

Male-Male Competition Causes Parasite-Mediated Sexual Selection for Local Adaptation

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ABSTRACT: Sexual selection has been suggested to accelerate local adaptation and promote evolutionary rescue through several ecological and genetic mechanisms. Condition-dependent sexual selection has mainly been studied in laboratory settings, while data from natural populations are lacking. One ecological factor that can cause condition-dependent sexual selection is parasitism. Here, we quantified ectoparasite load (*Arrenurus* water mites) in a natural population of the common bluetail damselfly (*Ischnura elegans*) over 15 years. We quantified the strength of sexual selection against parasite load in both sexes and experimentally investigated the mechanisms behind such selection. Then we investigated how parasite resistance and tolerance changed over time to understand how they might influence population density. Parasites reduced mating success in both sexes, and sexual selection was stronger in males than in females. Experiments show that male-male competition is a strong force causing precopulatory sexual selection against parasite load. Although parasite resistance and male parasite tolerance increased over time, suggestive of increasing local adaptation against parasites, no signal of evolutionary rescue could be found. We suggest that condition-dependent sexual selection facilitates local adaptation against parasites and discuss its effects in evolutionary rescue.

Keywords: condition dependence, evolutionary rescue, local adaptation, parasitism, sexual selection.

Introduction

Sexual selection can promote local adaptation (Servedio 2004; Servedio and Boughman 2017) and facilitate evolutionary rescue (Candolin and Heuschele 2008) by purging the genome from deleterious mutations (Whitlock and Agrawal 2009). If the strength of sexual selection is stronger on males than on females and given that population fitness is more closely linked to female than male fitness

(Harts et al. 2014), then females can benefit from sexual selection on males while avoiding the costs of reduced female fitness (Agrawal 2001; Siller 2001; Whitlock and Agrawal 2009; Servedio and Boughman 2017; Cally et al. 2019). However, even though females may contribute more to short-term population growth (Harts et al. 2014), males contribute to long-term population growth by increasing local adaptation (Aguilée et al. 2013, 2016). Sex differences in local adaptation are therefore gaining increased research attention among ecologists and evolutionary biologists (Connallon et al. 2018; Svensson et al. 2018).

Overall organismal condition is likely to be influenced by both environmental and genetic factors, and condition should reflect genetic variation across the entire genome (Rowe and Houle 1996). Moreover, overall condition is likely to contribute more to individual mating success than any single trait (MacLellan et al. 2009; Whitlock and Agrawal 2009). As mating success requires males to succeed in several energetically costly behaviors (searching for females, male-male competition, courtship, female coercion, etc.; Andersson 1994), male mating success is likely to be highly condition dependent (Rowe and Houle 1996; Parrett et al. 2019). Sexual selection on condition-dependent traits is therefore expected to promote local adaptation (Rowe and Houle 1996; Lorch et al. 2003; Whitlock and Agrawal 2009; Servedio and Boughman 2017; Parrett et al. 2019).

The overall condition of an organism can be negatively affected by parasite load, and this in turn can affect mating success (Able 1996; Møller et al. 1999). For instance, field studies of red grouse (*Lagopus lagopus*) revealed that parasite load reduced body condition, which in turn resulted in reduced expression of secondary sexual characters (Vergara et al. 2012). Likewise, in natural populations of a damselfly (*Enallagma ebrium*), increased parasite load reduces male mating success (Forbes 1991). Sexual selection against parasites and pathogens (Joye and Kawecki 2019) is of general interest, as individuals with low parasite loads could

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have higher condition and higher genetic and/or phenotypic quality.

Moreover, parasite load and its consequences can be sex specific, which can have important evolutionary and demographic consequences. In laboratory-bred populations of *Drosophila melanogaster*, experimental infection with the bacterium *Pseudomonas aeruginosa* revealed sex differences in parasite-mediated sexual selection (Sharp and Vincent 2015). If the parasite load affects males more strongly than females, then selection on males can facilitate local adaptation without the demographic consequences that selection in females could cause. Parasite-mediated sexual selection might therefore reduce the risk of extinction by facilitating local adaptation and promoting evolutionary rescue (Forbes and Baker 1991; Vergara et al. 2012; Sharp and Vincent 2015).

