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Environmental variation shapes and links parasitism to sexual selection

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Abstract
Parasite-driven population divergence in hosts can be exacerbated by environmental factors affecting host parasitism, as well as by increasing sexual selection against parasitized hosts. Environmental factors can influence parasitism directly by affecting parasite survival, and indirectly by affecting host condition, which can in turn shape host sexual selection. To disentangle these potential alternative paths, we used a damselfly (host) - water mite (parasite) system to examine how environmental factors directly and indirectly drive heterogeneity in parasitism across populations and influence the strength of sexual selection acting against parasitized males. We found substantial heterogeneity in parasitism across populations, driven mainly by lake pH, and damselfly density. Although this heterogeneity in parasitism did not translate directly into variation in sexual selection, the density of predatory fish increased sexual selection strength, likely through the effects on damselfly condition. These results imply that parasitism alone may not cause differences in sexual selection across populations, but when linked with underlying environmental conditions, parasitism can increase the strength of selection. More broadly, these results suggest that elucidating how parasitism may drive sexual selection requires consideration of the intwined effects of ecological processes.

Keywords Parasite-host interactions · Mating success · Environmental effects · Insects

Introduction

The causes of sexual selection can vary among populations, as female mate choice, male signalling, male competition, and the expression of secondary sexual traits often depend on environmental context (Andersson 1994; Badyaev and Qvarnström 2002; Kokko et al.

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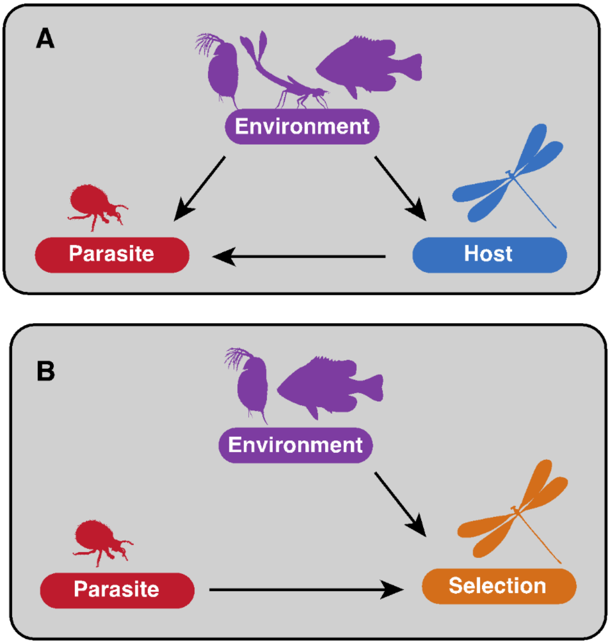

Fig. 1 The direct and indirect effects of environmental variation shaping sexual selection through parasitism. Environmental factors can affect parasitism directly, affecting parasite survival during the free-living stage, and indirectly, affecting host condition and their ability to defend against parasites (**A**). Moreover, the strength and direction of sexual selection can also be affected by environmental factors that reduce host condition and the strength of parasitism they are exposed to (**B**)

2002; Chaine and Lyon 2008; Cornwallis and Uller 2010; Siepielski et al. 2022). Parasitism is a key interaction that can affect the strength and direction of sexual selection because infection can decrease host condition, the expression of secondary sexual traits, and mating success (Hamilton and Zuk 1982; Åbro 1982; Forbes and Baker 1991; Vergara et al. 2012; Gómez-Llano et al. 2020; Dougherty 2021). Much as overall condition affects sexual signalling in males, condition can also affect female mate choice (Jennions and Petrie 1997; Hingle et al. 2001; Hunt et al. 2005; Cotton et al. 2006; Dakin and Montgomerie 2014) and male-male competition for access to females (Gómez-Llano et al. 2020). In many cases, parasitism itself will often be driven by environmental features, increasing or decreasing its intensity (Smith 1988; Arneberg et al. 1997, 1998; Pietrock and Marcogliese 2003; Poulin 2006; Wolinska and King 2009; Tack and Laine 2014; Preisser 2019). Thus, if the effects of parasites differ among populations because of underlying environmental variation, this can in turn affect the strength and direction of sexual selection among populations (Fig. 1).

