

Gregarine parasitism in two damselfly hosts: Comparison between species, sexes, and sites (Odonata: Calopterygidae)

Kamil Hupało^{1,3}, Michał Rachalewski¹, Dagmara Rachalewska²
& Grzegorz Tończyk¹

¹Department of Invertebrate Zoology and Hydrobiology, University of Lodz,
12/16 Banacha, 90-237 Łódź, Poland

²Department of Ecology and Vertebrate Zoology, University of Lodz, Poland

³Corresponding author; <hrupeq@gazeta.pl>

Received 13th July 2014; revised and accepted 16th October 2014

Abstract. We compared gregarine parasitism in imagines of *Calopteryx splendens* (Harris, 1780) and *C. virgo* (Linnaeus, 1758) collected at two sites with sympatric populations in the Spała Landscape Park, Łódź Province, Poland, in July 2012. Gregarine prevalence, intensity, wing load, and aggregation were compared between host species, sexes and sites. Among 140 individuals of both species collected from both sites, 81 (57.8%) hosted gregarines. The distribution of the parasites was aggregated ($k=1.0064$) and the highest intensity reached 40 parasites in a single host. There was no difference in gregarine prevalence between species. However, prevalence was different between sexes in both species. Females of *C. splendens* were more often parasitised at site 1, whereas in *C. virgo* males the prevalence was significantly higher at site 2. Secondly, the intensity of parasite infestation and aggregation rate was higher in *C. splendens* at both sampling sites, but we found no differences between sexes except at site 2 where males of *C. splendens* exhibited higher intensity. Thirdly, we found that the parasitism did not affect the damselflies' wing load. Our study revealed differences in patterns of gregarine infection between species, sexes and sampling sites, which confirm that this system of parasitism is complex and influenced by many factors such as physiology and behavior of the host, environmental conditions or availability of gregarine infectious stages.

Key words. Zygoptera, *Calopteryx splendens*, *Calopteryx virgo*, parasites

Introduction

Dragonflies are hosts to several groups of endoparasites, like tapeworms, horsehair worms, trematodes, and gregarines (CORBET 1999: 125 ff., 320 ff.; LOCKLIN & VODOPICH 2010), of which the last two have been studied in detail (FORBES & ROBB 2008). Gregarines are apicomplexans, inhabiting a great variety of marine, freshwater and terrestrial invertebrates, and occur-

ring in most invertebrate groups (CLOPTON 2002). Within arthropods, insects are the most commonly infested group, particularly orthopterans and odonates (LOCKLIN & VODOPICH 2010).

Gregarine infestations can occur both in adult damselflies and dragonflies and in their larvae (ÅBRO 1974). Odonate hosts ingest gregarine spores (oocysts) adhering to the legs of their prey, i.e. small dipterans (ÅBRO 1976; SIVA-JOTHY & PLAISTOW 1999). These spores are filled with sporozoites that afterwards develop into trophozoites, the gregarine feeding form. In the midgut of the host, trophozoites attach to the epithelium and start food ingestion. After maturation, they become gamonts, which can eventually mate to form gametocysts, containing infective sporozoites, and which are passed out with faeces. Following gametogenesis and fertilization, sporozoites form oocysts that can infest new hosts (ÅBRO 1971; FORBES & ROBB 2008; LOCKLIN & VODOPICH 2010). In a single host hundreds of trophozoites can be found, which harm the host by blocking its gut and by promoting bacterial infections, occasionally visible as brown spots on the host's abdomen (ÅBRO 1971). Within Odonata, mainly damselflies are infested by gregarines (FOERSTER 1938; ÅBRO 1974, 1996).

Gregarine–odonate interactions have been most studied in *Calopteryx* spp. (ÅBRO 1996; SIVA-JOTHY & PLAISTOW 1999; CLOPTON 2004; ILVONEN et al. 2011). Most of the past studies focus on measuring the prevalence of gregarines. ÅBRO (1996) also compared infestations between sexes in *Calopteryx virgo*. ILVONEN et al. (2011) were the first to identify differences in gregarine prevalence between sympatric and allopatric populations of two *Calopteryx* species. However, the number of studies considering multiple factors of gregarine infestation is scarce and for this reason we have compared prevalence, intensity, aggregation, and wing load.

