VOL. 199, NO. 1 THE AMERICAN NATURALIST JANUARY 2022

Environmental Conditions during Development Affect Sexual Selection through Trait-Fitness Relationships

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Submitted April 8, 2021; Accepted August 12, 2021; Electronically published November 23, 2021

Online enhancements: supplemental PDF. *Dryad data:* https://doi.org/10.5061/dryad.5qfttdz62.

ABSTRACT: Sexual selection can be shaped by spatial variation in environmental features among populations. Differences in sexual selection among populations generated through the effects of the environment could be shaped via four paths: differences in mean absolute fitness, differences in the means or variances of phenotypes, or differences in the absolute fitness–trait function relationship. Because sexual selection occurs only during the adult life stage, most studies have focused on identifying environmental features that influence these metrics of fitness and trait distributions among adults. However, these adult features could also be affected by environmental factors experienced in early life stages that then shape the trajectory for sexual selection during the adult life stage. Here we investigated how among-population variation in environmental conditions during the juvenile (larval) stage of two species of *Enallagma* damselflies shapes sexual selection on male body size. We found that environmental factors related to predation pressures, lake primary productivity, and habitat availability play a role in shaping spatial variation in sexual selection. This acts mainly through how the environment affects absolute fitness–body size associations, not spatial variation in mean fitness or body size means and variances. These results demonstrate that the underpinnings of sexual selection in the wild can arise from environmental conditions during prereproductive life stages.

Keywords: causes of selection, damselfly, divergence, *Enallagma*, mate choice, sexual selection.

Introduction

Sexual selection has played a prominent role in the diversification of many speciose taxa, including Hawaiian *Drosophila* (Boake 2005), African lake cichlids (Salzburger 2009), birds (Price 2008), and *Enallagma* damselflies (McPeek 2008), as well as in divergence among populations of many species (Boughman 2001; Masta and Maddison 2002; Svensson et al. 2004, 2006). Comparative studies have shown that sexual selection is often stronger (Hoekstra et al. 2001; Kingsolver et al. 2001; Siepielski et al. 2011*a*) and exhibits less temporal variation than selection through other fitness components (but see Morrissey and Hadfield 2011; Siepielski et al. 2011*a*), which should drive population divergence. Critical for understanding the processes underlying population divergence through sexual selection is an understanding of the causes of spatial variation in sexual selection.

Much like selection through survival or other fitness components, sexual selection via male-male competition or female mate choice may be shaped by environmental variation among populations. Sexual selection through male-male competition is often predicted to vary with the environment, as changes in environmental conditions (e.g., resource availability) could affect the strength of interactions among males competing for access to potential mates (Gillespie et al. 2014; Miller and Svensson 2014). Selection through female mate choice should also exhibit spatial variation because these choices directly benefit females and their benefits vary across environments (Andersson 1994). For instance, female preferences (Qvarnström 2001; Kokko et al. 2002; Chaine and Lyon 2008) and the expression of many sexually selected traits (Andersson 1994; Badyaev and Qvarnström 2002) are often environmentally context dependent. Importantly, male-male competition and female choice are unlikely to act independently of one another (Hunt et al. 2009), and both can vary simultaneously with the environment. However, our understanding of the causes and consequences of spatial variation in sexual selection via female choice is less clear. This is especially the case for sexual selection in which males provide no direct benefits to females, as in indirect benefits models (Mead and Arnold 2004; Kokko et al. 2006).

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American Naturalist, volume 199, number 1, January 2022. © 2021 The University of Chicago. All rights reserved. Published by The University of Chicago Press for The American Society of Naturalists. https://doi.org/10.1086/717294

One indirect way sexual selection may arise is if sexual selection via female choice emerges as a consequence of species recognition mechanisms (McPeek and Gavrilets 2006). When females evolve a preference for a particular trait, conspecific males that have different trait values are less likely to successfully reproduce. If males and females share this or correlated traits (e.g., body size), this could also lead to the evolution of assortative mating. Moreover, if this trait is shared across sexes and there is trait variation among females within a population, this could further accentuate sexual selection. These population-level tendencies could account for why assortative mating by body size is common in nature (Arnqvist et al. 1996).

We have hypothesized such a scenario to explain sexual selection on *Enallagma* damselfly (Odonata: Zygoptera) male body size (Steele et al. 2011). We previously showed that the distribution of female body sizes throughout the breeding season for a single population defined the function for male mating success based on male body sizes (Steele et al. 2011), which is a critical component of male fitness (Lande 1981; Andersson and Simmons 2006). When mean male body size differed from mean female body size, males experienced directional selection to match female body sizes (Steele et al. 2011). Although males also engage in scramble competition for mates (we have observed as many as four males attempting to mate with a single female), males do not directly fight with one another; rather, the "scramble" is for securing the proper hold on the female for mating. Support for the hypothesis that the strength and direction of selection males experience is driven in part by the difference in body size between males and females would be strengthened with comparative studies spanning multiple populations and species and an evaluation of how environmental factors can shape selection among populations via the relationship between male and female body sizes. By determining what environmental features might shape body size differences among populations as well as differences among males and females, we can identify putative ecological drivers of sexual selection.

Although sexual selection on body size acts during the adult life stage, for organisms with complex life cycles, such as damselflies, environmental factors during the juvenile stage can shape the distribution of adult size phenotypes (Sokolovska et al. 2000; Thompson and Fincke 2002; Hassall 2013; Therry et al. 2014). For example, Anholt (1990) found that damselflies raised in high-density, low-food conditions emerged at smaller body sizes, implying that variation in food availability, habitat cover, lake productivity, and competitor density influence adult body size. In addition, high predator densities increase selection for lower activity levels and prey attack rates in larval damselflies (Strobbe et al. 2011; Siepielski et al. 2020) and stress responses to the threat of predation or competitors affect larval digestive physiology (McPeek et al. 2001), all of which may affect body size at emergence via feedbacks on growth and developmental rates. Thus, spatial variation in environmental conditions and the intensity of selective pressures among lakes can directly or indirectly affect larval size distribution, thereby setting the stage for sexual selection on body size during the adult life stage (Gillespie et al. 2014). Exploring this link between ecology and sexual selection is necessary for developing a more mechanistic understanding of how and why phenotypes shape fitness (Cornwallis and Uller 2010; Miller and Svensson 2014; Scordato et al. 2014; Giery and Layman 2019).

Because selection is defined by the functional relationship between fitness and phenotypes, differences in selection among populations could be shaped via four facets: differences in mean absolute individual fitness, differences in the distributions (means and variances) of phenotypes, or differences in the absolute fitness–trait function relationship (Steele et al. 2011; Hunter et al. 2018). Investigating how these various components underlying a fitness landscape are in turn associated with intrinsic factors or environmental variation among populations would then provide a way to understand what may be the causes of spatial variation in selection in the wild (Wade and Kalisz 1990; MacColl 2011; Steele et al. 2011; Siepielski et al. 2013; Hunter et al. 2018). Despite variation in selection arising through these paths, most studies have taken the approach of only examining the association between estimates of selection coefficients (e.g., the estimated trait-fitness function) and potential causal factors. Consequently, our understanding of the contributions of differences among populations in absolute fitness and trait distributions in shaping selection along environmental gradients is lacking.

