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Cross-sex genetic correlations and the evolution of sex-specific local adaptation: insights from classical trait clines in *Drosophila melanogaster*

Clémentine Lasne,[1,2] Sandra B. Hangartner,[1] Tim Connallon,[1,*] and Carla M. Sgrò[1,*]
[1] *School of Biological Sciences, Monash University, Clayton, Victoria 3800, Australia*
[2] *E-mail: clementine.lasne@monash.edu*

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Natural selection varies widely among locations of a species' range, favoring population divergence and adaptation to local environmental conditions. Selection also differs between females and males, favoring the evolution of sexual dimorphism. Both forms of within-species evolutionary diversification are widely studied, though largely in isolation, and it remains unclear whether environmental variability typically generates similar or distinct patterns of selection on each sex. Studies of sex-specific local adaptation are also challenging because they must account for genetic correlations between female and male traits, which may lead to correlated patterns of trait divergence between sexes, whether or not local selection patterns are aligned or differ between the sexes. We quantified sex-specific divergence in five clinally variable traits in *Drosophila melanogaster* that individually vary in their magnitude of cross-sex genetic correlation (i.e., from moderate to strongly positive). In all five traits, we observed parallel male and female clines, regardless of the magnitude of their genetic correlation. These patterns imply that parallel spatial divergence of female and male traits is a reflection of sexually concordant directional selection imposed by local environmental conditions. In such contexts, genetic correlations between the sexes promote, rather than constrain, local adaptation to a spatially variable environment.

KEY WORDS: Body size, cline, cross-sex genetic correlations, sexual dimorphism, stress resistance.

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It has long been recognized that different traits do not necessarily evolve independently of one another (Lande 1979). The genetic correlation between traits quantifies the extent of this nonindependence, and the degree to which the evolutionary response of one trait will be influenced by selection on another (Falconer and Mackay 1996; Lynch and Walsh 1998). Genetic correlations can potentially facilitate or constrain evolutionary responses to selection (Lande 1979; Duputié et al. 2012), and therefore play pivotal roles in adaptive evolutionary divergence of populations to new or changing environments (Hellmann and Pineda-Krch 2007; Duputié et al. 2012). Empirical estimates of selection and genetic variation reveal varied evolutionary consequences of genetic correlations. While genetic correlations between traits constrain adaptation within some contexts of environmental change (Etterson and Shaw 2001), they facilitate adaptation in others (Agrawal and Stinchcombe 2009). Nevertheless, the interplay between environmentally variable selection and genetic correlations is not well understood, despite potentially important impacts on evolutionary trajectories under climate change (Hellmann and Pineda-Krch 2007; Duputié et al. 2012).

Genetic correlations play a similarly crucial role in the evolution of sex-specific adaptations, including the evolution of sexual dimorphism. The cross-sex genetic correlation (r_{mf}) is commonly used to estimate the amount of genetic coupling between the sexes for any trait (Lande 1980; Fairbairn 2007; Poissant et al. 2010). Empirical estimates of r_{mf} highlight a consistent pattern: r_{mf} is nearly always positive, and typically large, suggesting marginal

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[*] These authors share equal cosupervision of the research; author order was decided by a coin toss.

scope for independent evolution of female and male traits (Lande 1980; Poissant et al. 2010; Griffin et al. 2013). Nevertheless, for traits experiencing similar patterns of selection in males and females, a strong and positive r_{mf} will facilitate rapid adaptation in both sexes (Lande 1980). These scenarios of sex-specific divergence are particularly interesting in the context of environmental change; if changing environmental conditions cause maladaptation of males and females, and directional selection is aligned between the sexes, then a large and positive r_{mf} should promote rapid adaptation (Connallon 2015; Connallon and Hall 2016).

Despite the potential importance of r_{mf} for adaptive evolution, testing whether r_{mf} constrains or facilitates adaptation is a major challenge. First, while current empirical evidence indicates that r_{mf} is almost always positive, estimates vary in magnitude among traits (Poissant et al. 2010). For example, r_{mf} is generally lower for physiological traits compared to morphological traits (average r_{mf} estimates for physiological and morphological traits are 0.47 and 0.76, respectively, though individual estimates for morphological traits are often indistinguishable from $r_{mf} = 1$; see Poissant et al. 2010). Second, the influence of r_{mf} on adaptation critically depends on whether directional selection is concordant or discordant between the sexes. Current direct estimates of phenotypic selection suggest that sex differences in the direction of selection are common (Cox and Calsbeek 2009), though some of these inferred differences may reflect the imprecision of selection estimates (Morrissey 2016). Nevertheless, such studies are limited to a relatively small range of taxa and traits where estimates of selection are feasible (see Cox and Calsbeek 2009). While studies using laboratory populations also allow for direct tests of sex-specific selection and adaptation in novel environments (Delcourt et al. 2009; Long et al. 2012; Berger et al. 2014; Punzalan et al. 2014; Holman and Jacomb 2017; Martinossi-Allibert et al. 2017), they are few in number and provide less insight into conditions of adaptation in nature (discussed in Bonduriansky and Chenoweth 2009).