The main aim of this study was to compare gregarine infestation of *Calopteryx splendens* (Harris, 1780) and *C. virgo* (Linnaeus, 1758), which have slightly different habitat requirements. Whereas *C. virgo* prefers cool, shaded, rapidly-flowing, narrow brooks often in forest or meadows, *C. splendens* inhabits partially open running waters and avoids cool and shaded ones (ZAHNER 1959, 1960). Despite these differences, sympatric populations exist due to the patchiness of riverside habitats (e.g., BERNARD et al. 2009: 50 ff.), thus enabling comparative studies of populations from the same

sampling site. The goal of this study was to determine how the environment can mediate gregarine infection in odonate hosts. We studied individuals from two sympatric populations of *C. virgo* and *C. splendens*, existing in relative proximity. We estimated the prevalence, intensity of infestation, aggregation of parasites and wing load, which indicates the maturity of an adult (GRABOW & RÜPPELL 1995; LOCKLIN & VODOPICH 2010).

Materials and methods

Individuals were collected at two sampling sites in Łódź Province, central Poland, on 14- and 15-vii-2012 at the Pilica River, the longest tributary of the Vistula River, and the Słomianka River, a tributary of the Pilica. Both sites were located in the Spała Landscape Park, 7 km from each other. Both sites offered different habitat conditions for damselflies. The study site on the Pilica River (site 1) was located near the middle of its course, representing an open river with reeds dominant in the riparian zone, in the center of the village of Spała (51°31'15.31"N, 20°08'04.45"E). In comparison, the Słomianka River (site 2; 51°30'27.28"N, 20°11'56.65"E) was smaller, with abundant littoral vegetation, which shaded almost the whole stream. Within each site, water temperature, dissolved oxygen, pH and electrical conductivity were measured with a WTW Multi 350i pocket meter (Tab. 1).

The damselflies were identified immediately after their capture. Subsequently, they were transported alive to the laboratory and decapitated on the day of collection. A total of 140 specimens were investigated, 70 (40 males, 30 females) of *C. splendens* and 70 (40 males, 30 females) of *C. virgo*. Immediately after decapitation, the abdomen of every individual was dissected to determine the level of gregarine infestation. The intestine was smeared on a slide with a drop of water and microscopically analysed (Nikon Eclipse E100, magnification 40×), the trophozoites and gamonts were counted without further identification.

Wing load ($\text{mg body weight} \times \text{wing surface area}^{-1}$) was used to evaluate the maturity of odonate imagines. To determine the wing surface area, hind wings were photographed and then the length of each wing was measured with COOLview 2.7.4 software (PRECOPTIC Co.). All damselflies were weighed to the nearest 0.01 g. The wing load for each specimen was calcu-

Table 1. Characteristics of the two sampling sites of this study in the Spała Landscape Park, Łódź Province, central Poland, as determined on 14- and 15-vii-2012.

	Site 1, Pilica	Site 2, Słomianka
Conductivity [$\mu\text{S}/\text{cm}$]	388	396
Water temperature [$^{\circ}\text{C}$]	15.3	11.6
pH value	8.591	7.915
Oxygen rate [mg/l]	9.30	8.55

lated in order to evaluate differences between parasitised and unparasitised dragonflies.

Statistical methods

Differences in gregarine prevalence (the proportion of infested hosts) between species, sexes and sampling sites were tested using a χ^2 test ($\alpha=0.05$). This test was also used to compare differences in parasite intensity (the number of parasites per infested individual), wing loads of infested versus uninfested individuals, between sexes, sampling sites and species and parasite aggregation.

The possible impact of the number of parasites on wing load of a single individual was estimated using linear regression analysis, performed in R software (R DEVELOPMENT CORE TEAM 2009).