Here we take a comparative approach to understand how the environment shapes spatial variation in sexual selection. Comparative studies (e.g., studies involving multiple species) of selection are particularly useful in helping strengthen observational studies that evaluate putative causal aspects of selection in lieu of direct experimental studies. Using comparisons among numerous populations of two damselfly species in the genus *Enallagma*, we evaluated the following. First, we compared male and female adult body sizes among lakes and examined how lake abiotic and biotic features during the juvenile stage influenced body sizes and differences in size between males and females. Second, we estimated spatial variation in sexual selection on male body size to examine how selection was related to differences in body size between males and females as well as environmental variation among lakes. To do so, we determined the environmental sensitivity of selection by decomposing selection into differences in mean fitness, differences in the distributions (means and variances) of phenotypes, and the absolute fitness–trait function relationship among populations (Hunter et al. 2018).

Material and Methods

Study System

We investigated spatial patterns of sexual selection among populations of two *Enallagma* damselfly species (*E. ebrium* and *E. geminatum*) that commonly co-occur in ponds with fish predators throughout the northeastern United States and southeastern Canada (McPeek and Brown 2000; Westfall and May 2006). *Enallagma* are univoltine and lay eggs in midsummer. Individuals then spend approximately 11 months as aquatic larvae and emerge the subsequent summer (middle to late June) as aerial adults. During the first few days of adulthood, males and females forage away from ponds to mature (Anholt 1991). *Enallagma* males are nonterritorial and return to the pond to actively search for females (Bick and Hornuff 1966), whereas females primarily forage away from ponds to acquire resources for egg production (Fincke 1982; Anholt 1992). When females return to ponds to mate, multiple males often engage in intense scramble competition for mating opportunities (Fincke 1982, 1986). Because females primarily visit ponds to mate and oviposit, the operational sex ratio at a pond is highly skewed toward males (Stoks 2001). Females may reject mating attempts when in tandem by moving about roughly until the male releases their grasp (Fincke 1997). Ultimately, females decide with whom they mate because they must willingly bend their abdomens to engage with the male secondary genitalia. In this study, we cannot distinguish between these potential causes of selection (male-male or male-female interactions); both likely contribute to our assessment of male mating success because only males possessing traits that allow for successful male-male competitive bouts will be subjected to female mate choice (Steele et al. 2011).

Characterizing Damselfly Body Size and Sexual Selection among Populations

Our procedures for quantifying selection on damselfly body size have been described in detail elsewhere (e.g., Steele et al. 2011) and are similar to those of many other studies of sexual selection in odonates (e.g., Cordero 1995; Svensson et al. 2004; Gosden and Svensson 2008; Steele et al. 2011; Siepielski et al. 2018). Here we summarize the key features of our methods. We used handheld nets to collect adult damselflies from eight populations of each of the two *Enallagma* species (table S1; tables S1–S6 are available online) that were either in tandem or found singly throughout the breeding season (mid-June to early August 2010 and 2011). These dates capture almost the entire breeding season for each generation and thus span the period of time that sexual selection on male body size may occur. Single males and tandems were collected between 1000 hours and 1900 hours, the time when damselflies are generally most active, on days that were partially or fully sunny and ≥18°C. Each lake was visited three or four times, and all individuals were combined in the subsequent analysis of selection to provide overall estimates of selection per generation (e.g., Steele et al. 2011). All damselflies were stored in 70% ethanol.

We photographed individuals in the laboratory under standardized lighting conditions and used ImageJ (ver. 1.43u; Media Cybernetics, Bethesda, MD) to measure eight morphological traits: 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. All measurements were made to the nearest 0.1 mm.

Because we collected as many paired damselflies as we could find and as many single damselflies as time allowed during the sampling period, this study provides an accurate assessment of daily mating activity. This technique of quantifying mating success is often used to quantify sexual selection on damselflies (e.g., Cordero 1995; Svensson et al. 2004; Gosden and Svensson 2008; Steele et al. 2011; Siepielski et al. 2018). However, this study does not measure lifetime mating success because males that were captured and not in tandem may have mated outside our collection periods and some matings may not have been observed. For the purposes of defining the fitness component, mating success, we considered males captured in tandem to be “mated” and to have a fitness of 1 and captured males that were not in tandem to have a fitness of 0.

To characterize size variation of damselflies, we used principal components analysis (PCA) on the correlation matrix of the eight morphological traits for each species each year. Separate PCAs were performed for each species; however, they captured similar patterns of trait variation across both species. All traits loaded negatively and fairly equitably on the first PC (PC1; tables S1, S2), and these associations were comparable among years. Thus, we considered PC1 to be an overall measure of body size, as is frequently done for damselflies (Svensson et al. 2004; Gosden and Svensson 2008; Steele et al. 2011), and refer to this composite trait as “size.” Although other PCs capture somewhat similar levels of variation, our specific hypotheses focus primarily on body size, so we focus our attention on this composite trait measure.

From these measures we estimated unstandardized selection differentials ($\hat{s}$) as the difference in mean values of mated and nonmated males. We used unstandardized selection differentials so as not to obscure potential paths through which the environment can affect trait-fitness associations generating selection (for a detailed description of this approach, see Hunter et al. 2018). The standard error of these estimates was determined as shown in Hunter et al. (2018).

Environmental Variation and Larval Damselfly Densities among Lakes

At each lake, we measured environmental factors that previous studies have shown can either directly or indirectly affect damselfly larval growth and mortality rates (McPeek 1990, 1998; McPeek et al. 2001; Siepielski et al. 2011*b*, 2016; Siepielski and McPeek 2013) and that can potentially affect adult body size (Anholt 1990, 1991). The methods used have been described elsewhere (see Siepielski et al. 2010, 2011*a*, 2011*b*), so we only briefly describe them here. We estimated the density of macrophytes in ten 0.25-m^2 quadrats in the littoral zone because they are essential habitat for damselflies, providing refuge from predators and foraging substrate for larvae (Crowley and Johnson 1992). Damselfly prey density on submerged macrophytes was estimated by taking six replicate prey samples with a 6-L box sampler (100-μm mesh). We also measured the density of fish predators by taking three standardized seine hauls (4.5 × 1.5-m beach seine net with 5-mm mesh) throughout the littoral zone of each lake. Finally, we quantified the net primary productivity of the littoral food web of each lake by estimating the growth rates (mg $\text{C} \times \text{d}^{-1}$) of attached algae on clay tiles. To estimate *Enallagma* larval densities, we sampled larvae using standardized 1-m-long sweeps with a D-frame dip net (28-cm net opening, 1 × 1-mm mesh) at a depth between 0.25 and 0.50 m. This method gives highly repeatable estimates of odonate abundances (Crowley and Johnson 1992; Stoks and McPeek 2003). On each sampling date, we took 10 replicate sweeps throughout macrophytes in the littoral zone of each lake. All captured animals were preserved in 70% ethanol. There were no strong correlations among these environmental factors among lakes (table S3).

Assessing the Role of Environmental Conditions and Male and Female Phenotypic Distributions in Sexual Selection

To determine whether there were differences in male and female body sizes among lakes, we used linear mixed effects models separately for males and females of both species. Male and female body size was our response variable, and lake was treated as a fixed factor. Year was included as a random effect to account for nonindependence.

To test whether male and female body sizes differed within lakes and among years, we used pairwise Welch's *t*-tests. To examine whether larval period environmental features could explain differences in both male and female body sizes, we used simple linear regression analyses. We used male and female body size as a response variable and the five different environmental variables: *Enallagma* density, lake productivity, macrophyte and fish density, and total prey.

