Ecological differentiation, interference, and coexistence in Odonata

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Overview

Recent work in coexistence theory has begun to more fully consider the diverse factors that may foster or retard species coexistence and the spatial scales over which this may occur. This chapter considers how ecological differentiation and interference may influence coexistence in Odonata. Studies of ecological differentiation have revealed how resource competition and predatorprey interactions may foster species coexistence, but they have also revealed evidence of neutrality among co-occurring odonate species. Both niche and neutral processes may simultaneously shape odonate assemblages, which can arise locally as well as regionally among different populations. Common forms of interspecific interference in Odonata include intraguild predation at the larval stage, and aggression (e.g. territorial fighting) and reproductive interference (e.g. attempted mating) at the adult stage. Currently, more is known about the evolutionary effects of interference between co-occurring species than about how interference impacts coexistence. In theory, intraspecific interference mechanisms, such as sexual conflict and territoriality, could promote coexistence by increasing intraspecific density-dependence relative to interspecific density-dependence. Conversely, interspecific interference could hinder local coexistence while promoting regional coexistence. Odonata is a promising taxon for advancing a general understanding of the role of interference in coexistence, in part because the types and intensity of interference vary within clades that exhibit minimal ecological differentiation. Ultimately, understanding how coexistence mechanisms structure Odonata communities will require investigating the roles of ecological differentiation and interference at both the larval and adult stages.

15.1 Introduction

From the bank of a pond or stream on a sunny day, one might see a half dozen or more colorful species of dragonflies and damselflies, perching, hovering, flying, hunting, mating—all within meters of each other. Species diversity is not exceptionally high in Odonata, compared to other insect orders, but it can certainly be more apparent to a casual observer. With a few notable exceptions, most odonates are generalist invertivores at both larval and adult stages (Corbet 1999). How is it possible for multiple species in the same feeding guild to co-occur? Are there feedback mechanisms that enable species to coexist stably? Or do species only co-occur transiently within a landscape of sources and sinks, connected by dispersal? We do not yet have clear answers to these questions, but the small spatial scale at which it is possible to study some species, particularly damselflies, combined with the tractability of experimental manipulations in the field, makes this a promising group for investigating factors that contribute to, and potentially maintain, species diversity at both local and regional scales.

The basic goals of this chapter are to succinctly review what is known about the mechanisms promoting coexistence in odonates and point to areas

Gregory F. Grether et al., *Ecological differentiation, interference, and coexistence in Odonata.* In: *Dragonflies and Damselflies.* Second Edition. Edited by Alex Córdoba-Aguilar, Christopher D. Beatty and Jason T. Bried, Oxford University Press. © Oxford University Press (2023). DOI: 10.1093/oso/9780192898623.003.0015 where more research is needed. It starts with a general introduction to modern coexistence theory. It then narrows in on specific factors that, in theory, might influence whether odonates coexist, including types of behavioral interference that are common in the field but rarely on the minds of theoretical ecologists. The empirical section roughly mirrors the order of presentation of topics in Section 15.2.

15.2 Coexistence theory

15.2.1 Local coexistence

Species that co-occur locally should not be assumed to coexist stably (Siepielski and McPeek 2010). In any natural assemblage, some co-occurring species might be "walking dead" (i.e. slowly going extinct, Hanski et al., 1996), or "sinks" maintained locally by immigration (Pulliam 1988), or subject to demographic neutrality (Hubbell 2001). Over time and across the landscape, species can shift between these categories. In the absence of rigorous empirical evidence for stable coexistence, the correct term to use is co-occurrence (Leibold and McPeek 2006).

Stable local coexistence requires each species in an assemblage to gain a demographic advantage when rare, such that it is buffered from extinction. The formal invasibility criterion is that each species can increase in population size as an "invader" (i.e. when rare) when all other "resident" species are at their respective single-species equilibria (Chesson 2000). Modern coexistence theory is a framework that explains the potential for competitors to coexist as a consequence of stabilizing effects and fitness differences (Chesson 2000). Stabilizing effects contribute to coexistence by reducing the demographic effects of interspecific competition while intensifying the effects of intraspecific competition. Stabilizing effects can result from ecological differences among species' niches, such as differences in resource use (e.g. prey items, foraging locations) or susceptibility to predators or pathogens (Adler et al., 2007). The signature of stabilization is that per-capita population growth rates (or surrogate vital rates) decline as species become common but increase as they become rare, which prevents competitive exclusion. In the absence of stabilizing effects, each species limits its own growth rate and the competing species' growth rate equally (see Figures 15.1 and 15.2 in Adler et al., 2007).