Clinal studies provide an indirect approach for inferring the directionality of adaptive phenotypic divergence between populations distributed across environmental gradients (Haldane 1948; Endler 1977; Mullen and Hoekstra 2008). Parallel clines across continents (Adrion et al. 2015) and stable clines through time (Hoffmann and Weeks 2007; Sgrò et al. 2010) imply that phenotypic divergence has evolved in response to spatially varying selection (Endler 1977). Stable genetic divergence in the face of gene flow reflects adaptation in response to local selection, and as such, clines indirectly reflect the direction of selection acting across the species' range. Clines provide valuable insights into the traits targeted by natural selection (Blanckenhorn et al. 2006; Hoffmann and Weeks 2007), the genes underlying these traits (e.g., Weeks et al. 2002; Hoekstra et al. 2004), and in ideal cases the strength of selection (Hoekstra et al. 2004; Mullen and Hoekstra 2008).

On the other hand, there has been minimal use of clines for studying sex-specific local adaptation and the potential role of r_{mf} in facilitating or constraining it, despite a variety of interesting theoretical implications regarding the interaction between sex-specific selection and environmental variability in space (see Harts et al. 2014; Miller and Svensson 2014; Connallon 2015; Servedio and Boughman 2017). Cline theory predicts that a positive r_{mf} can help both sexes locally adapt when their optima shift in parallel over space, or impede adaptation when sex-specific optima shift at different rates or in different directions across the species' range (Connallon 2015). Lab- and field-based estimates of body size clines suggest that cline slopes are often steeper in males than females (Blanckenhorn et al. 2006), which raises the intriguing possibility that spatially varying selection may differentially impact the sexes. However, it remains unclear what the contributions of genetic divergence versus plasticity are to these patterns. The extent to which the sexes are differentially adapted to local conditions remains unclear.

To date, most empirical studies that look into both male and female clinal divergence focus on body size (reviewed in Blanckenhorn et al. 2006)—a trait with a notoriously large r_{mf} (generally near one; Poissant et al. 2010). For such traits, it is difficult to tell whether clines accurately reflect patterns of spatial variation in sex-specific selection. In clinal studies that focus on traits with a high r_{mf}, parallel divergence is expected, regardless of the pattern of selection on each sex (Fig. 1B vs D; also see Fig. S1), so at best, we are only able to infer something about the sex-averaged direction of local selection. In contrast, traits with modest genetic correlations ($r_{mf} << 1$) can rapidly evolve clines in sexual dimorphism, and thereby reflect sex differences in selection across the range (Fig. 1A vs C) (Connallon 2015). By studying sets of traits that are known to exhibit consistent clinal divergence and that vary in r_{mf}, there is an opportunity to test for signals of genetic constraints to local adaptation. If spatially variable sexual dimorphism is observed in traits with modest r_{mf}, but not in traits with strong r_{mf} (Figs. 1C vs D), it suggests that strong genetic coupling between the sexes may mask empirical signals of spatially discordant local selection on female and male traits.

We estimated sex-specific patterns of genetic divergence in five key traits (cold, heat, desiccation and starvation resistance, and body size) that are known to be important in climatic adaptation in populations of *Drosophila melanogaster* from the latitudinal gradient in Eastern Australia (James et al. 1995; Hoffmann et al. 2001, 2002; Sgrò et al. 2010), as well as in India (Parkash and Munjal 1999; Parkash et al. 2012) and North America (Schmidt et al. 2005). Each trait is sexually dimorphic, and prior estimates of r_{mf} show that at least three have modest cross-sex genetic correlations (from Poissant et al. 2010, the estimate ranges are: $r_{mf} = 0.15$–0.38 for heat resistance; $r_{mf} = 0.54$–0.58 for cold resistance; $r_{mf} = 0.21$–0.58 for starvation resistance). By focusing