We took two approaches to investigate how variation in the strength and direction of linear selection was related to differences in environmental conditions and the difference in female and male body sizes among lakes. First, we regressed (unstandardized) estimated selection differentials against environmental features and body size differences:

$$\hat{s}_i = \mu + be_i + m_i + \epsilon_i,$$

where $\hat{s}_i$ is the estimated selection differential (the difference in mean PC1 between mated and nonmated males) for each population, i, and e_i is the value of the larval period environmental variable or difference in body size between male and females. The sampling error of each selection differential is included as $m_i \sim N(0, \text{SE}_i^2)$, and the residual error is included as $\epsilon_i \sim N(0, \sigma_\epsilon^2)$. This model was implemented separately for each species for each e_i in the metafor package (Viechtbauer 2010).

Our second approach estimated the sensitivity of the selection to changes in the environment (e.g., environmentally structured fitness functions; Hunter et al. 2018) and through which of the different paths (trait mean and variance, mean fitness, and fitness-trait relationship) they are more strongly affected by (i.e., full and partial sensitivities; Hunter et al. 2018). We briefly summarize the method here given that an extended explanation is presented in Hunter et al. (2018). First, we constructed three models to estimate how the (i) mean and (ii) logarithmic variance of male body size was affected by the environmental features noted above as well as (iii) how fitness was affected by the environment and male body size. The mean and logarithmic variance of male body size were both analyzed with a linear regression using the environmental variable as a fixed factor. The effect of the environment and male size in fitness was analyzed with a binomial model because our fitness measure is binary (mated = 1, single = 0). We used body size, the environment, and their interaction as fixed factors. With the coefficients of these models, we can predict the mean male body size in a given environment by

$$\bar{z}(e) = \alpha + \beta e,$$

the trait variance in a given environment by

$$\sigma_z^2 = \exp(\alpha + \beta e),$$

and the absolute fitness of a given trait value in a given environment by

$$W(z, e) = g'(\alpha + \beta_1 z + \beta_2 e + \beta_3 ez),$$

where g' is an inverse logit function. Then we introduce a change in the environment smaller than the natural (observed) range of the environmental variable. This change in the environment can act independently in each of the previous equations:

$$\begin{aligned} \bar{z}(e) &= \alpha + \beta(e + h_\mu), \\ \sigma_z^2 &= \exp(\alpha + \beta(e + h_\sigma)), \\ W(z, e) &= g'(\alpha + \beta_1 z + \beta_2(e + h_a) + \beta_3(e + h_b)z). \end{aligned}$$

With these equations we can estimate the absolute fitness (W) of a trait (z) in a given environment (e), and if multiplied by the probability density function of the trait in the environment we obtain the mean fitness ($\overline{W}_e$). The selection differential in any given environment can then be expressed as $S(e) = W^{-1}\mathrm{cov}(z, W)$ when $h_\mu = h_\sigma = h_a = h_b = 0$.

We estimated the full sensitivity of the selection differential to a given environmental variable by

$$\frac{dS(e)}{de} = \frac{S(e + h) - S(e)}{h},$$

where $S(e + h) = W^{-1}\mathrm{cov}(z, W, h)$ and $h_\mu = h_\sigma = h_a = h_b = 0.01$. Finally, we estimated the partial sensitivities by introducing an environmental change in one of the coefficients while maintaining the others constant:

$$\frac{dS(e, j)}{de} = \frac{S(e + h_j) - S(e)}{h_j}.$$

With this approach, we can estimate the partial sensitivity of the selection differential to a given environment through each of the four pathways. For example, the partial sensitivity through the effect of the environment in the trait mean would be given when $h_\mu = 0.01$ and $h_\sigma = h_a = h_b = 0$. To calculate average sensitivity, we estimated the full and partial sensitivities in all observed values of the environmental variables. We conducted all analyses in R (ver. 4.0.2; R Core Team 2020). Data and code to run analyses can be found in the Dryad Digital Repository (https://doi.org/10.5061/dryad.5qfttdz62; Siepielski et al. 2021).

Results

Are There Differences between Male and Female Body Size Within and Between Populations?

There was considerable variation in both mean male (*Enallagma ebrium*: $\chi^2 = 1{,}082.8$, $n = 9{,}422$, $\mathrm{df} = 7$, $P < .001$; *Enallagma geminatum*: $\chi^2 = 623.84$, $n = 2{,}218$, $\mathrm{df} = 7$, $P < .001$) and female (*E. ebrium*: $\chi^2 = 255.27$, $n = 2{,}129$, $\mathrm{df} = 7$, $P < .001$: *E. geminatum*: $\chi^2 = 168.74$, $n = 514$, $\mathrm{df} = 7$, $P < .001$) body sizes among lakes for both species (fig. 1). With the exception of Stocker Pond, New Hampshire, in 2010, females were consistently larger than males within lakes, and there was much variation in the magnitude of the size differences between males and females (table S4; fig. 1).

Do Abiotic and Biotic Features during the Larvae Stage Influence Male and Female Body Size Distributions and Sexual Size Dimorphism?

Differences among lakes in body sizes were associated with environmental factors, but these patterns differed among males and females. For both *E. ebrium* and *E. geminatum*, males became larger as fish densities increased (table 1; fig. 2). Notably, although other environmental factors did not significantly explain differences in male body size among lakes, the patterns themselves were generally similar among the factors and species (fig. 2). By contrast, no environmental factors significantly explained variation in female body sizes among lakes (table 1; fig. 2). Qualitatively, though, the general patterns of associations between female body sizes and lake features were similar to the patterns observed among males (fig. 2).

As with female body sizes, no environmental factors explained the difference in body size between males and females among lakes (table 2; fig. 3). Thus, although males consistently differed from females among lakes in that they were smaller, the magnitude of this difference was unrelated to any of the environmental features measured, even though some of these same features explained difference in male body size.

Does Sexual Selection Show Spatial Variation and Is It Related to Sexual Size Dimorphism and the Environmental Factors Varying among Lakes?

Selection tended to favor larger males in most populations in most years for both species (table S5; fig. S1, available online). Variation among populations in estimated selection on males was also related to environmental factors among lakes for both species (table 3; fig. 4). The regression-based analysis taking into account sampling error in selection differentials revealed that for *E. ebrium*, as fish densities and macrophyte densities increased among lakes, estimated selection differentials for larger males weakened and instead began to favor smaller males (fig. 4). For *E. geminatum*, as macrophyte densities increased among lakes, selection also weakened for larger males and instead began to favor smaller males. For *E. geminatum*, as lakes became more productive, selection for larger males strengthened (fig. 4).

There was no support for the hypothesis that differences in the strength and direction of selection were related to variation among lakes in the differences in