In coexistence theory terminology, fitness differences refer to frequency-independent demographic advantages and disadvantages that species have relative to each other. Fitness differences are manifested as inequalities in average per capita population growth rates between species and predict which species would go extinct in the absence of stabilizing effects (Chesson 2000). Fitness differences can arise from species differences in resource exploitation ability, susceptibility to shared predators, or reproductive capacity (Chesson and Kuang 2008). As fitness differences increase, stronger stabilizing effects are necessary for coexistence (Chesson 2000).

Species in an assemblage are considered ecologically equivalent if they have identical interaction strengths with all species outside the assemblage (e.g. predators, parasites, resources, mutualists) and the abiotic environment (McPeek and Siepielski 2019). When species are ecologically equivalent with no stabilizing effects operating and have identical fitness, neutral dynamics should eventually lead to the stochastic extinction of all but one species in a local community (Hubbell 2001). This stochastic march toward extinction can take so long that it may appear that local diversity is being maintained (McPeek and Gomulkiewicz 2005; Haney et al., 2015). Ecologically equivalent species can coexist stably, however, if their population growth rates are regulated in a negative density-dependent fashion by additional intraspecific processes or interactions with other species in the assemblage (Figure 15.1; McPeek 2012; McPeek and Siepielski 2019; Yamamichi et al., 2020; Gómez-Llano et al., 2021). For example, sexual conflict, mate competition, reproductive interference, and territoriality all have the potential to stabilize coexistence (see Sections 15.2.3 and 15.2.4). The canonical ecological differences among species (e.g. consuming different prey, being consumed by different predators) might not be key to understanding species coexistence after all (McPeek 2012; McPeek and Siepielski 2019; Gómez-Llano et al., 2021).

Much of the this framework has focused on understanding the potential for coexistence among pairs of competitors and species within a single trophic level. Moving beyond this pair-wise construct to > 2 species systems can be achieved through structural stability analyses (Barabás et al., 2016; Saavedra et al., 2017). Recent advances linking food web theory and niche-based coexistence mechanisms have also highlighted the need to better determine how multi-trophic interactions can affect the potential for species coexistence (Godoy et al., 2018; McPeek 2019). This focus on multi-trophic interactions is especially relevant for organisms with complex life cycles (e.g.



Figure 15.1 Illustration of factors that could potentially stabilize or destabilize coexistence in a hypothetical assemblage of two ecologically equivalent species.

Vertical arrows depict the addition and loss of individuals to the population through recruitment and dispersal. Horizontal arrows depict interspecific interactions that occur primarily within age or sex classes, namely, aggressive interference (AI) and exploitative competition (EC). Diagonal arrows depict interspecific interactions between age or sex classes, namely intraguild predation (IGP) and reproductive interference (RI). Curved arrows represent intraspecific interactions, namely cannibalism (Cn), mate competition (MC), and sexual conflict (SC). Plus (+) and minus (-) signs by vertical arrows represent positive and negative effects on the growth rate of the population. Elsewhere (+) and (-) represent positive or negative effects on the fitness of individuals. All forms of interspecific interference (i.e. AI, RI, and IGP) are likely to be asymmetric, meaning that one species is harmed more than the other. To illustrate a tradeoff that might stabilize co-occurrence, the thickness of the arrows indicates that species 1 is the superior IGP competitor but is harmed more by RI and AI than species 2. In the absence of such tradeoffs, asymmetries in interspecific interference destabilize coexistence (Section 15.2.3). By contrast, intraspecific interference (i.e. Cn, MC, and SC) can stabilize coexistence (Section 15.2.4). In the absence of stabilizing factors, species might still coexist regionally because of asymmetries in dispersal or habitat selection (Section 15.2.2). The EC arrows are gray to acknowledge that the evidence for exploitative competition in Odonata is meager (Section 15.3.3). The dashed horizontal line represents the larval/adult habitat boundary. Interactions that do not appear to be particularly common in Odonata, such as aggression between females, are not depicted. The diagram could be simplified for lentic species by removing larval dispersal and for species with scramble competition mating systems by removing AI. By definition, ecologically equivalent species have the same prey, predators and parasites and are affected in the same ways by those and all other biotic and abiotic factors external to the species assemblage (Section 15.2.1), which is why those factors are not depicted.

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odonates), which, because of their wide disparity in body sizes both among species and within species through ontogeny, vary in their roles as predators, competitors, and prey. Consequently, determining how changes in trophic interactions among life stages (de Roos and Persson 2013; de Roos 2021) and size structure in multi-channel food webs can promote coexistence or lead to extinction (Dijoux and Boukal 2021; Lindley et al., 2009) holds much promise for better understanding the maintenance of species diversity.