Parasite prevalence (parasite presence or absence) and load (number of parasites per individual) are often expected to vary spatially due to direct and indirect environmental effects. Direct effects increase parasite prevalence and load and are especially important in parasites with a free-living stage, as they are directly subject to environmental conditions which can determine their local abundance (Smith 1988; Arneberg et al. 1997, 1998; Pietrock and Marcogliese 2003; Poulin 2006; Wolinska and King 2009; Tack and Laine 2014; Preisser 2019). For example, low pH reduces survival (Rousch et al. 1997) of parasitic water mites (*Arrenurus* spp) of Odonates (damselflies and dragonflies), leading to lower parasite load in Odonates across pH gradients among lakes (McDevitt-Galles et al. 2018; LoScerbo et al. 2020). Indirect environmental effects can also modify the defensive responses of hosts to parasites. This can arise when parasite prevalence and load are mediated by environmental factors that shape host condition. For example, immune responses are often energetically costly (Zuk and Stoehr 2002; Sandland and Minchella 2003; Wolinska and King 2009; González-Santoyo and Córdoba-Aguilar 2012), and in resource poor environments immune responses can be weakened (Campero et al. 2008; De Block and Stoks 2008; Wolinska and King 2009; Hasik et al. 2021). Therefore, resource poor environments and environmental factors limiting resource acquisition could increase parasitism (Fig. 1A).

Environmental factors and parasitism can also cause differences in sexual selection against parasites between populations (Fig. 1B). Populations with different levels of parasitism often differ in the strength of selection as higher parasitism is more likely to lead to stronger directional selection (Coltman et al. 1999; Benkman 2013; Betts et al. 2018; Gómez-Llano et al. 2020). Moreover, environmental factors that affect individuals' condition can also affect the strength of selection and lead to population divergence, as female mate choice, male competition, immune response, and signalling are frequently condition-dependent (Åbro 1982; Jennions and Petrie 1997; Hingle et al. 2001; Hunt et al. 2005; Cotton et al. 2006; Vergara et al. 2012; Dakin and Montgomerie 2014; Dougherty 2021). Identifying the environmental features affecting parasitism and shaping sexual selection on hosts is therefore critical to understand their roles in promoting adaptive population divergence.

Damselflies and their ectoparasitic water mites are a good study system to investigate spatial variation in the pathways between environmental variation, parasitism, and sexual selection against parasitized individuals. Parasitism by water mites can affect flight performance and male condition, which can generate potential sexual selection against parasitized individuals (Åbro 1982; Forbes and Baker 1991; Forbes 1991; Willink and Svensson 2017; Gómez-Llano et al. 2020). Moreover, environmental conditions during the larval pre-reproductive stage, such as low resource availability, predation risk, and higher competitor densities, can affect a damselfly's condition and ability to defend against parasites (Rutherford et al. 2007; Campero et al. 2008; De Block and Stoks 2008; Hasik et al. 2021; Hasik and Siepielski 2022).

Therefore, we hypothesized that environmental conditions jointly shape parasitism and host sexual selection against parasitized individuals. This association could arise via two paths. First, environmental conditions could affect parasitism directly on the parasite free-living stage, and indirectly by affecting host condition necessary to defend against parasites (Fig. 1A). Second, the environment could affect selection against parasitized individuals directly through the effect of parasite prevalence and load on the strength of selection, and indirectly by reducing hosts condition required for competing, signalling, and choosing mates (Fig. 1B).

To test these hypotheses, we used two congeneric species of *Enallagma* damselflies (*E. ebrium* and *E. geminatum*) and their ectoparasitic water mites (*Arrenurus* spp). To determine the effect of environmental variation on parasitism, we first compared populations of *E. ebrium* and *E. geminatum* to determine if parasite prevalence and load varied among lakes. We then asked if different environmental features affect parasite prevalence and load directly, or indirectly through its effect on damselfly body size. Then, to determine if parasites can lead to spatial variation in sexual selection, we estimated selection acting against male parasite prevalence and load across populations. Finally, to test the effect of the environment on sexual selection against parasitized individuals, we determined how sexual selection was affected by environmental features that affect hosts' body size (e.g., Siepielski et al. 2022). By evaluating these hypotheses, we can better understand the role of ecological factors linking host parasitism dynamics to sexual selection against parasitized individuals.

Methods

Study system

E. ebrium and *E. geminatum* are commonly found throughout southeastern Canada and northeastern United States (Westfall and May 1996; McPeek and Brown 2000). Populations in this region are univoltine and individuals spend approximately 11 months as aquatic larvae, after which they emerge as free flying terrestrial adults during the summer months (mid-June to early August) when they reproduce. *Enallagma* are not territorial, but there is intense scramble competition between males to gain access to females (Steele et al. 2011; Siepielski et al. 2018, 2022). After copulation, females oviposit in emerging macrophytes (Corbet 1999). During the final instar of the larval stage, damselflies are exposed to attack by parasitic water mites (*Arrenurus* spp.). Water mites are commensals during the aquatic larval stage of the damselflies, attaching to the larvae and remaining in a phoretic stage until damselflies emerge as adults. During damselfly emergence, mites pierce the damselfly cuticle before it hardens and feed on the damselfly body fluids (Åbro 1979, 1982; Rolff 2000). Importantly, only the larval stage of the water mites is parasitic, after detachment, during the deutonymphal and adult stages, water mites are free-living predators (Smith 1988) exposed to environmental conditions (Pietrock and Marcogliese 2003). Therefore, local lake environmental features can affect the host-parasite interactions between damselflies and mites (De Block and Stoks 2008; LoScerbo et al. 2020; Hasik et al. 2021).