Pond damselflies (family Coenagrionidae) are characterized by strong sexual selection, arising from intense male-male scramble competition over access to females and the resulting male mating harassment (Corbet 1999; Gosden and Svensson 2007, 2008, 2009). Mating success is therefore highly likely to be condition dependent (Forbes 1991; Forbes and Baker 1991). Natural populations of pond damselflies are often infected by ectoparasitic water mites of the genus *Arrenurus* (Åbro 1979, 1982; Rolff 2000). High parasite loads in damselflies have been shown to affect agility and flight performance, which is necessary for mate search and competition for mates (Åbro 1982). Consistent with this, *Arrenurus* parasite load has been linked to poor mating success in the damselfly *Enallagma eribium* (Forbes 1991) and reduced female fecundity in *Ischnura elegans* (Willink and Svensson 2017). However, sex differences in the strength of sexual selection against parasitism and the possible ecological or behavioral mechanisms reducing male or female mating success have not been investigated in any previous study, to the best of our knowledge.

Here, we used multigenerational field data from a natural *I. elegans* population that has been monitored for 15 years to investigate how parasite load affects pre- and postcopulatory sexual selection, with the aim of understanding how selection on males and females could promote local adaptation and evolutionary rescue. First, we investigated whether male and female parasite load affect precopulatory sexual selection (mating success), postcopulatory sexual selection (fecundity), or both. Second, we asked whether male-male competition was an important driver of precopulatory sexual selection. To achieve these ends, we quantified the strength of selection against parasite load and compared the strength of pre- and postcopulatory sexual selection between the sexes in the field. Given the strong male-male competition in this species, we expected parasite loads to reduce male mating success,

while female parasite loads were expected to reduce fecundity. Next, we estimated male mating success in the presence and absence of male competition to assess the effect of parasites on male mating success. Finally, we asked whether sexual selection can lead to local adaptation through the evolution of parasite resistance and tolerance and whether local adaptation can promote evolutionary rescue by facilitating population recovery. Given sexual selection against parasite load, we would expect local adaptation to evolve through increased parasite tolerance, parasite resistance, or both. Such local adaptation would be more pronounced in the sex with the strongest sexual selection. Finally, if adaptation to parasitism occurs, we expect population productivity to increase through the effects of evolutionary rescue. We therefore analyzed whether population density in this field population of *I. elegans* has increased.

Methods

Study Organism

The common bluetail damselfly (*Ischnura elegans*) is a small insect species distributed throughout Europe, with its northernmost range limit in Scandinavia (Corbet 1999). The generation time of *I. elegans* is 1 year in the northern part of its range in Europe, with adults emerging between late May and early August, while the larvae overwinter in an aquatic stage (Corbet 1999). During the aquatic stage, water mites of the genus *Arrenurus* attach to the larvae and remain in a phoretic stage until adults emerge, when they attach to the cuticle on the ventral side and pierce it to feed on the host body fluids (Åbro 1979, 1982; Rolff 2000). These water mites are presumably harmless commensals during the aquatic larval stage, which is followed by a stage where they become parasites on the adult damselflies. Water mites are easily detected visually and have been reported to affect agility and flight performance in other species of *Coenagrion* and *Enallagma* damselflies (Åbro 1982).

Mating and reproduction in *I. elegans* consist of several behavioral steps. First, males search for females, which they attempt to clasp by the prothorax using structures known as claspers (Åbro 1979). Intense scramble competition between males to find and clasp females characterizes the mating system of *I. elegans* and other pond damselflies studied in the past (Åbro 1979). After clasping, the male and female form a tandem position, and the female can choose to bend her abdomen to reach the male genitalia and ensure mating and sperm transfer (Åbro 1979). During copulation, male damselflies remove sperm from previous matings before transferring their own sperm to a female (Fincke 1984; Corderos and Miller 1992). Finally, females oviposit on emergent vegetation in freshwater bodies (Åbro 1979).

Data Collection

Our field data come from a longitudinal study of a natural population of *I. elegans* in southern Sweden, in which we have collected parasite data over the last 15 years (2003–2018). The location is a large permanent freshwater pond located near the city of Lomma (55.684942, 13.085414). We visited this population in Lomma on multiple occasions (between 5 and 16 times, with a mean of 8.5) per year, during 15 reproductive seasons of *I. elegans*. Visits are weather dependent, as we visited the population during warm ($>15^{\circ}\text{C}$) days with no rain or strong wind, the favorable conditions for this damselfly. During these visits, we caught all damselflies we could using hand nets during time-recorded capture sessions. We estimated population densities by dividing the total catch with the catching time (i.e., number of individuals caught per minute). For each captured individual we identified the sex, mating status (single or in copula), and number of parasites. Males and females caught in copula were transported back to an indoor laboratory at the Department of Biology (Lund University). In the lab, we estimated fecundity by placing females in individual plastic cups with moisturized filter paper as oviposition substrate (Svensson et al. 2005). We allowed females to lay eggs for 48 h, after which we scanned and counted the eggs. In odonates, including *I. elegans*, males and females can mate multiple times, but males remove the sperm from previous copulations (Cordero 1990; Corderos and Miller 1992; Córdoba-Aguilar et al. 2003; Rivera et al. 2004); therefore, by using females found in copula we can be sure of the parasite load of both parents. We collected data of mating success and parasite loads from 2003 to 2018, but fecundity data could not be collected during the period between 2010 and 2013 due to financial constraints. We transported all males and females captured during a single visit to our laboratory, preventing recaptures of animals between capturing sessions.