15.2.2 Regional (non-local) coexistence

Local coexistence models assume that species interact in homogenous environments, but different species can prevail in different environments (Hart et al., 2017). Regional species coexistence theory takes spatial heterogeneity and metacommunity dynamics into consideration (also see Chapter 17). Species often exist in favorable and unfavorable environments, and each species has a competitive advantage in its favorable environment. Individuals often have the ability to move and disperse across the landscape, to escape deteriorating or unfavorable conditions. A species might be able to exclude other species in its favorable environment, while also persisting at low frequencies in unfavorable environments (Amarasekare 2003). Thus, species that cannot coexist locally could still coexist on a regional scale if each is competitively dominant in a different environment (Levins and Culver 1971; Yu and Wilson 2001; Amarasekare 2003).

Adaptive differences generating tradeoffs between species can facilitate regional coexistence. For example, some species might be better at colonizing new habitats, while others are slower to disperse but better at competing for resources. Efficient colonizers could disperse to a new habitat and exploit the resources before a superior resource-exploiting species arrives. Competition-colonization tradeoffs can promote regional coexistence if subordinate species colonize new areas and use resources before dominant species invade (Levins and Culver 1971; Yu and Wilson 2001; Amarasekare 2003).

Regional coexistence can also occur in homogeneous environments between species with little or no ecological differentiation. Habitat selection could lead to regional coexistence even in homogenous environments if species segregate in different parts of the landscape, thereby reducing or eliminating interspecific competition (Morris 2003). If the mere presence of heterospecifics imposes a cost for both species (e.g. increasing hybridization risk, decreasing probability of finding a suitable mate) and the species segregate to avoid such costs, this could promote regional coexistence (M'Gonigle et al., 2012; Ruokolainen and Hanski 2016; Kyogoku and Kokko 2020).

15.2.3 Interspecific interference and coexistence

Interference competition refers to a direct, costly interaction between individuals over access to a resource (Krebs 2001). Aggression is probably the most common type of interference competition in animals. Intraguild predation is a type of interference competition in which competitors are killed (Holt and Pollis 1997). A key difference between aggression and intraguild predation is that intraguild predators can benefit from the presence of intraguild prey by consuming them (Amarasekare 2002). While interspecific aggression usually serves a useful purpose, such as preventing a competitor from depleting a food patch, the expected fitness of both competitors would be higher in the other's absence.

Asymmetries in interference competition can compound or counteract asymmetries in resource exploitation ability. Coexistence between intraguild predators and prey is possible if the intraguild prey is the superior resource exploiter and the intraguild predator receives a net benefit from consuming the prey (Holt and Pollis 1997; Amarasekare 2002). Based on formal theory, interspecific aggression only hinders coexistence, but could override an asymmetry in exploitative competition and eliminate the superior resource exploiter (Amarasekare 2002). Going beyond formal theory, forms of interspecific competition that increase temporal or spatial habitat separation, such as dominance and territoriality, could promote local coexistence between resource competitors (Ashmole 1968; Ziv et al., 1993; Grether et al., 2013). Interference competition could also promote regional coexistence by preventing superior resource competitors from successfully colonizing new areas and driving resident species extinct (Grether et al., 2017).

Reproductive interference refers to sexual interactions between species, such as courtship, mating, and mate guarding (Gröning and Hochkirch 2008). Reproductive interference is positively frequency dependent because females of the rarer species are more likely to encounter heterospecific males (Kuno 1992). To the extent that female reproductive output affects population growth, reproductive interference could generate a positive feedback loop where the species that experiences more harm by the interaction spirals to extinction (Kuno 1992; Kyogoku and Nishida 2012; Kishi and Nakazawa 2013). Reproductive interference more readily leads to exclusion than does exploitative resource competition and could result in exclusion of the superior resource competitor (Kuno 1992; Kyogoku and Nishida 2012; Kishi and Nakazawa 2013).

However, reproductive interference might not be as antithetical to local coexistence as current theory suggests. If reproductive interference usually results in local extinction, it should be rare, but instead it is common in many taxa, including Odonata (Gröning and Hochkirch 2008; Shuker and Burdfield-Steel 2017; Drury et al., 2019). One explanation is that the costs of reproductive interference are relatively low, and coexistence is stabilized by other mechanisms (Yoshimura and Clark 1994). In Odonata and other taxa with complex life cycles, coexistence might be stabilized by resource partitioning, intraguild predation, or other mechanisms at the larval stage that are not easily perturbed by reproductive interference at the adult stage. Reproductive interference itself could also be part of a coexistence mechanism, such as when female avoidance of heterospecific males results in niche partitioning (Noriyuki and Osawa 2016; Ruokolainen and Hanski 2016), or a tradeoff exists between reproductive interference and resource competition (Kishi and Nakazawa 2013).