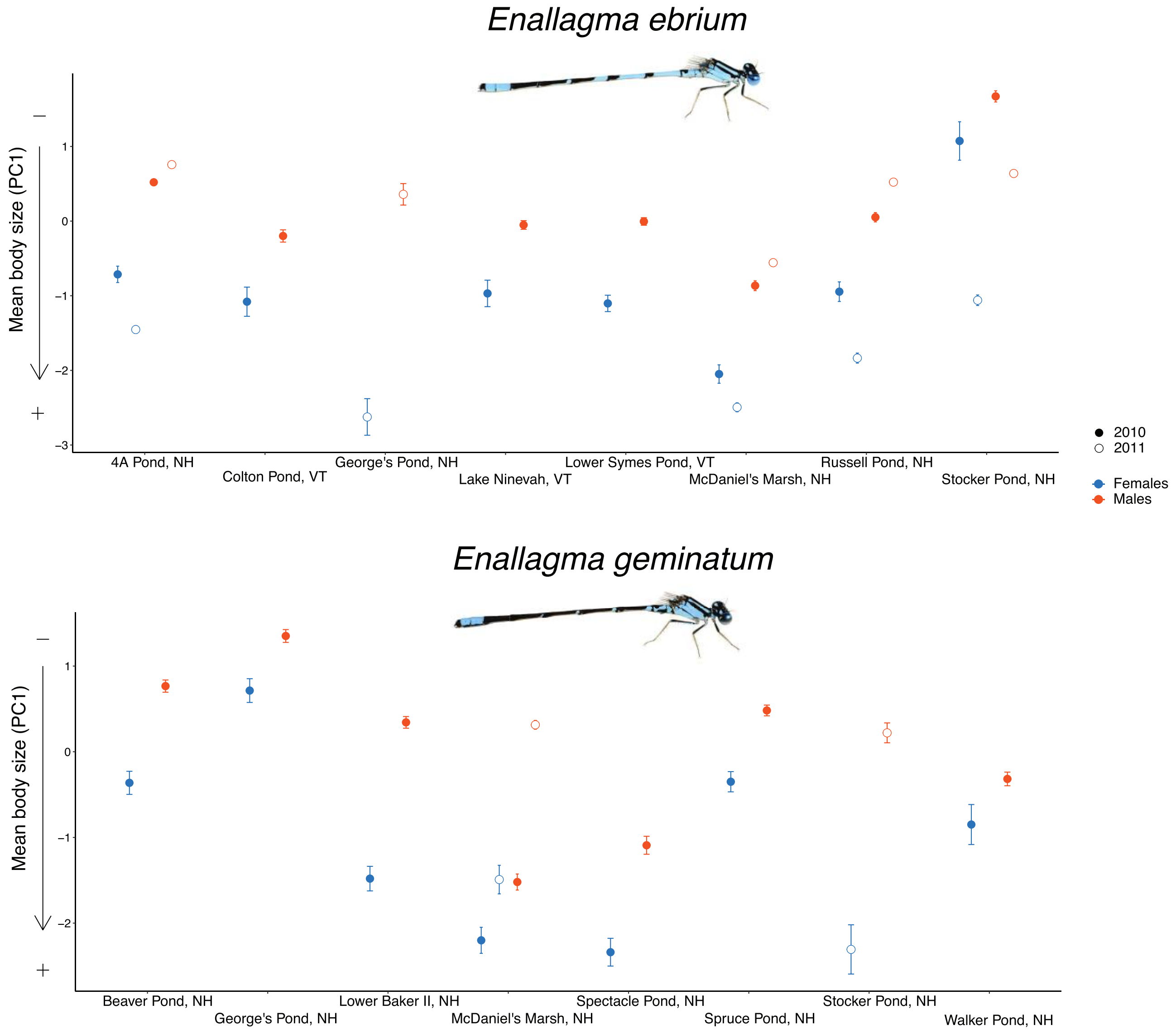

Figure 1: *A*, *Enallagma ebrium* male and female mean body size (PC1) and standard error in eight different lakes during 2010 and 2011. *B*, *Enallagma geminatum* male and female mean body size (PC1) and standard error in eight different lakes during 2010 and 2011. Note that more negative values of PC1 correspond with larger body sizes (see tables S1, S2). Damselfly illustrations by Ed Lam.

sizes between males and females among lakes (table 3; fig. 4). Thus, shared features of the environment that larvae experience can explain differences in selection among populations, but differences in body sizes between males and females among lakes does not.

Does the Environment Affect Patterns of Selection and, If So, through Which Pathway (Trait Mean and Variance, Mean Fitness, and Fitness-Trait Relationship)?

We considered only those environmental factors that accounted for differences in selection among populations from our regression-based analysis (table S6; fig. 5) to investigate environmentally structured fitness functions. Decomposing the trait mean and variance, absolute fitness, and trait-fitness relationships revealed that for both species, trait-fitness relationships had the largest partial sensitivities (table S6; fig. 5). That is, spatial variation in selection was largely attributed to differences in the functional relationships between absolute fitness (mating success) and body size. The effects of spatial variation in trait means and variances, or mean absolute fitness, contributed little to the sensitivity of selection to environmental features, except that mean absolute fitness and body size variances

Table 1: Results from linear regression analyses examining the effect of five different environmental variables on *Enallagma ebrium* and *Enallagma geminatum* body size (PC1) of males and females

Species, environmental variable	Estimate (SE)	t	P	R^2
	Males			
E. ebrium:				
Enallagma density	.001 (.003)	.268	.794	.007
Productivity	1.306 (2.9)	.441	.669	.019
Macrophyte density	−.0054 (.005)	−1.056	.316	.100
Fish density	−.055 (.01)	−3.15	.0103	.498
Prey density	.00093 (.004)	.224	.827	.005
E. geminatum:				
Enallagma density	.0052 (.01)	.37	.723	.019
Productivity	.339 (2.9)	.117	.91	.001
Macrophyte density	−.0082 .006)	−1.181	.276	.166
Fish density	−.0602 (.02)	−2.269	.057	.423
Prey density	.0036 (.005)	.66	.53	.058
	Females			
E. ebrium:				
Enallagma density	.0007 (.005)	.134	.895	.001
Productivity	6.06 (3.9)	1.545	.153	.192
Macrophyte density	−.004 (.007)	−.584	.572	.032
Fish density	−.05 (.03)	−1.558	.15	.195
Prey density	−.005 (.005)	−.951	.364	.082
E. geminatum:				
Enallagma density	−.001 (.01)	−.067	.949	.0006
Productivity	−2.51 (3.2)	−.769	.467	.001
Macrophyte density	−.009 (.008)	−1.179	.277	.165
Fish density	−.05 (.03)	−1.696	.134	.291
Prey density	.002 (.006)	.314	.762	.013

of *E. geminatum* slightly declined as macrophyte densities increased (fig. 5).

Discussion

Mating decisions frequently generate strong selection pressures in nature (Kingsolver et al. 2001; Andersson and Simmons 2006; Siepielski et al. 2011*a*). Because sexual selection acts only during the adult life stage, most studies have investigated how sexual selection might be shaped by environmental features experienced during the adult life stage and ignored preceding life stages (Gillespie et al. 2014). Yet since selection acts through fitness and phenotypic variation and it is defined by the functional association between these facets, environmental features that affect these components during the juvenile stage may shape sexual selection. In support of this idea, our results provide comparative evidence that environmental factors during the juvenile stage play a role in shaping variation in sexual selection among damselfly populations. This appears to act mainly through absolute fitness (mating success)–body size associations, not spatial variation in mean fitness or body size mean and variance. Below we discuss the results of our study by placing them into a broader conceptual framework aimed at more fully understanding the ecological underpinnings of sexual selection in the wild.