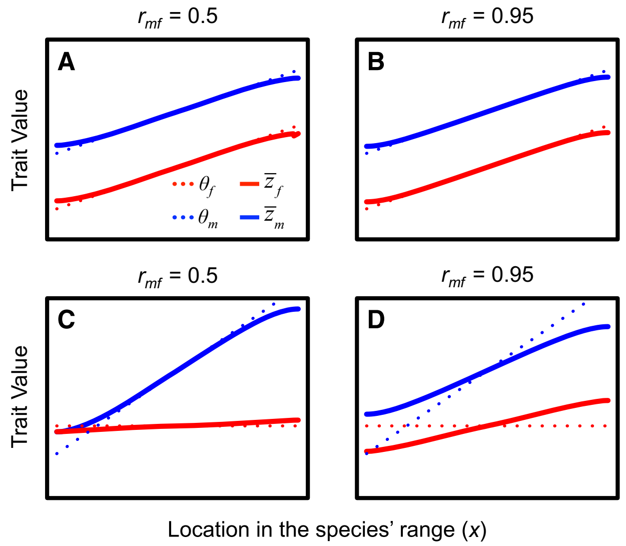

Figure 1. Hypothetical scenarios for the evolution of female and male trait clines. Broken lines show the female and male optima—θ_f and θ_m, for females and males, respectively—which vary linearly across the geographic gradient (x representing location in the gradient). Solid lines show equilibrium trait clines for each sex ($\bar{z}_f$, $\bar{z}_m$). Theoretical curves are based on the uniform population density model of Connallon (2015). Curves corresponding to an alternative, "abundant center" model of population density are provided in the supplementary material (see Fig. S1). In panels A and B, female and male trait optima shift in parallel, leading to the evolution of parallel female and male trait clines, under both high and low genetic correlations between the sexes. In panels C and D, where the trait optima for the sexes do not shift in parallel, we observe divergent sex-specific clines when the trait is partially correlated between the sexes ($r_{mf} = 0.5$, panel C), and maladaptive parallel clines when traits are strongly correlated between the sexes ($r_{mf} = 0.95$, panel D). Additional parameters include: $a = 3$ (sexual dimorphism at the range center), $SG/\sigma^2 = 2$ (the product of selection strength (S) and additive genetic variation (G), divided the mean squared dispersal distance (σ^2)), $b_{avg} = 1.5$ (the average of female and male trait optimum slopes), and $b_{SD} = 0$ in panels A and B or $b_{SD} = 3$ in panels C and D (the difference between male and female optimum slopes: $b_m - b_f$).

on traits with modest r_{mf}, we allow for the possibility of observing sex differences in clinal divergence—a signal of differential selection of females and males to local climatic conditions. We documented parallel male and female clines for the entire set of traits, regardless of the magnitude of r_{mf}, which suggests a strong alignment of selection between the sexes across the species' range (Fig. 1A–B).

Methods

DROSOPHILA COLLECTIONS AND MAINTENANCE

Eleven populations of *Drosophila melanogaster* were collected in April 2016 along the eastern Australian coast (Table S1). For each population, we used fifty field-inseminated females to initiate iso-female lines, with the exception of Bowen for which only 37 lines were established. All lines were treated with tetracycline [0.3 mg/mL] in lab generation F_2 to cure them of *Wolbachia*. After two generations of laboratory culture, 10 virgin females and males were pooled from each iso-female line of each population to initiate the 11 mass-bred populations. Each population was maintained across five 250 mL bottles (each containing 60 mL of agar-dextrose-potato-yeast medium) at 25°C and a 12:12 light/dark cycle. Densities were approximately 300 flies per bottle to ensure census population size of 1500 flies.

SELECTION OF TRAITS

We focused on the following five key traits—body size, and resistance to heat, cold, desiccation, and starvation—for three reasons. First, populations of *D. melanogaster* from the east coast of Australia are consistently phenotypically divergent for these traits in at least one sex, implying an important role for each in local adaptation (James et al. 1995; Hoffmann et al. 2001, 2002; Sgrò et al. 2010). Second, these traits vary in r_{mf}. Previous work has shown that body size is generally characterized by r_{mf} indistinguishable from one (Poissant et al. 2010), whereas the remaining traits have r_{mf} values that are typically intermediate in magnitude (Poissant et al. 2010; Williams et al. 2012; Hangartner et al. unpubl.). Importantly, and for the purpose of this study, we have estimates of r_{mf} for 4 of the 5 traits (body size, heat, cold, and desiccation resistance) from the Beerwah population, the same central clinal population used in this study (see supplementary information for details). We were therefore able to examine the relationship between r_{mf} and the extent of phenotypic divergence between populations and sexes. Finally, all traits are sexually dimorphic, which could reflect sexual dimorphism in female and male trait optima, and some scope for discordant selection between the sexes.

EXPERIMENTAL PROTOCOL

To control for density effects, populations were subjected to a series of short laying periods (24 hours each in 250 mL bottles containing 60 mL of medium) for two generations prior to trait assays. Adults from the parental generation were transferred into 250 mL specimen containers containing 12 mL of blue-dyed media. The food surface had been covered with live yeast paste to stimulate oviposition overnight (12 hours on average) at 25°C. For each trait assay, 300 eggs per population were transferred into 40 mL vials containing 7 mL of normal medium and placed at 25°C (12:12 light/dark) to complete development. With the exception of wing size, for which exactly 25 eggs were manually deposited in each vial, we transferred approximately 50 eggs per vial. Once flies eclosed from these vials, adults were allowed to mate for 24 hours prior to being separated under light CO_2 anesthesia before they were transferred to holding vials for 48 hours prior to the assays described below. Table S1 provides the number of generations of laboratory culture for each population, prior to the experiments. The experimental design for each trait is summarized below; further details can be found in Table S4.

HEAT RESISTANCE

Heat knockdown time was measured on 75 5-day-old individuals of each sex and population. Each fly was placed in 5 mL glass vials and submerged in a water bath at 39°C. This measure of heat resistance was chosen (rather than the dynamic, ramping method) because it has been repeatedly shown to exhibit clinal variation along the east coast of Australia in females (Hoffmann et al. 2002; Sgrò et al. 2010). Heat knockdown time was scored as the time until flies became immobilized (Hoffmann et al. 2002; Clemson et al. 2016). With the exception of Port Macquarie, which was not used for this experiment, populations were tested across 15 experimental runs, with each population and sex measured in each run.