15.2.4 Intraspecific interference and coexistence

Essentially anything that causes populations to selfregulate has the potential to facilitate local coexistence (McPeek 2012). This includes many types of intraspecific interference that behavioral ecologists have long studied for other reasons and community ecologists have mostly ignored, such as mate competition, sexual conflict, territoriality, infanticide, and siblicide (Gómez-Llano et al., 2021). It is well established that intraspecific territoriality and mating harassment could cause density-dependent population regulation (Bauer et al., 2005; López-Sepulcre and Kokko 2005). It therefore seems logical to deduce that intraspecific interference alone could stabilize coexistence between species (McPeek and Siepielski 2019; Yamamichi et al., 2020). Yamamichi and colleagues (2020) coined the term "intraspecific adaptation load" for the negative effect of individual-level selection on population growth. Using a simple game theory model, they demonstrate that the evolution of a selfish trait (i.e. one that benefits the bearer but reduces the fitness of conspecifics) could allow multiple species to coexist through negative frequency dependence at the community level (Yamamichi et al., 2020). However, not all forms of intraspecific interference are likely to reduce population growth and stabilize coexistence. For example, while territorial behavior is "selfish" and can prevent some individuals from breeding, it nevertheless could increase the growth rate of a population by increasing the foraging efficiency of breeders, by slowing disease transmission, or by reducing the frequency of more costly types of interference, such as mating harassment, sexually selected infanticide, or cannibalism (depending on the system).

15.3 Empirical studies on coexistence and competition in Odonata assemblages

15.3.1 Local coexistence

Most species have ecological requirements that dictate their occurrences and local abundances. If species are ecologically differentiated in ways that cause them to be regulated by unique features, then species' relative abundances and demographic rates (per capita births and deaths) should covary with environmental gradients in ways that explain changes in their relative abundances. Indeed, repeated patterns of changes in the constituent species within assemblages along biotic and abiotic gradients (Johnson and Crowley 1980; Johansson et al., 2006; Stoks and McPeek 2006; McCauley 2007; McCauley et al., 2008; McPeek 2008; Siepielski and McPeek 2013; Worthen and Chamlee 2020) suggest that different sets of factors act to regulate the occurrence and relative abundances of odonate species. Within water bodies that have been repeatedly sampled, odonate abundances are often highly consistent from year to year. For example, Crowley and Johnson (1992) analyzed the abundances of 13 species of odonates at one lake and found highly consistent abundances over 12 years in most species. However, manipulative field experiments are necessary to test for density-dependent population regulation, as simply showing that species are ecologically different does not mean those differences result in stable coexistence (Ousterhout et al., 2019).

While a number of studies have evaluated cooccurrence of odonate species and sought to link those patterns to ecological differences, few have experimentally evaluated key requirements for stable local species coexistence, such as negative frequency dependence in vital rates. Perhaps because of their often high abundances and ease of experimental manipulations in field settings, most past experimental work on stable local coexistence in Odonata was conducted in lentic coenagrionid damselfly assemblages (mainly *Enallagma, Ischnura,* and *Lestes*) at the larval stage, especially in North America (see Svensson et al., 2018 for an example with lotic calopterygid damselflies in Europe). As such, we focus on this collective body of work as an illustrative case study.

Throughout temperate North America, Ischnura and Enallagma damselflies frequently co-occur in lakes and ponds, and unique assemblages of Enallagma are found in lakes with dragonflies or fish as the top predators (McPeek 1998). Based on a series of field experiments, McPeek (1998) inferred that stabilizing effects promote coexistence of Enallagma and Ischnura in both fish and dragonfly lakes. Unlike Enallagma, Ischnura are abundant in both fish and dragonfly lakes (Johnson and Crowley 1980; McPeek 1989, 1990, 1998). Within each lake type, Enallagma experience lower mortality rates from native predators relative to Ischnura, but Ischnura are better at converting consumed prey into their own biomass, and so grow faster than Enallagma (McPeek 1998, 2004). Thus, Enallagma and Ischnura settle the growth/predation risk tradeoff in different ways (McPeek et al., 2001; Stoks et al., 2003; McPeek 2004; Stoks et al., 2005), and these differences stabilize coexistence, as hypothesized by models of tri-trophic interactions (Holt et al., 1994; Leibold 1996; McPeek 1996; Siepielski et al., 2010).

Siepielski and colleagues (2011) further tested for ecological differentiation that might promote local coexistence among Enallagma, Ischnura, and Lestes. Field experiments manipulating intra- and intergeneric densities of one species in each genus revealed that the growth rate of each genus was negatively densitydependent and only limited by increases in intra-, not intergeneric, densities. Such differences should promote stabilizing effects and prevent competitive exclusion. Intensive sampling of these damselfly assemblages across 40 lakes also showed that the relative abundances of each genus correlated with different abiotic and biotic factors. Such responses to the environment are consistent with the local population size of each genus being regulated by unique local ecological factors.