Experimental Mating Trials

To investigate whether male-male competition could cause parasite-mediated sexual selection, we carried out an experiment with two treatments: one without male-male competition (the no-competition treatment; one female with one male) and one with male-male competition (the competition treatment; one female with two males) during the summers of 2018 and 2019. We expected that if female mate choice were the main cause of differential male mating success, then parasitized males would have lower mating success than nonparasitized males in the no-competition treatment. Furthermore, if male-male competition were the main cause of parasite-mediated sexual selection, then we would find lower mating success of parasitized males in

the competition treatment compared with that in the no-competition treatment.

Parasitized and nonparasitized males and females were captured in the Lomma population and transported to Stenoffa Field Station (55.695145, 13.447076) in netted containers (Port-a-Bug containers; diameter, 10.2 cm; height, 22.9 cm). We used adult (sexually mature) individuals with no visible harm (e.g., broken wings). All animals were separated by sex and kept in an average density of 10 individuals per container during transportation. In the field station, we quantified the parasite load of each individual and set up a series of cages (Port-a-Bug cages; diameter, 25 cm; height, 30 cm) for mating trials. We added twigs and grasses to mimic natural vegetation and allow individuals to perch or rest as well as a plastic cup with a moisturized filter paper to prevent desiccation. For the no-competition treatment we added one female and one marked male (parasitized or nonparasitized). For the competition treatment we added two males (one parasitized and one nonparasitized) and one marked female. We marked the individuals with a fluorescent color dust in the genital area. This technique allowed us to identify the males that successfully mated by looking at traces of color dust in the genitalia under UV light 24 h after initiating the experiment. This method has been used previously to quantify female mating rates in *I. elegans* and male mating success in other damselfly species, such as *Enallagma cyathigerum* and the genus *Calopteryx* (Gosden and Svensson 2009; Gómez-Llano et al. 2018). All data used for this study are available in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.cjsxksn35>; Gómez-Llano et al. 2020).

Statistical Analysis

Precopulatory sexual selection was analyzed with generalized linear mixed models assuming a binomial distribution, using mating success (1 = mated, 0 = unmated) as the dependent variable and parasite load, sex, and their interaction as fixed effects. Year was included as a random factor. To investigate postcopulatory sexual selection we used a subset of the field data with only those females that were found mating. We used a model with a Poisson distribution, with the number of eggs as the response variable and parasite loads in the female and the partner as fixed effects. Again, year was included as a random factor. To test whether there was a difference in the proportion of successful matings of parasitized and nonparasitized males between the competition treatment and the no-competition treatment, we performed a Cochran-Mantel-Haenszel test.

To estimate the linear selection differential (Lande and Arnold 1983) on parasite loads, we regressed our two relative fitness measures (mating success and fecundity)

separately for each sex and standardized individual parasite loads separately in males and females. As significance levels can be unreliable when using binomially distributed variables such as mating success (Lande and Arnold 1983), we used binomial distributions to obtain the significance levels of the selection differentials of mating success (Brodie and Janzen 1996). Selection estimates are useful in meta-analyses that compare the strength of natural or sexual selection in different traits and/or taxa, as they provide standardized effect sizes that are comparable between studies (for examples, see Kingsolver et al. 2001; Janicke et al. 2016; Siepielski et al. 2017, 2019; De Lisle et al. 2018).

To investigate the consequences of parasite-mediated sexual selection for local adaptation, we constructed two different statistical models to analyze how parasite resistance and tolerance changed from 2003 to 2018. Parasite resistance was analyzed using a binomial distribution with parasite prevalence as the response variable and year, sex, and their interaction as fixed factors. Parasite tolerance was analyzed as the reduced negative effect of parasite prevalence, quantified through fecundity. We used egg count as the response variable assuming a Poisson distribution. Year, parasite prevalence in females and males, and the two-way interactions (year and parasite prevalence in females and year and parasite prevalence in males) were included as fixed factors. Given that a decrease in parasite prevalence could be caused by a decrease in parasite density, we performed a model using the mean seasonal parasite density as the response variable assuming a normal distribution and year as a fixed factor. Finally, to investigate whether local adaptation facilitated population recovery, we constructed a linear model with a normal distribution, using daily visit population density as the response variable and year as a linear predictor.

