

CHAPTER 6

Odonata immunity, pathogens, and parasites

Adam Z. Hasik, Jaakko J. Ilvonen, Adam M. Siepielski, and Rosalind L. Murray

Overview

Parasites and pathogens are a ubiquitous threat facing organisms within every ecological network. To protect themselves from parasites, organisms have evolved immune defenses. Insect immunity has received a great deal of attention, with numerous studies investigating the intersection of parasite pressure, immune function, and ecology. This chapter highlights how the investigation of odonate immunity has provided insight into how insect immunity operates within the ecological theatre under the threat of parasites. It first explains why odonates are an excellent model system for studies of immunity and parasites. It then reviews what is known of the parasites odonates harbor. Then, it covers the myriad mechanisms employed by odonates to defend themselves from their parasitic enemies. It also discusses key ecological and evolutionary studies that fall at the intersection of immunity and parasites.

6.1 Introduction

Parasites and pathogens (hereafter parasites) are part of every ecosystem. Host organisms have evolved immune defenses targeted toward reducing the costs associated with parasite infection. Insects have an innate immune function, which is generalized to resist many enemies (Siva-Jothy et al., 2005). Yet host organisms exist in complex ecological communities whereby they interact with not only their many parasites, but also competitors, predators, mutualists, and more.

Odonates are well suited for immunity and parasite studies. Their ecology is well known, and a wealth of studies have investigated the manner in which both dragonflies (Duong and McCauley 2016; McCauley et al., 2018; Murray et al., 2020) and damselflies (McPeck 1998; Gosden and Svensson 2009; Siepielski et al., 2020) persist in food webs, acquire resources, and complete their life cycle. The foundation provided by this detailed knowledge provides an ideal setting to

make connections between host–parasite interactions, immunity, and the other aspects of odonate ecology.

In addition to studies dedicated to understanding their ecology and role within ecological networks, odonates have been used as model study systems to investigate several parasites and immune parameters. Furthermore, odonates have a cosmopolitan distribution, making them an exemplar system to study how abiotic and biotic gradients contribute to changes in immunity and parasite pressure. Because they are so abundant and tractable for study, odonates are model organisms for both lab-based and field-based experimental and observational studies.

This chapter provides an overview of immunity and parasites in odonates. First, it explores the many parasites known to attack odonate hosts. Second, it reviews components of odonate immunity. Third, it examines the ecology and evolution of host–parasite interactions and odonate immunity. Finally, it highlights promising avenues for future research, both currently

under-studied areas and novel research areas for both odonate parasites and immunity.

6.2 Parasites

6.2.1 Viruses

Viruses exist in both larval and adult odonates (Rosario et al., 2013; Dayaram et al., 2015; Johnston et al., 2015). As a group, these findings demonstrate that odonate viruses are ubiquitous and are not specific to a given life stage or geographical location, nor do they have an association with shared ancestry. However, studies of viruses in odonates frequently examine abdomens (including the gut) and this may be a methodological issue, as odonates may accumulate viruses from the lower trophic levels. Such studies can help us understand the presence of viruses in general but become problematic if the goal is to discover viruses that infect odonates specifically. Indeed, Rosario and colleagues (2013) discovered a mastrevirus (typically a plant parasite) in *Erythemis vesiculosa* and *E. fusca*.

6.2.2 Bacteria

Few studies have explored the relationship between odonate hosts and their bacteria. Janssens and Stoks (2013, 2014) studied how a non-pathogenic *E. coli* bacteria affected odonate individuals. Collectively, they found that infection increased PO, reduced fat storage, and reduced internal accumulation of the bacterium, in addition to both decreasing and increasing growth rates (changes in body mass). These latter findings imply that infected individuals may speed up their growth to shorten their exposure time to the parasitic environment (Janssens and Stoks 2014).

6.2.3 Gregarines

Gregarines (Apicomplexa: Eugregarinorida) are protozoan **endoparasites** often found in both larval and adult odonates (Ilvonen et al., 2018; McDevitt-Galles et al., 2018). However, they have not been found in newly emerged adults (Åbro 1974; Locklin and Vodopich 2010), suggesting that either transmission from larvae to adults does not occur and the different gregarine species are stage specific, or that gregarines pass into the hemocoel of the **ecdysing** adults and re-emerge in the newly reformed gut afterwards. Hosts become infected by ingesting oocysts that are either transmitted by a prey vector (e.g. small dipterans, see Åbro 1976) or by drinking oocyst-infected water

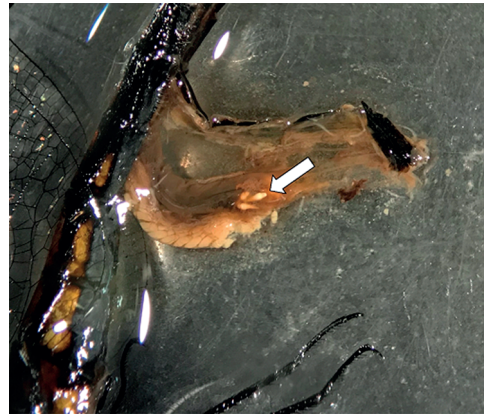


Figure 6.1 Female *Leucorrhinia intacta* dragonfly infected with gregarines (denoted by the white arrow). In this case, infection is so severe that the gut is almost completely full of gregarines. Image credit: Kari M. Kaunisto.

(Córdoba-Aguilar and Munguia-Steyer 2013). Infective stages of gregarines are then excreted into the local environment by their hosts.

Gregarines use their host's nutrients to develop, grow, and reproduce, which can be particularly costly for the hosts if they cannot compensate for those lost nutrients (Tsubaki and Hooper 2004). When infection is severe, gregarines can also cause ruptures and gut wall ulcerations, potentially blocking the intestinal tract in extreme cases (Figure 6.1; Åbro 1974). These negative effects likely reduce the host's fat accumulation, further reducing the host's general condition (Siva-Jothy and Plaistow 1999), egg production (Córdoba-Aguilar et al., 2003), or muscle formation (Schilder and Marden 2007b). However, these costs tend to be associated with severe gregarine infections, gregarines do not appear to have a marked effect on their hosts if their numbers are low enough (Locklin and Vodopich 2010).

6.2.4 Trematodes

Several studies have reported **trematodes** in different odonate species (Macy and Basch 1972; McDevitt-Galles et al., 2018; Rusconi et al., 2020), but how the presence of these parasites affects odonates remains unclear. However, some patterns of trematode–odonate interactions have been observed. First, odonate larvae often serve as second intermediate hosts or **paratenic hosts** for trematodes. Because of this, the numbers of trematodes infecting odonates tend to be associated with the environmental factors that

correlate with the definitive hosts of the trematodes (Koprivnikar et al., 2017). Second, single trematode species can infect several odonate species (Moravec and Skoriková 1998; Park et al., 2004; Rusconi et al., 2020). Finally, there are large differences in the level of trematode infections observed between odonate hosts (Rusconi et al., 2020). Surveys of odonates and trematodes continue to be useful for elucidating host–parasite interactions, although further studies are required to determine whether and how trematode infections impact odonate physiology and ecology.

