

Parasitism of *Enallagma civile* Hagen in Selys, 1853 (Zygoptera: Coenagrionidae) by *Arrenurus* water mites

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Research Article

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All relevant data are within the paper.

Abstract. We compared the prevalence and intensity of *Arrenurus sensu stricto* water mite parasites on *Enallagma civile* Hagen in Selys, 1853 (Zygoptera: Coenagrionidae) from 10 freshwater wetlands (playas) in two different land-cover contexts in western Texas from 2006–2007. Vulnerability to parasitism may be a consequence of disturbance, so we predicted that the more natural form of regional land cover (grasslands) surrounding playas should be associated with a lower water mite load than more disturbed land cover (tilled croplands). Additionally, we examined *Arrenurus* occurrence and intensity of infection by host sex. Overall prevalence was 38.46% of 130 damselflies sampled having mites; this varied by land-cover type but with opposite trends between years. Overall average parasite load was ~11 water mites per infected host (range: 1–40 mites); intensity was significantly higher in hosts from cropland playas in 2006, but there was no difference by surrounding land cover in 2007. Although there were consistent trends in both years of more males being parasitized than females, the highly uneven distribution of parasites on hosts and differences in average mite load between years generated variability that obscured any statistically significant patterns. Thus, land-cover context surrounding playas, but not host sex, had an impact on parasite load in one of the two years of our study. Future work is needed to identify the mechanisms by which land cover may affect water mite-odonate host-parasite relationships as well as the role of the odonate assemblage as a whole in dispersal of parasites in a temporally dynamic wetland network.

Key words. Dragonfly, *Arrenurus*, *Enallagma civile*, Odonata, land cover, playa, Texas, water mite

Introduction

Throughout the Great Plains of North America, there are ~80,000 ephemeral, freshwater wetlands known as playas that are regional foci for biodiversity (Bohlen et al., 1989). These shallow, lentic waterbodies are fed primarily by precipitation runoff, particularly during the regional rainy season from April through September, and are dry more often than they are wet (Johnson et al., 2011). Each of these prairie wetlands occupies an independent watershed, and the type of land cover surrounding these depressional wetlands strongly influences the presence, amount, and quality of water within playas (Bartuszevige et al., 2012, Collins et al., 2014, Starr & McIntyre, 2020). For example, playas surrounded by agriculture are subject to tillage and runoff that contains erosional sediments and agrochemicals, relative to those surrounded by grassland (Haukos & Smith, 1994). Such disturbances are suggested to have ecological consequences on aquatic organisms (e.g., in terms of parasitism, community structure, etc.) (see Chapman et al., 2015).

Odonates host a variety of internal and external parasites (reviewed in Corbet, 1999). Water mites from *Arrenurus sensu stricto* (Arachnida, Trombidiformes,

Arrenuridae, *Arrenurus*) are the most conspicuous and widespread group of ectoparasites that parasitize odonates (Smith & Oliver, 1986, Zawal, 2008, Zawal & Dyatlova, 2008, Andrew et al., 2015). With a near-global distribution and over 500 species (<https://www.gbif.org/species/2181035>), water mites are particularly associated with damselflies (multiple families) and libellulid dragonflies as hosts (Åbro, 1990, Forbes & Robb, 2008) (Fig. 1), with at least 55 species of *Arrenurus* parasitizing odonates (Corbet, 1999). Water mites occur in a wide variety of freshwater habitats (particularly lentic waterbodies); their free-swimming larvae attach themselves to late-instar odonate nymphs (Smith, 1988, Leung et al., 1999). Sometimes the water mites parasitize the nymphs (Zawal, 2006, Zawal & Szlauer-Łukaszewska, 2012), but parasitism more commonly occurs when the

odonate nymph emerges and ecloses as an adult. The water mite will pierce the teneral adult with a feeding tube, usually on the ventral surface of the thorax or abdomen. The water mite feeds on the host's hemolymph for as many as 20 days (Corbet, 1999), detaching when the host returns to water; the mite then completes its maturation and reproduces in water (Mitchell, 1959; Forbes & Robb, 2008).