Additionally, parasite aggregation (k) was estimated for all individuals, each species and each sampling site. When k is large (>20), the distribution is random; as k gets smaller, the parasite aggregation increases until k approaches zero and the aggregation reaches its highest value (WILSON et al. 2002).

Results

Among 140 collected individuals, 81 (57.8%) hosted gregarines. There was no significant difference in prevalence between the two species with 57.1% in *Calopteryx splendens* and 58.5% in *C. virgo*. However, difference in parasite prevalence between sexes in both species was detected (*C. splendens* males: 55%, females: 60%, $P<0.05$; *C. virgo* males: 62.5%, females: 53.3%, $P<0.05$) when all individuals from both sampling sites were combined

(Tab. 2). Differences in prevalence between individuals from site 1 compared to those from site 2 combined were almost significant ($P=0.0575$). Gregarine prevalence was significantly higher in females of *C. splendens* from site 1 than in those from site 2. No significant differences in prevalence between males in both species were found. Different patterns of prevalence between sexes were observed. In site 1, females of both species had higher parasite prevalence than males, whereas in site 2 females had lower parasite prevalence than males (Fig. 1).

There was a significant difference in intensity, or the median intensity with interquartile range (IQR), between species, but there was none between gender (*C. splendens* median ♂ = 6.0, IQR = 4.25–8.5; median ♀ = 5.0, IQR = 3.0–8.0; $P>0.05$; *C. virgo* median ♂ = 2.0, IQR = 1.0–3.0; median ♀ = 2.5, IQR = 1.0–4.25; $P>0.05$) (Tab. 2). No differences were found in median intensity between sampling sites.

Median wing load ($\text{mg} \times \text{m}^{-2}$ with IQR) for infested vs uninfested males was 5.077 (4.379–5.432) vs 4.377 (4.062–4.761) in *C. splendens* and 5.668 (4.980–7.077) vs 5.359 (5.106–6.176) for *C. virgo*, respectively. The corresponding wing load ($\text{mg} \times \text{m}^{-2}$ with IQR) for infested vs uninfested females was 5.001 (4.888–6.483) vs 5.152 (4.693–6.254) for *C. splendens* and 5.601 (5.030–6.540) vs 5.024 (4.857–6.787) for *C. virgo*, respectively. No differences were detected between the wing load of infested and uninfested individuals in relation to sex or to species (Tab. 2). A relation between wing load of a specimen and the amount of gregarines hosted was evaluated, but no significant tendency was found. There were no differences in wing load between sampling sites (Tab. 2).

The distribution of parasite intensity for both species combined was aggregated ($k=1.0064$) with one infected male of *C. splendens* having 40 parasites. The highest number of gregarines in one *C. virgo* host was seven. However, the distribution of gregarines was significantly less aggregated in *C. virgo* ($k=9.8014$) than in *C. splendens* ($k=1.3864$). Additionally, there was no clear pattern of aggregation between sexes: the males of *C. splendens* had significantly higher aggregation ($k=1.0811$) in comparison to conspecific females ($k=3.6021$), whereas aggregation in males of *C. virgo* was lower ($k=96.8$) than in conspecific females ($k=6.4286$). Moreover, para-