6.2.5 Water mites

Water mite larvae (Acari: Hydrachnida) are **ectoparasites** of adult odonates (Figure 6.2), leaving when the host returns to water to reproduce, after which the mites complete their life cycle as predatory adults (Smith et al., 2010). Larval water mites actively seek their hosts, and even track the emergence of their “preferred” host species (Smith 1988; Forbes et al., 2002). Depending on the species, water mites find their odonate host either in aquatic habitats by attaching to larval odonates as they emerge from the water (McDevitt-Galles et al., 2018) or in terrestrial habitats by waiting for an adult odonate to land on emergent vegetation (Forbes and Robb 2008). Larval water mites are opportunistic parasites, and single species can infect numerous odonate species (Zawal and Szlauer-Lukaszewska 2012; Zawal and Buczyński 2013), while a single odonate species can be infected by several

water mite species (Zawal and Szlauer-Lukaszewska 2012; Mlynarek et al., 2013).

Water mite parasitism is affected by both host traits (e.g. body mass) and environmental factors (e.g. pH, conductivity, dissolved oxygen, and air temperature, see Hasik & Siepielski 2022; LoScerbo et al., 2020; da Silva et al., 2021). There is also substantial variance in mite prevalence between and within species (Hasik & Siepielski 2022; Ilvonen et al., 2016; Worthen and Hart 2016; Ilvonen et al., 2018), although there appears to be no general trend toward either sex being more infected (Ilvonen et al., 2016).

Larval water mites ingest odonate **hemolymph** through a feeding tube that pierces the host’s cuticle (Fig. 14.2a in Forbes and Robb 2008). Infection with water mites not only reduces host survival, but can also hinder the host’s movements when infection is severe (Åbro 1982; Forbes and Baker 1991). Though it is a general defensive mechanism, resistance to water mites is known to vary. Specifically, resistance is greater when the host is rare (Forbes et al., 1999; Lajeunesse et al., 2004), increases with both the prevalence and intensity of parasitism (Nagel et al., 2010; Kaunisto et al., 2017), and increases with the degree of local adaptation to parasites (Gómez-Llano et al., 2020). Odonates resist larval water mites by encapsulating their feeding tubes, which blocks the mite’s access to hemolymph (Marmaras et al., 1996; Mlynarek et al., 2015). The effects of water mites on odonate hosts are varied and differential parasitism rates have been suggested as a mechanism that allows the coexistence of different color morphs within a species (Willink and Svensson 2017). Additionally, water mites can have a strong effect on intraspecific male–male competition and decrease mating success in both sexes (Gómez-Llano et al., 2020).

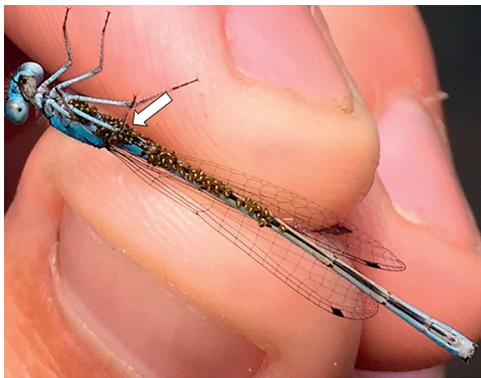


Figure 6.2 Male *Enallagma geminatum* damselfly with a “mite shirt.” This is when infection by mites (denoted by the white arrow) is so intense that many parts of the thorax and abdomen are obscured. Image credit: Adam Z. Hasik.

6.2.6 Parasitoids

There has been only one observation of an adult odonate being the target of a **parasitoid**. Von Ellenrieder and colleagues (2015) observed a tachinid fly larva emerge from an adult male *Hetaerina caja dominula* (Figure 6.3). **Egg parasitism**, on the other hand, is commonly observed in odonates (Harabiš et al., 2013; Harabiš et al., 2015; Harabiš et al., 2019). Odonate eggs are immobile and nutritious, a combination that makes them highly sought after by parasitoids. Parasitoid wasps of the order Hymenoptera are primarily generalist **idiobionts** that target a wide range of insect taxa, including odonate species. Prevalence of egg parasitism in odonates varies substantially from 0% to 92% (Reinhardt and



Figure 6.3 Adult male *Hetaerina caja dominula* damselfly parasitized by a tachinid fly larva. Image credit: von Ellenrieder et al., 2015.

Gerighausen 2001; Querino and Hamada 2009; Hara-biš et al., 2019) and depends on the host and parasite species, method of egg laying, and locality.

6.2.7 Coinfection

Few studies, limited to gregarines and water mite parasites, have explored the dynamics of odonate **coinfection**. Morrill and colleagues (2013) found no correlation between gregarines and live and resisted (dead) water mites, but they did find a negative correlation between the two parasites when using only live water mites. Conversely, Kaunisto and colleagues (2015) found a positive correlation between gregarine and water mite numbers, but a later study (Kaunisto et al., 2018) found a negative correlation between these two parasite types. Clearly, coinfection dynamics in odonate hosts would benefit from further investigation.

6.3 Odonate immunity

6.3.1 Overview of insect immunity

Insect immunity is principally an innate rather than adaptive system (Siva-Jothy et al., 2005; González-Santoyo and Córdoba-Aguilar 2012). That is, insects have generalizable defenses protecting against a wide array of parasites, as opposed to the more nuanced adaptive immunity that relies on prior exposure. Despite the more general nature of insect immunity, parasite-mediated selection still plays a role in the evolution of immunity. Indeed, insects are known to have “immune memory” similar to that of vertebrates (Lanz-Mendoza and Garduño 2018), such that individual insects are more successful at defending

against a parasite to which they have been previously exposed. Indeed, work by Nagel and colleagues (2010) has shown that previous parasitism by water mites accurately predicted expression of resistance in a population of *Lestes disjunctus*. Next, we summarize several components of odonate immunity, trade-offs between immunity and life history, and how they relate to local ecological conditions.

6.3.2 Components of odonate immunity

Though several components of odonate immunity are used as defenses against parasites, the vast majority of odonate studies have investigated the **phenoloxidase (PO)** cascade (Stoks et al., 2006; Contreras-Garduño et al., 2008b; De Block and Stoks 2008; Mlynarek et al., 2015; Hasik et al., 2021). This enzymatic cascade begins with the activation of PO and produces **melanin** as its end product, which is used to encase and kill foreign bodies.

