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Evolution of sexual dimorphism in phenotypic covariance structure in *Phymata*

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Sexual dimorphism is a consequence of both sex-specific selection and potential constraints imposed by a shared genetic architecture underlying sexually homologous traits. However, genetic architecture is expected to evolve to mitigate these constraints, allowing the sexes to approach their respective optimal mean phenotype. In addition, sex-specific selection is expected to generate sexual dimorphism of trait covariance structure (e.g., the phenotypic covariance matrix, P), but previous empirical work has not fully addressed this prediction. We compared patterns of phenotypic divergence, for three traits in seven taxa in the insect genus *Phymata* (Reduviidae), to ask whether sexual dimorphism in P is common and whether its magnitude relates to the extent of sexual dimorphism in trait means. We found that sexual dimorphism in both mean and covariance structure was pervasive but also that the multivariate distance between sex-specific means was correlated with sex differences in the leading eigenvector of P, while accounting for uncertainty in phylogenetic relationships. Collectively, our findings suggest that sexual dimorphism in covariance structure may be a common but underappreciated feature of dioecious populations.

KEY WORDS: **Divergence, genetic constraints, intralocus sexual conflict, latitudinal cline, P-matrix.**

Dioecious populations are typically faced with a fundamental problem: anisogamy predisposes males and females to different patterns of selection but, given a common genome, their independent evolution is constrained. At first glance, the diversity of secondary sex characters suggests a small role for genetic constraints on the independent evolution of male and female phenotypes. On one hand sexually antagonistic selection is pervasive and correlates with the extent of sexual dimorphism (Cox and Calsbeek 2009), however, it remains unclear whether the evolution of sexual dimorphism necessarily indicates release from constraints imposed by shared genetic architecture (Bedhomme and Chippindale 2007; Cox and Calsbeek 2009). In fact, some data indicate that the extent of shared genetic architecture is inversely related to sexual dimorphism, consistent with a prominent role for genetic constraints (Poissant et al. 2010). Surely, the issue of genetic constraints on sexual dimorphism is a matter of degree but it remains an active empirical question and subject of debate (Bonduriansky and Chenoweth 2009).

Most previous work on sexual dimorphism has been somewhat restricted in scope, typically focusing on the mean values of single (sexually homologous) traits. Both theory and data suggest that strictly univariate views can offer a distorted view of phenotypic evolution, including the importance of genetic constraints (Lande 1980; Blows and Hoffman 2005; Walsh and Blows 2009; Gosden et al. 2012; Wyman et al. 2013). Although the implications of sexual dimorphism in covariance structure was recognized early (Lande 1980; Cheverud et al. 1985), studies of this form of sexual dimorphism are still relatively rare (e.g., Steven et al. 2007; Wyman et al. 2013; Gosden and Chenoweth 2014).

To date, very little is known regarding the prevalence of covariance dimorphism and whether its incidence is comparable to the relatively common phenomenon of sexual dimorphism in

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mean phenotypes (Andersson 1994). A straightforward starting point is to compare standing patterns of variation (i.e., the phenotypic covariance matrix, **P**) between sexes and among species. The **P**-matrix summarizes the observed (population-level) variance in traits, along the diagonal elements of the matrix, as well as the pairwise relationships between traits (i.e., covariances), in the off-diagonals elements.

Analyses of **P**-matrices have proven valuable for comparative approaches to the evolution of trait covariances (e.g., Steppan et al. 2002; Berner et al. 2010; Kolbe et al. 2011). However, the use of **P** as a surrogate for the genetic variance–covariance matrix, **G**, has been subject to criticism (e.g., Willis et al. 1991; Roff et al. 2012). Although there is no guarantee that the two matrices will be similar, and the statistical power to estimate matrix similarity is typically limited (Steppan et al. 2002), empirical studies have often found some resemblance (e.g., Cheverud 1988; Roff 1996) and that **P** performs well for many applications (e.g., Schluter 1996; Phillips and Arnold 1999; Bégin and Roff 2003; Hohenlohe and Arnold 2008). For comparisons between sexes, employing the **P**-matrix to reveal some aspects of sexual dimorphism in genetic covariance structure may be justified if the sexes within a population are expected to experience, on average, similar environments (see Cheverud 1982; Pigliucci 2003; Pitchers et al. 2013).

