger body-sized species are more aggressive than smaller ones, and if the residence advantage prevail on heterospecific disputes.

MATERIAL AND METHODS

The behavioral observations were made in the Área de Proteção Ambiental (APA) São José, Minas Gerais, Brazil (21°07'00''S and 44°12'10''W). The climate presents a dry season from April to September and a rainy season in the summer. Mean annual temperature is about 19°C with maximum between 21°C and 22°C. The APA (4758 ha) comprises a contact zone between Cerrado and Semidecidual Seasonal Atlantic Forest. Water courses are abundant mostly with perennial drainages.

I conducted this study between January and March, period of year with the highest abundances of dragonflies (De Marco & Latini 1998). I observed individual behaviour between 9:00 and 14:00 h to control effects of luminosity and humidity (Heinrich & Casey 1978; May 1979). I sampled four similar swamps with different altitudes, and all of them were disturbed areas, where originally there was Cerrado and Galery Forest.

Territorial Behaviour

The sampling unit for behavioural observations was the sequence of behaviours registered during one minute of focal observation of an individual (Altmann 1974). The moment of each behaviour start was noted, allowing the estimation of time spent in each activity. Individuals were selected at different locations of the swamps to avoid pseudoreplication (repeated observations of the same individual). I observed 54 males for *E. fusca*, 24 for *E. famula*, 65 for *E. latimaculata*, 44 for *E. media* and 45 for *E. pallida*.

I classified behavioural activities following De Marco (1998), such as: *i)* perch: including all classes of perch; *ii)* patrolling: flying back and forward through an area; *iii)* transition flight: passing through an area without patrolling and *iv)* territorial defence (agonistic interaction): chasing another individual. I distinguished the territorial defence between conspecific (intraspecific dispute) and heterospecific (heterospecific dispute) males. The territorial disputes were considered only when I was able to determine the resident male and the winner (males that remained in the territory at the end of disputes). I used a Chi-square analysis to test differences on ability of males to win disputes among different species and between residents and intruders.

Body Size

Five individuals of each species were collected and dried at 40ºC. Differences among mean weight of species were tested using a single classification analysis of variance. To test the hypothesis that larger species are more aggressive, I used a Linear Regression comparing mean proportion time spent on aggressive behaviour (patrol and territorial disputes) and mean dry weight for these species. Despite the obvious common ancestry shared by these species, I could not use a comparative analysis to test this hypothesis because there is no a phylogeny proposed to this group.

RESULTS

Males of *Erythrodiplax* species exhibited similar territorial defence behaviour and the five species spent most of their time perched (Fig. 1), spending little time in aggressive

Table I. Mean time (s) spent in aggressive behaviour (intra-, heterospecific territorial disputes and patrol) by *Erythrodiplax* species at the APA São José, Tiradentes, MG, Brazil. The Min-Max column indicates the 95% confidence interval. Superscript letters show equals treatments, based on confidence interval. N indicates the sample size.

Species		Intraspecific disputes		Heterospecific disputes		Patrol	
		Mean	Min-Max	Mean	Min-Max	Mean	Min-Max
E. famula	(N = 24)	3.31 [a]	1.07 - 5.56	0.94 [a]	0.19 - 1.70	9.92 [a]	5.84 - 13.99
E. fusca	(N = 54)	1.83 [a]	0.74 - 2.93	0.93 [a]	0.36 - 1.50	7.92 [a]	5.84 - 10.00
E. latimaculata	(N = 65)	0.44 [b]	-0.01 - 0.89	0.76 [a]	0.15 - 1.37	2.92 [b]	1.94 - 3.90
E. media	(N = 44)	2.75 [a]	1.40 - 4.09	0.53 [a]	0.07 - 0.99	9.11 [a]	6.71 - 11.50
E. pallida	(N = 45)	0.66 [b]	0.08 - 1.24	0.75 [a]	-0.25 - 1.76	4.32 [b]	2.64 - 6.01