All models analyzing fecundity were performed using Bayesian generalized mixed models with Markov chain Monte Carlo (MCMC) estimation, given the dispersion and smaller sample size. We used an uninformative prior and performed 100,000 iterations, with a burn-in of 10,000 and a thinning interval of 10. We evaluated convergence by plotting the chains and assessing whether they mixed properly, using the package MCMCglmm (Hadfield 2010). Models of mating success and density were analyzed with lme4 (Bates et al. 2015). All of the statistical analyses were carried out in the R statistical environment (R Development Core Team 2018).

Results

We collected a total of 4,387 individuals: 2,655 males (1,006 parasitized; ~38%) and 1,732 females (817 parasitized; ~47%). We estimated the fecundity of 554 females,

which were captured in copula in the field. As we aimed to analyze the effect of male and female parasite load on fecundity, only females captured together with their partner and for which we were able to estimate the parasite load were used in the fecundity analysis. The mating trial experiments were carried out using 116 females and 186 males from the Lomma population.

Sex Differences in the Effects of Parasite Load on Mating Success and Fecundity

Precopulatory sexual selection was estimated as male and female mating success (a cross-sectional measure, based on the proportion of copulating individuals in the field). As predicted, we found a significant negative effect of parasite load on mating success (estimate = -0.025 , $P < .001$). We also found a significant effect of sex, where the average mating success of nonparasitized males was significantly lower than that of nonparasitized females (estimate = -0.652 , $P < .001$), reflecting that a higher fraction of females were found mating near the water bodies where sampling typically takes place. Interestingly, the interaction between parasite load and sex (i.e., testing for a sex difference in slopes) was also significant (estimate = -0.026 , $P = .012$), revealing that the fitness costs of parasite load in mating success was higher in males than in females (fig. 1A; table S1; tables S1–S6 are available online).

Postcopulatory sexual selection against parasitism was estimated from individual fecundity data obtained from females found in copula and their corresponding mates. Contrary to our expectations, we did not find a significant effect of either male ($P_{\text{MCMC}} = .82$) or female ($P_{\text{MCMC}} = .17$) parasite load on fecundity (fig. 1B; table S2).

Selection differentials (standardized slopes) for mating success against parasite load were significantly stronger in males than in females ($P < .001$; fig. 1B; table 1), consistent with the steeper slope for males than for females in figure 1A. We could not find a significant difference in the selection differentials of fecundity on parasitized males ($P_{\text{MCMC}} = .75$) or females ($P_{\text{MCMC}} = .13$; fig. 1B; table 1, pt. A).

Effect of Male-Male Competition on Selection against Parasite Load

We compared the effects of parasite load on male mating success in the presence of male competition (mating trials with one female and two males) and the absence of male competition (one female and one male). We found that the male mating success of parasitized males was higher in the no-competition treatment than in the competition treatment ($\chi^2 = 32.61$, $P < .001$; fig. 2A; table 2). Overall,