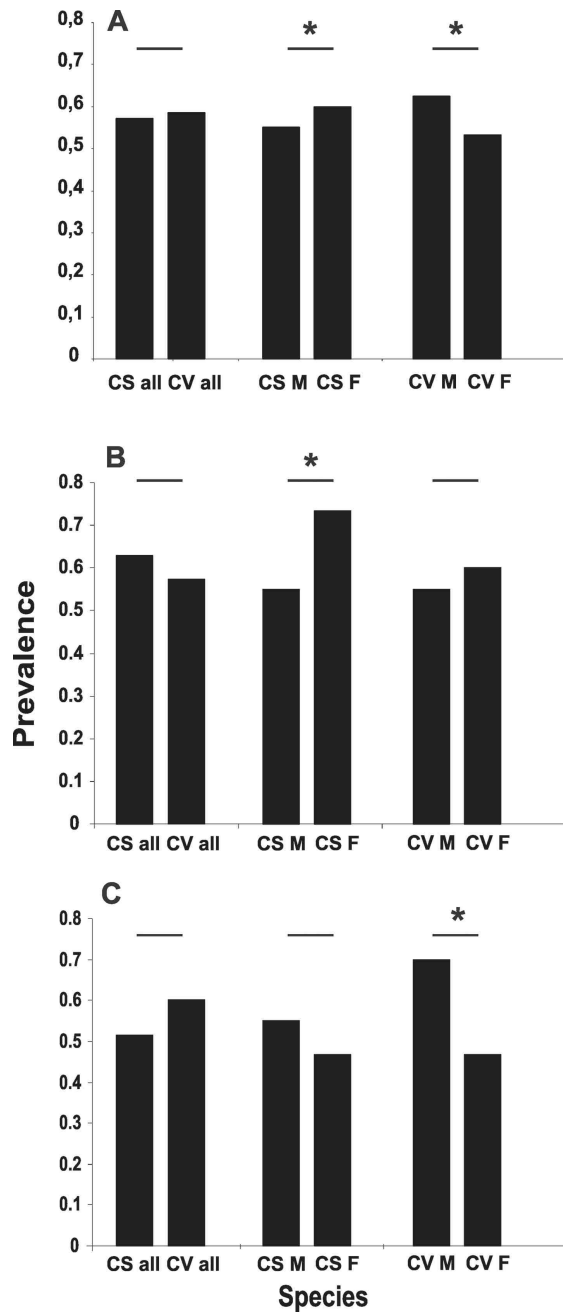


Figure 1. Gregarine prevalence of *Calopteryx* species at two study sites in the Spała Landscape Park, Łódź Province, central Poland; CS – *C. splendens*; CV – *C. virgo*; M – males; F – females; **A** – both sites combined; **B** – Gregarine prevalence in individuals at site 1; **C** – Gregarine prevalence in individuals at site 2. Significant differences are marked with an asterisk.

Table 2. Number of individuals of *Calopteryx splendens* and *C. virgo* infested and uninfested with gregarines, collected on 14- and 15-vii-2012 at two sites in the Spała Landscape Park, Łódź Province, central Poland. Additionally, the table shows gregarine prevalence, median intensity (Int Med) with interquartile ranges (IQR), maximum intensity (Int Max), and median wing loads with interquartile ranges for infested (WL Median_{inf}) and uninfested individuals (WL Median_{uninf}) of both species, sexes, and sites.

Species	Infected	Not infected	Prevalence	Int Med (with IQR)	Int Max	WL Median _{inf}	WL Median _{uninf}
<i>C. splendens</i> , all	40	30	0.571	5 (3.75-8.25)	40	5.001 (4.596-5.613)	4.693 (4.084-5.304)
males	22	18	0.55	6 (4.25-8.5)	40	5.077 (4.379-5.432)	4.377 (4.062-4.761)
females	18	12	0.6	5 (3.0-8.0)	17	5.001 (4.888-6.483)	5.152 (4.693-6.254)
<i>C. virgo</i> , all	41	29	0.586	2 (1.0-4.0)	7	5.662 (4.980-6.928)	5.195 (4.947-6.283)
males	25	15	0.625	2 (1.0-3.0)	6	5.668 (4.980-7.077)	5.359 (5.106-6.176)
females	16	14	0.533	2.5 (1.0-4.25)	7	5.601 (5.030-6.540)	5.024 (4.857-6.787)
<i>C. splendens</i> , site 1	22	13	0.629	5 (3.0-6.75)	17	4.896 (4.379-5.004)	4.691 (4.109-4.770)
males	11	9	0.55	5 (3.5-6.0)	7	4.421 (4.115-5.119)	4.204 (4.018-4.734)
females	11	4	0.733	5 (3.0-8.5)	17	4.981 (4.798-5.001)	4.828 (4.693-5.058)
<i>C. virgo</i> , site 1	20	15	0.571	2 (1.0-3.0)	7	6.318 (5.119-7.397)	5.215 (4.885-6.798)
males	11	9	0.55	1 (1.0-2.0)	4	7.292 (5.713-7.594)	5.297 (5.082-6.457)
females	9	6	0.6	3 (1.0-4.0)	7	5.539 (5.081-6.846)	5.035 (4.805-6.525)
<i>C. splendens</i> , site 2	18	17	0.514	7 (4.0-9.0)	40	5.770 (5.118-6.604)	4.736 (4.076-5.858)
males	11	9	0.55	9 (5.5-10.5)	40	5.366 (4.893-6.181)	4.447 (4.073-4.890)
females	7	8	0.467	4 (1.0-8.0)	9	6.616 (5.637-7.382)	5.677 (4.571-7.233)
<i>C. virgo</i> , site 2	21	14	0.6	2 (1.0-4.0)	6	5.344 (4.735-5.855)	5.167 (4.957-6.190)
males	14	6	0.7	2.5 (1.0-4.0)	6	5.221 (4.771-5.766)	5.719 (5.167-6.068)
females	7	8	0.467	2 (1.0-4.5)	6	5.662 (5.001-6.094)	5.024 (4.918-6.397)