There was considerable variation in male and female body sizes among populations for both species. Differences in body size covaried with environmental features for males but not females, and no environmental features explained differences in body sizes between males and females within populations among lakes. For both species male body size increased as fish densities increased, with much of the variation in body size well explained by this factor. There are several reasons why greater fish predator densities may account for this variation. The direct consumptive effects of greater fish densities increasing mortality during the larval stage (Ousterhout et al. 2018) could reduce damselfly densities and thus reduce both direct interference competition and indirect resource competition (Anholt 1990; McPeek 1998). Reduced competition could therefore lead to larger adult body sizes, to the extent that adult body size is food limited—a pattern supported by experimental studies (Anholt 1990). Moreover, increased fish densities can decrease

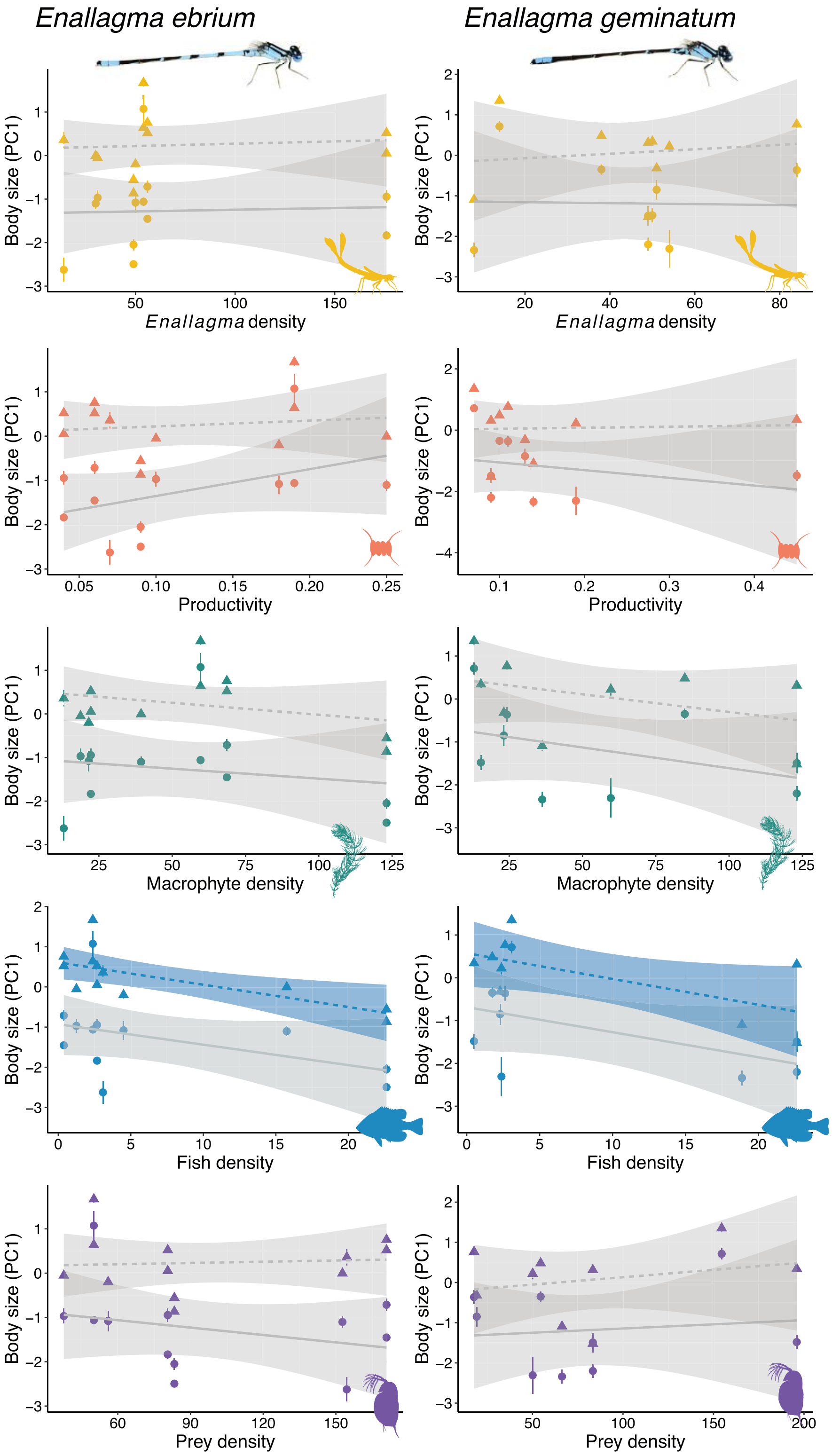

Figure 2: Effects of environmental factors on *Enallagma ebrium* (*left*) and *Enallagma geminatum* (*right*) male and female body size (PC1). Symbols (circles for females and triangles for males) denote estimated population mean values with their associated standard error. Lines show predictions from linear regression analyses, and colored regressions denote statistically significant associations. Regression parameter estimates can be found in table 1.

Table 2: Regression analysis examining the effect of five different environmental variables in sex differences in body size (male PC1 minus female PC1) of *Enallagma ebrium* and *Enallagma geminatum*

Species, environmental variable	Estimate (SE)	t	P	R^2
E. ebrium:				
Enallagma density	.0002 (.004)	.065	.949	.004
Productivity	−4.76 (2.8)	−1.646	.1308	.213
Macrophyte density	−.0008 (.005)	−.15	.883	.002
Fish density	−.004 (.02)	−.175	.864	.003
Prey density	.006 (.004)	1.598	.141	.203
E. geminatum:				
Enallagma density	.006 (.01)	.605	.564	.049
Productivity	2.85 (1.9)	1.5	.1773	.243
Macrophyte density	.001 (.005)	.244	.814	.008
Fish density	−.001 (.02)	−.065	.949	.0006
Prey density	.001 (.004)	.369	.723	.019

damselfly growth rates, as fish select for reduced foraging rates in damselflies (Strobbe et al. 2011; Siepielski et al. 2020), and nonconsumptive effects can cause physiological stress responses that suppress digestive physiology and slow growth (McPeek et al. 2001). Slower growth rates would prolong the developmental period and lead to larger body sizes, as frequently observed in other insect populations (Blanckenhorn and Demont 2004; De Block and Stoks 2004; Strobbe and Stoks 2004; Therry et al. 2014).

It is unclear why male, but not female, body size differences among lakes are correlated with fish densities. Across lakes, for both species male and female body sizes are positively correlated (*Enallagma ebrium*: $r = 0.665, P = .018$; *Enallagma geminatum*: $r = 0.770$, $P = .015$). Thus, we would have expected the same overall associations between environmental factors and body size to be apparent. This lack of concordance suggests that female body sizes are shaped by additional factors that males are not experiencing. One possibility is that sex-specific differences in foraging ecology during the adult life stage further shapes differences in body size between sexes. Females odonates are consistently heavier than males (Anholt et al. 1991) and, unlike male body size, female body size—specifically body mass and abdominal width—continues to increase as they feed to acquire prey resources for egg production (Anholt 1992). Because males forage near waterbodies and females primarily forage away from waterbodies, females may also experience weaker resource competition, thereby generating more variation in adult female body size. Thus, there may be differences among lakes in prey resources for adult females, and this shapes variation in their body sizes. Many species have such sex-specific differences in foraging ecology (Shine 1989; Giery and Layman 2019). Because foraging ecology can directly or indirectly shape differences in body size, which is often a target of selection, it may be a key ecological factor underlying the dynamics of sexual selection (Giery and Layman 2019).

Differences in environmental factors among lakes were also associated with sexual selection on male body size. For both species, selection generally favored larger males when macrophyte densities were lower and smaller males when macrophyte densities were higher. This pattern may be associated with habitat availability because macrophytes, in addition to providing a foraging substrate for larvae, are also locations where mating and oviposition often occur. While our measure of macrophyte density did not discriminate between emergent and submerged vegetation, it may be that when macrophyte densities are lower, more intense scramble competition among males arises, favoring larger, more dominant males. Ultimately, however, the decision to mate is contingent on the female accepting the male. Although selection in both species was similarly associated with macrophytes, they also exhibited unique facets. For *E. ebrium*, selection favored larger males at lower fish densities and smaller males at higher fish densities—this pattern was also apparent for *E. geminatum* but was not statistically significant. For *E. geminatum*, sexual selection favored smaller males in less productive lakes and larger males in more productive lakes. The latter finding is intriguing, as it suggests that sexual selection imposed by female mate choice might shape body size difference for performing in lakes of varying productivity (see also Gillespie et al. 2014). Presumably, if a lake is resource limited and so has low productivity, smaller individuals that have lower resource requirements might be favored. Thus, selection during the adult life stage may have further synergistic consequences during the juvenile life stage (Price and Grant 1984).

