


## LETTER

# Temperature drives pre-reproductive selection and shapes the biogeography of a female polymorphism

Erik I. Svensson,<sup>1\*</sup> 

Beatriz Willink,<sup>1†</sup>

Mary Catherine Duryea<sup>1§</sup> and

Lesley T. Lancaster<sup>2</sup>

<sup>1</sup>Department of Biology Lund University, SE-223 62 Lund, Sweden

<sup>2</sup>School of Biological Sciences, University of Aberdeen, Aberdeen AB24 2TZ, UK

<sup>†</sup>Present address: School of Biology, University of Costa Rica, San Jose, Costa Rica 11501-2060 California, USA

<sup>§</sup>Southern New Hampshire University, Manchester, New Hampshire, USA 03106

\*Correspondence: E-mail: erik.svensson@biol.lu.se

### Abstract

Conflicts of interests between males and females over reproduction is a universal feature of sexually reproducing organisms and has driven the evolution of intersexual mimicry, mating behaviours and reproductive polymorphisms. Here, we show how temperature drives pre-reproductive selection in a female colour polymorphic insect that is subject to strong sexual conflict. These species have three female colour morphs, one of which is a male mimic. This polymorphism is maintained by frequency-dependent sexual conflict caused by male mating harassment. The frequency of female morphs varies geographically, with higher frequency of the male mimic at higher latitudes. We show that differential temperature sensitivity of the female morphs and faster sexual maturation of the male mimic increases the frequency of this morph in the north. These results suggest that sexual conflict during the adult stage is shaped by abiotic factors and frequency-independent pre-reproductive selection that operate earlier during ontogeny of these female morphs.

### Keywords

Biogeography, climate, colour polymorphism, frequency-dependent selection, ontogeny, pre-reproductive selection, sexual conflict, temperature.

Ecology Letters (2020) 23: 149–159

The peer review history for this article is available at <https://publons.com/publon/10.1111/ele.13417>

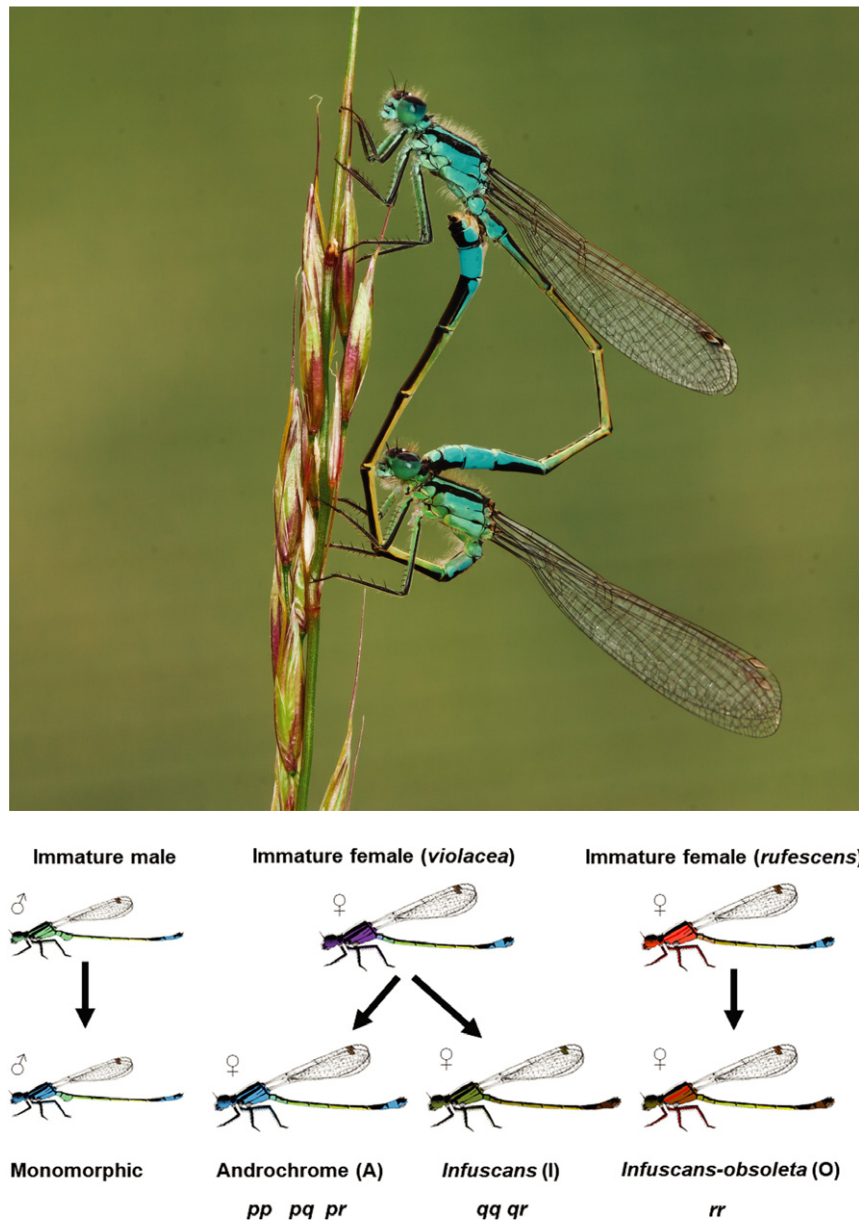
## INTRODUCTION

Sexual conflict is a major force that shapes male and female sexual interactions and in many species females incur fitness costs of mating or mating harassment (Rice 1996; Arnqvist & Rowe 2005). Experimental studies and comparative analyses (Arnqvist & Rowe 2002a, 2002b, b) suggest that sexual conflict could promote the rapid evolution of female and corresponding male traits, contributing to speciation (Arnqvist *et al.* 2000; Gavrillets 2000), but sexual conflict could also elevate extinction risk (Rankin *et al.* 2011), since female fitness is closely linked to population performance and stability (Le Galliard *et al.* 2005; Harts *et al.* 2014; Takahashi *et al.* 2014). However, evidence for a strong link between sexual conflict and speciation remains equivocal (Ritchie 2007). Theory also shows that an alternative outcome of sexual conflict is the evolution of distinct female (and sometimes also male) genetic clusters (or morphs) (Gavrillets & Waxman 2002; Svensson *et al.* 2005; Le Rouzic *et al.* 2015; Iversen *et al.*, 2019). An increasing number of examples of such polymorphisms that have evolved as a response to sexual conflict have now been demonstrated in several insect taxa (Svensson *et al.* 2005, 2009; Reinhardt *et al.* 2007; Karlsson *et al.* 2013).

One form of such mating polymorphisms is intersexual mimicry, in which some male or female individuals express a phenotype resembling the opposite sex (Gosden & Svensson 2009; Neff & Svensson 2013). Intersexual mimicry provides a fitness advantage either for males to obtain 'sneaky' matings through deception by looking like females (Neff & Svensson

2013), or, in the case of females, to avoid excessive male mating harassment by looking like males, especially when male densities are high and mating harassment of females is intense (Gosden & Svensson 2009; Svensson *et al.* 2009). Such intraspecific and intersexual mimicry is expected to show negative frequency-dependency, similar to more well-known interspecific Batesian mimicry systems, where benefits of mimicry are expected to break down if mimics becomes very common (Finkbeiner *et al.* 2018).