COLD RESISTANCE

Chill-coma recovery time was assessed by placing 40 5-to-6-day-old individuals of each sex and population in dry eppendorf (1.5 mL) tubes and exposing them to 0°C through full immersion in a water bath with cooled 10% glycol solution for 5 hours (Gibert and Huey 2001; Clemson et al. 2016). Flies were then removed and allowed to recover at 25°C, where the time for each fly to right itself (stand up) was recorded. Populations were tested over eight experimental runs, with each population and sex measured in each run.

DESICCATION RESISTANCE

Forty 5-day-old flies of each sex and population were individually placed into empty 5 mL glass vials covered with fine gauze. A total of 880 vials were equally divided between three sealed glass tanks with silica gel maintained at 1.5–3% relative humidity (Hallas et al. 2002). Desiccation resistance was scored as the time until death, assayed through hourly checks until all flies died (Hallas et al. 2002).

STARVATION RESISTANCE

Fifty 4-day-old flies of each sex and population were individually transferred from normal media into 40 mL plastic vials containing nonnutritive agar medium (Goenaga et al. 2010). To avoid potentially confounding effects of desiccation, vials were covered with wet towels during the experiment. Starvation resistance was scored as mortality time, assayed at 8-hour intervals until all flies died (Goenaga et al. 2010).

WING SIZE

The right wing of 30 5-day-old flies of each sex and population was removed with fine forceps, mounted onto a glass slide covered with double-sided tape, and protected with a glass cover slip. Each wing was photographed using a Leica M80 stereo microscope (Leica, Heerbrugg, Switzerland) mounted with a digital camera. Eight vein landmarks were obtained for each wing with *x* and *y* coordinates extracted using tpsDIG2 software, version2.17 (Rohlf 2006). Centroid size (the square root of the sum of the squared distances between each landmark and the centroid, and a proxy for wing size) was estimated using the CoordGen8 software (Sheets 2003).

STATISTICAL ANALYSES

Prior to analyses, all traits were assessed for homogeneity of variances and normality using Levene's and Shapiro–Wilk tests. All traits except for cold resistance met assumptions of normality and equal variances; we subsequently log-transformed cold resistance. Analyses of variance (ANOVA) were used to test for differences between populations and sexes. All statistical analyses were performed in SPSS version 25.0 (SPSS Inc., Chicago, IL, USA). Population (unordered by latitude) and sex were treated as fixed effects. For both cold and heat resistance, run was treated as a random effect since there were more than six levels (eight and 15 runs, respectively). For desiccation resistance, tank was treated as a fixed effect since there were only three levels (Bolker et al. 2009).

Regression analyses, with latitude and sex as the predictor variables, were used to test for sex-specific latitudinal patterns of divergence in all traits. The least square trait means for each population and sex from the ANOVA's described above were used as the dependent variable in these analyses. Because we detected a significant effect of run on heat resistance, and tank on desiccation resistance, we performed a mathematical correction for these effects prior to (a) performing regression analyses, and (b) calculating sexual dimorphism indices (described below) for both traits. Specifically, following Sgrò et al. (2010), individual values of each trait in males and females were multiplied by the ratio of the sex-specific grand mean (over all runs/tanks) divided by the sex-specific run or tank mean (Sgrò et al. 2010; van Heerwaarden et al. 2012). Linear and polynomial regressions were then fitted to male and female data for all traits. Akaike's information criterion (AIC) was used to evaluate goodness of fit of linear and quadratic regressions.

SEXUAL DIMORPHISM

We used the Sexual Dimorphism Index (SDI; see Lovich and Gibbons 1992; Poissant et al. 2010) to quantify sexual dimorphism for each trait in each population. The SDI is obtained by subtracting one from the ratio of the trait value of the larger sex to

Table 1. Two-way analyses of variance (ANOVA) testing for differences in stress resistance and wing size between populations and sexes.

Trait	Source	d.f.	SS	*F*	*P* value
Wing size (mm)	Population	10	0.506	30.835	<0.001
	Sex	1	8.022	4888.405	<0.001
	Population × Sex	10	0.022	1.315	0.218
	Error	627	1.029		
Desiccation resistance (hours)	Population	10	357.9	5.819	<0.001
	Sex	1	6418.8	1043.703	<0.001
	Run	2	106.5	8.655	<0.001
	Population × Sex	10	57.4	0.933	0.502
	Error	838	5153.7		
Starvation resistance (hours)	Population	10	87,787	19.828	<0.001
	Sex	1	531,640	1200.816	<0.001
	Population × Sex	10	12,855	2.904	0.0013
	Error	1074	475,494		
Chill coma recovery time (log-transformed)	Population	10	0.366	3.495	<0.001
	Sex	1	0.232	22.135	<0.001
	Run	7	0.086	1.177	0.314
	Population × Sex	10	0.105	1.006	0.436
	Error	833	8.717		
Heat knockdown time (minutes)	Population	9	2515	4.413	<0.001
	Sex	1	5001	78.978	<0.001
	Run	14	2124	2.396	0.003
	Population × Sex	9	856	1.502	0.142
	Error	1463	92,637		