sites present in individuals from site 2 were significantly more aggregated ($k=0.74674$) than in those from site 1 ($k=2.72063$).

Discussion

Gregarine prevalence and intensity varies among dragonfly species and between sexes (ÅBRO 1996; HECKER et al. 2002; LAJEUNESSE et al. 2004; CANALES-LAZCANO et al. 2005; LAJEUNESSE 2007; ILVONEN et al. 2011). Physiological and behavioural conditions may determine the exposure to and ingestion of gregarine oocysts or alter the tolerance to attached trophozoites (LOCKLIN & VODOPICH 2010). Within one species there are often gender differences in life history, physiology and behaviour (ZUK & MCKEAN 1996). ÅBRO (1996) was the first to find disparities in gregarine infestation in *Calopteryx*. He noticed that females of *Calopteryx virgo* hosted more parasites and often used lower parts of the habitat than males, which may have exposed females more to oocyst ingestion (ÅBRO 1996). In our study we found no significant differences for both prevalence and intensity between sexes in *C. virgo* in either sampling site. The same was true for *Calopteryx splendens*, except at site 2 where males harbored more parasites than females. This leads to the assumption that apart from behavioural and physiological differences between sexes, environmental conditions may also play a major role in gregarine parasitism.

Habitat-specific environmental conditions can affect the transmission of parasites within host populations (HALMETOJA et al. 2000; LAFFERTY & KURIS 2005; MORLEY 2007; AMANO et al. 2008). Environmental parameters, such as water current, electrical conductivity and temperature, might affect the distribution, availability, and viability of infective oocysts and this may contribute to differences in parasitism between populations. The difference in gregarine prevalence and intensity between *Calopteryx* species recorded at site 1 and site 2 (Tab. 2) is noticeable. Most physicochemical parameters measured at both sites were similar, apart from water temperature (Tab. 1). The Słomianka River, a narrow and largely shaded stream overgrown by vegetation, has much lower water temperature in comparison to the Pilica River, which is a wide, open river exposed to sunlight. In addition, Pilica has a wide riparian zone which offers better conditions not only for *Calo-*

pteryx damselflies, but also for other insects like dipterans which may transmit gregarines adhering to their legs (ÅBRO 1976; SIVA-JOTHY & PLAISTOW 1999). *Calopteryx* females and most dipterans tend to fly and forage near the woodland floor and water surface, and this may explain the fact that in site 1 females of both *Calopteryx* species were more infested with parasites than at other sites (ÅBRO 1996). Therefore, infection rate may be a function of the environment as well as species-specific physiology and behaviour.

High aggregation is by far the most predominant pattern across natural host–parasite relationships (POULIN 2006). In our study *C. splendens* individuals hosted more gregarines, which were more aggregated, than in *C. virgo* individuals. Moreover, intensity of infestation and aggregation values differed between sampling sites for both species.