Many genera of dragonflies and damselflies are characterised by strong sexual conflict, intersexual mimicry and several genetic female colour morphs that coexist locally within populations (Svensson *et al.* 2009; Corbet 1999). In many species of pond damselflies in the globally distributed genus *Ischnura*, for example, one male-like female morph (androchrome females, hereafter called "male mimic") almost always occurs at lower frequency than the alternative female morph (gynochrome females) (Sanchez-Guillen *et al.* 2011). Thus, most species have two female colour morphs: a minority male mimic (androchrome) and a majority female-like (gynochrome) morph (Sanchez-Guillen *et al.* 2011). Some species like the widely distributed common bluetail damselfly (*Ischnura elegans*) even has three such female colour morphs, of which only one is a male mimic (Fig. 1) (Svensson *et al.* 2005; Le Rouzic *et al.* 2015). In *I. elegans*, and in several other species of *Ischnura*, colour morph development is governed by a single autosomal locus with three alleles in a dominance hierarchy and with sex-limited expression to females (Fig. 1) (Sanchez-Guillen *et al.* 2005; Svensson *et al.* 2009). However, such



**Figure 1** Sexual conflict and female colour polymorphism in *Ischnura* damselflies. Upper picture: the common bluetail damselfly (*I. elegans*) is characterised by strong sexual conflict over mating between males and females. During mating, the male (upper) and the female (lower; a male mimic, or “A-female”, see below) can remain attached to each other for several hours. Lower picture: as a result of sexual conflict over mating, many species of *Ischnura* damselflies exhibit female colour polymorphisms, with two or (in the case of *I. elegans*) three heritable female colour morphs. Such colour polymorphisms are maintained by frequency-dependent sexual conflict among adult females, in which common females suffer from excessive male mating harassment, resulting in lower female fitness. Females show age-related colour changes during the course of their ontogeny (Fig. S1), but the three adult female morphs at maturity is the result of a single autosomal locus with three alleles in a dominance hierarchy, with expression limited to females (males are monomorphic and do not express this polymorphism). Androchrome females (A-females) are male mimics and carry at least one *p*-allele, which is dominant over the *q* and *r*-alleles. The three female morphs are denoted A, I and O throughout this paper.

female morphs differ also in several other traits, apart from colour, including parasite loads, female fecundity, cold acclimation ability, mating behaviours and resistance and tolerance towards male mating harassment (Gosden & Svensson 2009; Lancaster *et al.* 2017; Willink & Svensson 2017).

The maintenance of these female colour polymorphisms is believed to be due to balancing selection (Svensson 2017), with empirical evidence for negative frequency-dependent selection in several species (Svensson *et al.* 2005; Takahashi

*et al.* 2010; Le Rouzic *et al.* 2015) and with some additional and complementary role for density-dependent selection (Gosden & Svensson 2009; Galicia-Mendoza *et al.* 2017). However, all of the proposed mechanisms for how negative frequency-dependent selection arises in these polymorphic systems rely on arguments for evolutionary change arising from selection driven by male mating harassment on females during the adult (reproductive) stage (Robertson 1985; Van Gossum *et al.* 2001; Fincke 2004; Takahashi & Watanabe 2009; Iserby

*et al.* 2011; Takahashi *et al.* 2010, 2014; Gering 2017). We know little about how selection might operate on earlier life stages, such as during the pre-reproductive development period of females, in spite of the fact that we know that opposing selection pressures during ontogeny is common in populations of many other organisms (Schluter *et al.* 1991; Barrett *et al.* 2008; Sinervo & McAdam 2008).

Recently, researchers interested in various forms of sexual conflict have turned their attention to the role of temperature in modulating such conflict in some laboratory insect systems (Berger *et al.* 2014; García-Roa *et al.* 2019). The aim of this study was to investigate how temperature might influence and explain geographic variation in female colour morph frequencies in the polymorphic species *I. elegans*. Specifically, we combined field studies of natural populations with mesocosm studies to investigate how frequency-independent pre-reproductive selection operating early in female colour development could influence adult morph frequencies. Such frequency-independent pre-reproductive selection could potentially oppose the well-known and previously demonstrated frequency-dependent selection, which is driven by sexual conflict and that is operating on the adult female morphs later in ontogeny (Svensson *et al.* 2005; Takahashi *et al.* 2014; Le Rouzic *et al.* 2015).

## METHODS

### Study organism

The common bluetail damselfly (*Ischnura elegans*) is a common insect in Europe with a broad geographic distribution, ranging from the UK in the west to Japan and several other countries in Asia (Indonesia, Malaysia, India and Pakistan) in the east (<http://www.iucnredlist.org/details/165479/0>). In Europe, *I. elegans* occurs from Cyprus, Greece, Italy and Spain in the south to Scandinavia in the north (Gosden *et al.* 2011; Askew 1988). Southern populations of *I. elegans* are multi-voltine with several generations per year, whereas populations in northern Europe are generally univoltine, with only one generation per year (Parr 1970; Shama *et al.* 2011; Fitt *et al.* 2019). *I. elegans* is characterised by three female-limited colour morphs, one of which is typically a male mimic (Fig. 1). The genetic basis of female colour polymorphism in *I. elegans* and its close relatives (*I. graellsii* and *I. genei*) has been revealed in controlled breeding experiments over several generations and arises from genetic variation at a single autosomal locus with three alleles in a dominance hierarchy and with sex-limited expression to females (Cordero 1990; Sanchez-Guillen *et al.* 2005; Sanmartín-Villar & Cordero-Rivera 2016). In addition to fixed genetic colour differences among adult female colour morphs (Fig. 1), there are also pronounced ontogenetic colour changes within the three female morphs during their sexual maturation period (Fig. S1).

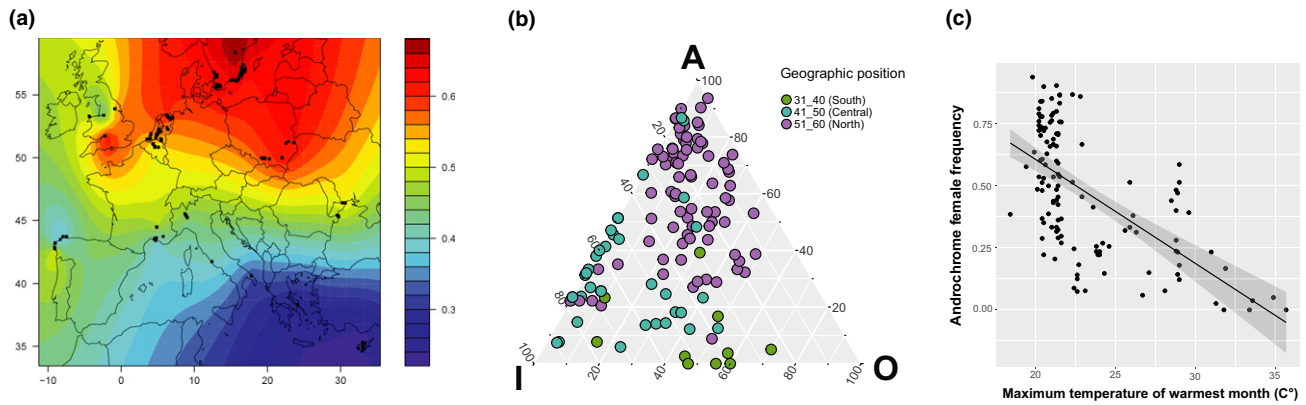
The three female morphs can be distinguished during their immature stage based on the melanin patterning on their blue abdomen patches (Fig. S1). Specifically, the two female gynochrome (female-like) morphs (I- and O-females) cover their blue abdominal patch with pigment as they become sexually mature, whereas the androchrome female morph (A-females, male mimic) retains this blue abdomen patch (Fig. S1). This

blue abdomen patch is also present on males throughout their entire lives (Fig. 1). Retaining of this male colour signal in androchrome females is an important part of male mimicry as it causes female resemblance to males and experimental phenotypic manipulations have revealed that the presence of this blue patch reduces male mating harassment (Willink *et al.* 2019a). Thorax colour also changes in these morphs during the course of their ontogeny (Cordero *et al.* 1998). Thorax colour changes from violet to blue in A-females, from violet to green in I-females and from pink to brown in O-females (Fig. 1) (Cordero *et al.* 1998; Svensson *et al.* 2009). Female colour maturation is tightly correlated with female reproductive maturity, as immature-coloured females of all morphs have high levels of reproductive failure and lay few eggs, if any at all, if given the opportunity (Willink *et al.* 2019a).