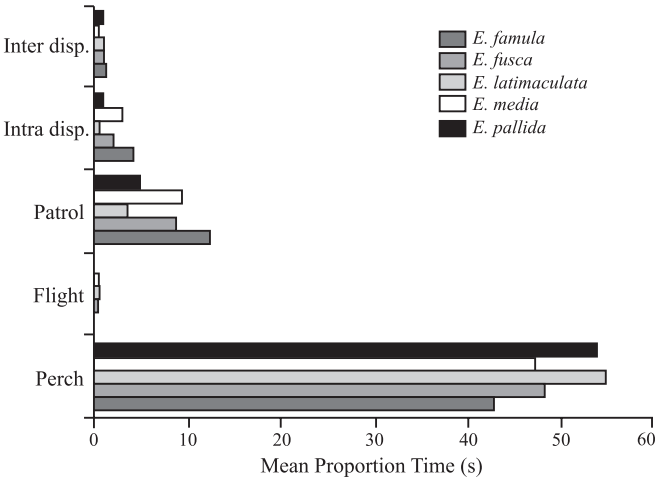

Fig. 1. Mean time (s) spent in the activities: perch, flight, patrol, intra- and interespecific territorial disputes by males of *E. fusca* (N = 54), *E. famula* (N = 24), *E. media* (N = 44), *E. pallida* (N = 45) and *E. latimaculata* (N = 65), at the APA São José, Tiradentes, MG, Brazil.

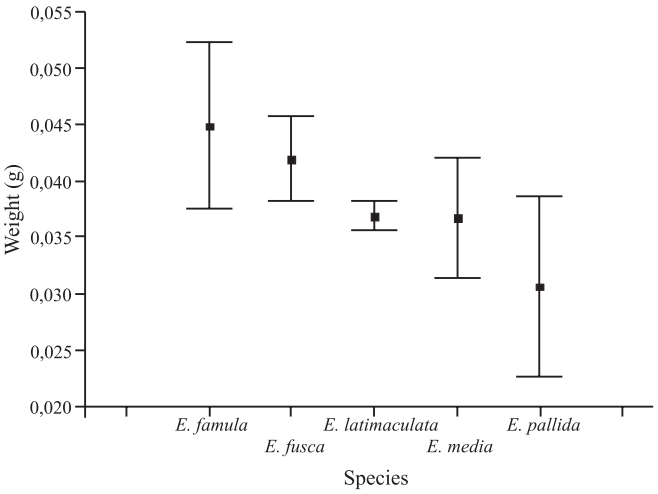

Fig. 2. Mean weight (g) for the five *Erythrodiplax* species at the APA São José, Tiradentes, MG, Brazil. Bars represent 95% confidence interval, and means are significantly different according to the analysis of variance (F = 5.05; d.f.= 4, 22; P<0.01).

behaviour. *E. famula, E. media* and *E. fusca* males spent more time in territorial disputes and patrol than *E. latimaculata* and *E. pallida* (Table I), but, all species spent little time in heterospecific territorial disputes (Table I), so differences on aggressive behaviour among these species are mainly due to intraspecific aggressiveness.

There are significant differences in body weight among species (F = 5.05; d.f. = 4, 22; P < 0.01). *E. famula* and *E. fusca* are larger than the other *Erythrodiplax* species, presenting similar body size (Fig. 2). *E. latimaculata, E. media* and *E. pallida* present similar body size, but, the last species presented the smaller individuals (Fig. 2). Despite these differences, the mean weight does not explain the time spent in patrol and territorial disputes for *Erythrodiplax* species (N = 5; t = 1.25; P = 0.29; R^2 = 0.35). Males of all species won or lost heterospecific disputes at the same frequency (χ^2 =8.6; d.f.=7; P=0.28; Table II). Territorial owners won heterospecific territorial disputes more frequently than intruders (Table III) and there are no differences in this pattern between the five species (χ^2=3.3; d.f.=4, P=0.50). Similarly, the resident *Erythrodiplax* males won intraspecific territorial disputes more frequently than intruders (Table III) and this effect was similar between the studied species (χ^2=6.06; d.f.=4; P=0.19).