Data collection

Data for this study is a subset of the data used in Siepielski et al. (2022), specifically, we used a subset of populations in which parasite data was available (see below). While Siepielski et al. (2022) studied the effects of different environmental features on damselfly body size and sexual selection, here we focused on the effect of environmental features in parasitism and sexual selection against parasitized individuals. Because this data is a subset of Siepielski et al. (2022), the details for field procedures are only explained briefly here.

Damselfly sampling

Damselflies were collected from 10 populations of *E. ebrium* and eight population of *E. geminatum* in Vermont and New Hampshire, USA, using hand nets during the reproductive season (mid-June to early August 2010), when damselflies were active, between 1000 and 1900 h excluding overcast and above 18°C days. Each day as many males as possible were captured and recorded if they were found as single (non-mated = 0) or in tandem (mated = 1) as a measure of mating success. Although this widely-used measure of sexual selection does not reflect lifetime mating success, as males could have mated previously or after collection, it does provide an average of the males that are successful at competing and acquiring mates, and has commonly been used as reliable estimates of sexual selection in damselflies (e.g., Steele et al. 2011; Gómez-Llano et al. 2020; Svensson et al. 2020; Siepielski et al. 2022). Captured individuals were preserved in 70% ethanol and photographed under standardized lighting conditions and above a ruler to take morphometric measures using ImageJ. The morphometric measures considered were: head width, tarsus length, thorax length and width, forewing length, abdomen length, and abdomen widths at the junction of the fourth and fifth and the eighth and ninth abdominal segments. Principal component analysis (PCA) of these measures was used to generate an overall composite measure of male body size. From this PCA, all traits loaded negatively and therefore larger PC1 values represent smaller body size (Table S1). Parasite presence was noted during collection and parasite load was taken as the number of parasites per individual, as observed from the photographs. Although this latter measure is a proxy of the total parasite load, as it gives us only a partial (minimal) count of the total parasites (visible part of the individuals), because the ventral part (commonly the most parasitized area) was fully visible, we expect these to be reliable measures.

Numerous environmental factors can affect parasite mortality and larval damselfly growth and body size (Baker 1989; Forbes and Baker 1991; Rousch et al. 1997; McPeek 2004; De Block and Stoks 2008; LoScerbo et al. 2020). Here we focus on those factors that previous studies have implicated in directly affecting parasitism in damselflies or damselfly body size. Parasitism can be directly affected by pH, as more acidic environments can decrease mite hatching success and survival due to damage of the egg coating (Rousch et al. 1997; LoScerbo et al. 2020), as well as decreasing host density (e.g., density-dependent parasitism; Arneberg et al. 1997, 1998). Because smaller individuals are more likely to be parasitized due to reduced immune responses (Hughes et al. 2016; LoScerbo et al. 2020), environmental factors affecting damselfly body size could indirectly affect parasite prevalence and load. Therefore, we analysed the indirect effect of fish density as it was the only environmental factor previously found to affect body size in these species (Siepielski et al. 2022). Environmental factors can not only affect parasitism, but also the strength of sexual selection against parasitized individuals. We therefore tested the effect of parasite prevalence and load on sexual selection, as the intensity of parasite-host interactions can affect the strength of selection against parasitized individuals (Benkman 2013). Finally, we also estimated the effect of fish density, as it was found to affect adult body size in these species (Siepielski et al. 2022), and adult body size is correlated to condition (Baker 1989) and condition can affect sexual selection (Vergara et al. 2012; Gómez-Llano et al. 2020; Dougherty 2021).

Environmental conditions

Methods for the collection of environmental factors, except for pH and parasite prevalence and load, are specified elsewhere (Siepielski et al. 2010), so we only briefly summarize them here. Host density (*Enallagma* larval density) was estimated by counting the number of larvae in 10 standardized 1-m long sweeps through macrophytes in the littoral zone of each lake using a D-frame dip net (28 cm width 1 × 1 mm mesh). Predatory fish density was estimated with three standardized seine hauls through the littoral zone of each lake. Lake pH was measured using a YSI probe (YSI ProPlus; YSI Inc.). Parasite load per lake was estimated as the mean parasite load per individual for each species separately in each lake.