However, what must ultimately be explained are patterns in local and regional species-level diversity,

whereby multiple species of each genus frequently co-occur. Two to four Ischnura species co-occur at most lakes across eastern North America; two to three Enallagma species co-occur in fishless ponds and lakes; and five to twelve Enallagma species co-occur at virtually every pond and lake with fish that has been surveyed (Johnson and Crowley 1980; McPeek 1989; McPeek 1990; Shiffer and White 1995; McPeek 1998; Siepielski et al., 2010). Similarly, two species of Lestes commonly co-occur in lakes with fish, and perhaps two to five or more in temporary ponds and wetlands where dragonflies are top predators (Stoks and McPeek 2006). Add into this mix the Argia, Nehalennia, and all the dragonflies with multiple species per genus that frequently co-occur, and the task before us is even more daunting.

Studies considering the potential for coexistence among species within a genus have revealed a number of key features. Siepielski and colleagues (2010) examined the potential for coexistence within the most speciose group of damselflies-Enallagma (see also Johnson et al., 1984). Experimentally manipulating the relative abundances of E. ebrium and E. vesperum larvae, two species that frequently co-occur throughout their geographic ranges and shared a recent common ancestor 10-15 million years ago, showed that neither species had faster growth rates nor lower mortality rates at low relative abundance (Figure 15.2). However, the summed total abundance of the two species was regulated-increasing total abundance caused growth rates to decline and mortality rates to increase (Figure 15.2). Thus, these species do not appear to be independently regulated by unique sets of ecological factors. These dynamics are precisely as expected for neutral species because the total abundance of all such ecologically equivalent species (not individual species) is the regulated quantity in a food web. Consistent with this, changes in relative abundance, growth rates, and mortality rates of species among 20 lakes were not explained by environmental factors. When combined with the mentioned studies, this work shows that both niche and neutral processes can occur simultaneously in a given species assemblage (Leibold and McPeek 2006; Siepielski et al., 2010).

Whether or not species can locally coexist also varies geographically. For example, experimental manipulations of the relative abundances of the same two *Enallagma* species (*E. signatum* and *E. vesperum*) in two different lakes with a shared fish predator showed that when each species was manipulated to low relative abundance it experienced lower mortality in one lake,



but not in the other (Figure 15.3). No differences in growth rates in relation to relative abundance were detected, indicating that resource competition may not be a key factor affecting the potential for coexistence (see also Johnson et al., 1984; Ousterhout et al., 2019). These results show that ecological differentiation potentially promoting coexistence (differences in survivorship in response to a shared predator) may only occur in some populations. Coexistence is inherently a question about co-occurring populations, and thus one should not attempt to reach general conclusions about species coexistence from single locations. **Figure 15.2** Two damselfly species, *Enallagma ebrium* and *E. vesperum*, showing strong responses to the manipulation of total abundance for per capita (a) mortality and (b) growth rates but no effects of relative abundance manipulations. Each symbol represents the responses of the two species in an experimental replicate. The symbols identify total abundance (open symbols, high total abundance; solid symbols, low total abundance) and relative abundance (squares, *E. vesperum* high relative abundance; triangles, *E. ebrium* high relative abundance) treatment replicates. The experiment was performed September–November 2008 at McDaniel's Marsh, Enfield, New Hampshire, USA. Figure and figure legend reproduced with modification from Siepielski et al., 2010.

Collectively, this series of related studies within one fairly small group of odonates shows that much can be learned about the potential for local coexistence by focusing on genera, species, and populations within species. While these studies have revealed patterns consistent with coexistence (or neutrality), it is important to note that none of these studies has provided definitive evidence for stable local coexistence. Whether other odonate assemblages exhibit similar patterns is an outstanding question, and future studies should adopt combined experimental and observational approaches (see Ousterhout et al., 2019) to test these ideas.

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Figure 15.3 Experimental evidence that the stabilizing effects of niche differences vary between populations. Photographs of damselflies used in the experimental studies of spatial variation in niche differentiation: (a) *Enallagma signatum* and (b) *E. vesperum*. The length from the head to the end of the abdomen of each species is approximately 25mm. No differences in per capita mortality (c) or growth rate (e) at low relative abundance or across total abundance treatments were detected in Michigan (MI). (d) Per capita mortality rates were significantly lower at low relative abundance in Arkansas (AR) in the low total abundance treatment, but not the high total abundance treatment. (f) Per capita growth rates did not differ at low relative abundance or across total abundance treatments in AR. Shown are mean +/- standard error; SEMs are smaller than the size of the symbol for some treatments.