Nitric oxide (NO) is used to induce cellular and humoral immune responses and cause damage to parasite DNA (Rivero 2006). NO has been used in far fewer studies of odonate immunity (Contreras-Garduño et al., 2008b; Córdoba-Aguilar et al., 2009; Córdoba-Aguilar et al., 2012), yet NO can exhibit differential expression to PO. For example, Córdoba-Aguilar and colleagues (2009) found that NO expression decreased somewhat during periods of limited resource availability, although PO was much more variable over the same period. There are also trade-offs between NO and certain aspects of host life-history, as *Hetaerina americana* females express 10× more NO than females that were submerged underwater (to emulate oviposition behavior, see Córdoba-Aguilar et al., 2012), despite no difference in PO expression among the two treatments. A more complete understanding of the influence of ecology on odonate immunity requires studies measuring NO. Researchers can then ask questions about which immune defenses are up- or down-regulated and under which contexts.

In addition to PO and NO, the hemolymph of odonates contains many hydrolytic enzymes used in defense against parasites. For example, Dhanalakshmi and Reniprha (2019) used zone-of-inhibition assays to show that dragonfly hemolymph had antimicrobial properties against bacteria. In a process like melanization, hemocytes phagocytize and encapsulate invading parasites (Robb and Forbes 2006; De Block and Stoks 2008). Studies investigating hydrolytic enzymes have found that, much like other components of immunity in odonates, females tend to have

heightened hemocyte concentrations and antibacterial activity compared to males (Robb and Forbes 2006, but see Rolff 2001). This could be due to either increased investment into immunity, or instead be a side-effect of the need for both PO and hemocytes for egg tanning, which is an important component of egg viability (Robb and Forbes 2006).

Hydrolytic enzymes in odonates also appear to be an age-dependent component of immune function. Mature damselflies have greater hemocyte concentration than newly emerged juveniles (Rolff 2001), and mature individuals suffering an immune challenge expressed greater concentrations than controls, despite there being no difference between the two treatments as newly emerged juveniles (Robb and Forbes 2006). Johnson and Rolff (2013) found that *Coenagrion puella* injected with *E. coli* up-regulated nine different immune genes, including genes responsible for hydrolytic enzymes and antimicrobial peptides. Up-regulation only during an immune challenge is likely adaptive, as a constant expression of a given component of immunity can result in self-harm for the host (Sadd and Siva-Jothy 2006).

While not a component of odonate immunity per se, exterior structures also play an important role in defending the host against parasites. The first line of defense is the cuticle, the hardened exoskeleton that many parasites must overcome to gain access to the host. Indeed, the thickness of dragonfly cuticles relative to those of damselflies may explain the comparatively low prevalence of ectoparasites in dragonflies (Ilvonen and Suhonen 2016; Ilvonen et al., 2018; LoScerbo et al., 2020). While fewer studies have investigated these exterior structures, another promising avenue for future study is the antimicrobial structures on dragonfly wings. These nanotextured surfaces shred bacteria (Bandara et al., 2017; Kamarajan and Muthusamy 2020), providing an antiseptic surface and another avenue of defense.

6.4 Ecology and evolution of immunity and parasites

6.4.1 PO and food webs

Numerous studies have examined how biological interactions such as predation and competition affect PO in odonates (Duong and McCauley 2016; Murray et al., 2020; Hasik et al., 2021). For example, male *Hetererina americana* damselflies compete for and defend territory that females use for oviposition (Contreras-Garduño et al., 2006; Contreras-Garduño et al., 2007;

Contreras-Garduño et al., 2008a). Territorial males that successfully defend and maintain a territory have an encapsulation ability ~50% greater than non-territorial males, yet these territorial bouts with other males can reduce encapsulation ability by ~60% (Contreras-Garduño et al., 2006). Encapsulation ability is correlated with fat reserves (Contreras-Garduño et al., 2006), and thus territorial male damselflies seem to prioritize competitive ability at the expense of immune function.

Though conspecific competition can decrease PO expression, predators can increase PO. Indeed, dragonfly larvae wound other dragonfly larvae when they attempt to consume them. Because wound repair requires PO-facilitated melanization, predator cues from these dragonflies increase melanization ability (Duong and McCauley 2016), and the mere presence of dragonfly predators increases melanization (Murray et al., 2020). Importantly, these effects of predators are likely restricted to invertebrate predators of odonates, as fish predators typically consume, not wound, larval odonates. Thus, it is unlikely that odonates living with fish will prime their immunity in the same manner.

Investigations of the effects of environmental factors at the larval stage have uncovered inconsistent relationships between resource availability, growth, and PO. For example, Hasik and colleagues (2021) found that PO in larval *E. signatum* was reduced in lakes with limited prey availability, yet there was no effect of increasing intraspecific competition on PO (Figure 6.4). Campero and colleagues (2008) exposed larval *Coenagrion puella* to a period of transient food stress, which caused a reduction in PO as adults. Jiménez-Cortés and colleagues (2012) provided larval *H. americana* with either two or five prey items and then measured body size and PO in adults and found that larvae experiencing resource limitation expressed reduced PO. These differences may be due to the length of resource limitation, as the larvae in Campero et al., (2008) were starved for a brief period and then returned to a normal diet, while those in Jiménez-Cortés et al., (2012) were given a constant reduced amount of food. It could be that growth is prioritized over PO in the short term, while neither growth nor PO can recover from extended periods of resource-limitation. Regardless, the contradictory and inconsistent relationships between PO and growth require further study to understand if PO is uncoupled from growth (as in Campero et al., 2008 and Hasik et al., 2021) or more closely tied to it (as in Jiménez-Cortés et al., 2012).