However, for all of these selection-environmental couplings we documented, there was no general correspondence between selection and body size differences among lakes. That is, spatial variation in sexual selection in relation to these environmental features does not seem to account for spatial variation in body size differences among lakes.

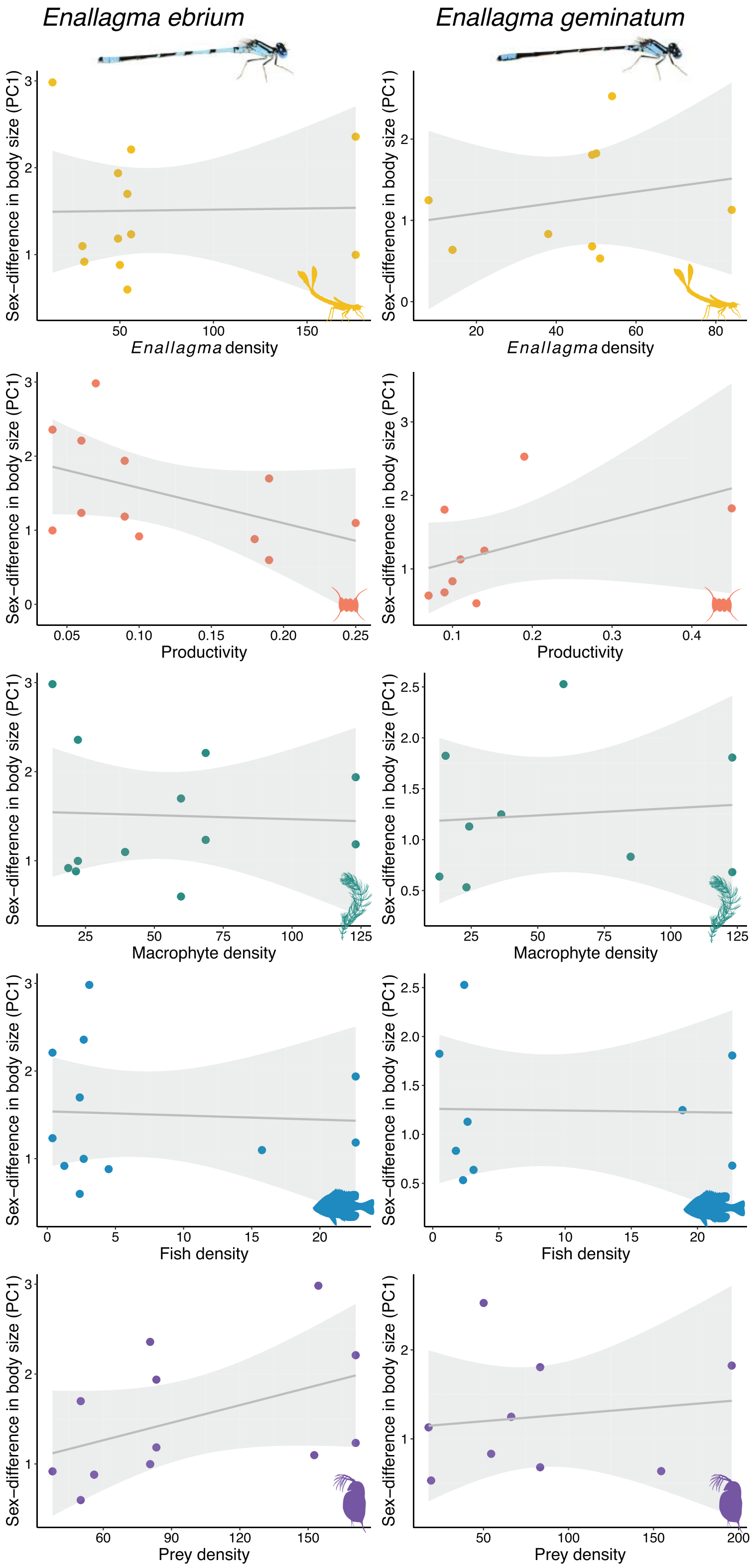

Figure 3: Effect of environmental factors on sex differences in body size (male PC1 minus female PC1) of *Enallagma ebrium* (*left*) and *Enallagma geminatum* (*right*). Points represent estimated population mean values of the difference between males and females. Lines show predictions from regression analyses; no regressions were statistically significant. Regression parameter estimates can be found in table 2.

Table 3: Results from models relating selection differentials of *Enallagma ebrium* and *Enallagma geminatum* to environmental variables

Species, environmental variable	Estimate (SE)	z	P	Pseudo R^2	I^2
E. ebrium:					
Enallagma density	−.0005 (.002)	−.209	.834	0	.5
Productivity	.316 (1.9)	.164	.869	0	.51
Sex difference PC1	−.0203 (.20)	−.098	.921	0	.51
Macrophyte density	.008 (.002)	3.806	<.001	1	0
Fish density	.029 (.01)	2.733	.006	.78	.15
Prey density	−.001 (.002)	−.719	.472	0	.47
E. geminatum:					
Enallagma density	−.004 (.009)	−.458	.646	0	.62
Productivity	−3.41 (1.19)	−2.853	.004	.78	.23
Sex difference PC1	−.231 (.32)	−.72	.471	0	.6
Macrophyte density	.007 (.004)	1.928	.053	.42	.45
Fish density	.028 (.02)	1.419	.155	.2	.53
Prey density	−.002 (.003)	−.588	.556	0	.61

Note: I^2 is the amount of heterogeneity relative to the total variance, and pseudo R^2 is the heterogeneity accounted for by a given environmental variable.

Body sizes are frequently heritable traits, so we expected to see that our estimated selection-environmental couplings explained population divergence. A critical assumption is that contemporary patterns of selection, such as those we documented, are what is currently driving population divergence. However, this need not necessarily be the case. For example, if populations have adapted to their local environment, they may display distinct phenotypes, but directional selection should be relatively weak (Bolnick and Nosil 2007). Indeed, because "selection erases its traces" (Haller and Hendry 2014), any alignment of selection with ecological or intrinsic differences (e.g., body size) may not be detectable. It may be that ongoing selection simply reflects a kind of fine-tuning that continues indefinitely as populations experience subtle changes in the environment, and large-scale changes in the environment may be needed to generate the kind of selection that results in detectable correlations between selection and population divergence (Kinnison and Hendry 2001; Estes and Arnold 2007; Uyeda et al. 2011; Haney and Siepielski 2018). Experimental approaches, such as reciprocal transplant experiments between contrasting environmental conditions, can help reveal these correlations because they essentially force a population to be maladapted (Nosil and Crespi 2006; Caruso et al. 2017; Ferris and Willis 2018). Similarly, because our approach for identifying putative environmental drivers of selection was inherently observational, future studies should conduct manipulative experiments to investigate the causal role of these environmental conditions (Wade and Kalisz 1990; Caruso et al. 2017). Numerous studies have documented spatial variation in selection among populations (Siepielski et al. 2013), but the extent to which spatial variation in ongoing selection mirrors patterns of trait divergence among populations has not been broadly evaluated.

We must also emphasize that we have focused only on one component of fitness affected by sexual selection. Viability selection, selection through other fitness components (Andersson 1994; Kokko et al. 2002; Siepielski et al. 2011*a*, 2011*b*), or other forms of sexual selection (Hunt et al. 2009) on body size may also be important, as may selection acting during the larval stage (McPeek 1997; Fincke and Hadrys 2001; Strobbe et al. 2011; Siepielski et al. 2020). This may be especially important for traits such as body size, which likely influence several fitness components, all of which frequently vary among life stages (Arnold and Wade 1984; Garcia et al. 2009; Chevin et al. 2017; Gamelon et al. 2018).