As many as 100% of adult odonates encountered at a waterbody may have at least one parasitic mite (Corbet, 1953), with > 200 water mites per host possible (Andrew et al., 2015). Some studies have shown that parasite load of *Arrenurus* water mites is higher on female odonates (Robb & Forbes, 2005, Andrew et al., 2015), which was attributed to females spending more time as a final instar nymph than males before emerging and to

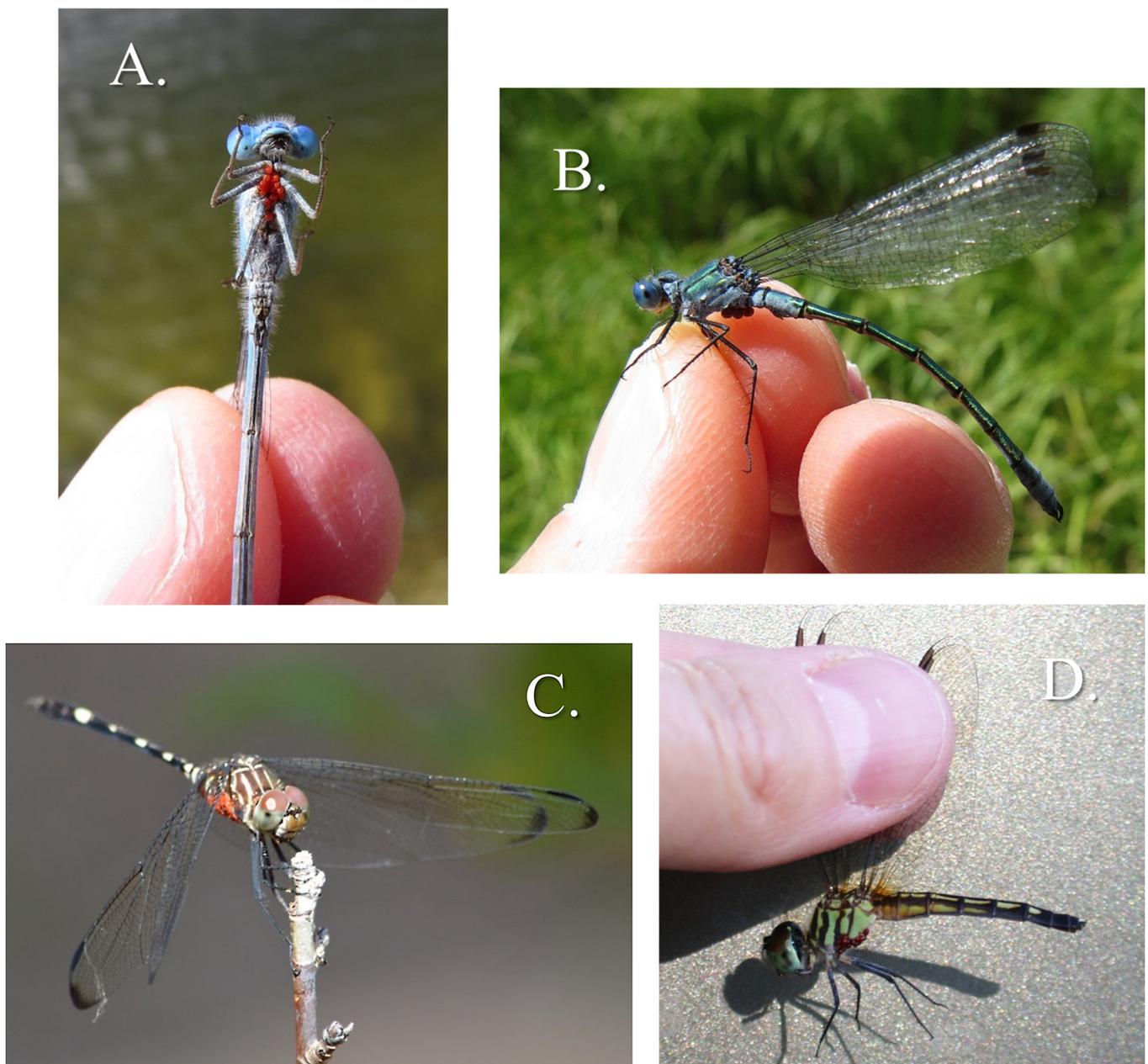


Figure 1. Examples of odonates parasitized by *Arrenurus* water mites (red spheres). A – *Enallagma civile* Hagen in Selys, 1853 (Coenagrionidae), Texas (USA); B – *Lestes dryas* Kirby, 1890 (Lestidae), Utah (USA); C – *Dythemis velox* Hagen, 1861 (Libellulidae), Texas (USA); D – *Pachydiplax longipennis* (Burmeister, 1839) (Libellulidae), Texas (USA). Photos by N.E. McIntyre.