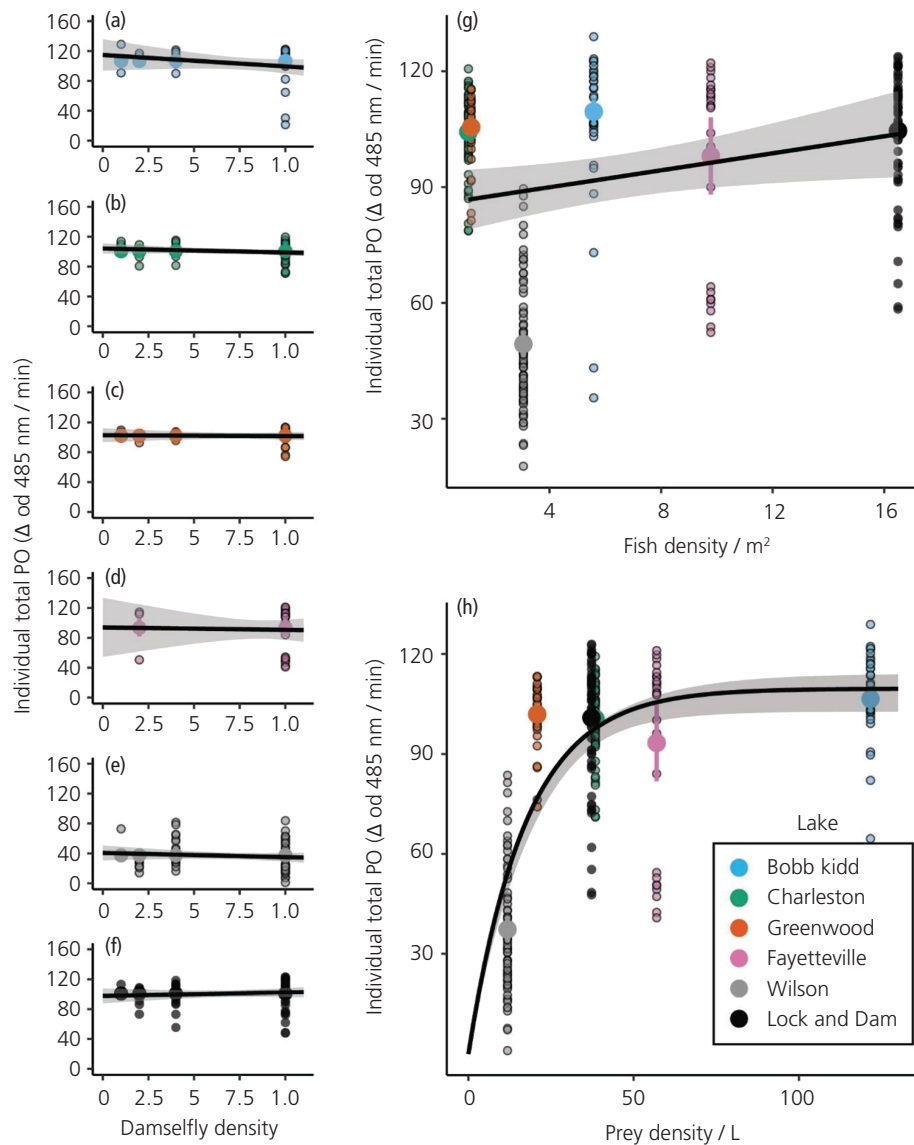


Figure 6.4 Total PO of larval *E. signatum* increased with prey availability (panel **h**) but did not decline as resource competition (panels **a-f**) or fish predator density (panel **g**) increased. Gray bands in all panels denote 95% CI, larger dark points in (**a-f**) denote density treatment means and one s.e., while larger dark points in (**g**) and (**h**) denote lake means and one s.e. Small, light points in all plots denote total PO activity values from individual damselflies. Image credit: Hasik et al., 2021, reprinted/adapted by permission from Springer Nature.

6.4.2 Metacommunity structure

Odonate parasites rely on their hosts for dispersal. Indeed, *Arrenurus* water mites utilize their insect hosts for dispersal (Bohonak et al., 2004) and gregarines are transported with their odonate hosts as they move from one suitable habitat to another (Cielocha et al., 2011). Because of this, odonates likely

determine the metacommunity structure of their parasites. Though no odonate studies have quantified host-parasite dynamics within metacommunities, hosts shape parasite metacommunity structure in other systems (Dallas and Presley 2014; Bolnick et al., 2020), including water mites attacking other insects (Baines et al., 2020). Metacommunity structure in odonates and

their parasites is likely to follow a hierarchical structure both among and within populations and species (e.g. Bolnick et al., 2020). For example, at the regional scale there exists a pool of species. These species are limited by their ability to disperse from one habitat to another, and further limited within these habitats via ecological filtering (McCauley 2007; Siepielski and McPeck 2013; Renault et al., 2018). Within a given community, hosts and their parasites are then going to be affected by the local abiotic and biotic factors driving host–parasite interactions. It follows that the metacommunity structure of odonate parasites is determined by their hosts, which is in turn determined by the local environment.

6.4.3 Coevolution

Though several studies have investigated interactions among odonate hosts and their parasites, the field currently lacks studies on coevolution between the two. Most studies have focused solely on odonate hosts, and few observational studies have investigated host–parasite interactions from the perspective of mite parasites (e.g. Forbes et al., 1999; Forbes et al., 2002; Lajeunesse et al., 2004). Forbes et al., (1999) investigated associations between the dragonfly host species *Symptetrum obtrusum* and *S. internum* and water mite parasite *A. planus* to understand if there were differences in the ability of *A. planus* to engorge on each host. They found that *A. planus* attacked both host species, yet *A. planus* was more successful at parasitizing *S. obtrusum* (only ~7% of mites resisted) compared to *S. internum* (~93% of mites resisted). Further work by Forbes et al., (2002) showed that *A. planus* appears to track the more susceptible *S. obtrusum* over the course of the season, such that mite numbers peaked during the period of maximum preferred-host availability. Interestingly, *S. obtrusum* was much more common during the study and *S. internum* was rarely encountered, suggesting that host availability could be important for understanding these patterns—mites may be adapting to the most common host species at the cost of adaptation to the less common (and more resistant) host species. Indeed, Lajeunesse et al. (2004) showed that infection by another mite species (*Limnochares americana*) was both more prevalent and intense in the more common host species (*Leucorrhinia frigida*) than the rare host (*Nannothemis bella*) in field surveys. Experimental infection trials showed that *L. americana* mites were more successful on *L. frigida* than *N. bella*, as the latter host species tended to resist the mites. Although these studies raise interesting questions about the nature of co-evolution among odonates and their parasites,

little work exists in this area, especially with regard to the perspective of the parasites and parasite fitness. Clearly, future studies are needed if we are to better understand the nature of host–parasite coevolution in odonates.

6.5 Future research directions

In addition to those key gaps we noted previously, we next outline several future research directions.

6.5.1 Genetics

The cryptic nature of infection by many odonate parasites makes detection difficult, and there is also no clear consensus on how many virus, bacteria, gregarine, and water mite species attack odonate hosts. Yet the rise of eDNA in freshwater systems (reviewed in Rees et al., 2014) will make detection and identification of many parasites more feasible. Such work has already been shown to be tractable for gregarines infecting other insect species (Singer et al., 2020).

Regarding immunity, an investigation of gene upregulation is necessary to understand which genes (if any) may be under selection. Previously, Johnston and Rolff (2013) utilized RNAseq to demonstrate that *C. puella* damselflies make use of two pathways to respond to wounding and an immune challenge, respectively. Nine immune genes related to melanization and antimicrobial peptides were upregulated when wounded (Johnston and Rolff 2013). These results open the door for an exciting avenue for future studies to investigate if and how immune genes are under selection in natural populations.

6.5.2 Microbiome

The gut microbiome plays important roles in host populations, providing nutrients, disrupting the ability of parasites to colonize the gut, and aiding immune defenses (reviewed in Engel and Moran 2013). Not only can parasites affect microbiome community composition (Fredensborg et al., 2020), but changes in the local environmental conditions (i.e. temperature) have been shown to correlate with changes in the gut microbiome and immunity (Ferguson et al., 2018). Indeed, the microbiome plays a major role in both the fitness and overall health of animals (Mueller and Sachs 2015; Lloyd-Price et al., 2016). However, further study is needed to know if and how microbiomes interact with host immunity and parasites in odonates. Previous studies suggest that adult dragonflies may have

more diverse microbiomes than other insects (Deb et al., 2019), and the gut microbiome of larvae differs from that of the adults (Nobles and Jackson 2020). These differences are potentially due to variation in prey availability during the two life stages (Deb et al., 2019). Such variation in the gut microbiome may have implications for how each life-stage interacts with its parasites. Interestingly, work with *Libellula pulchella* has shown that infection with gregarines can trigger metabolic syndrome (Schilder and Marden 2006, 2007a), a condition characterized by chronic changes in metabolism that often leads to obesity. Specifically, infection by gregarines interacts with the gut microbiome, resulting in chronic activation of p38 MAPK (a stress signaling pathway, see Schilder and Marden 2007a) and subsequent deposition of lipids around the flight muscles, which reduces muscle performance.