that of the smaller sex. Corrected data were used to calculate heat and desiccation resistance SDI values. For each trait, individual SDI values were calculated by randomly assigning an individual female value to an individual male value (each score was only used once). If, for any given trait, a population presented unequal numbers of male and female scores, scores of the most common sex were randomly removed from the dataset to equalise numbers of male and female values. For each trait, variation between populations in sexual dimorphism was examined by performing ANOVAs with population (unordered by latitude) as a fixed effect. Latitudinal patterns in SDI for all traits were then assessed via regression analyses, with SDI least square means for each trait and population (from the ANOVAs) used as the data points, as described above.

Results

MALE AND FEMALE CLINES

Population and sex significantly affected all traits (Table 1; Fig. 2A–E). Females were significantly larger and more resistant than males to desiccation and starvation stress (Fig. 2A–C); males were more resistant to cold and heat stress (Fig. 2D–E). The significant interaction between sex and population detected for starvation resistance (Table 1) was likely driven by smaller differences between males and females from the northernmost population, Innisfail, relative to other populations (Fig. 2C).

Significant—or near significant—latitudinal divergence was detected in both sexes for all five traits (Table 2; Fig. 2A–E). Mean chill coma recovery time, desiccation resistance and starvation resistance changed linearly with latitude, with resistance increasing with latitude. Wing size and heat knockdown time showed quadratic clinal patterns in both sexes, with wing size primarily changing across high latitudes, and heat knockdown time decreasing from cline ends toward the range center (Fig. 2A and E).

SPATIAL VARIATION IN SEXUAL DIMORPHISM

Each sexual dimorphism index (SDI) remained positive across populations for all traits, indicating a consistent direction of sexual dimorphism across the range (Fig. 2F–J). Cold resistance was the least sexually dimorphic trait (SDI < 0.05 in all populations), whereas desiccation resistance was the most sexually dimorphic (females 50% more resistant, on average). Wing size showed the narrowest range of SDI values across populations, whereas starvation resistance exhibited the widest range (Fig. 2F and H).

There was a significant effect of population on SDI for starvation resistance (Table S2: $F_{10,535} = 4.545$, $P < 0.001$), yet there was no clinal pattern in sexual dimorphism (Fig. 2H; Table S3).