### General field work procedures

We performed field work around Lund (southern Sweden) in a series of natural populations of *I. elegans* that are part of a long-term population study that was initiated in the year 2000 by E.I. Svensson (Svensson & Abbott 2005; Svensson *et al.* 2005; Abbott *et al.* 2008; Gosden & Svensson 2008, 2009; Le Rouzic *et al.* 2015; Willink & Svensson 2017). Field work for this study was carried out during three reproductive seasons of *I. elegans* in the summers (June and July) of 2015–2017. This field observational study was complemented with a mesocosm study at Stenoffa Ecological Field Station (see further below). Field data on morph frequency variation and changes in morph frequencies during generations come from a total of 16 populations that are part of our core long-term population study (Le Rouzic *et al.* 2015). General field work routines are described in detail elsewhere (Svensson & Abbott 2005; Svensson *et al.* 2005; Le Rouzic *et al.* 2015; Willink & Svensson 2017). Briefly, we visited and revisited each of our populations at weekly intervals to catch and record densities, female colour morph frequencies, sex ratios and age class frequencies (tenerals, immatures and adults) and used standardised (time-recorded) sampling sessions to take into account total catching effort (Willink & Svensson 2017). By using data from these standardised field-sampling routines, we quantified morph frequency variation between populations and recorded morph frequency changes during the course of ontogeny, from the sexually immature stage to the adult reproductive stage (Fig. S1). All populations were visited multiple times across all field seasons in an effort to minimise any potential biases due to possible morph differences in catchability or detectability linked to specific weather conditions on specific days. Our previous work has revealed that population densities estimated using this approach are not biased by daily temperature fluctuations (Fitt & Lancaster 2017).

In addition to field work in southern Sweden, we also compiled a large biogeographic data set on female colour morph frequency variation across a number of populations along a latitudinal South-North gradient in Europe. We updated a previous biogeographical survey which contained data on adult female morph frequencies across all of Europe (Gosden *et al.* 2011) by adding eleven more populations (three from France, five from Cyprus) to this data set. This large



**Figure 2** Biogeographic variation in female colour morph frequencies of *I. elegans* and local microclimatic factors. (a) Across Europe, the frequency of the male mimic (A-females) increases at higher latitudes and near the northern range limit (Table S1) (b) Morph frequency variation in Europe divided in to three latitudinal bands. Each corner in the ternary plot represents a hypothetical population fixed for one morph (100%), but no such populations have been found, and the majority of populations are trimorphic, with a few dimorphic populations. (c) The local population frequency of the male mimic (A-females) is negatively related to maximum temperature during the warmest month (Bio5; Table S2), suggesting that these females are more cold-tolerant (or less heat-tolerant) than the two other female colour morphs.

biogeographic data set contained information from 129 populations across 11 countries in Europe with a total of 15 714 morphotyped adult females of *I. elegans* (Supporting Material). All these populations were georeferenced and contained longitudinal and latitudinal locality information. We used this spatial information to extract temperature information from bioclimatic data (Hijmans *et al.* 2005) for each locality and relate such local temperature information to local morph frequencies (Fig. 2). We used standard temperature measures from the Bioclim database (Hijmans *et al.* 2005) and related these to geographic variation in morph frequencies. Of these temperature variables, Bio1 (“Annual mean temperature”) has previously been shown by us to be the predictor with the highest contribution in Maxent species distribution modelling of the geographic range of *I. elegans* (62.1% contribution to the model) (Lancaster *et al.* 2015), and both Bio1 and to an even higher degree Bio5 (“Maximum temperature during the warmest month”) are both associated with significant molecular genetic differentiation and local adaptation along a latitudinal cline from southern Sweden, up to its northern range limit (Dudaniec *et al.* 2018). However, we were also interested in the effects of more temporally fine-grained temperature measures that might be relevant to the sexual maturation period during summer and the timing of colour development of the female colour morphs. We therefore investigated how all the eleven temperature variables in Bioclim (Bio1-B11) performed in explaining geographic variation in morph frequencies of *I. elegans*. As these different temperature measures are typically highly correlated with each other (see Supporting Material), we only present the relationship with the variable that performed best in explaining geographic variation in morph frequencies, as judged by the lowest value of the Akaike Information Criterion (AIC).

### Mesocosm study

Beginning in the summer of 2015 and continuing in 2016 and 2017, we performed mesocosm studies, in which we marked

individuals with unique numbers on their wings, recaptured them daily and measured morph-specific female colour maturation rates and survivorship from the immature stage to the final colour stage that is reached at sexual maturity (Fig. 1; Fig. S1) (Cordero *et al.* 1998; Svensson *et al.* 2009). These mesocosm studies were performed in large outdoor insectaries ( $3 \times 3 \times 3 = 27 \text{ m}^3$ ) at Stensoffa Ecological Field Station, outside Lund. These large outdoor insectaries mimicked natural conditions. Cages were covered with nets with a mesh size that enabled small insects (primarily moths and flies) to enter, which provided natural food in the form of live prey for the damselflies (Takahashi *et al.* 2014; Svensson *et al.* 2018). Each cage also contained 2–3 small and shallow plastic water tanks with resting substrate in the form of floating vegetation, where the damselflies could perch and obtain water.

We individually marked and released immature female *I. elegans* of these three female colour morphs. All survivors were recaptured every day until they either died or reached the adult colour-maturation stage. We recorded time (in days) until the different individuals of the three different morphs reached the final colour-maturation stage or were no longer found alive. In total, we marked and released 450 immature individual *I. elegans* females from five populations in these cages, during 2015–2017. Of these marked individuals, 144 (32%) belonged to the A-morph, 215 (48%) belonged to the I-morph and 91 (20%) belonged to the O-morph, and a total of 162 (36%) survived until sexual maturity. Males were not present in these female-only mesocosms as we were interested in intrinsic female morph differences in pre-reproductive females and the presence of males might confound our findings. This is justified as males do typically avoid mating with such immature females, when given a choice in experimental settings (Willink *et al.* 2019a). To ensure that males did not affect our results, our mesocosm cages were not in the vicinity of any natural pond, meaning that females did not encounter any males, neither physically nor visually during their colour maturation process.

We compared the three female morphs with respect to development time until maturity and survival until maturity (binomial variable: 1 = survived, 0 = did not survive) using previously published information about the colour developmental stages (Cordero *et al.* 1998; Svensson *et al.* 2009; Willink *et al.* 2019a). We incorporated information about the daily mean temperatures during the entire colour development period of individual females during the summers 2015–2017, which we obtained from the closest weather station in Malmö (southern Sweden: <http://opendata-download-metobs.smhi.se/explore/>). In addition to the daily mean temperatures that females experienced during their colour development period, we also incorporated information about the daily mean temperatures they experienced the three days preceding their captures in the field, following our previous study in which we found that this time period influenced individual acclimation (Lancaster *et al.* 2017).