6.5.3 Climate change

A study of 105 odonate species predicted a poleward migration rate of 4.5km/year under the intermediate greenhouse gas emission scenario (Li and Park 2020). If odonates track favorable climatic conditions and move further toward the poles, several alterations in the outcome of host-parasite interactions are possible. Namely, odonates may suffer from increased parasitism. Water mite parasitism generally increases with mean diurnal temperature (da Silva et al., 2021), and if temperatures continue to rise and odonates cannot track favorable conditions or locally adapt to warmer temperatures, they may be subjected to additional parasitism. Furthermore, seasonality is an important predictor of both water mite and gregarine parasitism (Locklin and Vodopich 2010; Stolbov et al., 2020), pointing to another avenue by which parasitism may increase or decrease with changes in temperature, although this depends on both host and parasite species.

Beyond direct interactions with parasites, climate change may have indirect effects via effects on immunity. Moore and colleagues (2021) found that male dragonflies are selected to have less wing ornamentation in warmer climates, yet females do not face the same selection pressure. Because wing pigmentation is produced with melanin, this may be evidence for an environment-mediated tradeoff. That is, warmer temperatures result in less wing ornamentation, reducing male quality on average as wing spots are a sexually selected trait known to correlate with fat reserves, the ability to maintain a territory, and mating success (Contreras-Garduño et al., 2007; Contreras-Garduño

et al., 2008a; Córdoba-Aguilar et al., 2009). However, this may leave hosts less vulnerable to (and more able to defend against) parasites. This is possible, as certain odonate species have been shown to better resist water mite infection at increased temperatures (Robb and Forbes 2005). Thus, while increasing temperatures may reduce male quality via effects on wing spot pigmentation, male odonates may be better suited to defend themselves against parasites, resulting in selection on parasites to evolve more effective ways to exploit their odonate hosts.

6.6 Conclusions

Parasites are an ever-present part of the lives of odonates, during both their larval and adult stages. Consequently, odonates possess many immune defenses to mitigate the costs associated with these multifarious attacks. The usefulness of odonates for both experimental and observational studies has allowed us to learn a great deal about how both host-parasite interactions and immunity operate within complex ecological communities. However, there is more that we have yet to uncover. Namely, more work is needed to understand components of odonate immunity beyond PO. Additionally, the prior focus on ectoparasitic mites and endoparasitic gregarines means that our understanding of the many other parasites of odonates is limited. While previous studies provide the basis for understanding odonate immunity and parasites, the field is ready for further work to understand how interactions within communities can mediate host-parasite interactions and odonate immunity.

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References

- Åbro, A. (1974). The gregarine infection in different species of Odonata from the same habitat. *Zoologica Scripta* 3: 111–20.
- Åbro, A. (1976). The mode of gregarine infection in Zygoptera (Odonata). *Zoologica Scripta* 5: 265–75.

- Åbro, A. (1982). The effects of parasitic water mite larvae (*Arrenurus* spp.) on zygopteran imagoes (Odonata). *Journal of Invertebrate Pathology* **39**: 373–81.
- Baines, C. B., Diab, S., and McCauley, S. J. (2020). Parasitism risk and infection alter host dispersal. *The American Naturalist* **196**: 119–31.
- Bandara, C. D., Singh, S., Afara, I. O., Wolff, A., Tesfamichael, T., Ostrikov, K., and Oloyede, A. (2017). Bactericidal effects of natural nanotopography of dragonfly wing on *Escherichia coli*. *ACS Applied Materials & Interfaces* **9**: 6746–60.
- Bohonak, A. J., Smith, B. P., and Thornton, M. (2004). Distributional, morphological and genetic consequences of dispersal for temporary pond water mites. *Freshwater Biology* **49**: 170–80.
- Bolnick, D. I., Reserits, E. J., Ballare, K., Stuart, Y. E., and Stutz, W. E. (2020). Scale-dependent effects of host patch traits on species composition in a stickleback parasite metacommunity. *Ecology* **101**: e03181.
- Campero, M., De Block, M., Ollevier, F., and Stoks, R. (2008). Correcting the short-term effect of food deprivation in a damselfly: mechanisms and costs. *Journal of Animal Ecology* **77**: 66–73.
- Cielocha, J. J., Cook, T. J., and Clopton, R. E. (2011). Host utilization and distribution of nubenocephalid gregarines (Eugregarinorida: Actinocephalidae) parasitizing *Argia* spp. (Odonata: Zygoptera) in the central United States. *Comparative Parasitology* **78**: 152–60.
- Contreras-Garduño, J., Buzatto, B. A. Serrano-Meneses, M. A., Nájera-Cordero, K., and Córdoba-Aguilar, A. (2008a). The size of the red wing spot of the American rubyspot as a heightened condition-dependent ornament. *Behavioral Ecology* **19**: 724–32.
- Contreras-Garduño, J., Canales-Lazcano, J., and Córdoba-Aguilar, A. (2006). Wing pigmentation, immune ability, fat reserves and territorial status in males of the rubyspot damselfly, *Hetaerina americana*. *Journal of Ethology* **24**: 165–73.
- Contreras-Garduño, J., Canales-Lazcano, J., Jiménez-Cortés, J. G., Juárez-Valdez, N., Lanz-Mendoza, H., and Córdoba-Aguilar, A. (2008b). Spatial and temporal population differences in male density and condition in the American rubyspot, *Hetaerina americana* (Insecta: Calopterygidae). *Ecological Research* **24**: 21–9.
- Contreras-Garduño, J., Lanz-Mendoza, H., and Córdoba-Aguilar, A. (2007). The expression of a sexually selected trait correlates with different immune defense components and survival in males of the American rubyspot. *Journal of Insect Physiology* **53**: 612–21.
- Córdoba-Aguilar, A., Jiménez-Cortés, J. G., and Lanz-Mendoza, H. (2009). Seasonal variation in ornament expression, body size, energetic reserves, immune response, and survival in males of a territorial insect. *Ecological Entomology* **34**: 228–39.
- Córdoba-Aguilar, A. and Munguia-Steyer, R. (2013). The sicker sex: understanding male biases in parasitic infection, resource allocation and fitness. *PLoS ONE* **8**: e76246.
- Córdoba-Aguilar, A., Ruiz-Silva, D., González-Tokman, D., Contreras-Garduño, J., Peretti, A., Moreno-García, A. M., Rantala, M. J., Koskimäki, J., Kortet, R., and Suhonen, J. (2012). No firm evidence of immunological costs of insect oviposition and copulation: a test with dragonflies (Zygoptera). *Odonatologica* **41**: 7–15.
- Córdoba-Aguilar, A., Salamanca-Ocaña, J. C., and Lopezaraiza, M. (2003). Female reproductive decisions and parasite burden in a calopterygid damselfly (Insecta: Odonata). *Animal Behaviour* **66**: 81–7.
- da Silva, G. G., Poulin, R., and Guillermo-Ferreira, R. (2021). Do latitudinal and bioclimatic gradients drive parasitism in Odonata? *International Journal for Parasitology* **51**: 463–70.
- Dallas, T. and Presley, S. J. (2014). Relative importance of host environment, transmission potential and host phylogeny to the structure of parasite metacommunities. *Oikos* **123**: 866–74.
- Dayaram, A., Potter, K. A., Pailles, R., Marinov, M., Rosenstein, D. D., and Varsani, A. (2015). Identification of diverse circular single-stranded DNA viruses in adult dragonflies and damselflies (Insecta: Odonata) of Arizona and Oklahoma, USA. *Infection, Genetics and Evolution* **30**: 278–87.
- De Block, M. and Stoks, R. (2008). Short-term larval food stress and associated compensatory growth reduce adult immune function in a damselfly. *Ecological Entomology* **33**: 796–801.
- Deb, R., Nair, A., and Agashe, D. (2019). Host dietary specialization and neutral assembly shape gut bacterial communities of wild dragonflies. *PeerJ* **7**: e8058.
- Dhanalakshmi, G. and Reniprha, A. (2019). The antibacterial effect of dragonfly larvae *Diplocodes trivialis* (Rambur) haemolymph the food borne pathogens in raw meat. *International Research Journal of Engineering and Technology* **6**: 2784–9.
- Duong, T. M. and McCauley, S. J. (2016). Predation risk increases immune response in a larval dragonfly (*Leucorhinia intacta*). *Ecology* **97**: 1605–10.
- Engel, P. and Moran, N. A. (2013). The gut microbiota of insects – diversity in structure and function. *FEMS Microbiology Reviews* **37**: 699–735.
- Ferguson, L. V., Dhakal, P., Lebenzon, J. E., Heinrichs, D. E., Bucking, C., and Sinclair, B. J. (2018). Seasonal shifts in the insect gut microbiome are concurrent with changes in cold tolerance and immunity. *Functional Ecology* **32**: 2357–68.
- Forbes, M. R., Muma, K. E., and Smith, B. P. (1999). Parasitism of *Sympetrum* dragonflies by *Arrenurus planus* mites: maintenance of resistance particular to one species. *International Journal for Parasitology* **29**: 991–9.
- Forbes, M. R., Muma, K. E., and Smith, B. P. (2002). Diffuse coevolution: constraints on a generalist parasite favor use of a dead-end host. *Ecography* **25**: 345–51.