For a given subset of quantitative traits, and under the simplifying assumption that environmental covariances are equal for the sexes, the evolution of sex differences in **P** can result from at least two nonexclusive mechanisms. First, sexual dimorphism in **P** could arise from selection on the additive genetic variance–covariance matrix, **G** (Lande 1979; Phillips and Arnold 1989). Second, sexual dimorphism in **P** can evolve, despite the sexes sharing a common environment, through sex-limited alleles or modifiers that have sex-specific and/or nonadditive effects. For example, males and females may exhibit differences in their genetically based plastic responses to environmental input that will be manifested as differences in phenotypic covariances. Rowe and Houle (1996) illustrated how the allocation of resources among costly traits will evolve to depend on resource acquisition and in a manner that optimizes trade-offs among components of fitness. Bonduriansky (2007) extended this to consider sex specificity in these trade-offs, showing that within- and between-sex trait distributions (means and covariances) can strongly depend upon environmental sources of variation. Empirical studies in other taxa indicate that the degree to which environmental input mediates secondary sex traits expression does, indeed, show a strong genetic basis (e.g., David et al. 2000; Kotiaho et al. 2001) and often diverges within lineages (Wilkinson and Taper 1999).

It is important to emphasize that these two types of sexual dimorphism—in trait means and in their covariances—are separate evolutionary phenomena. That is, the sexes can diverge in covariance structure even when trait means do not and vice versa. Nonetheless, there are plausible biological scenarios where these two moments of the phenotypic distribution might themselves bear an association. For example, as the ecological disparity between males and females becomes more marked, one might expect increasing sexual dimorphism in both the trait means (i.e., greater distance between sex-specific optima) and the trait covariances (i.e., greater sex differences in the trait combinations that confer high fitness). We are aware of only one empirical study, to date, that explicitly considered the relationship between sexual dimorphism in trait means and sex-specific variability (Wyman and Rowe 2014). To our knowledge, the possibility that the degree of multivariate sexual dimorphism in trait means might be correlated with divergence between sexes in their trait covariance structure has not been explicitly tested.

As is often the case in comparative studies, attributing observed patterns of divergence to specific mechanisms of selection poses a considerable challenge. However, one classical approach to inferring targets and mechanisms of selection is to study natural variation across a biogeographical scale (Endler 1986). For example, traits such as size and coloration have been shown to vary predictably across latitudes, as a consequence of gradients in season length and climate (e.g., Rapoport 1969; Brakefield 1984; Blanckenhorn and Demont 2004).

Here we used a genus of insects, the ambush bugs (*Phymata* spp. in the Reduviidae), to illustrate the potential ubiquity and diversity of sexual dimorphism in covariance structure for a subset of sexually homologous size and color pattern traits, known to have important consequences for various components of fitness. In addition to characterizing both types of multivariate sexual dimorphism in each species, we specifically asked whether among-species divergence in their degree of multivariate sexual dimorphism (i.e., of the trait means) was correlated with dimorphism in their respective covariance structure, **P**.

Detailed studies of sex-specific selection are limited to only a few *Phymata* species, but previous work implicates body size to be an important correlate of some key life-history traits (Dodson and Marshall 1984a,b) and that color pattern plays a key role in thermoregulation and sexual selection (Punzalan et al. 2008b, 2010). Therefore, we also inspected latitudinal trends, within and between species in the expression of these traits to infer possible selective causes of sex and species differences in dimorphism.

Methods

STUDY SYSTEM BACKGROUND AND DATA COLLECTION

The genus *Phymata* has a mostly New World distribution that includes approximately 100 species. We focused on a subset of North American taxa that have either taxonomic (nomenclature)

and/or geographic affinities: *Phymata americana americana* Melin, *P. americana coloradensis*, Melin, *P. americana metcalfi* Evans, *P. fasicata fasciata* Gray, *P. fasiciata mystica* Evans, *P. pennsylvanica* Handlirsch, and *P. vicina* Handlirsch (see Supporting Information S1). For the present purposes, the distinction between populations (subspecies) and species is arbitrary and, for simplicity, each taxon is hereafter referred to as a "species" with subspecific names elevated and (for brevity) the genus name often omitted.