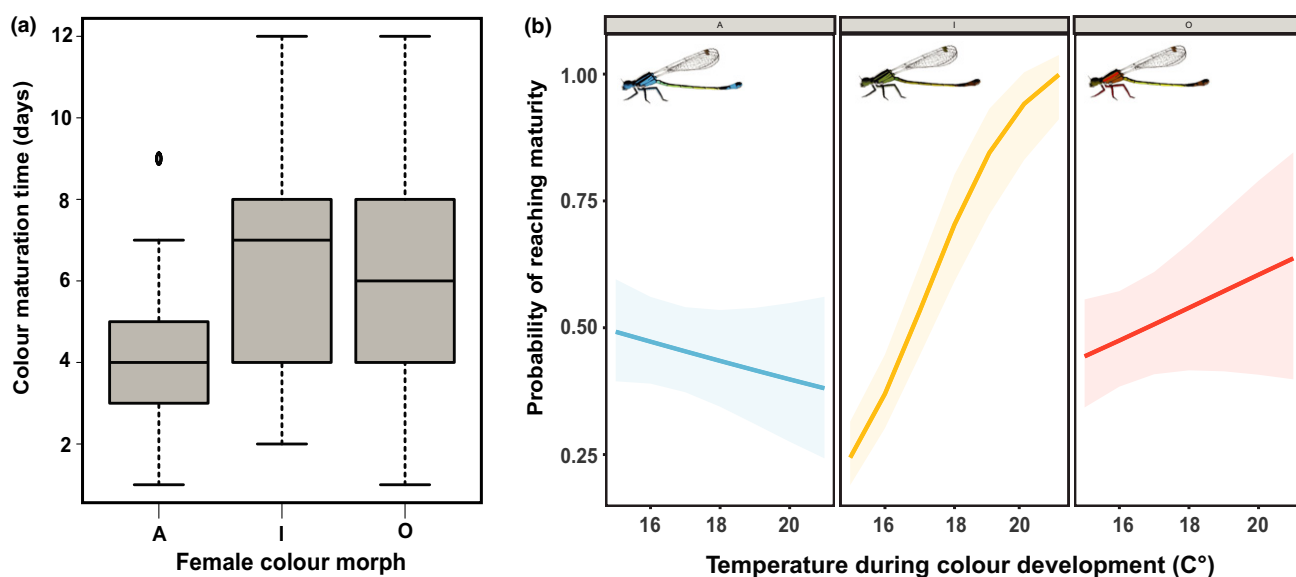
### Quantifying pre-reproductive survival and estimating selection coefficients of female colour morphs in field populations

We estimated relative fitness on a per-morph basis using a cross-sectional selection analysis approach (Lande & Arnold 1983), where we compared the morph frequencies among immature females (prior to sexual maturity) and sexually mature females (judged by their colour maturation stage) (Cordero *et al.* 1998; Svensson *et al.* 2009; Willink *et al.* 2019a) (Fig. 4a and b). An increase in the relative frequency of one morph from the immature to the mature stage within a local population would be consistent with higher pre-reproductive survival, compared to morphs that decrease in

frequency (within-generation selection). Based on the within-generation frequency changes for these three morphs, we calculated two closely related parameters: relative morph fitness and pre-reproductive selection coefficient on each morph, using classical approaches in ecological genetics (Linnen & Hoekstra 2009). We estimated these two parameters using data from 2015 to 2017 in 16 intensively monitored field populations, that are part of a long-term population study of *I. elegans* initiated in the year 2000 (Le Rouzic *et al.* 2015). In total, we sampled and identified 4625 females to colour-development category and morph. Of the total, 3078 were A-females (67%), 1310 were I-females (28%) and 237 were O-females (5%).

### Statistical analyses

All statistical analyses in this paper were performed using various packages (nlme, lme4, MCMCglmm) in the “R” statistical environment (R Development Core Team 2014). We used generalised linear mixed models when analysing geographic variation in morph frequencies (Fig. 2c), differences in development time between the morphs (Fig. 3a) and morph-specific survivorship to maturity in relation to temperature in mesocosm cages (Fig. 3b; Tables 1, 2). In the mesocosm studies (Fig. 3; Tables 1, 2), we included the year, population of origin and experimental cage as random factors, and female colour morph and temperature variables were fixed effects. When we analysed geographic variation in androchrome frequencies (Fig. 2a and b) and how local microclimatic variation (temperature) affected androchrome frequencies (Fig. 2c), we also used a mixed model with population (Table S1) and



**Figure 3** Mesocosm studies revealing differences between female colour morphs in development time and differential temperature sensitivity. The three female colour morphs were kept in large outdoor cages from their immature stage and the colour development time to reach sexual maturity was recorded, as well as temperature and the probability of reaching maturity. (a) The male mimics (A-females) had significantly shorter colour development time and reached sexual maturity faster than the two other female colour morphs, which did not differ from each other (Table S2). (b) The male mimic is less sensitive to temperature in terms of its probability of reaching sexual maturity (left panel), compared to the two other female morphs (middle and right panels) whose survivorship increases with higher temperatures (Table 1). Data comes from 450 individually marked females that were followed throughout their entire lives in these mesocosm cages. Temperatures ranged between 7.5 °C and 32.1 °C in these cages, and the average daily mean temperature experienced by the individual females varied between 14.1 °C and 21.2 °C.

**Table 1** Development time from the immature stage to final colour maturation stage of the three female colour morphs in mesocosm experiments. Significant effects are indicated in bold ( $P < 0.05$ )

Fixed effects	D.f.	SS	F	$\chi^2$	P
Female colour morph	2	25.417	12.709	29.462	< <b>0.001***</b>
Developmental temperature	1	8.454	8.454	8.454	<b>0.004**</b>
Random effects	Levels	Variance	SD		
Cage	7	0.02641	0.16251		
Population	5	0.00000	0.00000		
Year	3	0.00665	0.08155		

Generalised linear mixed models were used to examine how the duration and success of development to colour maturity (sexual maturity) depends on female colour morph and temperature in our mesocosm experiments with females of *I. elegans* (Fig. 3a and b). Experimental cage number, population origin and year were included as random factors in these models (Tables 1, 2). In the analysis of development time, the interaction between female colour morph and developmental temperature was not significant, and a model that included this interaction had a higher AIC than the present model, hence it is not shown here. We also constructed a model incorporating past temperature prior to capture as we did in the next model (Table 2), but this variable was not significant on its own or through any of the interactions with female colour morph and developmental temperature, and hence this variable was not included in the final model shown above. The male mimic (A-females) had significantly shorter development time than the two gynochrome female morphs (Fig. 3a; Tukey post hoc tests: A vs. I:  $P < 0.001$ ; A vs. O:  $P = 0.003$ ), whereas these two gynochrome female morphs did not differ significantly from each other (Tukey post hoc test: I vs. O:  $P = 0.23$ ).

population and latitude block (Table S2) to control for spatial autocorrelation and statistical non-independence of closely located populations within the same latitudinal band. Europe was divided in to seven latitudinal blocks of equal length (each block encompassing 5°), ranging from Cyprus in the south to Sweden in the north (Table S2).

Female morph frequencies at the pre-reproductive and reproductive developmental stages were estimated using a categorical (i.e. multinomial) mixed-effect model fitted by MCMC. We used a flat Kronecker prior for the two-way marginal probabilities (i.e. A- vs. I-females, I- vs. O-females and A- vs. O-females) in each developmental stage (Hadfield 2015). In this model, we included a random interaction between the latent morph-frequency variable and the sampling population, thereby allowing natural populations to differ in their morph frequencies. Relative fitness was calculated as the frequency ratio between the reproductive and immature stages, across the entire posterior distribution of morph frequency estimates. Cross sectional selection coefficients ( $s$ ) for each morph were also calculated across posterior estimates following standard ecological genetics literature (Linnen & Hoekstra 2009) as:

$$S = \frac{\Delta p}{(p' \times (1 - p) - p \times q \times r)}$$

where  $\Delta p$  is the change in frequency of the focal morph between the immature and mature stages,  $p'$  and  $p$  are the focal morph frequencies at the reproductive and immature stages respectively, and  $q$  and  $r$  are the frequencies of the two other morphs during the immature developmental stage. We

**Table 2** Survivorship to maturity in mesocosm experiments in relation to female colour morph and temperature during colour development. Significant effects are indicated in bold ( $P < 0.05$ )

Fixed effects	D.f.	SS	F	$\chi^2$	P
Female colour morph (FM)	2	2.548	1.274	2.806	0.25
Developmental temperature (DT)	1	3.961	3.961	4.153	<b>0.041*</b>
Past temperature (PT)	1	0.273	0.273	0.441	0.51
FM x DT	2	5.260	2.630	10.744	<b>0.005**</b>
FM x PT	2	11.005	5.503	13.518	<b>0.001**</b>
DT x PT	1	12.391	12.391	12.391	<b>0.0004***</b>
Random effects	Levels	Variance	SD		
Cage	7	0.04226	0.2056		
Population	5	0.06402	0.2530		
Year	3	0.16944	0.4116		