Statistical analysis

Environmental effects on parasite prevalence and load

Because the study species were not always found in the same lakes, we analysed each species separately. We estimated differences in parasite prevalence among populations using a binomial distribution (presence = 1, absence = 0) and for parasite load we used a negative binomial (number of parasites per individual) due to overdispersion. In both models, we used lake as a fixed factor. We then used Tukey adjusted pairwise post-hoc tests for comparisons between lakes.

To identify the direct and indirect effects of environmental features in parasite prevalence and load we used structural equation models (SEM) using the "*lavaan*" package (Rosseel 2012). We regressed (1) pH, *Enallagma* density, and male body size on parasite prevalence and parasite load, separately, and (2) fish density on male body size. We included pH and *Enallagma* densities as environmental variables, as they can affect parasite prevalence and load (Arneberg et al. 1997, 1998; Rousch et al. 1997; LoScerbo et al. 2020), male body size was included as it is positively correlated with immune function and defence against parasites, including mites (González-Santoyo and Córdoba-Aguilar 2012; Preisser 2019; LoScerbo et al. 2020). We tested the indirect effect of fish density on parasite prevalence and load through its effect on damselfly body size (Siepielski et al. 2022).

Environmental effects on sexual selection

We estimated species and lake specific selection gradients (Lande and Arnold 1983) separately for parasite prevalence and load following the method developed in Janzen and Stern (1998). Mating success was assigned as a binary response variable (mated = 1, not mated = 0) and parasite prevalence or load and male body size as independent variables. These estimates of selection gradients allow us to estimate directional selection acting on parasite prevalence and load while taking into account any effects of body size (Lande and Arnold 1983), which we know is important because male body size can be a target of sexual selection (Steele et al. 2011; Siepielski et al. 2022).

To test how environmental conditions affect the strength and direction of sexual selection against parasite prevalence and load, we regressed the selection gradients (*β*, for parasite prevalence or load) from the above analyses against environmental conditions at each lake:

$$B_{ji} = \mu + be_i + m_i + \in_i,$$

,where *β* is the selection gradient of species *j* in lake *i*, *e* is the environmental condition during the larval (i.e., fish density) or adult (i.e., parasite prevalence and load) life stage. As we were interested in the effect of parasitism, we only considered the effects of direct selection on parasite prevalence and load, controlling for body size. The sampling error of the selection gradient was included as $m_i \sim N\left(0,\ SE_i^2\right)$ and the residual error as $\in_i \sim N\left(0,\ \sigma_i^2\right)$. This analysis therefore allows us to examine how sexual selection on parasitized individuals varies among populations while taking into account sampling error of the estimated selection coefficients. In this way, because selection coefficients are all standardized, they can be viewed as a measure of effect size.

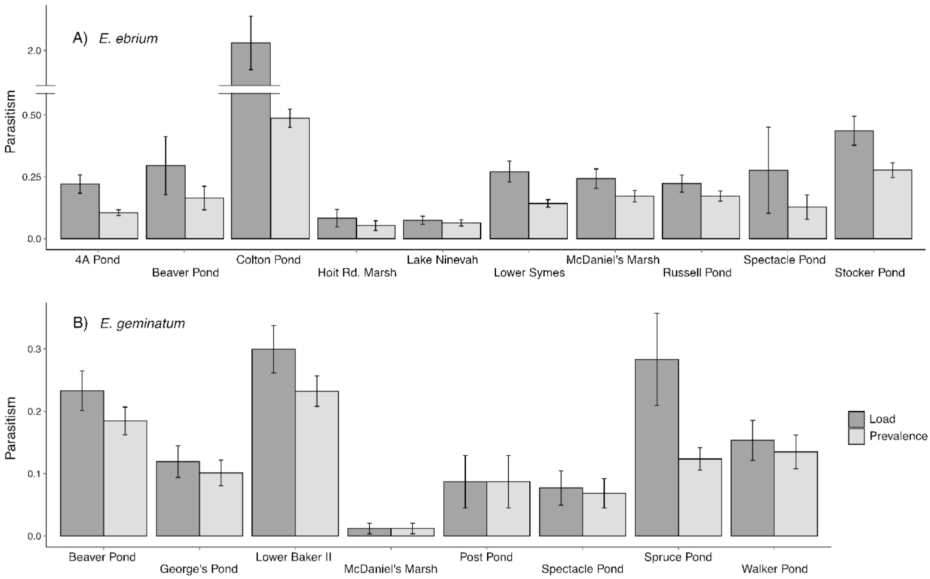

Fig. 2 Variation in parasite pressure among populations of *E. ebrium* (**A**) and *E. geminatum* (**B**). We found differences in parasite prevalence (dark grey) and load (light grey) among lakes. Shown are means and +/- 1 standard errors. Note scale of Y axis in *E. ebrium*

The analyses were performed in R (R Core Team) using the packages: "lme4" (Bates et al. 2015), "car" (Fox and Weisberg 2018) for estimating differences in parasitism across populations, "lavaan" (Rosseel 2012) for the SEM, "psa" (Kawano 2022) to estimate selection gradients and "metafor" (Viechtbauer 2010) to estimate the effects of environmental variables on the selection gradients.