These *Phymata* spp. differ substantially in size and coloration (see Supporting Information S2), but we focused on a subset of three traits for which previous studies have identified as likely targets of direct selection. Observed sexual size dimorphism in several species could be partly explained by fecundity selection favoring large female size (Dodson and Marshall 1984a; Punzalan et al. 2008c), whereas color dimorphism in one species is attributable to selection favoring dark male coloration (Punzalan et al. 2008c, 2010) because of its thermal advantages for mate search (Punzalan et al. 2008b). Phylogenetic relationships among *Phymata* are currently unknown.

Data were obtained for preserved specimens from six museums (Supporting Information S1). For each specimen, we recorded geographic origin and then photographed it under standardized lighting conditions, with size and color references included in each (dorsal and lateral) photograph. Complete locality and morphological data were collected for a total of 972 individuals (females/males) of *americana* (94/134), *coloradensis* (54/62), *fasciata* (45/36), *metcalfi* (33/82), *mystica* (66/53), *pennsylvanica* (105/151), and *vicina* (9/48). Following the protocol of Punzalan et al. (2008c), images were analyzed using Scion® Image (on Microsoft© XP) to obtain measures of pronotum width (PN), a measure of body size (Mason 1973) as well as two color pattern traits: mean darkness of a circular patch on the dorsal (MD) surface of the pronotum and lateral (ML) surface of the thorax (i.e., the mesopleuron) (Fig. 1). Although dark coloration is not limited to these regions, these measures provide proxies for the melanism of two discrete (i.e., pro- and mesothoracic segments) and potentially independent developmental units in heteropterans (e.g., Cheseboro et al. 2009; Prudhomme et al. 2011), while allowing objective comparisons across sex and species (i.e., homologous characters). Detailed methods for trait measures and image analyses are described in the Supporting Information S3. Traits were approximately normally distributed and were not transformed, though it was appropriate to standardize data for some analyses (discussed below).

Divergence of trait means and intraspecific latitudinal effects

As an overall test for species, sex, and (linear) latitudinal effects on multivariate (mean) divergence, we first conducted a MANCOVA with the three traits as response variables, species (fixed effect), sex (fixed effect), latitude (covariate) and the species × sex interaction as independent variables (i.e., we refer to this as a "global" MANCOVA). Given the significance of the species × sex interaction, we proceeded with a series of analyses that treated each species separately, while also considering possible sex-specific latitudinal clines; that is, MANCOVA with sex, latitude and the sex × latitude interaction as predictors and the three traits as response variables. To facilitate interpretation of the multivariate (mean) sex differences, we conducted additional univariate analyses; for each trait and species, we performed an ANCOVA, again with sex as the main effect and with latitude and sex × latitude as additional covariates/predictors. These analyses were performed using JMP® version 11.0 (SAS Institute).

Estimating trait covariances, independent of latitude

Not surprisingly, average trait values differed among species, between sex as well as latitude (see Results). For the **P**-matrix comparisons we wished to make, it was ultimately necessary to remove these effects as well as those that result from trait scaling (i.e., the expected positive relationship between the variance of a trait with its mean). We accomplished this by considering sex separately (within species) and dividing each trait by its sex-specific mean (i.e., mean standardization). Subsequently, we calculated the residuals of these mean-standardized values after linear regressions (separately for each trait) on latitude and calculated the covariances from these. An equivalent approach is to first residualize trait values and then add these values to the species/trait mean values prior to the mean standardization; both approaches give identical covariance matrices. This approach of using of latitude-corrected residual variation is analogous to procedures used elsewhere, whereby **P** was estimated after correcting for linear measures of size (e.g., Berner et al. 2010; Kolbe et al. 2011). Standard errors of the elements of **P** were estimated using a delete-one jackknife approach (Manly 1997) implemented in R, using the package "bootstrap" version 2015.2 (Efron and Tibshirani 1993).