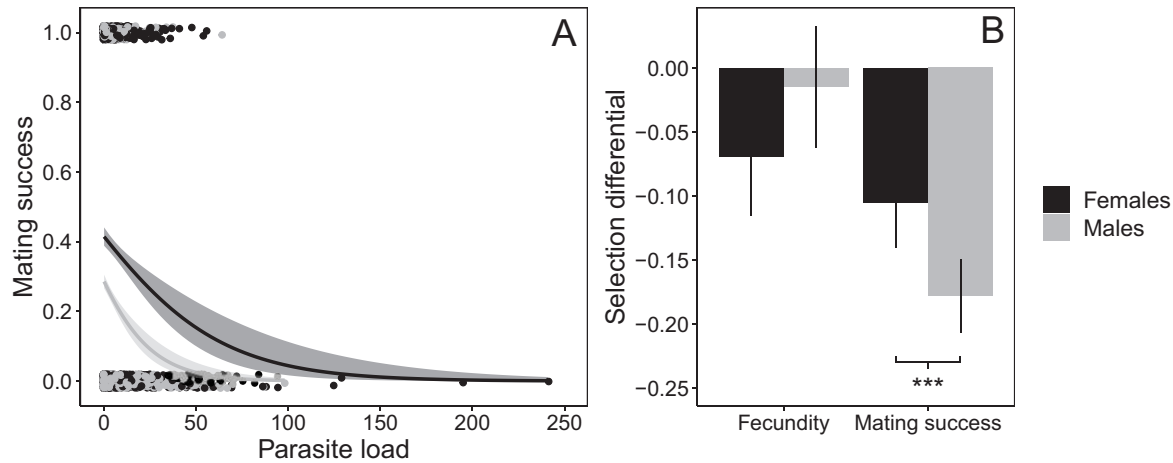


Figure 1: Parasite load reduced both male and female mating. A, We show a more negative effect of parasites in males than in females (i.e., steeper slope of the relationship between mating success and parasite load). Points show individual observations, and the regression line shows predicted values with 95% confidence intervals. B, Selection differentials (standardized separately for males and females) against parasite load for mating success were significantly different from zero in males and females and were stronger in males than in females, while the selection differentials for fecundity were not different from zero or between sexes. Error bars show standard errors.

the selection differential against parasite load was stronger in the competition treatment ($s = -0.43$) than in the field ($s = -0.17$), and the strength of sexual selection in the field was in turn stronger than that in the no-competition treatment ($s = 0.018$; fig. 2B; table 1, pt. B).

Increasing Local Adaptation of Parasite Resistance and Parasite Tolerance?

Given the strong sexual selection against parasite load that we documented above (figs. 1, 2), we would expect local adaptation to increase parasite resistance, parasite tol-

erance, or both. We found evidence for increased parasite resistance in both males and females, as revealed by a significantly declining per capita parasite prevalence in both sexes across the entire study period (estimate = -0.026 , $P = .008$; fig. 3A), but there was no significant interaction between sex and year (estimate = 0.008 , $P = .51$; fig. 3A). This indicates that parasite resistance increased to the same extent in both sexes during these 15 years (fig. 3A; table S3). We also analyzed temporal changes in parasite tolerance using our fecundity data. We found a significant effect of the interaction between year and parasite prevalence in males ($P_{\text{MCMC}} = .042$). The average fecundity of parasitized males increased during this time period, while the fecundity of nonparasitized males remained constant (fig. 3B). Interestingly, there was no such significant temporal trend in females during the same time period ($P_{\text{MCMC}} = .28$; table S4, pt. A). These results were even stronger when using a subset of the data (from 2003 to 2007) in which the annual sample sizes were considerably larger (table S4, pt. B). Finally, when analyzing temporal changes in parasite density we found no effect of year (estimate = -3.909 , $P = .56$). This shows that although parasite prevalence has decreased across years, it is not due to a decrease in parasite density, as it has remained stable across years (table S5).

Has Local Adaptation Led to Evolutionary Rescue?

Population density in Lomma declined steadily and significantly from 2003 to 2018 (estimate = -0.03 , $P = .002$;

Table 1: Precopulatory (mating success) and postcopulatory (fecundity) selection differentials against parasite load in males and females in the field (pt. A) and male precopulatory selection in the field and under experimental conditions in the competition and no-competition treatments (pt. B)

	Differential	SE
A. Fitness component, sex:		
Mating success:		
Males	-.178	.028
Females	-.105	.035
Fecundity:		
Males	-.014	.045
Females	-.068	.046
B. Environment:		
Field	-.178	.028
Competition	-.438	.076
No competition	.018	.032