Results

Parasite pressure

We quantified parasite prevalence and load of a total of 2873 *E. ebrium* males in ten lakes, and 1648 *E. geminatum* in eight lakes. We found significant differences in parasite prevalence and load between lakes in both *E. ebrium* (prevalence: $\chi^2=139.9$, df=5, $p<0.001$; load: $\chi^2=216.5$, df=5, $p<0.001$; Fig. 2A, Table S2A) and *E. geminatum* (prevalence: $\chi^2=21.5$, df=3, $p<0.001$; load: $\chi^2=13.2$, df=3, $p=0.004$; Fig. 2B, Table S2B).

Environmental effects on parasite prevalence and load

We found both direct and indirect environmental effects on parasitism. In *E. ebrium*, pH had a positive effect on both parasite prevalence (Fig. 3A) and load (Fig. 3B). The density of *Enallagma* damselflies also had a significant effect on parasite prevalence, but not on load. Finally, although fish density had a negative effect on body size (PC1), in agreement with previous research (Siepielski et al. 2022), it did not generate an indirect effect on parasite

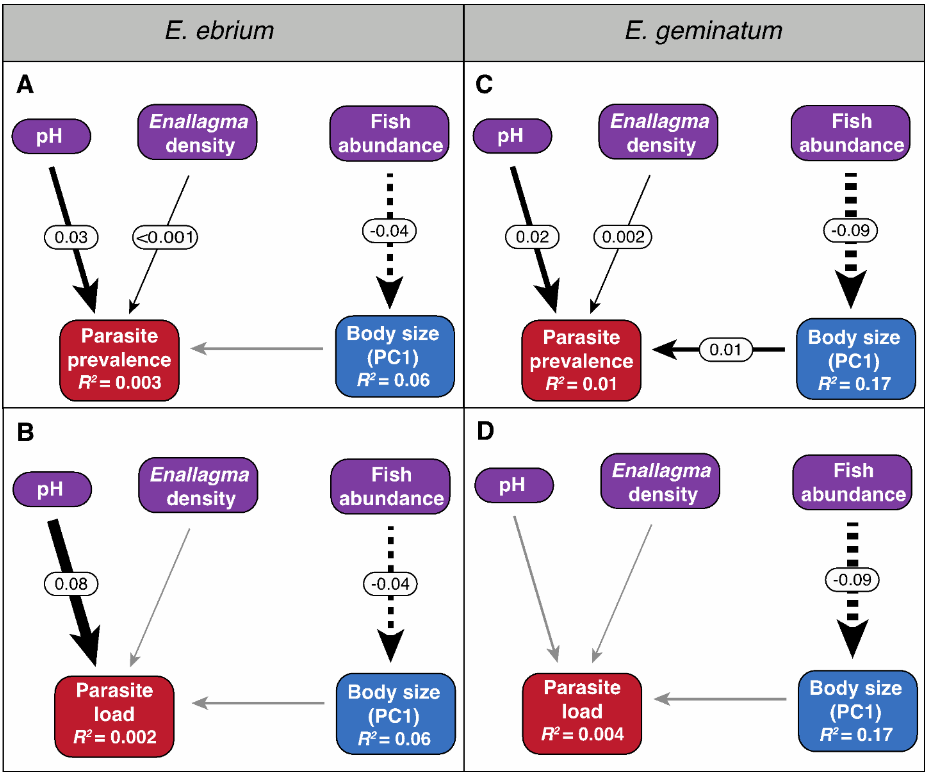

Fig. 3 Results from SEM models of the direct and indirect effects of environmental factors on parasite prevalence and load. In *E. ebrium* (left) there was a positive effect of damselfly density and pH on parasite prevalence (**A**) but only pH on parasite load (**B**). In *E. geminatum* (right), the positive effect of damselfly density and pH was significant only on prevalence (**C**) not load (**D**). Although fish density had a significant effect on body size (PC1) in both species, body size only influenced parasite prevalence on *E. geminatum* and not parasite load or on *E. ebrium.* Statistically significant and non-significant effects are shown in black and grey arrows, respectively. Values are the effect sizes of statistically significant effects. Line widths are proportional to the effect size. Dashed lines show negative effects and solid lines positive effects. Note that the direction of the effects was consistent in both species in prevalence and load

prevalence or load, as body size had no effect on parasite prevalence nor load (Fig. 3A-B Table S3A). In *E. geminatum*, pH and *Enallagma* density similarly had a positive effect on parasite prevalence and fish density had an indirect effect through its effect on body size (Fig. 3C). However, we found no evidence for any direct or indirect effects of any of the environmental variables on parasite load (Fig. 3D, Table S3B).