Although we found that environmental features influenced body sizes among lakes, there were no detectable features of the environment that explained body size differences between males and females that also explained differences in selection. Thus, we found no support for the hypothesis that differences in male and female body sizes generate selection on males. Of course, we cannot distinguish between the potential causes of selection (male-male or male-female interactions), as both likely contribute to male mating success because only males possessing traits that allow for successful male-male competitive bouts scrambling for females will be subjected to female mate choice. In damselflies, the reproductive structures (e.g., male cerci and female mesostigmal plates) that serve as strong prezygotic isolating barriers (Barnard et al. 2017) scale with body size (Siepielski et al. 2018). Therefore, we expected that males should experience strong directional selection for larger

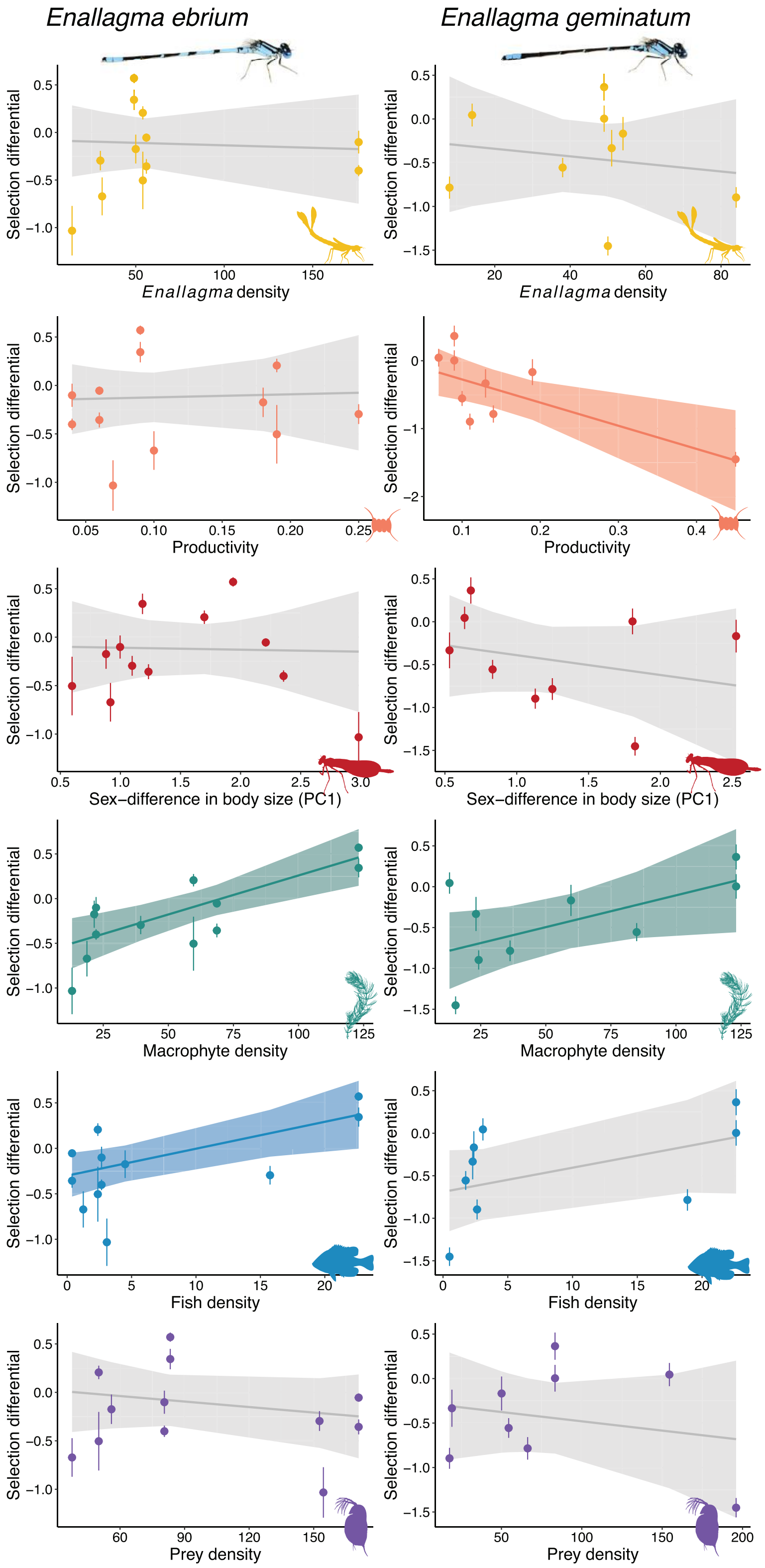

Figure 4: Effect of environmental variables and sex differences in body size on unstandardized selection differentials ($\hat{s}$). Points represent estimated selection differentials with their associated standard error. Lines show predictions from regression analyses. Significant ($P < .05$) regressions are shown as colored lines and shaded areas. Regression parameter estimates can be found in table 3.