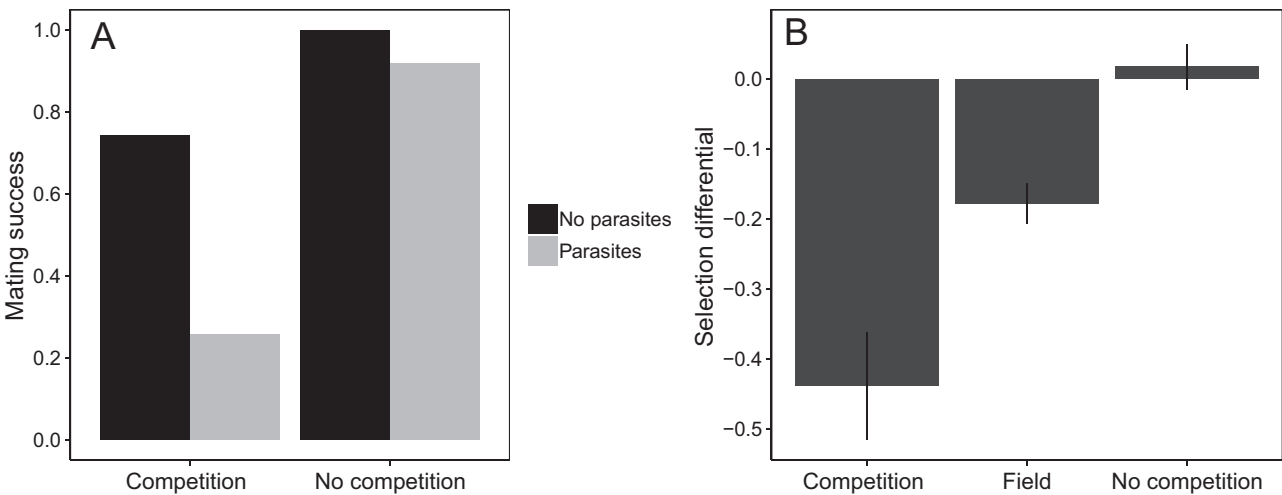


Figure 2: Proportion of successful matings of parasitized and nonparasitized males in the competition treatment and the no-competition treatment. *A*, The proportion of successful matings of parasitized males was lower in the competition treatment than in the no-competition treatment, suggesting that male-male competition is the main cause of precopulatory sexual selection against parasite load. *B*, Selection differentials of precopulatory sexual selection against parasitized males was stronger in male-male competition than in the absence of male-male competition, and selection strength in the field fell in between. Standard errors are shown around the three selection estimates.

fig. 4; table S6). No signs of recovery could be found, as adding a quadratic term turned out to be nonsignificant.

Discussion

Theory and limited empirical evidence suggest that condition-dependent sexual selection can improve population mean fitness (Forbes and Baker 1991; Lorch et al. 2003; Whitlock and Agrawal 2009; Servedio and Boughman 2017; Parrett et al. 2019). Most previous studies investigating the links between sexual selection, local adaptation, and population fitness have been performed in laboratory settings using a few model organisms and a restricted set of taxa (Sharp and Agrawal 2008; MacLellan et al. 2009; McGuigan et al. 2011; Berger et al. 2016; Martinossi-Allibert et al. 2018, 2019; Cally et al. 2019; but see Parrett et al. 2019). Here, we used field data from a long-term population study and used individual variation in parasite load as a measure of condition to investigate the

role of sexual selection in promoting local adaptation of males and females. Our approach is similar to some previous studies of parasite-mediated and condition-dependent sexual selection (Vergara et al. 2012; Sharp and Vincent 2015).

Previous studies have shown that parasite load can reduce overall condition (Forbes 1991; Forbes and Baker 1991; Vergara et al. 2012) and increase mutation load (Cooper et al. 2005; Young et al. 2009; Sharp and Vincent 2015). Parasite-resistant males are likely to exhibit higher condition and might, on average, be more adapted to the local environment and/or have a lower mutation load. Given that parasite-resistant males (in high condition) might be more successful in obtaining a larger proportion of the matings because of their advantage in male-male competition (figs. 1, 2), sexual selection against parasite load would be expected to increase average condition and lead to well-adapted males, which in turn should increase adaptation and mean fitness of the population (fig. 3). The results presented here are in agreement with a recent field study of dung beetles that documented strong population-level benefits of precopulatory sexual selection on traits that are important in male-male competition (Parrett et al. 2019).

We note that although parasitized females suffered from lower mating success than nonparasitized females (fig. 1), the relationship between fitness and mating success is likely to be more complex in females than in males, due to strong male mating harassment and sexual conflict (Gosden and Svensson 2009). Lower female mating success might not necessarily indicate lower female fitness, as females suffer from repeated mating and harassment from males (Yun

Table 2: Mating success of parasitized and nonparasitized males in the competition and no-competition treatments

	Nonmated	Mated
Competition:		
Nonparasitized	18	52
Parasitized	52	18
No competition:		
Nonparasitized	0	21
Parasitized	2	23