We investigated how the probability of reaching maturity (binomial variable: 0 = did not reach maturity; 1 = did reach maturity) depends on female colour morph (FM), temperature during colour development (DT), past temperature experienced prior to capture (“acclimation”; PT) and all the three two-way interactions between these three variables. The three-way interaction (FM × DT × PT) was not significant and such a complete model had significantly higher AIC than the model presented above. The significant interaction between female colour morph and temperature during colour development in the mesocosm experiments is illustrated in Fig. 3b, and shows that the survivorship of I-females increased significantly with temperature, in contrast to the two other female morphs. Post hoc tests ( $P$ -value adjustment method: holm) of morph differences in the slopes of how probability of reaching maturity was affected by developmental temperature showed that A-females differed significantly from I-females, which showed a positive relationship with temperature (Fig. 3b;  $P = 0.003$ ), whereas A- and O-females did not differ significantly from each other ( $P = 0.37$ ). There was a non-significant tendency for I-females to have a steeper slope than O-females ( $P = 0.08$ ).

considered the relative fitness and selection coefficients of two female morphs as significantly different if the values for one morph were higher than for the other in more than 95% of the posterior distribution of model estimates. All data and computer code behind the statistical analyses in this paper has been made openly available and uploaded on the Dryad data repository (Svensson *et al.* 2019).

## RESULTS

### Geographic variation in colour morph frequencies

Analysis of geographic variation in the local population frequencies of the male mimic in *I. elegans* across Europe reveals that the male mimics reach their highest frequencies near the species' northern range limit in Scandinavia, where they are often the majority morph with 60–80% of all females (Fig. 2a and b; Table S1). Although there is also considerable regional variation between populations within latitudinal bands (Lancaster *et al.* 2017), this overall large-scale geographic pattern is robust to such local deviations (Fig. 2a and b; Table S1). We further found a strong and highly significant positive relationship between local temperatures and the frequency of the male mimic across the biogeographic range in Europe (Fig. 2c; Table S2). Of the different temperature variables, the

best predictor of the local frequency of the male mimic was maximum temperature during the warmest month (Bio5: Table S2), which probably best captures the temperatures that females experience in the summers during colour maturation (Fig. 3a and b). Notably, temperature during the warmest month showed a better statistical fit to the data (as judged by lower AIC-values) than the annual mean temperature (Bio1), which also showed a highly significant relationship with the local frequency of the male mimic (Table S2, Fig. S2). Interestingly, mean temperature of the coldest month (Bio6) - which reflects temperature during winter when these damselflies are in their aquatic larval stage - was not significantly related to the local frequency of the male mimic (Table S2). This might suggest that thermal conditions during the adult stage are more important than thermal conditions earlier in ontogeny in shaping biogeographic variation in morph frequencies.

### Survivorship to maturity in mesocosms

We performed mesocosm studies in the northern part of the geographic range of *I. elegans*, and complemented these studies by tracing within-generation morph frequency dynamics across a series of populations that have been subject to a long-term study, starting in the year 2000 (Svensson *et al.* 2005; Le Rouzic *et al.* 2015). We found that the male mimic had significantly shorter development time to sexual maturity than the two gynochrome morphs, which did not differ significantly from each other (Fig. 3a, Table 1). We also found that the rate and probability of reaching sexual maturity was dependent on temperature, morph and the interaction between morph and temperature (Fig. 3b, Table 2). Whereas the male

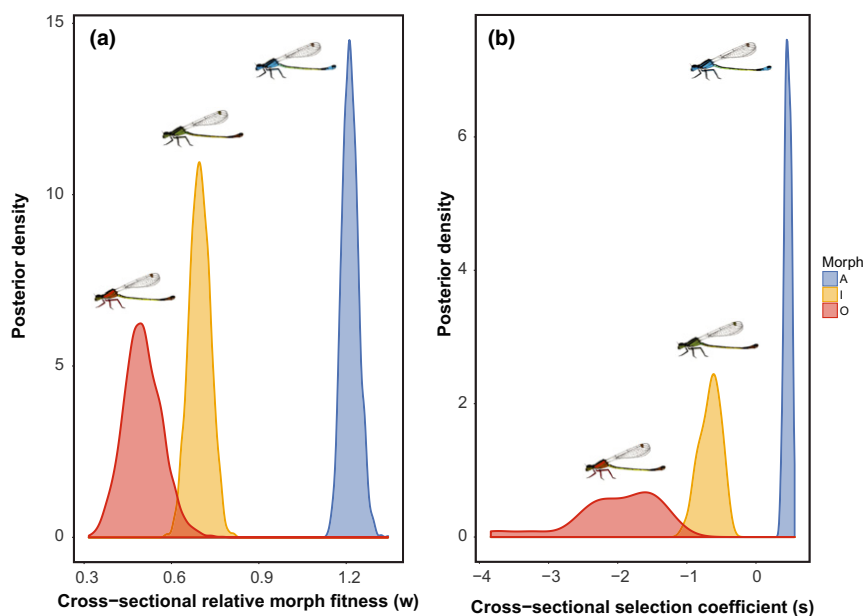
mimic showed evidence of being relatively canalised and less sensitive to thermal conditions in terms of reaching sexual maturity, the two gynochrome female morphs showed higher thermal sensitivity with increasing survival at high temperatures (Fig. 3b, Table 2).

### Pre-reproductive selection in the field

We complemented our mesocosm experiments with a cross-sectional selection study in our field populations, in which we estimated the relative fitness of the three female morphs and associated selection coefficients, based on morph frequency changes during the ontogeny. This cross-sectional selection analysis across three seasons and 16 populations revealed that the male mimic increased in frequency from the sexually immature to the sexually mature adult stage, and we thus found evidence for positive pre-reproductive selection in favour of the A-females (Fig. 4a and b).

### DISCUSSION

Our analyses of the large-scale geographic variation in female morph frequencies of *I. elegans* across its range in Western Europe (Fig. 2; Table S1 and S2) strongly suggested that the male mimicking female morph is better adapted to cooler microclimates than the two other female morphs. Consistent with this interpretation, male mimics have a higher acclimation ability in response to recent cold spells than the two other female morphs (Lancaster *et al.* 2017). A similar latitudinal geographic pattern with a higher frequency of the male mimic at higher latitudes has also been documented in the closely related subtropical species *I. senegalensis* in Japan



**Figure 4** Pre-reproductive survivorship and selection prior to sexual maturity in natural populations of *I. elegans* in northern Europe, near the species range limit. (a) Probability density functions of relative fitnesses of the three female morphs, based on a cross-sectional selection analysis where we compared the frequency changes between the immature age class and the sexually mature females. Shown are the posterior densities of the estimates based on a MCMCglmm analysis. (b) The same data set as in A, but expressed as selection coefficients. The relative fitnesses and selection coefficients differ significantly between the morphs, with the male mimics experiencing positive survival selection prior to sexual maturity, resulting in a higher frequency among the adult females than the two other morphs (see Methods and Results).

(Takahashi *et al.* 2011). These observational data in combination with our mesocosm studies (Fig. 3) suggest that the colour morph locus might interact with other loci influencing thermal adaptation in this ectothermic insect species. Our recent experimental gene expression studies have revealed that genes governing the production of heat shock proteins (*Hsp*) are differentially upregulated in relation to heat- and cold shocks, and in complex and different ways depending on geographic range position (Lancaster *et al.* 2016). Furthermore, our recent gene expression studies performed during ontogenetic colour maturation of these female colour morphs (Fig. 1, Fig. S1) have revealed that the morph locus shows extensive pleiotropy and interacts with many other genes behind vital physiological and reproductive functions during development (Willink *et al.* 2019b). This previous work of ours in combination with the novel results in this study suggests that the morph locus might also be involved in epistatic relationships with loci for thermal adaptation, something that we plan to investigate in the future. We also note that the best predictor of geographic variation in local morph frequencies was the maximum temperature during the warmest month (Bio5; Fig. 2c), rather than annual mean temperature (Bio1; Fig. S2) or mean temperature during the coldest month (Bio6), which was not significant (Table S2). This suggests that it is temperature conditions during the adult stage, rather than during the much longer larval stage, that are most important in affecting morph frequencies, consistent with the results from our mesocosm and field studies (Figs 3 and 4).