DISCUSSION

An intruder would exclude a resident from its territory only if it had a higher territory defender's quality [Resource Holding Power - RHP (Parker 1974)] (Alonzo 2004; Lindström & Pampoulie 2004), but, this event looks like rare. This pattern may occurs: i) when resource is concentrated and throughout constant disputes, individuals with highest quality occupied territories with more resources (Kemp & Wiklund 2004; Koskimäki *et al.* 2004); ii) when territory property increases individual quality, for example, due to more food availability (Metcalfe *et al.* 2003) or, iii) when costs from territorial disputes are different to intruder and resident (Parker 1974).

For Odonata species, the territory defender's quality is frequently correlated to differences in body size. Larger males present frequently a higher lifetime mating success for diverse Libellulidae species, like *Sympetrum rubicundulum* (Say, 1839) (Van Buskirk 1987), *Plathemis lydia* (Drury, 1773) (Marden 1989), *Libellula luctuosa* Burmeister, 1839 (Moore 1996) and *Orthetrum chrysostigma* (Uhler, 1858) (Miller 1983). Moreover, this effect of body size on lifetime mating success means highly connected to territoriality (Sokolovska *et al.* 2000). In fact, space or resource competition is clearly

Table II. Number and percentage of success in heterospecific territorial disputes for *Erythrodiplax* species at the APA São José, Tiradentes, MG, Brazil.

Heterospecific disputes	Species winner				
	E. pallida	*E. media*	*E. latimaculata*	*E. fusca*	*E. famula*
E. pallida/ E. media	4 (57.1%)	3 (42.9%)	-	-	-
E. pallida/E. latimaculata	3 (50%)	-	3 (50%)	-	-
E. fusca/E. pallida	7 (77.8%)	-	-	2 (22.2%)	-
E. fusca/E. latimaculata	-	-	7 (63.6%)	4 (36.4%)	-
E. latimaculata/E. media	-	1 (20%)	4 (80%)	-	-
E.latimaculata/E. famula	-	-	3 (75%)	-	1 (25%)
E. fusca/E. famula	-	-	-	6 (42.9%)	8 (57.1%)
E. fusca/E. media	-	5 (83.3%)	-	1 (16.7%)	-

Table III. Number and percentage of success in heterospecific and intraspecific territorial disputes for intruder and resident males of *Erythrodiplax* species at the APA São José, Tiradentes, MG, Brazil.

	Heterospecific disputes		Intraspecific disputes	
	Intruder	Resident	Intruder	Resident
E. famula	2 (22.2%)	7 (77.8%)	4 (23.5%)	13 (76.5%)
E. fusca	1 (7.7%)	12 (92.3%)	8 (33.3%)	16 (66.7%)
E. latimaculata	5 (29.4%)	12 (70.6%)	2 (50%)	2 (50%)
E. media	3 (33.3%)	6 (66.7%)	3 (16.7%)	15 (83.3%)
E. pallida	2 (14.3%)	12 (85.7%)	0 (0%)	9 (100%)

related to population dynamics, so, aggressiveness should vary in function of body size (Parr 1983; Marden & Cobb 2004; Koskimäki *et al.* 2004).

However, in this study, in both intra- and heterospecific territorial disputes, the residents frequently won and maintained their territories. So, the individual residence prevails on heterospecific disputes, despite any morphological or behavioural differences and despite any competitive asymmetry among the species. Heterospecific aggressiveness may result from a complex interactions of asymmetries depending of kind of resources are limited (Aikio 2004) and body size prevalence must be replaced by residence like determinant source of asymmetry. Competitive asymmetry among species results from a trade-off between the territory size and the ability to compete for resources into the overlapping area (Aikio 2004). Individuals of larger territories will have larger overlapping areas, spending more energy to establish and to maintain their territories, what may decrease their ability to compete for resources and this trade-off may allow the coexistence of species with competitive asymmetries (Aikio 2004).