adult females spending more time in very close proximity to water during oviposition (Robb & Forbes, 2006). However, other work has failed to detect a difference in parasite load by sex (Ilvonen et al., 2016), and still other papers have found differences in parasitism by sex to vary by host species and parasite species (Baker et al., 2008; Zawal et al., 2017a, 2017b). Water mite parasitism has been shown to negatively affect odonate host body condition, flight ability, longevity, and fecundity in some studies but not in others (Forbes, 1991; Forbes & Baker, 1991; Bonn et al., 1996; Forbes & Robb, 2008). Furthermore, high variance in water mite abundance has been documented even within relatively localized areas (James et al., 2009). This variation means that there is still much that remains to be understood about water mite parasitism in odonates.

One such area that merits greater clarification is on the role of landscape disturbance on parasitism by water mites. There have been some studies on water mite parasitism on odonates in North America, but very few have examined the influence of land-cover type on water mite presence and intensity, and those that did find, surprisingly, higher rates of parasitism in less-disturbed wetlands (James et al., 2009; Worthen & Turner, 2015). With this limited knowledge, more investigation into the drivers of odonate-mite relationships is warranted to understand complex host-parasite interactions for taxa across various regions and aquatic systems, especially within the context of a dynamic wetland system with anthropogenically modified/disturbed habitats. The objectives of our study were thus to compare water mite prevalence (i.e., occurrence) and intensity (i.e., load) at wetlands within different land-cover contexts of varying degrees of anthropogenic modification. We used the playa network as a model of odonate responses to agricultural modifications to wetlands across the landscape.

Methods

Sampling occurred May–August 2006–07 at 10 playas in Briscoe and Swisher counties in western Texas (Fig. 2), five of which were surrounded by tilled agriculture (primarily cotton and maize) and five in grassland-dominated watersheds (pastures grazed by domestic livestock). Most sites were visited once per month during the sampling period each year. Because of the highly intermittent nature of playa inundation (Johnson et al., 2011), sampling could only occur when water was present in the playa basin, so some sites were sampled more frequently than were others; three playas were sampled in only one of the two years, with nine playas sampled in 2007 and eight in 2006. Playas were designated as cropland (tilled agriculture) or grassland based on the dominant (> 75% surface area coverage) immediate land-cover type in a circular buffer 31,416 m² in area (200 m diameter) around each playa. Five cropland-dominated playas and four grassland ones were sam-

pled in 2007; four cropland and four grassland were surveyed in 2006. Because this is a shortgrass prairie biome, playas surrounded by grasslands most closely represent natural, undisturbed habitats compared to ones in agricultural areas. Sites were separated by at least 300 m (Fig. 2).

During each site-visit at wet playas, sampling took place at the water's edge (littoral zone) by walking around the perimeter of each playa. We focused on adult *Enallagma civile* Hagen in Selys, 1853 (Zygoptera: Coenagrionidae), the most widespread and abundant odonate species in our region (Reece & McIntyre, 2009). We used aerial nets to collect 130 mature (i.e., non-teneral) adult *E. civile* (53 females, 77 males; vouchers are in the Department of Biological Sciences, Texas Tech University). More males are represented than females, partly because males are more conspicuous than females and because we are here making use of individuals collected for another study that focused on males. The number of attached water mites on each individual was counted. For prevalence, presence/absence of water mites was determined for each host individual, and for intensity, the number of mites was counted per infected damselfly individuals only (uninfected individuals were not included in this assessment of parasite load). Prevalence and intensity were then compared between land-cover types and sexes. Variation in damselfly age may result in an underestimation of infection intensity if our samples contained both old-