Reproduced with modification from Bried and Siepielski 2019. Photographs by Steve Krotzer.

15.3.2 Regional coexistence

Empirical evidence of regional coexistence in odonates is limited and mostly based on studies with dragonflies. Using a series of artificial ponds, McCauley (2007) showed that higher connectivity promoted species richness, but dispersal limitation generated a pattern in which more distant ponds contained different species. The species isolation caused by limited dispersal could promote regional species coexistence as it would limit interactions among competitors that could lead to competitive exclusion. Moreover, local processes such as predator type (dragonfly or fish) could further limit species establishment and increase habitat differentiation and regional species coexistence (McCauley 2007). Limited dispersal ability and the effect of predators in species assemblages has also been studied in Enallagma and Lestes damselflies (McPeek 1989; McPeek 1990; Conrad et al., 1999; Stoks and McPeek 2003), but more research is needed to determine how

these characteristics affect regional coexistence. More broadly, work is needed in the metacommunity context (see Chapter 17) to study how species' dispersal differences trade off and interact with niche differences, environmental heterogeneity, and stochasticity to promote regional coexistence.

15.3.3 Exploitative competition among larvae

To demonstrate exploitative competition, it is important to show that increases in consumer density drive prey resources down and cause negative densitydependence in consumer demography. Studies in *Enallagma* and *Ischnura* have shown negative densitydependence in growth rates or survivorship with increasing intra- or interspecific densities, and that such negative density-dependence weakens with prey supplementation (Anholt 1990; McPeek 1998). Studies in dragonflies (e.g. *Pachydiplax longipennis*) have also found evidence for negative density-dependence in survivorship and growth rates (Van Buskirk 1987). However, the combined effect of density and prey supplementation were not apparent, indicating that the strength of negative density-dependence was not shaped primarily by food limitation.

Studies with dragonflies have also concluded that strong exploitative competition is unlikely. Johnson and colleagues (1985) manipulated intra- and interspecific densities of two dragonflies (Tetragoneuria cynosura and Celithemis elisa) and found negative densitydependence in survivorship, but not growth rates. They also found little evidence for local prey depletion and any such prey depletion was not affected by odonate density (Johnson et al., 1987)-a pattern found in similar experiments with Enallagma traviatum and E. divagans (Johnson et al., 1984). Similarly, Siepielski and colleagues (2020) found that individual growth rates of E. signatum increased with increases in natural prey density among lakes, implying prey limitation, but the strength of negative density-dependence in response to conspecific densities was not affected by prey densities.

In summary, the available evidence suggests that exploitative competition occurs, at least occasionally during the larval stage, within and between some, but not all, species. However, exploitative competition has not been directly implicated in competitive exclusion, nor has it been shown to be a factor underlying the potential to stabilize coexistence in Odonata, at least in the larval stage. For example, there is no evidence that exploitative competition has resulted in character displacement to consume different prey. Only in combination with other regulating factors, such as mortality from shared predators (e.g. McPeek 1998, 2004; Siepielski et al., 2010, 2011), does exploitative resource competition seem to underlie the potential for stable coexistence, but much work remains to understand these interacting processes in odonates.

15.3.4 Interference competition among larvae

Two types of interference competition have been shown (or hypothesized) to occur between Odonata species at the larval stage: feeding interference and intraguild predation. Larvae of some species have been reported to defend feeding territories, and sizedependent dominance has been documented in others (reviewed in Grether 2019). We are not aware of reports of interspecific territoriality or dominance at the larval stage, but if it occurs, it would likely be a form of feeding interference. Feeding interference may also occur when larvae respond to the presence of larger (and potentially predatory) species by becoming less active (McPeek 1998). Feeding interference would be expected to reduce larval growth rates and survival in the smaller species. Differential responses to dragonflies might be part of what allows *Ischnura* and *Enallagma* damselflies to inhabit the same lakes in North America (reviewed in Crumrine et al., 2008; McPeek 2008).

Intraguild predation has been proposed as an integral part of multiple coexistence mechanisms in Odonata. Intraguild predation can be unidirectional, such that one species consistently preys on the other, or it can be bidirectional and size-dependent, such that both species prey on smaller individuals of the other species (reviewed in Crumrine et al., 2008). When intraguild predators are cannibalistic, this could stabilize or destabilize coexistence between intraguild predators and their prey, depending on whether cannibalism counteracts or exacerbates a competitive asymmetry (Rudolf 2007). To test for such effects, Crumrine (2010) carried out a laboratory experiment with larvae of three species: a damselfly, Ischnura verticalis (prey), and two dragonflies, Anax junius (intraguild predator) and Pachydiplax longipennis (intraguild predator of I. verticalis and prey of A. junius). Cannibalism in A. junius reduced the density and activity of small A. junius and thereby increased survival of P. longipennis. Because A. junius outcompetes P. longipennis for the shared resource (I. verticalis), cannibalism seems likely to promote coexistence (Crumrine 2010). Whether cannibalism by intraguild predators helps account for local species diversity in natural odonate communities remains to be determined.