- Forbes, M. R. and Robb, T. (2008). Testing hypotheses about parasite-mediated selection using odonate hosts. In: *Dragonflies & damselflies: model organisms for ecological and evolutionary research*. Córdoba-Aguilar, A. (ed), pp. 175–88. Oxford University Press, New York.
- Forbes, M. R. L. and Baker, R. L. (1991). Condition and fecundity of the damselfly, *Enallagma ebrium* (Hagen): the importance of ectoparasites. *Oecologia* **86**: 335–41.
- Fredensborg, B. L., Fossdal Í Kálvalið, I., Johannesen, T. B., Stensvold, C. R., Nielsen, H. V., and Kapel, C. M. O. (2020). Parasites modulate the gut-microbiome in insects: a proof-of-concept study. *PLoS One* **15**: e0227561.
- Gómez-Llano, M., Narasimhan, A., and Svensson, E. I. (2020). Male-male competition causes parasite-mediated sexual selection for local adaptation. *The American Naturalist* **196**: 344–54.
- González-Santoyo, I. and Córdoba-Aguilar, A. (2012). Phenoloxidase: a key component of the insect immune system. *Entomologia Experimentalis et Applicata* **142**: 1–16.
- Gosden, T. P. and Svensson, E. I. (2009). Density-dependent male mating harassment, female resistance, and male mimicry. *The American Naturalist* **173**: 709–21.
- Harabiš, F., Dolný, A., Helebrandová, J., and Rusková, T. (2015). Do egg parasitoids increase the tendency of *Lestes sponsa* (Odonata: Lestidae) to oviposit underwater? *European Journal of Entomology* **112**: 63–8.
- Harabiš, F., Rusková, T., and Dolný, A. (2019). Different oviposition strategies of closely related damselfly species as an effective defense against parasitoids. *Insects* **10**: 26.
- Harabiš, F., Sigut, M., and Dolný, A. (2013). Density-distribution patterns of egg parasitoids in freshwater habitats. *Acta Musei Silesiae. Scientiae Naturales* **62**: 65–72.
- Hasik, A. Z., Tye, S. P., Ping, T., and Siepielski, A. M. (2021). A common measure of prey immune function is not constrained by the cascading effects of predators. *Evolutionary Ecology*: 1–18.
- Hasik, A. Z., and A. M. Siepielski. 2022. A role for the local environment in driving species-specific parasitism in a multi-host parasite system. *Freshwater Biology* 67:1571–1583.
- Ilvonen, J. J., Kaunisto, K. M., and Suhonen, J. (2016). Are sexes equally parasitized in damselflies and dragonflies? *Oikos* **125**: 315–25.
- Ilvonen, J. J., Kaunisto, K. M., and Suhonen, J. (2018). Odonates, gregarines and water mites: why are the same host species infected by both parasites? *Ecological Entomology* **43**: 591–600.
- Ilvonen, J. J. and Suhonen, J. (2016). Phylogeny affects host's weight, immune response and parasitism in damselflies and dragonflies. **33**: 160421.
- Janssens, L. and Stoks, R. (2013). Exposure to a widespread non-pathogenic bacterium magnifies sublethal pesticide effects in the damselfly *Enallagma cyathigerum*: From the suborganismal level to fitness-related traits. *Environmental Pollution* **177**: 143–9.
- Janssens, L. and Stoks, R. (2014). Non-pathogenic aquatic bacteria activate the immune system and increase predation risk in damselfly larvae. *Freshwater Biology* **59**: 417–26.
- Jiménez-Cortés, J. G., Serrano-Meneses, M. A., and Córdoba-Aguilar, A. (2012). The effects of food shortage during larval development on adult body size, body mass, physiology and developmental time in a tropical damselfly. *Journal of Insect Physiology* **58**: 318–26.
- Johnson, P. R. and Rolff, J. (2013). Immune- and wound-dependent differential gene expression in an ancient insect. *Developmental & Comparative Immunology* **40**: 320–4.
- Johnston, P. R., Mikolajewski, D. J., and Rolff, J. (2015). Identification of viruses associated with larvae of the dragonfly *Leucorrhinia dubia*, and damselfly *Coenagrion puella* from RNA sequencing data. *International Journal of Odonatology* **18**: 81–8.
- Johnston, P. R. and Rolff, J. (2013). Immune- and wound-dependent differential gene expression in an ancient insect. *Developmental & Comparative Immunology* **40**: 320–4.
- Kamarajan, B. P. and Muthusamy, A. (2020). Survival strategy of *Pseudomonas aeruginosa* on the nanopillar topography of dragonfly (*Pantala flavescens*) wing. *AMB Express* **10**: 1–12.
- Kaunisto, K. M., Kaunisto, P., Ilvonen, J. J., and Suhonen, J. (2017). Parasitism, immune response, and egg production of the spearhead bluet (*Coenagrion hastulatum*) damselfly. *Canadian Journal of Zoology* **95**: 367–72.
- Kaunisto, K. M., Kaunisto, P., Vahtera, V., and Suhonen, J. (2015). Populations of the damselfly *Coenagrion hastulatum* at the edge of the species range have fewer gregarine and water mite parasites. *Freshwater Biology* **60**: 794–801.
- Kaunisto, K. M., Morrill, A., and Forbes, M. R. (2018). Negative covariance between water mite and gregarine parasitism for adult dragonflies, *Leucorrhinia intacta* (Hagen): an age-related pattern? *Parasitology Research* **117**: 3909–15.
- Koprivnikar, J., Urichuk, T. M. Y., and Szuroczki, D. (2017). Influences of habitat and arthropod density on parasitism in two co-occurring host taxa. *Canadian Journal of Zoology* **95**: 589–97.
- Lajeunesse, M. J., Forbes, M. R., and Smith, B. P. S. (2004). Species and sex biases in ectoparasitism of dragonflies by mites. *Oikos* **106**: 501–8.
- Lanz-Mendoza, H. and Garduño, J. C. (2018). Insect innate immune memory. In: *Advances in comparative immunology*. Cooper, E. (ed), pp. 193–211. Springer, Cham.
- Li, F. and Park, Y.-S. (2020). Habitat availability and environmental preference drive species range shifts in concordance with climate change. *Diversity and Distributions* **26**: 1343–56.
- Lloyd-Price, J., Abu-Ali, G., and Huttenhower, C. (2016). The healthy human microbiome. *Genome Medicine* **8**: 1–11.
- Locklin, J. L. and Vodopich, D. S. (2010). Patterns of gregarine parasitism in dragonflies: host, habitat, and seasonality. *Parasitology Research* **107**: 75–87.
- LoScerbo, D., Farrell, M. J., Arrowsmith, J., Mlynarek, J., and Lessard, J.-P. (2020). Phylogenetically conserved host traits and local abiotic conditions jointly drive the geography of parasite intensity. *Functional Ecology* **34**: 2477–87.