Sexual selection against parasitized individuals

We estimated selection gradients for parasite prevalence and load of each species across lakes. We found that selection gradients for both parasite prevalence and load were mostly non-significant in both species (Fig. 4, Table S4A). In *E. ebrium*, we found only one population with significant selection gradients, interestingly, favouring parasitized males (Lower Symes Pond). In *E. geminatum*, we found only one lake with significant selection against

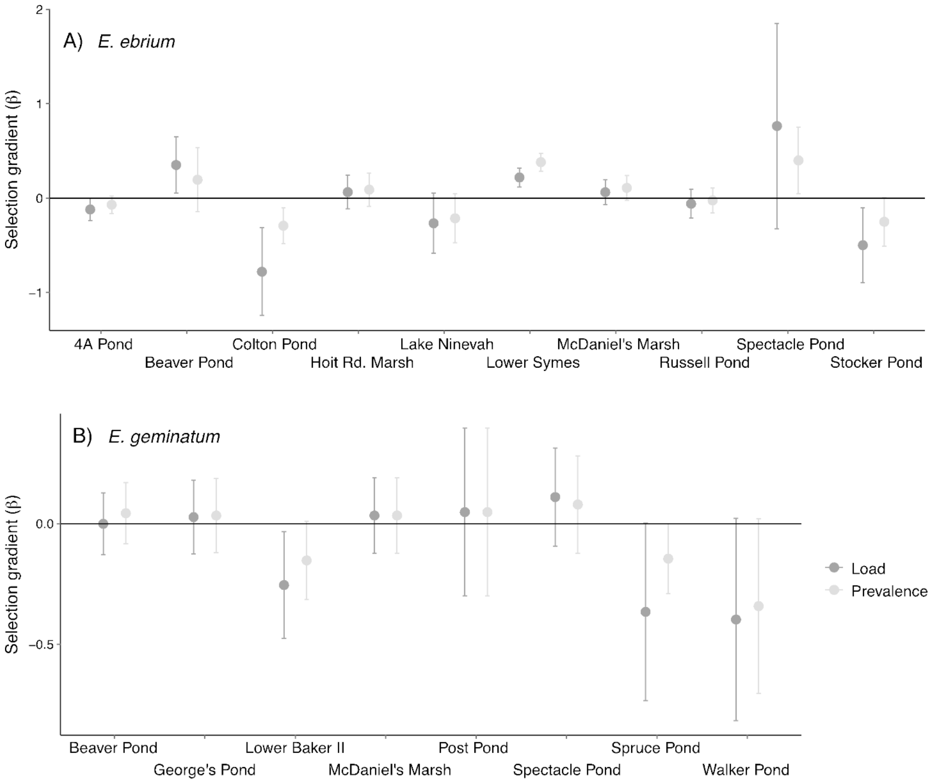

Fig. 4 Selection gradients on parasite prevalence (light grey) and load (dark grey) were non-significant in most populations of *E. ebrium* (**A**) and *E. geminatum* (**B**). If selection gradients are positive, parasitized males were more likely to be found in copula than non-parasitized males, the opposite when selection is negative. Shown are selection gradients +/- 1 standard error

parasite load (Lower Baker II). Directional selection in each lake was largely consistent for parasite prevalence and load (Fig. 4, Table S4B).

Environmental effects on sexual selection

We then analysed the effect of different environmental factors on the direction and strength of sexual selection against parasitized males. We found a consistent positive effect of fish density increasing selection for parasitized males when using both parasite prevalence and load in *E. ebrium* but not in *E. geminatum*, although there was a trend in the same direction (Fig. 5). Population mean parasite prevalence and load were also associated with increased selection against parasitized males in both species, although this trend was not significant in either *E. ebrium* or *E. geminatum* (Fig. 5; Table S5B).