Factors that influence the relative size distributions of intraguild predators could potentially stabilize or destabilize coexistence. Two such factors are temperature and phenology. By varying water temperature in the laboratory, Suhling and Suhling (2013) determined that the range-expanding dragonfly Crocothemis erythraea has a thermal advantage over the native dragonfly Leucorrhinia dubia. The thermal advantage of C. erythraea was attributed primarily to an asymmetry in intraguild predation. Rasmussen and colleagues (2014) used larvae of two dragonfly species to test the hypothesis that shifts in hatching phenology affect coexistence between intraguild predators. The researchers simulated species differences in hatching phenology by placing Tramea carolina larvae of different size classes in mesocosms with early instar Pantala flavescens larvae. Large species differences in simulated arrival time (i.e. size) resulted in the "early arriving" species preying on and usually excluding the "late arriving" species. With

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small species differences in arrival time, intraguild predation was more symmetrical and neither species was excluded. Thus, annual variation in the direction of species differences in phenology might promote coexistence, but directional changes in phenology caused by anthropogenic climate change (reviewed in Parmesan 2007) would likely result in the eventual loss of whichever species arrives later (Rasmussen et al., 2014).

15.3.5 Interspecific aggressive and reproductive interference at the adult stage

Reproductive interference, caused by males pursuing and/or clasping females of other species, is very common (Tynkkynen et al., 2008). What effect this has on the fecundity of females, and therefore the likelihood of coexistence versus sexual exclusion (i.e. local extinction), has not been established. Van Gossum and colleagues (2007) studied reproductive interference between two species of Nehalennia damselflies, the more common of which (N. irene) has two female color morphs (gynomorph and andromorph). It was

determined that N. irene males preferentially attempt to clasp gynomorphs of their own species while males of the rarer species (N. gracilis) do not discriminate between females of the two species. The authors inferred that most harassment of N. gracilis females is by N. irene males and offer this as an explanation for the rarity of N. gracilis. However, if the population densities of the two species were equal, N. irene andromorphs should experience more heterospecific clasping attempts, and both N. irene color morphs should receive more mating harassment in total than N. gracilis females. Thus, if the asymmetry in male mate recognition was the cause of the difference in population density, N. irene should be the rarer of the two species.

Species that interfere with each other reproductively often interfere with each other aggressively as well (Tynkkynen et al., 2008; Drury et al., 2015; Grether et al., 2020). Research on rubyspot damselflies (Hetaerina spp.) has provided the strongest supporting evidence to date for the hypothesis that interspecific territorial aggression can evolve in response to (or be maintained by) interspecific mate competition (Figure 15.4; Drury



Figure 15.4 Evidence for a link between reproductive and aggressive interference in rubyspot damselflies (Hetaerina spp.). Each point represents a sympatric population. Where females of sympatric species differ less in wing pigmentation, male territory holders are more likely to clasp tethered heterospecific females and are also more aggressive to tethered heterospecific male intruders. Photo: A tethered female Hetaerina cruentata in tandem with a male Hetaerina vulnerata. Reproduced with permission from Drury et al., 2015. Photo credit: Andrew Chao.

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et al., 2015; Grether et al., 2020). Why, though, does reproductive interference itself persist? The hypothesis inspired by, and subsequently tested in, rubyspot damselflies is that this is a type of evolutionary dilemma or catch-22: males clasp heterospecific females when they cannot distinguish them from conspecific females, and in that predicament, there is no selection on females to diverge phenotypically (Drury et al., 2019).

How do species with high levels of reproductive and aggressive interference coexist? Or do such species not actually coexist and instead only co-occur transiently? Identifying and testing for mechanisms that might allow such species to coexist stably is one way that this question might be approached. Perhaps coexistence is stabilized by predation, resource partitioning, or intraguild predation at the larval stage. If the populations are regulated by larval density dependence, interference at the adult stage might be of little consequence. Unfortunately, Odonata researchers tend to focus on either larvae or adults, and few genera have been studied intensively at both life stages. Integration of research across the life cycle, replication at the level of species pairs, and a combination of observational studies and field experiments, will probably be necessary to answer the question of whether coexistence is stabilized (or precluded) by interactions between species at the larval or adult stages (Gómez-Llano et al., 2021).