Dragonfly males dispute for territories with perches and/or oviposition substrates, aiming as final objective the mate acquisition and this cannot compensate heterospecific aggressiveness. Even if males of odonate larger species had enough advantages to exclude males of smaller species from their territories, the spent of energy in these disputes must not increase individual mating success because the final resource – females - is not disputed. Despite any costs associated to species co-occurrence, heterospecific aggressiveness may not evolve mainly because males are able to use visual cues to distinguish between hetero- and conspecific males (Schultz & Switzer 2001; Tynkkinen *et al.* 2004).

So, the low heterospecific aggressiveness of studied *Erythrodiplax* species must derive from the residence advantage between opponents, particularly, because in a system with mating territorial defence, intraspecific competition must be so more intense, that coexistence among similar species must be allowed, just as the classic Lotka-Volterra competition model predicted.

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REFERENCES

Aikio, S. 2004. Competitive asymmetry, foraging area size and coexistence of annuals. **Oikos 104**: 51–58.

Alcock, J. 1982. Post-copulatory mate guarding by males of the damselfly *Hetaerina vulnerata* Selys (Odonata: Calopterygidae). **Animal Behaviour 30**: 99–107.

Alcock, J. 1987. Male reproductive tactics in the libellulid dragonfly *Paltothemis lineatipes*: temporal partitioning of territories. **Behaviour 103**: 157–173.

Alonzo, S. H. 2004. Uncertainty in territory quality affects the benefits of usurpation in a Mediterranean wrasse. **Behavioral Ecology 15**: 278–285.

Altmann, J. 1974. Observational study of behavior: sampling methods. **Behaviour 49**: 227–267.

Corbet, P. S. 1962. **A biology of dragonflies.** London. Witherby. 247 p.

Corbet, P. S. 1999. **Dragonflies: behavior and ecology of Odonata.** Ithaca, Comstock Publ. Assoc. 829 p.

De Marco, P. Jr. 1998. The Amazonian campina dragonfly assemblage: patterns in microhabitat use and behaviour in a foraging habitat (Anisoptera). **Odonatologica 27**: 239–348.

De Marco, P. Jr. & A. O. Latini. 1998. Estrutura de guildas e riqueza de espécies em uma comunidade de larvas de Anisoptera (Odonata), p. 101–112. *In*: J. Nessimian & A. L. Carvalho (eds.). **Ecologia de Insetos Aquáticos**. Séries Oecologia Brasiliensis, vol. V. Rio de Janeiro. PPGE-UFRJ. 310 p.

De Marco, P. Jr.; A. O. Latini & D. C. Resende. 2005. Thermoregulatory constraints on behavior: patterns in a Neotropical dragonfly assemblage. **Neotropical Entomology 34**: 155–162.

De Marco, P. Jr. & D. C. Resende. 2002. Activity patterns and thermoregulation in a tropical dragonfly assemblage. **Odonatologica 31**: 129–138.

Fincke, O. 1992. Consequences of larval ecology for territoriality and reproductive success of a neotropical damselfly. **Ecology 73**: 449–462.

Gordon, D. M. 1997. The population consequences of territorial behavior. **Trends in Ecology & Evolution 12**: 63–66.

Heinrich, B. & T. M. Casey. 1978. Heat transfer in dragonflies: 'fliers' and 'perchers'. **Journal of Experimental Biology 74**: 17–36.

Hsu, Y.; R. L. Earley & L. L. Wolf. 2006. Modulation of aggressive behaviour by fighting experience: mechanisms and contest outcomes. **Biological Reviews 81**: 33–74.

International Dragonfly Fund. **World species list.** 2003. http://www.calopteryx.de/idf/. Access 18 May 2007.

Johnson, D. M. & P. H. Crowley. 1980. Habitat and seasonal segregation among coexisting odonate larvae. **Odonatologica 9**: 297–308.

Kemp, D. J. & C. Wiklund. 2004. Residency effects in animal contests. **Proccedings of the Royal Society of London 271**: 1707–1711.

Koskimäki, J.; M. J. Rantala; J. Taskinen; K. Tynkkynen & J. Suhonen. 2004. Immunocompetence and resource holding potential in the damselfly, *Calopteryx virgo* L. **Behavioral Ecology 15**: 167–173.

Lindström, K. & C. Pampoulie. 2004. Effects of resource holding potential and resource value on tenure at nest sites in sand gobies. **Behavioral Ecology 16**: 70–74.