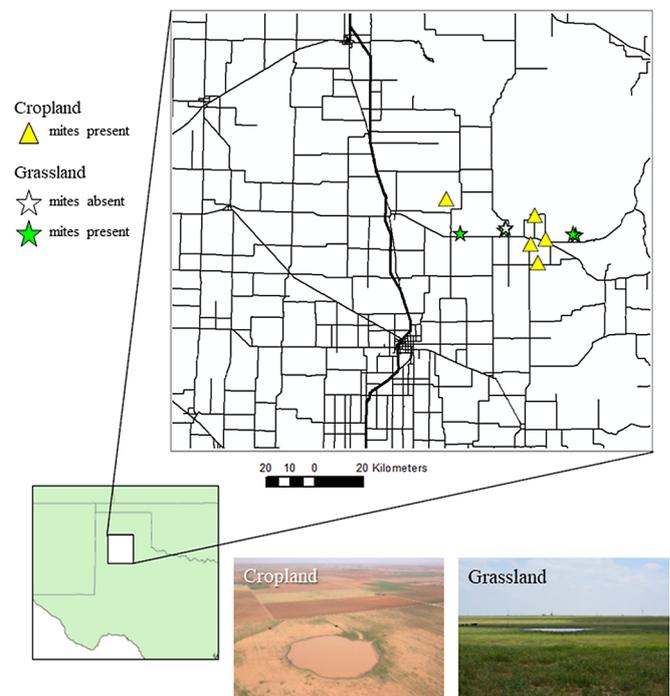


Figure 2. Locations of the 10 playas in Texas that were surveyed for water mites on *Enallagma civile*, denoted by surrounding land-cover type. The playa where no mites were encountered is represented by white symbols whereas playas where mites were found are denoted by filled symbols. Black lines are paved roads; the developed area in the lower-central portion of the inset map is Plainview, Texas.

er individuals (with mites already detached) as well as younger ones (Kaunisto et al., 2018). Because *E. civile* cannot be aged beyond the post-teneral stage, we have no way of examining the effects of host age.

Data and analytical code are available at <https://github.com/enallagma/watermites>. All statistical analyses were performed in R 4.0.3 (R Core Team, 2020) and RStudio 1.4.1717 (RStudio Team, 2021). A Fisher’s exact test ('stats' package in base R) was used to analyze the relationships between mite prevalence and land-cover type and sex (as recommended by Rózsa et al., 2000 and Reiczigel et al., 2019). Prevalence values are reported with 95% Clopper-Pearson confidence intervals, based on a binomial distribution ('GenBinomApps' package; Lewitschnig & Lenzi, 2020). Bootstrapped two-sample t-tests ('MKinfer' package; Kohl, 2020) with 95% bias-corrected and accelerated bootstrap confidence intervals ('coxed' package; Kropko & Harden, 2020) were used to compare mean intensity of water mites parasitizing *E. civile* by land-cover type and by sex as per recommendations by Rózsa et al. (2000). Because not all sites held water in both years, we analyzed patterns separately by year. *P*-values were Bonferroni-adjusted as $\alpha/4$ (0.0125), with adjustments performed separately for the prevalence and intensity dependent variables. Finally, we used the Moran’s I test of spatial autocorrelation ('ape' package; Paradis & Schliep, 2019) to determine whether mite prevalence and intensity were related to site proximity (i.e., whether there was spatial bias in infection).

Results

Water mites were encountered at nine of our 10 sites, being absent from one grassland site (Fig. 2). There were 43 site-visits from 2006–2007: at four playas, all *E. civile* individuals (N = 9) found were parasitized, at 16 site-visits there were no individuals found with parasites (N = 34), and at 22 site-visits both parasitized (N = 40) and non-parasitized (N = 47) individuals were found. Thus, on most site-visits, we encountered both parasitized and non-parasitized *E. civile* at the same wetland. There were more *E. civile* collected at cropland playas (32) than grassland ones (16) in 2006, but in 2007, there was an equitable sample size (41 damselflies from cropland, 41 from grassland). A total of 554 mites were found across the 130 *E. civile* individuals examined, with a 38.46% overall frequency of damselflies with at least one parasite (range for infected hosts: 1–40 mites per individual, with an average of 11–12) (Tables 1–2).

In examining how parasitism varied with land cover surrounding playa wetlands, water mites were more prevalent at cropland playas than at ones in grasslands in only one of our two years (2006), with the opposite trend being seen in 2007. Differences in occurrence of damselflies with mites did not significantly differ with land-cover type (Fisher’s exact test, 2006: $p = 0.1964$;

Table 1. Prevalence (frequency of hosts with at least one parasite) of *Arrenurus* water mite parasitism of *Enallagma civile*, with 95% Clopper-Pearson confidence intervals and number of *E. civile* individuals examined (both infected and uninfected) as a function of two land-cover types surrounding playa wetlands and host sex.