- Macy, R. W. and Basch, P. F. (1972). *Orthetrotrema monostomum* gen. et sp. n., a Progenetic Trematode (Dicrocoeliidae) from Dragonflies in Malaysia. *The Journal of Parasitology* **58**: 515–18.
- Marmaras, V. J., Charalambidis, N. D., and Zervas, C. G. (1996). Immune response in insects: the role of phenoloxidase in defense reactions in relation to melanization and sclerotization. *Archives of Insect Biochemistry and Physiology* **31**: 119–33.
- McCauley, S. J. (2007). The role of local and regional processes in structuring larval dragonfly distributions across habitat gradients. *Oikos* **116**: 121–33.
- McCauley, S. J., Hammond, J. I., and Mabry, K. E. (2018). Simulated climate change increases larval mortality, alters phenology, and affects flight morphology of a dragonfly. *Ecosphere* **9**: e02151.
- McDevitt-Galles, T., Calhoun, D. M., and Johnson, P. T. J. (2018). Parasite richness and abundance within aquatic macroinvertebrates: testing the roles of host- and habitat-level factors. *Ecosphere* **9**: e02188.
- McPeck, M. A. (1998). The consequences of changing the top predator in a food web: a comparative experimental approach. *Ecological Monographs* **68**: 1–23.
- Mlynarek, J. J., Iserbyt, A., Nagel, L., and Forbes, M. R. (2015). Differential water mite parasitism, phenoloxidase activity, and resistance to mites are unrelated across pairs of related damselfly species. *PLoS One* **10**: 0115539.
- Mlynarek, J. J., Knee, W., and Forbes, M. R. (2013). Relative geographic range of sibling species of host damselflies does not reliably predict differential parasitism by water mites. *BMC Ecology* **13**: 1–10.
- Moore, M. P., Hersch, K., Stricharoen, C., Lee, S., Reice, C., Rice, P., Kronick, S., Medley, K. A., and Fowler-Finn, K. D. (2021). Sex-specific ornament evolution is a consistent feature of climatic adaptation across space and time in dragonflies. *Proceedings of the National Academy of Sciences of the United States of America* **118**: e2101458118.
- Moravec, F. and Skoříková, B. (1998). Amphibians and larvae of aquatic insects as new paratenic hosts of *Anguillicola crassus* (Nematoda: Dracunculoidea), a swimbladder parasite of eels. *Diseases of Aquatic Organisms* **34**: 217–22.
- Morrill, A., Mlynarek, J. J., and Forbes, M. R. (2013). Explaining covariation between endo- and ecto-parasites in spreadwing damselflies (Zygoptera: Lestidae). *Canadian Journal of Zoology* **91**: 761–5.
- Mueller, U. G. and Sachs, J. L. (2015). Engineering microbiomes to improve plant and animal health. *Trends in Microbiology* **23**: 606–17.
- Murray, R. L., Tah, S., Koprivnikar, J., Rowe, L., and McCauley, S. J. (2020). Exposure to potentially cannibalistic conspecifics induces an increased immune response. *Ecological Entomology* **45**: 355–63.
- Nagel, L., Tonia, R., and Forbes, M. R. (2010). Inter-annual variation in prevalence and intensity of mite parasitism relates to appearance and expression of damselfly resistance. *BMC Ecology* **10**: 5.
- Nobles, S. and Jackson, C. R. (2020). Effects of life stage, site, and species on the dragonfly gut microbiome. *Microorganisms* **8**: 183.
- Park, B., Kim, E., Cho, M., Park, J., Lee, J., Eo, S., and Chae, J. (2004). Prevalence and phylogeny of metacercariae of trematode in adult dragonflies in Chungbuk Province, Korea. In: *Animal health: a breakpoint in economic development? Proceedings of the 11th International Conference of the Association of Institutions for Tropical Veterinary Medicine and 16th Veterinary Association Malaysia Congress, August 23–27*. Fatimah Iskander, C. T. N., Abu, J., Hassan, L., Arshad, S. S., Dhalwadi, G. K., bin Salim, N., Yusoff, R., Aziz, S. A., Omar, A. R., Daud, H. M., Khan Goriman Kahn, M. A., Rahman, S. O. A., and Meng, G. Y. (eds), pp. 368–9. Universiti Putra Malaysia Press, Serdang.
- Querino, R. B. and Hamada, N. (2009). An aquatic microhymenopterous egg-parasitoid of *Argia insipida* Hagen in Selys (Odonata: Coenagrionidae) and biological observations in the Central Amazon, Brazil. *Neotropical Entomology* **38**: 346–51.
- Rees, H. C., Maddison, B. C., Middleditch, D. J., Patmore, J. R. M., and Gough, K. C. (2014). Review: The detection of aquatic animal species using environmental DNA – a review of eDNA as a survey tool in ecology. *Journal of Applied Ecology* **51**: 1450–9.
- Reinhardt, K. and Gerighausen, U. (2001). Oviposition site preference and egg parasitism in *Symptecma paedisca* (Odonata: Lestidae). *International Journal of Odonatology* **4**: 221–30.
- Renault, D., Laparie, M., McCauley, S. J., and Bonte, D. (2018). Environmental adaptations, ecological filtering, and dispersal central to insect invasions. *Annual Review of Entomology* **63**: 345–68.
- Rivero, A. (2006). Nitric oxide: an antiparasitic molecule of invertebrates. *Trends in Parasitology* **22**: 219–25.
- Robb, T. and Forbes, M. R. (2005). On understanding seasonal increases in damselfly defence and resistance against ectoparasitic mites. *Ecological Entomology* **30**: 334–41.
- Robb, T. and Forbes, M. R. (2006). Age-dependent induction of immunity and subsequent survival costs in males and females of a temperate damselfly. *BMC Ecology* **6**: 1–13.
- Rolff, J. (2001). Effects of age and gender on immune function of dragonflies (Odonata, Lestidae) from a wild population. *Canadian Journal of Zoology* **79**: 2176–80.
- Rosario, K., Padilla-Rodriguez, M., Kraberger, S., Stainton, D., Martin, D. P., Breitbart, M., and Varsani, A. (2013). Discovery of a novel mastrevirus and alphsatellite-like circular DNA in dragonflies (Epirocta) from Puerto Rico. *Virus Research* **171**: 231–7.
- Rusconi, J. M., Di Battista, C., Balcazar, D., Rosales, M., and Achinelly, M. F. (2020). *Amphimermis enzoni* n. sp. (Nematoda: Mermithidae) parasitizing damselflies and dragonflies in Argentina. *The Journal of Nematology* **52**: 1–9.