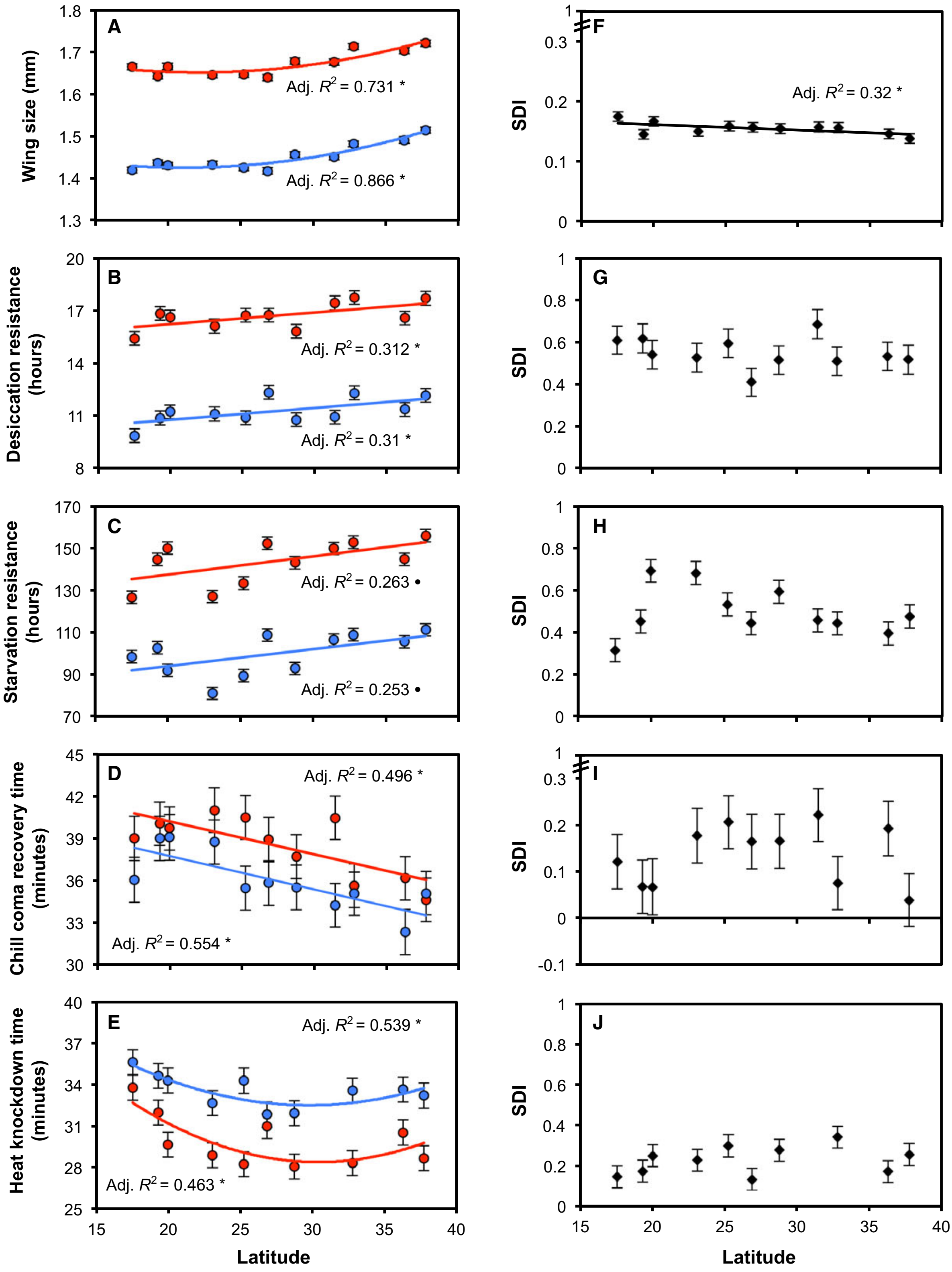

Figure 2. Sex-specific clines and population divergence in sexual dimorphism. Left column: association between latitude and sex-specific trait means (± 1 SE; females in red and males in blue) for (A) wing size, (B) desiccation resistance (corrected data), (C) starvation resistance measured as survival time, (D) cold resistance measured as recovery time, and (E) heat resistance (corrected data) measured as heat knockdown time. Right column: association between latitude and the sexual dimorphism index (SDI; population mean SDI ± 1 SE) for (F) wing size, (G) desiccation resistance, (H) starvation resistance, (I) cold resistance, and (J) heat resistance.

Table 2. Regression analysis testing for association between latitude and male and female trait means.

		Linear component		Quadratic component				
Trait	Sex	Slope $b \pm$ SE	*P* value	Slope $b \pm$ SE	*P* value	Intercept	Adj. R^2	*P-value*
Desiccation resistance	Females	0.0663 ± 0.0282	0.043	–	–	14.911	0.312	0.043
	Males	0.0676 ± 0.0289	0.044	–	–	9.414	0.310	0.044
Starvation resistance	Females	0.871 ± 0.407	0.061	–	–	120.166	0.263	0.061
	Males	0.812 ± 0.387	0.066	–	–	77.76	0.253	0.066
Chill coma recovery time	Females	–0.235 ± 0.071	0.009	–	–	44.947	0.496	0.009
	Males	–0.239 ± 0.065	0.005	–	–	42.546	0.554	0.005
Wing size	Females	–0.0136 ± 0.0068	0.079	0.0003 ± 0.0001	0.036	1.802	0.731	0.002
	Males	–0.0133 ± 0.0053	0.035	0.0003 ± 0.0001	0.011	1.565	0.866	<0.001
Heat knockdown time	Females	–1.579 ± 0.642	0.043	0.026 ± 0.0115	0.059	52.44	0.463	0.047
	Males	–1.157 ± 0.378	0.018	0.0194 ± 0.0068	0.024	49.763	0.539	0.028

Overall adjusted R-squared values and *P* values are given in the last two columns.

While there was no significant effect of population on sexual dimorphism for wing size (Table S2), there was a significant linear association between sexual dimorphism and latitude (Table S3: adj. $R^2 = 0.32$, $P = 0.04$; Fig. 2F), driven by the northernmost population, Innisfail; the association was no longer significant after removing the Innisfail population (adj. $R^2 = 0.12$, $P = 0.17$). None of the other traits exhibited population or clinal variability in sexual dimorphism (Table S2, S3; Fig. 2G–J).

Discussion

Environmental variation generates spatial heterogeneity in phenotypic selection, and favors adaptive divergence between subpopulations of widely distributed species (Siepielski et al. 2013, 2017). It is currently unclear whether patterns of selection for local adaptation typically differ between the sexes—an intriguing possibility with implications for the efficiency of adaptation in response to continuous environmental change (Connallon 2015). We measured sex-specific genetic clines in five key ecological traits that vary in the strength of their cross-sex genetic correlation, r_{mf}. Although all traits were sexually dimorphic, male and female trait clines were parallel for each trait, regardless of the magnitude of r_{mf}. This consistent parallelism implies that spatially variable selection is concordant between the sexes, at least for traits relevant to thermal stress, desiccation and starvation resistance, and body size. Below, we outline the implications of these observations for local adaptation, and discuss these new results within the context of prior empirical research on sexual dimorphism and the evolution of clines in ecologically important traits. We close with an appeal for further studies that directly link genetic correlations with population divergence of female and male traits.