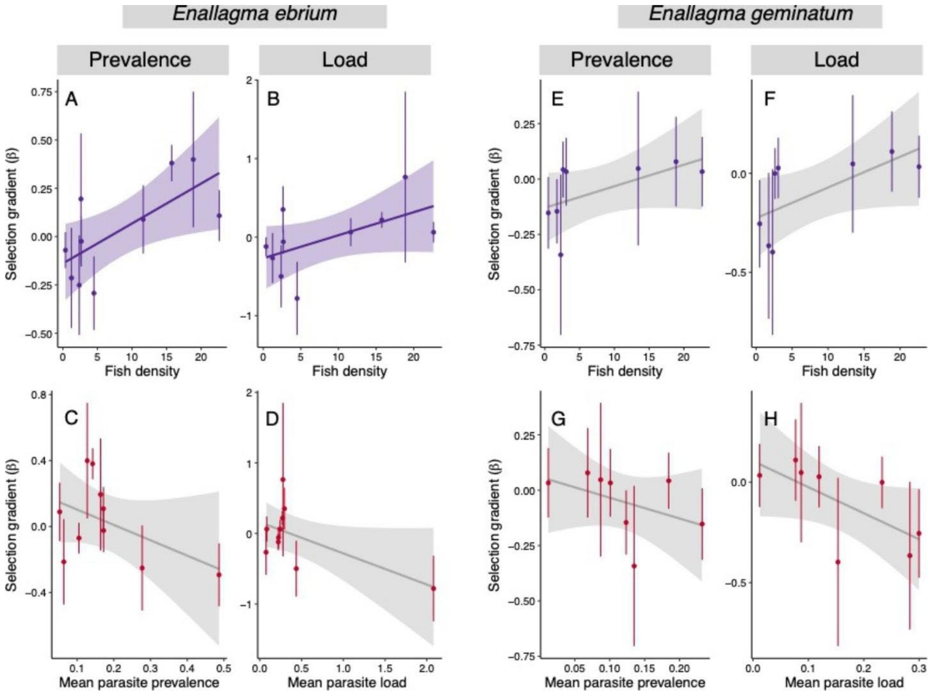

Fig. 5 Effects of environmental factors on sexual selection in *E. ebrium* (**A-D**) and *E. geminatum* (**E-H**). Fish density had a positive effect increasing selection favouring parasitized males, this was true when selection gradients were measured on parasite prevalence and load, although this effect was significant only in *E. ebrium* (**A-B**) and not in *E. geminatum* (**E-F**). The effect of mean parasite prevalence and load was not statistically significant for either *E. ebrium* (**C-D**) nor *E. geminatum* (**G-H**), although the effect direction was consistent between species. Points and error bars show the selection gradients (and +/- 1 standard errors) on parasite prevalence and load per population. Lines show predicted selection coefficient for a particular measure of parasitism in relation to environmental variables and 95% confidence interval with coloured lines depicting statistically significant effects

Discussion

We hypothesized that environmental conditions shape parasite prevalence and load directly and indirectly through host condition. We found partial support for this hypothesis, as we found that environmental conditions, especially lake pH, account for heterogeneity in parasitism (prevalence and load) across host populations, but we found little evidence of indirect effects through body size. Moreover, we hypothesized that the environment would affect selection against parasitized individuals directly through the effect of parasitism on the strength of sexual selection, and indirectly via its effects on body size. Our results show weak sexual selection on either parasite prevalence or load in both species. Moreover, parasite prevalence and parasite load in the population had no effect on the strength of sexual selection, but higher fish densities increased the strength of sexual selection among lakes. Together, our results suggest that environmental factors can affect parasitism and the strength of sexual selection, but the paths between these factors are not intuitive.

Parasite prevalence and load varied extensively among populations, in agreement with previous studies (Kaunisto and Suhonen 2013; Willink and Svensson 2017; LoScerbo et al.

2020; Khan and Herberstein 2022). This heterogeneity in parasitism was partially explained by environmental factors. Specifically, higher water pH and density of damselfly competitors consistently favoured higher parasitism in both species. Water mite hatching success and survival increases at higher pH (Rousch et al. 1997), while the higher density of damselflies can benefit parasites as they are more likely to find and infect hosts (e.g., hosts are a resource). The idea that environmental features affect parasites has been widely recognized (Soper 1929; Harvell et al. 2002; Altizer et al. 2006; Tack and Laine 2014). For example, higher winter temperatures increase survival of the fungal parasite affecting ribwort plantain (*Plantago lanceolata*), leading to increase disease prevalence (Penczykowski et al. 2015), but high temperatures can also be detrimental for parasites; for example, reducing bacterial load on fruit flies (Lazzaro et al. 2008). In general, the direct effects of the environment are expected to be stronger in parasites with a free-living stage such as water mites (Harvell et al. 2002; Pietrock and Marcogliese 2003), which would explain the substantial heterogeneity in parasite prevalence and load across lakes in our study.