Similar to the results of LOCKLIN & VODOPICH (2010), we found that the wing load of infected individuals did not significantly differ from that of uninfected individuals (Tab. 1). Gregarine parasitism appears neither to increase nor to decrease the weight of the host. However, it is known that gregarines may have a negative impact on the host's fitness (ÅBRO 1987, 1990; SIVA-JOTHY & PLAISTOW 1999) by decreasing survival and mating success of male hosts (CÓRDOBA-AGUILAR 2002; CÓRDOBA-AGUILAR et al. 2003; MARDEN & COBB 2004; FORBES & ROBB 2008). On the other hand, in some cases, gregarine infection has no apparent impact on the host (RODRIGUEZ et al. 2007; LOCKLIN & VODOPICH 2010). Further long-term investigations of the influence of gregarines on their odonate hosts are necessary to improve understanding of gregarine and dragonfly ecology.

A possible explanation of the differences in parasite infestation between co-existing species may be the so-called parasite-mediated competition theory (HALDANE 1949; BARBEHENN 1969). This states that two similar and competing species can coexist if parasites affect the stronger competitor more, thus providing an advantage to the weaker one. When *C. splendens* and *C. virgo* coexist sympatrically, there is competition for territories, and uninfested populations of *C. virgo* seem to be stronger (TYNKKYNNEN et al. 2004, 2006). ILVONEN et al. (2011) showed that in sympatric populations in Finland, *C. virgo* had a high prevalence of gregarines thus weakening their competitiveness. In our study no significant differences in parasite preva-

lence between species was found, but the intensity of gregarine infection was higher in *C. splendens* individuals in both studied populations. These findings suggest either that *C. splendens* is a better competitor than *C. virgo* in certain habitats or that the parasite-mediated competition theory is not applicable in all cases.

In conclusion, our study shows that there are differences in patterns of gregarine infestation between species, sexes and sampling sites. Notably, all the differences between species and sexes at one site are reversed at the other site. However, these differences cannot be explained either by the host's behaviour and physiology alone or by the parasite-mediated competition theory. The most probable explanation is that environmental factors mediate the level of infestation in individuals. Variation in gregarine infestation of odonate populations offers many opportunities for further studies. There are certain questions that still need to be answered concerning this host-parasite system. Is there only one gregarine species which infects *Calopteryx* species or do *Calopteryx* species serve as hosts to multiple gregarine species? Where exactly are the feeding sites of adult males and females of both *Calopteryx* species? Which species are the intermediate hosts for gregarines? On which of the intermediate hosts does *Calopteryx* feed? Further investigation of these questions is crucial for a better understanding of Odonata and Gregarina interactions. Our study emphasizes the particular importance that environmental factors may play in gregarine parasitism.

Acknowledgments

We are grateful to Michał Grabowski for helpful comments on the manuscript. We also thank Marek Nowicki, Aleksandra Prasek, Anna Rychter, Martyna Pszeniczna, and Rafał Świechowski for help in sampling.

References

- | | |
|--|---|
| ÅBRO A. 1971. Gregarines: Their effects on damselflies (Odonata: Zygoptera). <i>Entomologica scandinavica</i> 2: 294-300 | ÅBRO A. 1976. The mode of gregarine infection in zygoptera (Odonata). <i>Zoologica scripta</i> 5: 265-275 |
| ÅBRO A. 1974. The gregarine infection in different species of Odonata from the same habitat. <i>Zoologica scripta</i> 3: 111-120 | ÅBRO A. 1987. Gregarine infection of zygoptera in diverse habitats. <i>Odonatologica</i> 3: 119-128 |