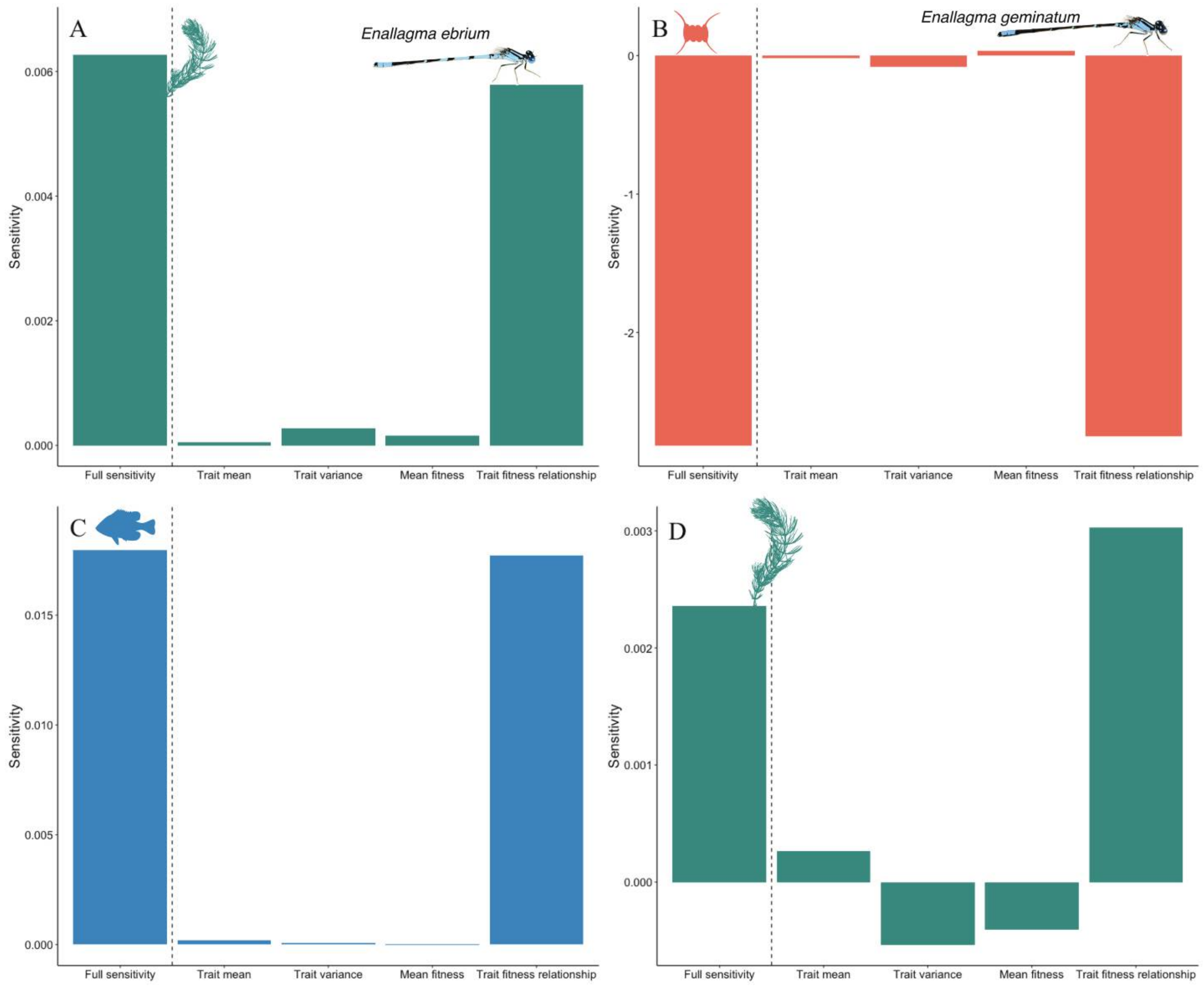

Figure 5: Sensitivity analyses depicting the partial contributions of each of the different pathways (trait mean, trait variance, mean fitness and trait fitness relationship) and total contribution (full sensitivities) through which different environmental factors affect selection estimates in *Enallagma ebrium* and *Enallagma geminatum* (see also table S5). Shown are full and partial contributions by which different environmental variables (*A*, *D*, macrophyte density; *C*, fish density; *B*, productivity) affect selection estimates in *E. ebrium* (*A*, *C*) and *E. geminatum* (*B*, *D*).

bodies when males were much smaller than females—a pattern we found support for in a single population throughout two breeding seasons (Steele et al. 2011). In this latter study, the differences in body size between males and females through time in that single population were comparable to the differences among populations documented here. Therefore, it is unlikely that the differences between males and females among populations studied here were simply not large enough. Rather, temporal and spatial variation in selection may simply not mirror each other and instead respond differently to environmental factors (Siepielski et al. 2019). One additional possibility is that alternative reproductive strategies (Gross 1996) could be favored when males are consistently mismatched relative to female body sizes. However, alternative strategies (e.g., courtship flights) have not been observed or reported in these species. Moreover, males cannot force females to mate, so how such a strategy might work is not clear based on our understanding of the biomechanics of reproduction.

Understanding the environmentally driven causes of selection in the wild is a formidable but important goal, as it provides a way of linking ecological and evolutionary processes. Many studies have adopted the approach of regressing selection coefficients on aspects of the environment (Wade and Kalisz 1990; Caruso et al. 2017; Siepielski et al. 2017; Hunter et al. 2018). While these studies have been insightful in understanding how ecological factors may shape selection and adaptive evolution in the wild (Chevin et al. 2010; MacColl 2011), they do not provide a complete view from which to understand how and why selection may be varying (Steele et al. 2011; Hunter et al. 2018). By quantifying and decomposing the sensitivity of sexual selection to the environment, we found that spatial variation in selection was shaped by trait–absolute fitness relationships, not through spatial variation in trait distributions or individual mean mating success. At present, there are few existing studies that have adopted this approach to draw comparisons with. Hunter et al. (2018) showed that temporal variation in viability selection in Soay sheep (*Ovis aries*) was primarily driven by the effects of density on mean fitness, not through trait-fitness relationships. Ehrlén and Valdés (2020) found that temporal variation in selection on phenology of the perennial herb *Lathyrus vernus* was influenced by both varying trait distributions and mean absolute fitness. However, most of the among-year variation in selection was explained by the effects of climatic factors on trait-fitness relationships.

More generally, decomposing the underlying causes of selection in this way will allow future synthesis studies aimed at understanding whether selection is varying mainly because of the effects of some environmental feature influencing trait distributions, mean fitness, or trait-fitness relationships. Much like how the development of the Lande and Arnold (1983) approach of using standardized selection coefficients has been foundational in uncovering the major features of selection, quantifying and decomposing the environmental sensitivity of selection will provide even deeper insight into understanding the causes of selection in the wild.

Acknowledgments

We thank Caitlin Barber, Richard Clark, Curtis McPeek, and Andrew Mertens for help with fieldwork. Michael Morrissey kindly provided much help with statistical analyses. Simon Tye, Christine Miller, and one anonymous reviewer provided helpful comments on the manuscript. This work was supported by the National Science Foundation (grant DEB-1748945 to A.M.S., grant DEB-0714782 to M.A.M.).

Statement of Authorship

A.M.S. conceptualized and designed the study, conducted fieldwork and analyses, and wrote the first draft of the manuscript. M.G.-L. conducted analyses and data visualization and reviewed and edited the manuscript. M.A.M. helped with conceptualizing the study and reviewed and edited the manuscript.

Data and Code Availability

All data and code to run the analyses can be found in the Dryad Digital Repository (https://doi.org/10.5061/dryad.5qfttdz62; Siepielski et al. 2021).

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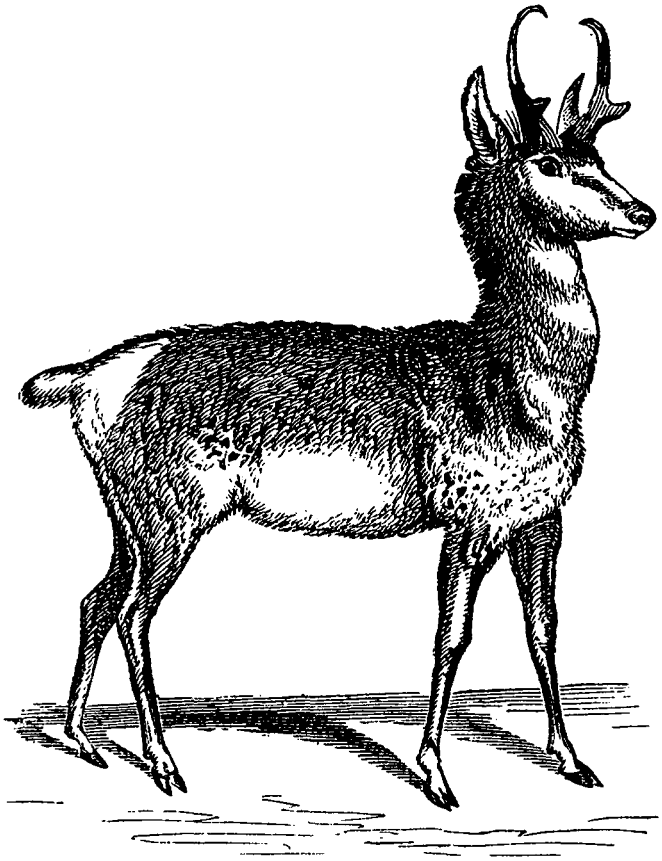

“Like the cow and sheep there is a horn-core formed by the prolongation of the frontal bone, and occupying about two-thirds of the interior of the horn. When the horn drops off, the horn-core is found covered with a thick skin, and coated with hair, the same as the face of the animal, with a small portion of the tip having already begun to harden; this acting as a wedge, forces the horn off.” From “The Prong-Horn Antelope” by W. J. Hays (*The American Naturalist*, 1868, 2:131–133).