Environmental features can also affect parasitism indirectly. Because previous work suggested that larger damselflies have lower parasite loads (Forbes 1991), we hypothesized that predator density would also have an indirect effect on parasitism given that greater fish density is associated with larger body sizes, likely by reducing damselfly resource competition, in male *Enallagma* (Siepielski et al. 2022), and body size is correlated with immune function (LoScerbo et al. 2020). However, we only found a small effect of body size in parasite prevalence, but not parasite load, for *E. geminatum* and no effect on either measure for *E. ebrium*. Why we found no effect on *E. ebrium* and a limited effect on *E. geminatum* is not clear. Our study was observational and it is possible that other environmental variables limit the effect of predators on immune function that shape prevalence and parasite load, including presence of multiple parasites, resource availability and habitat complexity (Stoks et al. 2006; Kaunisto and Suhonen 2013; Buchanan et al. 2017; LoScerbo et al. 2020). Regardless, environmental features show a stronger and more consistent direct effect on parasitism than proxies of immune function (e.g., body size). Although most studies have focused on the effects of broader, regional environmental conditions, such as temperature (e.g., Harvell et al. 2002; Laine 2004; Wolinska and King 2009), our results imply that local environmental conditions, such as pH and damselfly density, can also affect parasite prevalence and load (*see also* Hasik and Siepielski 2022).

We found weak sexual selection acting on parasite prevalence and load in our study. In both species, only one population showed directional selection, yet in opposite directions, favouring parasitized individuals in *E. ebrium* and against parasitized individuals in *E. geminatum*. In general, research on the effect of parasitism on damselfly male mating success is also somewhat mixed: selection against parasitized males has been found in some studies (Forbes 1991; Honkavaara et al. 2009; Gómez-Llano et al. 2020) and not in others (Rolff et al. 2000; Khan and Herberstein 2022), or found in some years but not in others (Andres and Cordero 1998). Environmental variables can increase or decrease selection against parasitized individuals if they affect the costs of defences against parasites (Sandland and Minchella 2003; Mitchell et al. 2005; Lazzaro and Little 2009; Wolinska and King 2009; Hughes et al. 2016) and drive parasite-host coevolution (Paplauskas et al. 2021). Interestingly, we found a positive effect of fish density increasing selection favouring parasitized males. This is somewhat surprising because the presence of predatory fish reduces damselfly foraging activity (McPeek 2004; Siepielski et al. 2022), and limited food intake can exacerbate the costs of immune function and increase selection against parasitized individuals (*see* Sandland and Minchella 2003; Wolinska and King 2009). However, in these species fish predation also leads to larger male body size, likely by reducing foraging competition for limiting food resources (Siepielski et al. 2022). Therefore, higher predator densities can increase food availability, facilitating immune responses that can favour parasitized males. Regardless, our research show that parasites alone have limited potential to shape selection on mating success, but in the presence of predators the strength of selection increases.

One possible explanation for the weak selection found in our populations and the positive effect of fish density on sexual selection is based on the higher mortality of parasitized teneral damselflies (Leung and Forbes 1997). High teneral mortality due to parasitism means that surviving individuals had to be in good condition and favoured by selection (i.e., the "invisible fraction" Hadfield 2008). Thus, parasitized adults were able to survive the teneral stage and reach maturity, and therefore differences between non-parasitized and surviving parasitized males could be minimal, limiting sexual selection. Fish density could disturb that balance, as high fish densities lead to larger individuals by reducing foraging competition that limits access to growth limiting resources (McPeek 1998; Siepielski et al. 2022) - more resources would reduce the costs of defences against parasites, reducing any negative effect of parasites on surviving adult damselflies. To fully disentangle the effects of parasites and environmental conditions further, research directly manipulating host conditions and measuring teneral and adult survival in combination with mating success would be necessary.

Sexual selection has long been thought to be driven by parasitism (Hamilton and Zuk 1982; Clayton 1991; Andersson 1994; Zuk and McKean 1996; Moller et al. 1999), and recent work has increasingly sought to link ecological dynamics to sexual selection (Qvarnström 2001; Gillespie et al. 2014; Miller and Svensson 2014; Moore et al. 2019; Siepielski et al. 2022) and parasitism (Pietrock and Marcogliese 2003; Poulin 2006; Wolinska and King 2009; Penczykowski et al. 2015; Hasik and Siepielski 2022). Yet evidence that directly or indirectly links ecological conditions to parasitism and sexual selection among populations is limited, especially in natural populations (Laine and Tellier 2008). Our results help to fill this gap and show that environmental conditions can affect parasite prevalence and load, and although sexual selection against parasitized males was generally weak, environmental conditions can increase the strength of sexual selection. The latter is a key finding – as it implies that our ability to understand how the dynamics of parasitism and sexual selection are linked requires that we focus on developing an understanding of how the local environment can couple these two interactions shaping fitness.

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Author Contribution A.M.S and M.G.L conceptualized the study, A.M.S and M.A.M conducted the fieldwork and data collection. M.G.L performed the analysis and wrote the manuscript with input from A.M.S and M.A.M.

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Data and code availability Link to be provided upon acceptance.

Declarations

Conflict of Interest There is no conflict of interests.

Ethical approval NA.

Consent to participate and publish NA.

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