Marden, J. H. 1989. Body building dragonflies: costs and benefits of maximizing flight muscle. **Physiological Zoology 62**: 505–521.

Marden, J. & J. R. Cobb. 2004. Territorial and mating success of dragonflies that vary in muscle power output and presence of gregarine gut parasites. **Animal Behaviour 68**: 857–865.

May, M. L. 1977. Thermoregulation and reproductive activity in tropical dragonflies of the genus *Micrathyria*. **Ecology 58**: 787–798.

May, M. L. 1979. Insect thermoregulation. **Annual Review of Entomology 24**: 313–349.

May, M. L. 1991. Thermal adaptations of dragonflies, revisited. **Advances in Odonatology 5**: 71–88.

McCauley, S. J. 2007. The role of local and regional processes in structuring larval dragonfly distributions across habitat gradients. **Oikos 116**: 121–133.

Metcalfe, N. B.; S. K. Valdimarsson & I. J. Morgan. 2003. The relative roles of domestication, rearing environment, prior residence and body size in deciding territorial contests between hatchery and wild juvenile salmon. **Journal of Applied Ecology 40**: 535–544.

Michiels, N. K. & A. A. Dhondt. 1990. Costs and benefits associated with oviposition site selection in the dragonfly *Sympetrum danae* (Odonata: Libellulidae). **Animal Behaviour 40**: 668–678.

Mikolajewski, J. D. & J. Johansson. 2003. Morphological and behavioral defenses in dragonfly larvae: trait compensation and cospecialization. **Behavioral Ecology 15**: 614–620.

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.

Moore, A. J. 1996. The evolution of sexual dimorphism by sexual selection: the separate effects of intrasexual selection and intersexual selection. **Evolution 44**: 315–331.

Osborn, R. & M. J. Samways. 1996. Determinants of adult dragonfly assemblage patterns at new ponds in South Africa. **Odonatologica 25**: 49–58.

Parker, G. 1974. Assessment strategy and the evolution of fighting behaviour. **Journal of Theoretical Biology 47**: 223–243.

Parr, M. J. 1983. An analysis of territoriality in libellulid dragonflies (Anisoptera: Libellulidae). **Odonatologica 12**: 39–57.

Pritchard, G. & A. Kortello. 1997. Roosting, perching, and habitat selection in *Argia vivida* Hagen and *Amphiagrion abbreviatum* (Selys) (Odonata: Coenagrionidae), two damselflies inhabiting geothermal springs. **Canadian Entomologist 129**: 733–743.

Resende, D. C. & P. De Marco, Jr. 2008. Residence and territorial characteristics of Libellulidae species in a Neotropical Assemblage. **Odonatologica 37**: 213–220.

Schultz, J. K. & P. Switzer. 2001. Pursuit of heterospecifics targets by territorial amberwing dragonflies (*Perithemis tenera* Say): a case of mistaken identity. **Journal of Insect Behavior 14**: 607–620.

Singer, F. 1990. Reproductive costs arising from incomplete habitat segregation among three species of *Leucorrhinia* dragonflies. **Behaviour 115**: 188–202.

Sokolovska, N.; L. Rowe & F. Johansson. 2000. Fitness and body size in mature odonates. **Ecological Entomology 25**: 239–248.

Tynkkinen, K.; M. J. Rantala & J. Suhonen. 2004. Interspecific aggression and character displacement in the damselfly *Calopteryx spledens*. **Journal of Evolutionary Biology 17**: 759–767.

Van Buskirk, J. 1986. Establishment and organization of territories in the dragonfly *Sympetrum rubicundulum* (Odonata:Libellulidae). **Animal Behaviour 34**: 1781–1790.

Van Buskirk, J. 1987. Influence of size and date of emergence on male survival and mating success in a dragonfly, *Sympetrum rubicundum*. **American Midland Naturalist 118**: 169–176.

Waage, J. K. 1988. Confusion over residency and the escalation of damselfly territorial disputes. **Animal Behaviour 36**: 586–595.

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