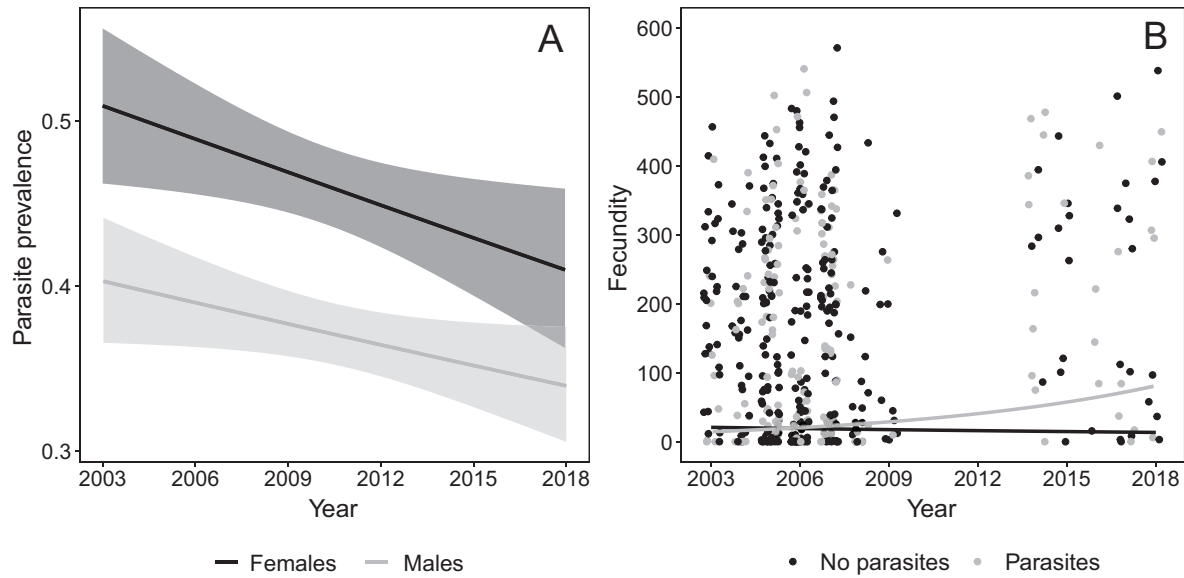


Figure 3: Temporal changes in parasite prevalence in both sexes and male parasite tolerance. *A*, Parasite prevalence (proportion parasitized) decreased over time, and this decline was similar in males and females. *B*, Parasite tolerance increased over time in males. This result was confirmed using a subset of the data (from 2003 to 2007) in which the per-year sample size is larger (see the supplementary analysis, available online). Points show individual observations, and the regression line shows predicted values with 95% confidence intervals in shaded areas.

et al. 2018), and higher mating success could then potentially reduce female fitness. However, if female mating rates would be above their fitness optima because of male mating harassment, we would expect parasitized females to have

similar mating success as nonparasitized females. That parasitized females mate at a lower frequency than nonparasitized females suggest that selective males discriminate against such females, which might be perceived as less attractive and of lower quality.

The results of this study show that sexual selection against parasitism, acting through mating success, is stronger in males than in females, while the effects of parasitism on fecundity selection was weak (fig. 1*B*). Although this latter result agrees with a previous result in a different species of damselfly (Åbro 1982), it contrasts with a previous study of *I. elegans* in the same area, where a significant negative effect of these ectoparasites on female fecundity was found (Willink and Svensson 2017). This discrepancy is likely to be due to the different focus of both studies. In our study, we used data from one heavily infested population and tracked the effects of the parasites through time. In the previous study, the authors compared populations that varied in the degree of parasite pressure, including populations with no parasites (Willink and Svensson 2017). Therefore, the previous study shows the effect of parasites in populations with, presumably, different degrees of adaptation to the parasite, including non-adapted populations. Our results, however, show evidence of local adaptation reducing the negative effects of parasites through time.

Parasite resistance (i.e., minimizing parasitic infection) and tolerance (i.e., reducing the fitness costs of parasite load) have traditionally been thought of as alternative

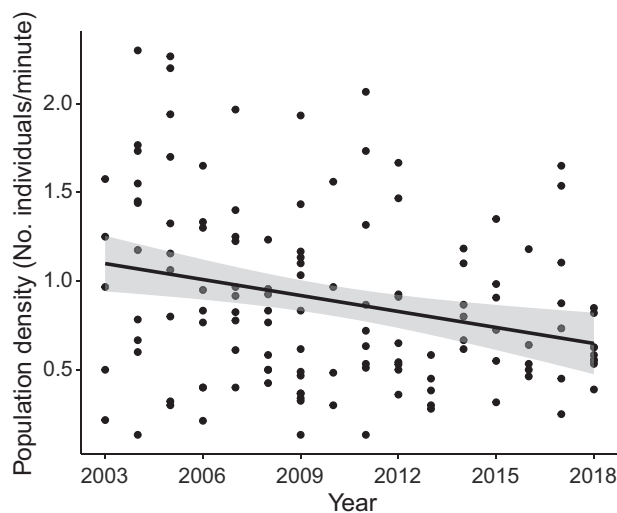


Figure 4: The population density of *Ischnura elegans* in Lomma has decreased significantly since 2003. Points show population density per visit, estimated by dividing the total catch (number of individuals) by the sampling effort (time spent catching). The regression line shows predicted values assuming a normal distribution, and the shaded region shows the 95% confidence intervals.

defense mechanisms in which investing in one mechanism will make the other redundant (Råberg et al. 2007, 2009; Svensson and Råberg 2010). The results of the present study are in contradiction with such a trade-off in both males and females. In females, although parasite resistance increased during the time period (fig. 3A), tolerance did not change. In males, both parasite resistance and tolerance increased (fig. 3), which is interesting since parasite-mediated sexual selection on mating success is stronger in males (fig. 1). These results suggest that such a trade-off between defense mechanisms does not exist, and individuals can evolve multiple responses to the same selective pressure. These sex differences in the temporal change to parasites raises interesting questions about sex differences in local adaptation (Svensson et al. 2018) and opens the door for follow-up studies of sex differences in the genes underlying parasite resistance and tolerance.