The biogeographic patterns we present here and the link to local temperature suggest that the male mimic has increased in frequency at higher latitudes due to higher physiological and reproductive performance in colder climates, whereas it is kept at low frequency at lower latitudes where temperatures are higher (Fig. 2). The morph differences in the rate of sexual development and colour maturation (Fig. 3a) might partly reflect the costs of pigment production such as pterins and maybe also melanin (Roff & Fairbairn 2013; Henze *et al.* 2019), since the male mimicking females do not deposit as much pigment on their abdomen tips as the gynochrome morphs (Fig. S1). Thus, the male mimicking females may become sexually mature more quickly and reach their final reproductive colour stage faster, compared to the gynomorphs (Table 1). We note, however, that there are also many other physiological, developmental and reproductive differences between the male mimicking females and the gynomorphs, making it difficult to exactly pinpoint the mechanism behind the faster development of the A-females (Gosden & Svensson 2009; Willink & Svensson 2017; Willink *et al.* 2019b).

Consistent with the large-scale biogeographic link between the frequency of the male mimic and mean temperature of the warmest month (Fig. 2c), both the rate and probability of reaching maturity depended on temperature, morph and their interaction in our mesocosm studies (Fig. 3b; Table 2). Specifically, the probability of reaching maturity for the male mimic was independent across a broad temperature range, whereas the two gynochrome female morphs showed higher thermal sensitivity and increasing survivorship with higher temperature (Fig. 3b; Table 2). Taken together, these data suggest that low temperatures at high latitudes have favoured the male mimic

and its frequency has increased in the north, due to its shorter development time, lower developmental sensitivity to temperature, and greater acclimation ability in response to cold weather (Lancaster *et al.* 2017).

If low temperatures at high latitudes in combination with shorter development time of the male mimic has increased its frequency (Figs 2 and 3), we predicted that there should be a within-generation selective increase in frequency of the male mimic in these cool northern field populations, due to the higher probability of A-females to reach the adult reproductive stage. Our cross-sectional selection analysis strongly supported this prediction, as the male mimic increased in frequency from the sexually immature to the mature adult stages and hence experienced significant and positive pre-reproductive survival selection (Fig. 4a and b). Such pre-reproductive selection and conflicting selection pressures between different ontogenetic stages of the life-history has been documented in other organisms (Schluter *et al.* 1991; Barrett *et al.* 2008; Sinervo & McAdam 2008) and might be a general feature of many natural populations, including *I. elegans*.

Female morphs in *I. elegans* and other taxa often differ in multiple traits apart from colour, including thermal physiology, fecundity, behaviour and parasite loads (Gosden & Svensson 2009; Lancaster *et al.* 2017; Willink & Svensson 2017). For instance, the male mimic has lower fecundity than the two gynochrome female morphs (Willink *et al.* 2019a), which could reflect costs of mimicry due to the more male like shape of these male mimics (Gosden & Svensson 2009). The lower fecundity of the male mimic could also be a cost of their earlier sexual maturity and faster colour development that we have demonstrated in this study (Fig. 3a). These and other phenotypic morph differences might have partly evolved as a result of correlational selection for different adaptive trait combinations in the different morphs (Sinervo & Svensson 2002). When the benefits of different trait combinations in the different morphs differ across geographic space, frequency-independent directional selection in favour of one trait (such as thermal physiology) can interfere with or can even partly counteract frequency-dependent selection on the female polymorphism at the adult stage, especially when colour is genetically or phenotypically correlated with other traits (Lancaster *et al.* 2017). When such episodes of frequency-dependent selection that operate early in the ontogeny either opposes or is aligned with the direction of the later frequency-dependent selection during reproduction, it can have large consequences for population mean fitness, maladaptation and the prospects of evolutionary rescue (Svensson & Connallon 2019). In the case of *I. elegans* in northern Europe, the male mimic has apparently increased to higher frequencies than in any other *Ischnura* species or population that has been studied to date (Sanchez-Guillen *et al.* 2011). This increase of male mimics is most likely the result of its higher cold weather-responsive acclimation capacity and shorter maturation time, although this thermal benefit and shorter development advantage might be partly counteracted by their lower fecundity (Willink *et al.* 2019b).

The high frequency of the male mimic in the north might also decrease the efficacy of male mimicry, as expected from theory and from research on interspecific mimicry systems (Finkbeiner *et al.* 2018). As a consequence, we expect higher



male mating harassment on male mimics and potentially also higher population extinctions rates in the north. Our previous manipulations of morph frequencies in mesocosm experiments did indeed show evidence for reduced population fitness when female morph frequencies become very biased (Takahashi *et al.* 2014) and population morph frequencies are also increasingly biased at the range limits of *I. elegans* (Gosden *et al.* 2011), consistent with such a scenario. Our data suggest that these high-latitude populations are not at their evolutionary equilibrium but are torn between the opposing forces of directional and frequency-independent selection for thermal adaptation that favours the male mimic (Fig. 4a and b). This pre-reproductive selection is in a tension against negative frequency-dependent selection at the adult stage that maintains the polymorphism and which prevents the male mimic from going to fixation (Svensson *et al.* 2005; Le Rouzic *et al.* 2015). As a result of these opposing selection pressures, our populations might experience a fitness load due to a conflict between pre-reproductive frequency-independent selection that increases the frequency of the male mimic with the progress of ontogeny, but where male mating harassment among adults might ultimately prevent the fixation of this morph. These results suggest that abiotic factors experienced during development might influence the dynamics of sexual conflict among adults and illustrates that adopting a biogeographic perspective can be fruitful to understand such evolutionary dynamics. The study of sexual conflict has been heavily dominated by laboratory studies of model organisms in controlled and stable laboratory environments (Rice 1996; Arnqvist & Rowe 2005) but recently the role of temperature, climate and other ecological factors in modulating various forms of sexual conflict has gained increased attention (Berger *et al.* 2014; Perry *et al.* 2017; De Lisle *et al.* 2018; García-Roa *et al.* 2019). The novel results in this study suggest that temperature can also influence the morph frequency composition among adults through frequency-independent pre-reproductive selection operating earlier in ontogeny.

## CONCLUSIONS

Our integrative study links climatic factors and biogeographic patterns to this female colour polymorphism with strong implications for the dynamics of sexual conflict and frequency-dependent selection on the adult morphs. Our results underscore the need to incorporate abiotic factors and pre-reproductive selection that operates earlier in development and the possibility of conflicting selection pressures during the course of ontogeny, which can have profound consequences for the evolutionary dynamics of sexual conflict among adults.

## ACKNOWLEDGEMENTS

We are grateful to the many field assistants, PhD students and postdocs who have participated in the field work and thereby directly and indirectly contributed to this study over many years, since 2000 when it was started. We also wish to thank David and Rosalyn Sparrow who kindly hosted B. Willink during a field trip to Cyprus in 2017 and who provided valuable field work help and guidance, enabling us to

gather information about morph frequencies of *I. elegans* at one of the southernmost localities of this species in Europe.

## FUNDING INFORMATION

Funding for this study has been provided by research grants from The Swedish Research Council (VR: grant no. 2016-03356), Carl Tryggers Foundation (CTS), Gyllenstiernska Krappertstiftelsen (grant no. KR2018-0038), Stina Werners Foundation and Erik Philip Sörensens Stiftelse to E.I.S.

## COMPETING INTERESTS

The authors declare no competing interests.