	Prevalence	95% CI	Number of infected <i>E. civile</i>	Number of uninfected <i>E. civile</i>
Cropland			30	43
2006	0.44	0–0.60	14	18
2007	0.39	0–0.53	16	25
Grassland			20	37
2006	0.19	0–0.42	3	13
2007	0.41	0–0.59	17	24
Female			17	36
2006	0.28	0–0.58	7	18
2007	0.36	0–0.53	10	18
Male			32	44
2006	0.43	0–0.50	10	13
2007	0.42	0–0.55	23	31
Overall	0.38	0–0.46	50	80

Table 2. Mean intensity (average number of mites per infected individual host) of *Arrenurus* water mite parasitism of *Enallagma civile*, with 95% bias-corrected and accelerated bootstrap confidence intervals) as a function of two land-cover types surrounding playa wetlands and host sex.

	Intensity	95% CI
Cropland		
2006	14.14	-10.68–37.35
2007	11.00	-6.52–27.05
Grassland		
2006	4.33	-0.94–9.78
2007	9.82	-7.34–25.80
Female		
2006	10.00	-12.12–32.56
2007	11.20	-2.94–25.32
Male		
2006	14.10	-11.13–39.38
2007	10.04	-8.33–26.13
Overall	11.08	-8.15–28.20

2007: $p = 1$; Table 1). *Enallagma civile* at agriculturally dominated sites averaged more mites per individual than those at playas within a grassland context in both years (Table 2), but this trend was statistically significant only in 2006 (bootstrapped t-test, 2006: $p = 0.0088$; 2007: $p = 0.6779$).

Although there was a trend for more males than females to be infected with mites (Table 1), this was not

statistically supported in either year (Fisher's exact test, 2006: $p = 0.5427$; 2007: $p = 0.6379$). Additionally, intensity in parasite load between those hosts that were infected with mites was statistically equivalent between the sexes in both years (bootstrapped t-test, 2006: $p = 0.5339$; 2007: $p = 0.7001$; Table 2).

There was no significant spatial autocorrelation in either year in the prevalence (2006: Moran's $I = -0.1025$, $p = 0.0784$; 2007: $I = -0.0033$, $p = 0.6212$) or intensity of infection by site proximity (2006: $I = -0.0440$, $p = 0.4886$; 2007: $I = -0.0440$, $p = 0.4886$).

Discussion

The statistical analyses we used were extremely conservative, associated with high false-negative rates and wide confidence intervals when parasites are not evenly distributed across hosts (i.e., when most mites are found on only a few host individuals), leading to almost-inevitable failure to reject the null hypotheses of no difference in parasite prevalence or intensity with respect to any factors examined (land-cover type or host sex) (Rózsa et al., 2000). There were some trends in the data and a significant relationship between land-cover type and intensity of infection in 2006 (more mites associated with agricultural disturbance), but the variability with land-cover type and host sex across years that accounted for lack of statistical differentiation in most comparisons indicates that odonate-water mite relationships are spatiotemporally heterogeneous. This variability may be inherent in a naturally dynamic, intermittent wetland system like the playas of the Great Plains. Other studies of water mite parasitism of odonates have been conducted in more stable systems (permanent wetlands and/or a laboratory setting), and there have been no long-term studies of dynamics playing out over longer time scales. Ecological variability may take longer to manifest in stable settings, so our understanding of host-parasite relationships in odonates is incomplete. This is an area of odonate natural history that clearly merits further investigation.

In our study, average mite occurrence was only 38.46%, so most *E. civile* individuals that we sampled lacked water mites altogether. This pattern may be due to either of two reasons: because no mites successfully established an infection, or because there were no mites present at a site for the odonates to encounter. The definitive cause of the similarity in water-mite intensity by land cover in one year but not the other cannot be determined from our study, but it may be due to the fact that more cropland playas than grassland ones were surveyed in 2006 than in 2007. In 2006, intensity of infection was statistically associated with land-cover type. Having a more equitable representation of land cover in 2007 was associated with a lack of differentiation in prevalence and intensity of infection. Just as mite prevalence and abundance may vary with season (e.g., playa basins being wet one year and dry

the other), variation in land-cover type with respect to sampling intensity may likewise be at least partially responsible for the lack of a consistent relationship with land cover across both years.