We suggest that sexual selection on parasite load has facilitated local adaptation through parasite tolerance and resistance, although we have not yet found any evidence of evolutionary rescue, as there is no sign of population recovery (fig. 4). This could be due to a temporal lag between increasing resistance and tolerance and their positive effects in population growth. If so, we would expect population density to increase in the coming years. Our results, however, show no effect of parasite load on female fecundity, which supports alternative explanations for population decline rather than a temporal lag. Population growth is affected by several biotic and abiotic factors; in insects especially population declines have been reported as a consequence of climate change (Hallmann et al. 2017; Lister and Garcia 2018; Seibold et al. 2019; Sánchez-Bayo and Wyckhuys 2019), which could be responsible for the observed population decline.

The beneficial effect of sexual selection promoting adaptation can be hindered by sexual conflict if male-induced harm reduces female fitness and the advantage of high-condition females (Rundle et al. 2006; Chenoweth et al. 2015; Yun et al. 2018). High levels of parasitism could potentially reduce average male harm on females if parasitized males cannot pay the costs of searching and competing for females. Female fitness costs of male-induced harm would then be limited, and adaptation through sexual selection would be promoted. The potential for parasitism in reducing male mating harassment and thereby reducing sexual conflict could be an additional and fruitful new line of research.

The difference in the strength of parasite-mediated selection on males in the presence and absence of competition in experimental treatments and the field (fig. 2) reveal several important insights about the role of male-male competition and how environmental complexity might influence male mating success. Overall, parasite-

mediated sexual selection was stronger in magnitude in male-male competition than in the absence of male competition, with selection strength in the field falling somewhere in between (fig. 2B). These differences in sexual selection strength presumably reflect differences in male-male competition as well as environmental complexity, which is substantially higher in the field than in our experimental cages. In the field, females can hide from males in the spatially more complex environment, and male search costs of females are presumably also higher, weakening the effects of parasite-mediated sexual selection and potentially weakening both sexual selection on and sexual conflict over females (MacPherson et al. 2018; Yun et al. 2018, 2019).

It is important to note two possible caveats of our mating assays. In our experiments males and females were kept in cages for 24 h. This long period of time could make it difficult or costly for females to resist mating approaches from parasitized and nonparasitized males, increasing male mating success in the no-competition treatment. Another possible problem is that although we do not claim or attempt to eliminate female mate choice but rather to eliminate male-male competition, the treatments also differ in the opportunity for female choice. Female choice is expected to be stronger in the competition treatment (with two males) than in the no-competition treatment (with one male). However, two factors support our interpretation. First, we used wild-caught females in our experiments. These females were very likely to have been mated beforehand so they would suffer no fitness consequences if they avoided mating, which could in turn strengthen selection against the male in the no-competition treatment. Second, Gosden and Svensson (2009) found that male harassment and coercion leaves limited scope for female choice in this damselfly's mating system. Male mating success is determined predominantly by male-male aggression and the harassment and coercion of females.

In summary, our results show that sexual selection against parasite load, a trait likely to reflect male condition, is stronger in males than in females. We show that male-male competition is a strong driver of sexual selection against parasitized males in this species. This form of sexual selection might have promoted local adaptation in parasite resistance and tolerance in this population. However, no evidence of population recovery and evolutionary rescue could be found. The links between parasitism, sexual selection, local adaptation, and evolutionary rescue clearly deserve further theoretical and empirical attention (Candolin and Heuschele 2008; Bell 2012; Servedio and Boughman 2017).

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Statement of Authorship

M.G.-L., E.I.S., and A.N. designed the study. M.G.-L. and A.N. carried out the experiments. E.I.S. and many former field assistants and PhD students collected the long-term population data. M.G.-L. conducted the statistical analyses and wrote the text with substantial input from E.I.S. and A.N.

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A marked *Ischnura elegans* male used in this study. Males were marked with color powder, which is transferred to females during mating. This method allowed the authors to identify which males had mated and which had not. Photo credit: Aaditya Narasimhan.