## ETHICAL STATEMENT

All the experiments carried out in this study are in accordance with Swedish legislation, and research on insects does not require any ethical permits in Sweden.

## AUTHORSHIP

E.I.S. conceived the idea of this study, planned the mesocosm experiments and maintained the long-term population study. E.I.S., BW and MCD collected field data and carried out the mesocosm experiments. E.I.S., BW and LL performed the statistical analyses. E.I.S. wrote the first draft of this paper. All the other authors read and contributed to the writing of the final manuscript.

## DATA AVAILABILITY STATEMENT

Original data behind all the analyses in this paper and associated R-code have been uploaded on Dryad (<https://datadryad.org/>). Correspondence and requests for additional materials should be directed to E.I.S. ([erik.svensson@biol.lu.se](mailto:erik.svensson@biol.lu.se)). <https://doi.org/10.5061/dryad.gtht76hgt>.

## REFERENCES

- Abbott, J.K., Bensch, S., Gosden, T.P. & Svensson, E.I. (2008). Patterns of differentiation in a colour polymorphism and in neutral markers reveal rapid genetic changes in natural damselfly populations. *Mol. Ecol.*, *17*, 1597–1604.
- Arnqvist, G. & Rowe, L. (2002a). Antagonistic coevolution between the sexes in a group of insects. *Nature*, *415*, 787–789.
- Arnqvist, G. & Rowe, L. (2002b). Correlated evolution of male and female morphologies in water striders. *Evolution*, *56*, 936–947.
- Arnqvist, G. & Rowe, L. (2005). *Sexual Conflict*. Princeton University Press, Princeton.
- Arnqvist, G., Edwardsson, M., Friberg, U. & Nilsson, T. (2000). Sexual conflict promotes speciation in insects. *Proc. Natl Acad. Sci. USA*, *97*, 10460–10464.
- Aske, R.R. (1988). *The Dragonflies of Europe*. B. H. & A. Harley Ltd., Colchester, UK.
- Barrett, R.D., Rogers, S.M. & Schluter, D. (2008). Natural selection on a major armor gene in threespine stickleback. *Science*, *322*, 255–257.
- Berger, D., Grieshop, K., Lind, M.I., Goenaga, J., Maklakov, A.A. & Arnqvist, G. (2014). Intralocus sexual conflict and environmental stress. *Evolution*, *68*, 2184–2196.

- Corbet, P.S. (1999). *Dragonflies: Behaviour and Ecology of Odonata*. Harley Books, Colchester.
- Cordero, A. (1990). The inheritance of female polymorphism in the damselfly *Ischnura graellsii* (Rambur) (Odonata: Coenagrionidae). *Heredity*, 64, 341–346.
- Cordero, A., Carbone, S.S. & Utzeri, C. (1998). Mating opportunities and mating costs are reduced in androchrome female damselflies, *Ischnura elegans*. *Anim. Behav.*, 55, 185–187.
- De Lisle, P., Goedert, D., Reedy, A.M. & Svensson, E.I. (2018). Climatic factors and species range position predict sexually antagonistic selection across taxa. *Philos. Trans. R. Soc. B Biol. Sci.*, 373, 20170415.
- Dudaniec, R.Y., Yong, C.J., Lancaster, L.T., Svensson, E.I. & Hansson, B. (2018). Signatures of local adaptation along environmental gradients in a range-expanding damselfly (*Ischnura elegans*). *Mol. Ecol.*, 27, 2576–2593.
- Fincke, O.M. (2004). Polymorphic signals of harassed female odonates and the males that learn them support a novel frequency-dependent model. *Anim. Behav.*, 67, 833–845.
- Finkbeiner, S.D., Salazar, P.A., Nogales, S., Rush, C.E., Briscoe, A.D., Hill, R.I. *et al.* (2018). Frequency dependence shapes the adaptive landscape of imperfect Batesian mimicry. *Proc. R. Soc. B*, 285, 20172786.
- Fitt, R.N.L. & Lancaster, L.T. (2017). Range shifting species reduce phylogenetic diversity in high latitude communities via competition. *J. Anim. Ecol.*, 86, 543–555.
- Fitt, R.N.L., Palmer, S., Hand, C., Travis, J.M.J. & Lancaster, L.T. (2019). Towards an interactive, process-based approach to understanding range shifts: developmental and environmental dependencies matter. *Ecography*, 42, 201–210.
- Galicia-Mendoza, I., Sanmartín-Villar, I., Espinosa-Soto, C. & Cordero-Rivera, A. (2017). Male biased sex ratio reduces the fecundity of one of three female morphs in a polymorphic damselfly. *Behav. Ecol.*, 28, 1183–1194.
- García-Roa, R., Chirinos, V. & Carazo, P. (2019). The ecology of sexual conflict: Temperature variation in the social environment can drastically modulate male harm to females. *Funct. Ecol.*, 33, 681–692.
- Gavrilets, S. (2000). Rapid evolution of reproductive barriers by sexual conflict. *Nature*, 403, 886–889.
- Gavrilets, S. & Waxman, D. (2002). Sympatric speciation by sexual conflict. *Proc. Natl Acad. Sci. USA*, 99, 10533–10538.
- Gering, E.J. (2017). Male-mimicking females increase male-male interactions, and decrease male survival and condition in a female-polymorphic damselfly. *Evolution*, 71, 1390–1396.
- Gosden, T.P. & Svensson, E.I. (2008). Spatial and temporal dynamics in a sexual selection mosaic. *Evolution*, 62, 845–856.
- Gosden, T.P. & Svensson, E.I. (2009). Density-dependent male mating harassment, female resistance, and male mimicry. *Am. Nat.*, 173, 709–721.
- Gosden, T.P., Stoks, R. & Svensson, E.I. (2011). Range limits, large-scale biogeographic variation, and localized evolutionary dynamics in a polymorphic damselfly. *Biol. J. Linn. Soc.*, 102, 775–785.
- Hadfield, J. (2015). MCMCglmm course notes. R-project.org.
- Harts, A.M.F., Schwanz, L.E. & Kokko, H. (2014). Demography can favour female-advantageous alleles. *Proc. R. Soc. B Biol. Sci.*, 281, 20140005–20140005.
- Henze, M.J., Lind, O., Wilts, B.D. & Kelber, A. (2019). Pterin-pigmented nanospheres create the colours of the polymorphic damselfly *Ischnura elegans*. *J. R. Soc. Interface*, 16, 20180785.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.*, 25, 1965–1978.
- Iserbyt, A., Bots, J., Van Dongen, S., Ting, J.J., Van Gossum, H. & Sherratt, T.N. (2011). Frequency-dependent variation in mimetic fidelity in an intraspecific mimicry system. *Proc. R. Soc. B-Biol. Sci.*, 278, 3116–3122.
- Iversen, L.L., Svensson, E.I., Christensen, S.T., Bergsten, J. & Sand-Jensen, K. (2019). Sexual conflict and intrasexual polymorphism promote assortative mating and halt population differentiation. *Proc. R. Soc. B Biol. Sci.*, 286, 20190251.
- Karlsson, G.K., Kovalev, A., Svensson, E.I. & Gorb, S.N. (2013). Male clasping ability, female polymorphism and sexual conflict: fine-scale elytral morphology as a sexually antagonistic adaptation in female diving beetles. *J. R. Soc. Interface*, 10, 20130409.
- Lancaster, L.T., Dudaniec, R.Y., Hansson, B. & Svensson, E.I. (2015). Latitudinal shift in thermal niche breadth results from thermal release during a climate-mediated range expansion. *J. Biogeogr.*, 42, 1953–1963.
- Lancaster, L.T., Dudaniec, R.Y., Chauhan, P., Wellenreuther, M., Svensson, E.I. & Hansson, B. (2016). Gene expression under thermal stress varies across a geographic range expansion front. *Mol. Ecol.*, 25, 1141–1156.
- Lancaster, L.T., Dudaniec, R.Y., Hansson, B. & Svensson, E.I. (2017). Do group dynamics affect colour morph clines during a range shift? *J. Evol. Biol.*, 30, 728–737.
- Lande, R. & Arnold, S.J. (1983). The measurement of selection on correlated characters. *Evolution*, 37, 1210–1226.
- Le Galliard, J.F., Fitze, P.S., Ferriere, R. & Clobert, J. (2005). Sex ratio bias, male aggression, and population collapse in lizards. *Proc. Natl Acad. Sci. USA*, 102, 18231–18236.
- Le Rouzic, A., Hansen, T.F., Gosden, T.P. & Svensson, E.I. (2015). Evolutionary time-series analysis reveals the signature of frequency-dependent selection on a female mating polymorphism. *Am. Nat.*, 185E, E182–E196.
- Linnen, C.R. & Hoekstra, H.E. (2009). Measuring natural selection on genotypes and phenotypes in the wild. *Cold Spring Harb. Symp. Quant. Biol.*, 74, 155–168.
- Neff, B.D. & Svensson, E.I. (2013). Polyandry and alternative mating tactics. *Phil Trans R Soc B*, 368, 20120045.
- Parr, M.J. (1970). The life histories of *Ischnura elegans* (van der Linden) and *Coenagrion puella* (L.) (Odonata) in south Lancashire. *Proc. R. Entomol. Soc. Lond. Ser. Gen. Entomol.*, 45, 172–181.
- Perry, J.C., Garroway, C.J. & Rowe, L. (2017). The role of ecology, neutral processes and antagonistic coevolution in an apparent sexual arms race. *Ecol. Lett.*, 20, 1107–1117.
- R Development Core Team (2014). *A Language and Environment for Statistical Computing*. Austria, Vienna. <http://www.R-project.org>. ISBN3-900051-07-0.
- Rankin, D.J., Dieckmann, U. & Kokko, H. (2011). Sexual conflict and the tragedy of the commons. *Am. Nat.*, 177, 780–791.
- Reinhardt, K., Harney, E., Naylor, R., Gorb, S. & Siva-Jothy, M.T. (2007). Female-limited polymorphism in the copulatory organ of a traumatically inseminating insect. *Am. Nat.*, 170, 931–935.
- Rice, W.R. (1996). Sexually antagonistic male adaptation triggered by experimental arrest of female evolution. *Nature*, 381, 232–234.
- Ritchie, M.G. (2007). Sexual selection and speciation. *Annu. Rev. Ecol. Evol. Syst.*, 38, 79–102.
- Robertson, H.M. (1985). Female dimorphism and mating behaviour in a damselfly, *Ischnura ramburi*: females mimicking males. *Anim. Behav.*, 33, 805–809.
- Roff, D.A. & Fairbairn, D.J. (2013). The costs of being dark: the genetic basis of melanism and its association with fitness-related traits in the sand cricket. *J. Evol. Biol.*, 26, 1406–1416.
- Sanchez-Guillen, R.A., Van Gossum, H. & Rivera, A.C. (2005). Hybridization and the inheritance of female colour polymorphism in two ischnurid damselflies (Odonata: Coenagrionidae). *Biol. J. Linn. Soc.*, 85, 471–481.
- Sanchez-Guillen, R.A., Hansson, B., Wellenreuther, M., Svensson, E.I. & Cordero-Rivera, A. (2011). The influence of stochastic and selective forces in the population divergence of female colour polymorphism in damselflies of the genus *Ischnura*. *Hered. Edinb.*, 107, 513–522.
- Sanmartín-Villar, I. & Cordero-Rivera, A. (2016). The inheritance of female colour polymorphism in *Ischnura* genei (Zygoptera: Coenagrionidae), with observations on melanism under laboratory conditions. *PeerJ*, 4, e2380.