INTERSEXUAL GENETIC CORRELATIONS AS FACILITATORS OF CLINAL ADAPTATION

Imperfect genetic correlations between sexes for heat, cold, desiccation, and starvation resistance provide an opportunity for males and females to independently evolve along environmental gradients. The parallel clines observed for these four traits imply similar patterns of sex-specific selection across the eastern Australian latitudinal gradient. Wing size also exhibited strongly parallel male and female clines. The general absence of spatial variation in sexual dimorphism for wing size could be due to strong alignment of sex-specific selection across the species range, or to a strong r_{mf} constraining the independent evolution of male and female body size. Direct estimates of sex-specific selection on wing size would be needed to distinguish between these possibilities.

When male and female trait optima shift in parallel across a species range, a positive genetic correlation between the sexes should promote local adaptation of each sex to changing environmental conditions (see Connallon 2015). Although several environmental, demographic and genetic factors (including r_{mf}) impact the steepness of genetically based trait clines, theory predicts that traits with larger genetic correlations between the sexes will exhibit steeper clinal divergence, provided selection is concordant between the sexes and all else is equal between traits. To evaluate this prediction, we assessed the relation between sex-specific cline slopes (estimated here) and r_{mf} point estimates for all traits except starvation resistance (r_{mf} estimates were obtained from a separate study of the Beerwah population, near the centre of the latitudinal range; Hangartner et al. unpubl. data—methods described in Supplementary Material). Although r_{mf} point estimates were also available for the two cline end populations (Innisfail and Melbourne), they were qualitatively similar to those from the Beerwah population (not shown), and we therefore used

r_{mf} values from the geographically central population at Beerwah. To compare cline slopes between traits, we rescaled clinal divergence to units of the phenotypic standard deviation of the trait within the central population. To control for potential differences in additive genetic variance among traits, we divided cline slopes by the trait's heritability estimate (Hangartner et al. unpubl. data; see Fig. S2 legend).

Standardized cline slopes increased with r_{mf} (Fig. S2, sex-specific cline slopes increase with r_{mf}), which suggests that r_{mf} facilitates local adaptation, and/or that traits with relatively large r_{mf} are preferentially targeted by selection for clinal divergence (i.e., such traits are subject to stronger selection, or their optima shift more rapidly across the range than traits with low r_{mf}). Although we cannot disentangle the set of conditions determining cline slopes for our traits, the observed positive association between r_{mf} and cline steepness, which we view as tentative, serves as a point of discussion and a motivation for future tests of the role of r_{mf} in local adaptation.

SEXUAL DIMORPHISM AND CLINAL ADAPTATION

Studies of sex-specific clinal adaptation have traditionally focused on body size and other morphological traits that are relatively easy to measure (reviewed in Blanckenhorn et al. 2006). While many such studies have reported spatial and latitudinal variation in the degree of sexual size dimorphism (SSD), the direction of this variation can vary across taxa. Much of the evidence for sexually dimorphic clines come from field-based studies, which do not disentangle effects of genetic divergence and phenotypic plasticity; for example, SSD declines with latitude in the Frillfin goby (Lima-Filho et al. 2017), and increases with latitude in two species of *Salmo* (Jonsson and Jonsson 2015; Weir et al. 2016). Lab-based studies, which are less common, occasionally report evidence for genetically based divergence in SSD among populations (e.g., nonclinal population differences in SSD in cabbage beetles: Tang et al. 2017). Other studies report no significant divergence among populations in SSD (e.g., Tesche and Hodges 2015; Sniegula et al. 2016). The latter results for SSD are consistent with those of the present study; the sole clinal pattern in SSD observed here was driven by the northernmost tropical population (Innisfail), and disappeared when this population was excluded from analysis. Similar patterns of SSD were observed for *D. simulans* populations collected from the east coast of Australia (i.e., parallel male and female body size clines, and no cline in SSD; Arthur et al. 2008).

Few studies have examined sex-specific patterns of clinal divergence in nonmorphological traits; those that have are largely based on *Drosophila*, and report varying patterns of sexual dimorphism. For example, male gene expression tends to show stronger clinal divergence than female gene expression among populations of *D. serrata* from eastern Australia, resulting in an increase in transcriptome sexual dimorphism with latitude (Allen et al. 2017). In contrast, cuticular hydrocarbons (CHCs) show parallel linear or quadratic clines in males and females of *D. melanogaster* and *D. serrata*, respectively, from the east coast of Australia (Frentiu and Chenoweth 2010). Finally, sexual dimorphism in body size, heat, cold, desiccation and starvation resistance did not vary with latitude in *D. simulans* from eastern Australia, although these results are difficult to interpret because of nonlinear (female cold resistance only) and nonsignificant (starvation and heat resistance) clines (Arthur et al. 2008). The results from the above studies are consistent with the absence of clinal variation in sexual dimorphism in the stress resistance traits reported in the present study for *D. melanogaster* and for starvation resistance in *D. leontia* from India (Aggarwal 2014).