- Sadd, B. M. and Siva-Jothy, M. T. (2006). Self-harm caused by an insect's innate immunity. *Proceedings of the Royal Society B: Biological Sciences* **273**: 2571–4.
- Schilder, R. J. and Marden, J. H. (2006). Metabolic syndrome and obesity in an insect. *PNAS* **103**: 18805–9.
- Schilder, R. J. and Marden, J. H. (2007a). Metabolic syndrome in insects triggered by gut microbes. *Journal of Diabetes Science and Technology* **1**: 794–6.
- Schilder, R. J. and Marden, J. H. (2007b). Parasites, proteomics and performance: effects of gregarine gut parasites on dragonfly flight muscle composition and function. *Journal of Experimental Biology* **210**: 4298–4306.
- Siepielski, A. M., Hasik, A. Z., Ping, T., Serrano, M., Strayhorn, K., and Tye, S. P. (2020). Predators weaken prey intraspecific competition through phenotypic selection. *Ecology Letters* **23**: 951–61.
- Siepielski, A. M. and McPeck, M. A. (2013). Niche versus neutrality in structuring the beta diversity of damselfly assemblages *Freshwater Biology* **58**: 758–68.
- Singer, D., Duckert, C., Hedénec, P., Lara, E., Hiltbrunner, E., and Mitchell, E. A. D. (2020). High-throughput sequencing of litter and moss eDNA reveals a positive correlation between the diversity of Apicomplexa and their invertebrate hosts across alpine habitats. *Soil Biology and Biochemistry* **147**: 107837.
- Siva-Jothy, M. T., Moret, Y., and Rolff, J. (2005). Insect immunity: an evolutionary ecology perspective. *Advances in Insect Physiology* **32**: 1–48.
- Siva-Jothy, M. T. and Plaistow, S. J. (1999). A fitness cost of eugregarine parasitism in a damselfly. *Ecological Entomology* **24**: 465–70.
- Smith, B. P. (1988). Host-parasite interaction and impact of larval water mites on insects. *Annual Review of Entomology* **33**: 487–507.
- Smith, I. M., Cook, D. R., and Smith, B. P. (2010). Water mites (Hydrachnidia) and other arachnids. In: *Ecology and classification of North American freshwater invertebrates* (3rd edn). Thorp, J. H. and Covich, A. P. (eds), pp. 485–586. Academic Press, San Diego.
- Stoks, R., De Block, M., Slos, S., Van Doorslaer, W., and Rolff, J. (2006). Time constraints mediate predator-induced plasticity in immune function, condition, and life history. *Ecology* **84**: 809–15.
- Stolbov, V. A., Semerikov, F. I., and Tupitsyn, S. S. (2020). Parasitism of Odonata by *Arrenurus* water mites (Acariformes, Hydrachnidia, Arrenuridae) in Western Siberia. *Odonatologica* **49**: 323–32.
- Tsubaki, Y. and Hooper, R. E. (2004). Effects of eugregarine parasites on adult longevity in the polymorphic damselfly *Mnais costalis* Selys. *Ecological Entomology* **29**: 361–6.
- von Ellenrieder, N., Hauser, M. Kinnee, S., and O'Hara, J. E. (2015). First record of a parasitoid tachinid fly (Diptera: Tachinidae) on a dragonfly (Odonata: Calopterygidae). *Studia dipterologica* **21**: 335–41.
- Willink, B. and Svensson, E. I. (2017). Intra- and intersexual differences in parasite resistance and female fitness tolerance in a polymorphic insect. *Proceedings of the Royal Society B: Biological Sciences* **284**: 20162407.
- Worthen, W. B. and Hart, T. M. (2016). Resistance to *Arrenurus* spp. parasitism in odonates: patterns across species and comparisons between a resistant and susceptible host. *Journal of Insect Science* **16**: 37.
- Zawal, A. and Buczyński, P. (2013). Parasitism of Odonata by *Arrenurus* (Acari: Hydrachnidia) larvae in the Lake Świdwie, nature reserve (NW Poland). *Acta Parasitologica* **58**: 486–95.
- Zawal, A. and Szlauer-Lukaszewska, A. (2012). Water mite parasites (Hydrachnidia) of odonates from the nature reserve "Jezioro Szare," Northwestern Poland. *Odonatologica* **41**: 267–75.