- ÅBRO A. 1990. The impact of parasites in adult populations of Zygoptera. *Odonatologica* 19: 223-233
- ÅBRO A. 1996. Gregarine infection of adult *Calopteryx virgo* L. Odonata: Zygoptera. *Journal of natural History* 30: 855-859
- AMANO H., HAYASHI K. & KASUYA E. 2008. Avoidance of egg parasitism through submerged oviposition by tandem pairs in the water strider, *Aquarius paludum insularis* (Heteroptera: Gerridae). *Ecological Entomology* 33: 560-563
- BARBEHENN K.R. 1969. Host-parasite relationships and species diversity in mammals: an hypothesis. *Biotropica* 1: 29-35
- BERNARD R., BUCZYŃSKI P., TOŃCZYK G. & WENDZONKA J. 2009. A distribution atlas of dragonflies (Odonata) in Poland. Bogucki Wyd. Naukowe, Poznań
- BRIED J.T. & ERVIN G.N. 2007. Intraspecific models and spatiotemporal context of size-mass relationships in adult dragonflies. *Journal of the North American Benthological Society* 26: 681-693
- CANALES-LAZCANO J., CONTRERAS-GARDUNO J. & CÓRDOBA-AGUILAR A. 2005. Fitness-related attributes and gregarine burden in a non-territorial damselfly *Enallagma praevarum* Hagen (Zygoptera: Coenagrionidae). *Odonatologica* 34: 123-130
- CLAUSNITZER V. 2009. *Calopteryx splendens*. IUCN 2012. IUCN Red List of Threatened Species. Version 2012.1
- CLOPTON R.E. 2002. Phylum Apicomplexa Levine, 1970: Order Eugregarinorida Léger, 1900. In: Lee J.J., Leedale G., Patterson D. & Bradbury P.C. (Eds), Illustrated guide to the Protozoa. 2nd ed.: 205-288. Society of Protozoologists, Lawrence, KS
- CLOPTON R.E. 2004. *Calyxocephalus karyopera* g. nov., sp. nov. (Eugregarinorida: Actinocephalidae: Actinocephalinae) from the ebony jewelwing damselfly *Calopteryx maculata* (Zygoptera: Calopterygidae) in southeast Nebraska, USA: Implications for mechanical prey-vector stabilization of exogenous gregarine development. *Comparative Parasitology* 71: 141-153
- CORBET P.S. 1999. Dragonflies: behavior and ecology of Odonata. Cornell University Press, Ithaca, NY
- CÓRDOBA-AGUILAR A. 2002. Wing pigmentation in territorial male damselflies, *Calopteryx haemorrhoidalis*: a possible relation to sexual selection. *Animal Behaviour* 63: 759-766
- CÓRDOBA-AGUILAR A., SALAMANCA-OCAÑA J.C. & LOPEZARAIZA M. 2003. Female reproductive decision and parasite burden in a calopterygid damselfly (Insecta: Odonata). *Animal Behaviour* 66: 81-87
- FOERSTER H. 1938. Gregarinen in schlesischen Insekten. *Zeitschrift für Parasitenkunde* 10: 157-209
- FORBES M.R. SMITH K.E. & SMITH B.P. 1999. Parasitism of *Sympetrum* dragonflies by *Arrenurus planusmites*: maintenance of resistance particular to one species. *International Journal for Parasitology* 29: 991-999
- FORBES M.R. & ROBB T. 2008. Testing hypotheses about parasite mediated selection using odonate hosts. In: Córdoba-Aguilar A. (Ed.), Dragonflies & damselflies: models organisms for ecological and evolutionary research: 175-188. Oxford University Press, New York
- GRABOW K. & RÜPPELL G. 1995. Wing loading in relation to size and flight characteristics of European Odonata. *Odonatologica* 24: 175-186