15.3.6 Intraspecific interference at the adult stage

Intraspecific interference allows species to regulate their own population growth and promote species coexistence. Intraspecific interference can be generated by different behaviors such as territoriality, scramble competition, and sexual conflict. Unfortunately, researchers have seldom studied these behaviors in the context of species coexistence (Gómez-Llano et al., 2021), even if these behaviors can limit population growth. For example, male territorial competition is energetically costly, but it is also correlated with successful mating (Plaistow and Siva-Jothy 1996; Suhonen et al., 2008). Could higher male density and the associated costs of increased competition limit mating success and population productivity? An experimental study with two species of Calopteryx damselflies, C. splendens and the dominant and territorial C. virgo, found that male-male aggression due to territorial competition caused negative frequency dependent survival in C. virgo males (Figure 15.5). Svensson and colleagues (2018) suggest that this could limit



Figure 15.5 Evidence for negative frequency dependent survival in *Calopteryx virgo* damselflies, from an experiment in which the density (high vs. low) and relative frequency of *C. virgo* and *C. splendens*. males were varied in mesocosms. Photos: male *C. virgo* (top), male *C. splenden*.

Reproduced with modification from Svensson et al., 2018. *Photo credit*: Erik I. Svensson.

population growth and prevent the exclusion of the subordinate species, but evidence is needed that shows that variation in male survival affects population growth.

Sexual conflict could be a mechanism of intraspecific interference by which species can stably coexist. This is because when a species becomes common, sexual conflict increases causing negative frequency dependence. Sexual conflict then could act to maintain species diversity in a similar way as the maintenance of intraspecific female color polymorphism (Fincke 1994; Takahashi and Kawata 2013). Although the role of sexual conflict has theoretical support (Yamamichi et al., 2020), empirical evidence is lacking. However, most odonate reproductive interactions, including male mating harassment, occur near oviposition sites, which can be both limited and patchy. Therefore, even if species frequency might be low, the density within patches can be high and sexual conflict intense. This could limit the potential effect of sexual conflict maintaining species

diversity as harassment can be costly, even when species are rare.

15.4 Conclusions and recommendations

Our review of the theory and empirical evidence for coexistence mechanisms in Odonata has revealed a vibrant area of research where significant progress is being made but many important questions remain unanswered. While ecological differentiation may indeed be the key to coexistence in many taxa, not all ecological differences between species promote coexistence, and coexistence is also possible between ecologically equivalent species. As such, empiricists need to be cognizant of, and devise methods to test for, a wider range of coexistence mechanisms than those traditionally considered.

Intensive research on damselfly larvae in the ponds and lakes of North America yielded evidence for both stable coexistence and neutrality in the same species assemblages. Yet even in the best studied genera, we still often lack a mechanistic understanding of the underlying processes promoting coexistence. While mechanisms that reduce resource overlap between species feature prominently in the broader coexistence literature, there is little evidence that resource-based character displacement occurs in Odonata.

Local coexistence arises from local processes, which can vary geographically, even within the same species pairs. Consequently, caution should be exercised when attempting to reach general conclusions about species coexistence. Regional coexistence is less well-studied and remains an area where much progress can be made.

Reproductive and aggressive interference occur frequently among species at the adult stage, and significant progress has been made toward understanding why these mutually costly interactions have persisted over evolutionary time. As yet, however, little is known about how these forms of behavioral interference affect coexistence in Odonata.

The proposition that intraspecific adaptation load might promote coexistence among species that otherwise could not coexist is exciting and merits further study. Odonates are a promising taxon for advancing knowledge in this area due to their tractability for observational and experimental field studies.

The complex life cycle of Odonata presents some interesting challenges for both theoreticians and empiricists. How processes operating at different life stages interact to affect local and regional species diversity is an important direction for future research. For example, species differences in adult breeding phenology could be the source of species differences in larval size structure that enable coexistence to be stabilized by intraguild predation and cannibalism. Likewise, regional species diversity likely depends on factors that affect adult dispersal and reproduction as well as those that affect larval growth and survivorship.

Odonata are at the forefront of modern coexistence research and hold great promise for further elucidating the factors that determine whether species coexist stably and how these factors vary geographically and over time, but much work remains. Elucidating the mechanisms that structure odonate communities will require integrating research on ecological differentiation and both intra- and interspecific interference across the life stages at appropriate spatial and temporal scales. Rising to this challenge requires a broader range of expertise than individual research groups typically possess. In closing, we encourage community ecologists to pay more attention to animal behavior and behavioral ecologists to think more about how the behaviors they study affect coexistence.

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