- Schluter, D., Price, T.D. & Rowe, L. (1991). Conflicting selection pressures and life history trade-offs. *Proc. R. Soc. Lond. Ser. B*, 246, 11–17.
- Shama, L.N.S., Campero-Paz, M., Wegner, K.M., Block, M.D. & Stoks, R. (2011). Latitudinal and voltinism compensation shape thermal reaction norms for growth rate. *Mol. Ecol.*, 20, 2929–2941.
- Sinervo, B. & McAdam, A.G. (2008). Maturation costs of reproduction due to clutch size and ontogenetic conflict as revealed in the invisible fraction. *Proc. R. Soc. Lond. Ser. B-Biol. Sci.*, 275, 629–638.
- Sinervo, B. & Svensson, E. (2002). Correlational selection and the evolution of genomic architecture. *Heredity*, 16, 948–955.
- Svensson, E.I. (2017). Back to basics: using colour polymorphisms to study evolutionary processes. *Mol. Ecol.*, 26, 2204–2211.
- Svensson, E.I. & Abbott, J. (2005). Evolutionary dynamics and population biology of a polymorphic insect. *J. Evol. Biol.*, 18, 1503–1514.
- Svensson, E.I., Abbott, J. & Hardling, R. (2005). Female polymorphism, frequency dependence, and rapid evolutionary dynamics in natural populations. *Am. Nat.*, 165, 567–576.
- Svensson, E.I., Abbott, J.K., Gosden, T.P. & Coreau, A. (2009). Female polymorphisms, sexual conflict and limits to speciation processes in animals. *Evol. Ecol.*, 23, 93–108.
- Svensson, E.I. & Connallon, T. (2019). How frequency-dependent selection affects population fitness, maladaptation and evolutionary rescue. *Evol. Appl.*, 12, 1243–1258. <https://doi.org/10.1111/eva.12714>.
- Svensson, E.I., Gómez-Llano, M.A., Torres, A.R. & Bensch, H.M. (2018). Frequency dependence and ecological drift shape coexistence of species with similar niches. *Am. Nat.*, 191, 691–703.
- Svensson, E.I., Willink, B., Duryea, M.C. & Lancaster, L.T. (2019). Data from: temperature drives pre-reproductive selection and shapes the biogeography of a female polymorphism. *Dryad, Dataset*. <https://doi.org/10.5061/dryad.gtht76hgt>
- Takahashi, Y. & Watanabe, M. (2009). Diurnal changes and frequency dependence in male mating preference for female morphs in the damselfly *Ischnura senegalensis* (Rambur) (Odonata: Coenagrionidae). *Entomol. Sci.*, 12, 219–226.
- Takahashi, Y., Yoshimura, J., Morita, S. & Watanabe, M. (2010). Negative frequency-dependent selection in female color polymorphism of a damselfly. *Evolution*, 64, 3620–3628.
- Takahashi, Y., Morita, S., Yoshimura, J. & Watanabe, M. (2011). A geographic cline induced by negative frequency-dependent selection. *BMC Evol. Biol.* 11, 256.
- Takahashi, Y., Kagawa, K., Svensson, E.I. & Kawata, M. (2014). Evolution of increased phenotypic diversity enhances population performance by reducing sexual harassment in damselflies. *Nat. Commun.*, 5, 4468.
- Van Gossum, H., Stoks, R. & De Bruyn, L. (2001). Reversible frequency-dependent switches in male mate choice. *Proc. R. Soc. Lond. Ser. B-Biol. Sci.*, 268, 83–85.
- Willink, B. & Svensson, E.I. (2017). Intra- and intersexual differences in parasite resistance and female fitness tolerance in a polymorphic insect. *Proc. R. Soc. B.*, 284, 20162407.
- Willink, B., Duryea, M.C. & Svensson, E.I. (2019a). Macroevolutionary origin and adaptive function of a polymorphic female signal involved in sexual conflict. *Am. Nat.*, (in press).
- Willink, B., Duryea, M.C., Wheat, C. & Svensson, E.I. (2019b). Gene expression changes during female reproductive development in a colour polymorphic insect. *bioRxiv*. <https://doi.org/10.1101/714048>

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Editor, Greg Grether

Manuscript received 12 September 2019

Manuscript accepted 9 October 2019