Finally, the clinal patterns that we report for heat and cold resistance and body size are consistent with previous clinal studies of *D. melanogaster* from eastern Australia (largely based on single-sex estimates; James et al. 1995; Hoffmann et al. 2002; Sgrò et al. 2010; van Heerwaarden and Sgrò 2011). Our study reports, for the first time in Australian *D. melanogaster*, linear and positive clines in desiccation and starvation resistance. While positive clines for desiccation resistance have repeatedly been found for *Drosophila* species from the Indian subcontinent (reviewed in Rajpurohit et al. 2013), Hoffmann et al. (2001) found no significant association between latitude and either desiccation resistance or starvation resistance in Australian *D. melanogaster*. Similarly, Arthur et al. (2008) did not find a cline in desiccation resistance in *D. simulans* from the east coast of Australia. Interestingly, the positive clines for starvation resistance that we report here (temperate populations more resistant than tropical populations) is opposite to the starvation resistance clines reported for *D. simulans* from eastern Australia (Arthur et al. 2008) and Indian *Drosophila* species (Rajurohit and Nedved 2013; Aggarwal 2014). While temperate populations are more starvation resistant than tropical population of *D. melanogaster* from North America (Schmidt et al. 2005), consistent with the present study, Robinson et al. (2000) did not find a cline for starvation resistance in South American populations of *D. melanogaster*. These discrepancies for starvation resistance across studies and continents may reflect differences in selection pressures over time and across continents. It is also possible that the clines in starvation and desiccation resistant in Australian *D. melanogaster* reported here reflect selection imposed by The Millennial Drought—a prolonged period of dry conditions from 1996 to mid-2010, which affected much of southern Australia, and which was particularly severe in southeastern Australia (Australian Bureau of Meteorology www.bom.gov.au). It would be interesting to reassess desiccation and starvation resistance in populations of *D. simulans* from eastern Australia to determine whether clinal patterns have similarly shifted in response to these recent climatic conditions.

Conclusion

Our study places a spotlight on the consequences of r_{mf} for clinal divergence in traits important for adaptation to broad-scale climatic conditions. To the extent that such traits dominate in local adaptation, our data suggest that both sexes will obtain long-run evolutionary benefits from positive cross-sex genetic correlations. Strong intersexual genetic correlations are often perceived as constraints to the independent evolution of male and female phenotypes (e.g., Lande 1980; Wyman et al. 2013). Yet, in the context of spatially varying environmental selection, a large r_{mf} will facilitate rapid adaptation as long as the direction of selection is concordant between the sexes. These results are consistent with both theoretical (Lorch et al. 2003; Whitlock and Agrawal 2009; Connallon and Hall 2016) and empirical studies (Long et al. 2012; Berger et al. 2014) that suggest that r_{mf} can facilitate sex-specific adaptation in changing environments. Future work focusing on patterns of sex-specific spatial divergence in different taxa and traits will help determine whether patterns of local selection typically align between the sexes, and whether r_{mf} typically facilitates or constrains the evolution of sex-specific local adaptation.

AUTHOR CONTRIBUTIONS

C.L., T.C. and C.M.S. designed the study, analysed the data and wrote the manuscript. C.L. and S.B.H. coordinated the field trip and performed the lab experiments. S.B.H. contributed to data interpretation and editing of the manuscript.

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DATA ARCHIVING

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Supporting Information

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

Table S1. Population sampling locations (site coordinates), and generation time of experiments.
Table S2. One-way analyses of variance (ANOVA) testing for differences in sexual dimorphism between clinal populations.
Table S3. Regression analysis testing for association between latitude and sexual dimorphism in all traits.
Table S4. Summary table of the experimental design for each heat, cold, desiccation, and starvation resistance, and wing size.
Figure S1. Hypothetical scenarios for the evolution of female and male trait clines under an "abundant center" model of population density across the species' range. Theoretical curves are based on the abundant center density model of Connallon (2015). Additional details are the same as in Figure 1 of the main text.
Figure S2. Association between intersexual genetic correlations (r_{mf}) and sex-specific cline slopes. Cline slopes include the four traits where r_{mf} values are available from the Beerwah population, which is near the center of the species' range (data from Hangartner et al. unpublished), and include desiccation resistance (green), heat resistance (red), cold resistance (blue), and wing size (orange). Cline slopes for each sex were rescaled to units of the phenotypic standard deviation of the trait within the central population (i.e., a given data trait value X is rescaled as $y = (X - \mathrm{E}(X_R))/\sigma_R$ where $\mathrm{E}(X_R)$ is the trait mean in the central "reference" population, and σ_R is the trait's standard deviation (i.e., the phenotypic variance V_P) in the reference population of Beerwah). After recalculating LS means for each sex and population for all four traits, linear regressions were fitted to male and female rescaled data to calculate cline slopes. Cline slopes were then divided by the trait's heritability estimate (Hangartner et al. unpubl. data) to control for differences in additive genetic variance between sexes and traits. It is worth noting that the r_{mf} estimates extend beyond 1 due, in this instance, to the method of estimation, when in reality, correlation coefficients are constrained to fall within the range: $-1 < r < 1$. Nevertheless, the distribution of point estimates reflects the range of values along the continuum of r_{mf}, and illustrates the theoretical expectation that the strength of local adaptation increases with r_{mf}.