Disturbance via land cover modifications has been shown in other studies to be negatively associated with the occurrence of water mites. For example, Worthen and Turner (2015) documented that odonates of various species in more natural areas had higher rates of parasitism than those in more disturbed sites. James et al. (2009) similarly found higher rates of parasitism on *Ischnura verticalis* (Say, 1839) (Zygoptera: Coenagrionidae) from natural wetlands than from artificially constructed ones in urban areas. They suggested that anthropogenically modified wetlands might not host the proper environment for water mites, likely due to a lack of prey species for the mites' aquatic stage. Clearly more research is needed to elucidate how landscape structure may affect host-parasite relationships. At a fine scale, it is possible that differences in vegetation structure and composition concentrate odonates at the water and facilitate water mite attachment (Hassall et al., 2010), but it is difficult to identify specific factors differentiating the occurrence and intensity of parasitism in specific landscapes. Studies that simultaneously collect environmental data that could influence host-parasite relationships (e.g. type and coverage of aquatic vegetation, water depth, water chemistry, etc.) would be needed to provide a deeper understanding of the relationships that our study documented. A multivariate ordination of those data would be particularly useful in visualizing species-environment relationships, which may allow for important habitat variables to be identified. In addition to these fine-scaled spatial effects, occurrence and abundance of water mites can vary by season and presumably by year (Smith, 1988; Forbes & Baker, 1991), so data collection—and subsequent inferences drawn—are likely influenced by timing of sampling.

The prevalence of water mite infection was not statistically greater for males than females (that is, males were not significantly more frequently infected than were females), and there was no statistical difference in intensity of water mites between the sexes (that is, infected individuals had equivalent numbers of mites, regardless of host sex). Other studies have similarly found no sex bias in *Arrenurus* parasitism of odonates (Ilvonen et al., 2015; Worthen & Hart, 2016). However, fewer females than males were examined in our study, which may have contributed to the lack of statistical support to any patterns of parasitism by host sex; future studies would be needed to clarify this.

Adult odonates serve as important dispersal vectors for water mites, especially for ephemeral wetlands such as playas. For water mites in lentic waters with independent watersheds (like playas), mobile hosts would be their main dispersal mechanism. Relatively little is known about how far *Enallagma civile* adults can disperse, but they have been observed at least 137 m from

water (Bick & Bick, 1963), possibly far enough to spread mites among the ephemeral playa wetland network; more vagile dragonflies could certainly do so. Our two closest sites (two grassland playas) were only ~300 m apart (Fig. 2), so *E. civile* individuals could possibly have dispersed between them. Intriguingly, however, one of those sites never had any water mites present whereas the other did, which likely contributed to the lack of spatial autocorrelation that we saw. It would be interesting in future studies to determine how other members of the odonate assemblage (particularly more-vagile dragonflies) affect the occurrence and spread of water mites, particularly with respect to the potential for a dilution effect, whereby higher host species richness and abundance contribute to lower parasite prevalence (Ostfeld & Keesing, 2000), although more water mite life-history information with respect to habitat or host specificity would be needed to assess this possibility.

For most sites, there were infected and uninfected individuals present at the same site at the same time, and most *Enallagma civile* at a given site were not infected with mites. Playas are naturally intermittent wetlands. It is unknown what happens to water mites when a playa dries up completely, although at least one species of *Arrenurus* (*A. planus*) can be found in ephemeral ponds (Forbes et al., 1999) and can withstand periods of desiccation (Nagel et al., 2011), suggesting that water mites may be persistent at playas. However, playas can be dry for years at a time; if *Arrenurus* cannot survive such lengthy desiccation, then temporal autocorrelation in infection would be disrupted. In such a case, since dragonflies are assumed to be capable of greater dispersal distances than are damselflies, dragonflies would presumably be the primary means by which playas are re-infected.

Given our relatively small sample sizes and the potential for many unmeasured and/or indirect effects, the role of anthropogenic modifications of the environment on the coevolved relationship between odonate hosts and their water mite parasites is still as yet unclear. The playa wetland network presents multiple opportunities for future work that could elucidate how odonate hosts and their parasites respond to anthropogenic disturbances, contributing to our understanding of water mite ecology and host-parasite relationships.

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