- HALDANE J.B.S. 1949. Disease and evolution. *La Ricerca scientifica, Supplemento* 19: 68-76
- HALMETOJA A., VALTONEN E.T. & KOSKENNIEMI E. 2000. Perch (*Perca fluviatilis* L.) parasites reflect ecosystem conditions: a comparison of a natural lake and two acidic reservoirs in Finland. *International Journal for Parasitology* 30: 1437-1444
- HECKER K.R., FORBES M.R. & LÉONARD N.J. 2002. Parasitism of damselflies (*Enallagma boreale*) by gregarines: sex biases and relations to adult survivorship. *Canadian Journal of Zoology* 80: 162-168
- ILVONEN S., ILVONEN J.J., KAUNISTO K., M. KRAMS I. & SUHONEN J. 2011. Can infection by eugregarine parasites mediate species coexistence in *Calopteryx* damselflies? *Ecological Entomology* 36: 582-587
- LAFFERTY K.D. & KURIS A.M. 2005. Parasitism and environmental disturbances. In: Thomas F., Guegen F. & Renaud F. (Eds), *Parasitism and ecosystems*: 113-123. Oxford University Press, Oxford
- LAJEUNESSE M.J. 2007. Ectoparasitism of damselflies by water mites in central Florida. *Florida Entomologist* 15: 765-778
- LAJEUNESSE M.J., FORBES M.R. & SMITH B.P. 2004. Species and sex biases in ectoparasitism of dragonflies by mites. *Oikos* 106: 501-508
- LOCKLIN J.L. & VODOPICH D.S. 2009. Bidirectional gender biases of gregarine parasitism in two coexisting dragonflies (Anisoptera: Libellulidae). *Odonatologica* 38: 133-140
- LOCKLIN J.L. & VODOPICH D.S. 2010. Patterns of gregarine parasitism in dragonflies: host, habitat, and seasonality. *Parasitology Research* 107: 75-87
- MARDEN J.H. & COBB J.R. 2004. Territorial and mating success of dragonflies that vary in muscle power output and presence of gregarine gut parasites. *Animal Behaviour* 68: 857-865
- MORLEY N.J. 2007. Anthropogenic effects of reservoir construction on the parasite fauna of aquatic wildlife. *Ecohealth* 4: 374-383
- POULIN R. 2006. *Evolutionary ecology of parasites*. 2nd ed. Princeton University Press, Princeton
- RODRIGUEZ Y., OMOTO C.K. & GOMULKIEWICZ R. 2007. Individual and population effects of eugregarine, *Gregarina niphandrodes* (Eugregarinida: Gregarinidae), on *Tenebrio molitor* (Coleoptera: Tenebrionidae). *Environmental Entomology* 36: 689-693
- SIVA-JOTHY M.T. & PLAISTOW S.J. 1999. A fitness cost of eugregarine parasitism in a damselfly. *Ecological Entomology* 24: 465-470
- TYNKKYNEN K., RANTALA M.J. & SUHONEN J. 2004. Interspecific aggression and character displacement in the damselfly *Calopteryx splendens*. *Journal of Evolutionary Biology* 17: 759-767
- TYNKKYNEN K., KOTIAHO J.S., LUOJUMÄKI M. & SUHONEN J. 2006. Interspecific territoriality in *Calopteryx* damselflies: the role of secondary sexual characters. *Animal Behaviour* 71: 299-306
- WILSON K., BJØRNSTAD O.N., DOBSON A.P., MERLER S., POGLAYEN G., RANDOLPH S.E., READ A.F. & SKORPING A. 2002. Heterogeneities in macroparasite infections: patterns and processes. In: Hudson P.J., Rizzoli A., Grenfell B.T., Heesterbeek H. & Dobson A.P. (Eds), *The ecology of wildlife diseases*: 6-44. Oxford University Press, New York
- ZAHNER R. 1959. Über die Bindung der mitteleuropäischen *Calopteryx*-Arten (Odonata, Zygoptera) an den Lebensraum des strömenden Wassers. I. Der Anteil der Lar-

ven an der Biotopbindung. *Internationale Revue der gesamten Hydrobiologie und Hydrographie* 44: 51-130

ZAHNER R. 1960. Über die Bindung der mitteleuropäischen *Calopteryx*-Arten (Odonata, Zygoptera) an den Lebensraum des strömenden Wassers. II. Der Anteil der Imagines an der Biotopbindung. *Internationale Revue der gesamten Hydrobiologie und Hydrographie* 45: 101-123

ZUK M. & MCKEAN K.A. 1996. Sex differences in parasitic infection: patterns and processes. *International Journal for Parasitology* 26: 1009-1024