Our use of these residual variances to estimate **P** is meant to capture "average" patterns of intraspecific trait covariation, independent of latitude. We acknowledge that our dataset has some shortcomings, including possible violation of the assumption of equal environmental covariances. This may be especially true, given that data for males and females of a species were obtained from specimens that were collected from different localities as well as on different dates. As discussed previously, this could undermine the ability to extend empirical inferences (based on **P**) to underlying genetic architecture. However, we believe the present treatment illustrates the utility of between-sex comparisons of covariance structure and its relevance.

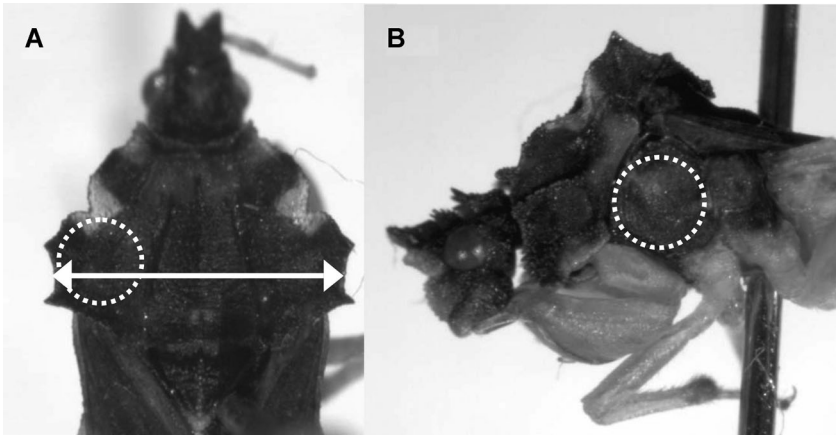

Figure 1. Closeup views of the thorax, viewed from dorsal (panel A) and lateral (panel B) aspects, from which size and color pattern traits were measured. The length of the white, solid (arrowed) line represents pronotum width (PN) and the dotted, white circles circumscribe the regions used to obtain measures of mean dorsal darkness (MD, panel A) and mean lateral darkness (ML, panel B).

Analyzing sexual dimorphism and among-species differences in P-matrices

To evaluate whether **P** was sexually dimorphic, for each species separately, we applied common principal components analysis (CPCA, Flury 1988), implemented using the software program provided by Phillips and Arnold (1999). Alternative methods for comparisons of covariance matrices among two or more samples (e.g., reviewed in Steppan et al. 2002, also see Hine et al. 2009; Marroig and Cheverud 2010; Roff et al. 2012; Aguirre et al. 2014), though we do not explore the differences among the all of these methods in the present article. As a straightforward test for sex differences in **P**-matrix structure, we used the CPCA "jump-up" approach, testing the hypothesis of "equality" versus "unrelated." As any given pair of matrices may exhibit similarities in aspects of covariance structure that are more subtle than strict equality (e.g., proportionality, one or more common eigenvectors), we used a model-building approach to determine the matrix structure of best fit in the CPCA hierarchy. Following common practice, we considered the (minimum) Akaike's Information Criterion score associated with each model to indicate the best descriptor of matrix similarity (Flury 1988; Phillips and Arnold 1999). As a complementary approach, we also performed comparisons following a random skewers method (Cheverud and Marroig 2007). Briefly, this method compares the average differences in predicted evolutionary response for a pair of matrices (samples), subjected to the same but random subset of linear selection vectors (i.e., assuming **P** is equal to **G**). Using the "phytools" version 0.4–21 package in R (Revell 2012), we subjected each male–female pair of matrices to 1000 random skewers and calculated the average vector correlation (c). For significance tests of c, we assumed a null hypothesis of identical matrices, following Calsbeek and Goodnight (2009) and Roff et al. (2012). To generate a null distribution of vector correlations (i.e., assuming no expected difference, or $c = 1$, between sex-specific **P**-matrices but with sampling error), at each ith iteration, we randomly assigned male and female multivariate trait observations to two matrices of the same size as the original data matrices. We determined significance according to the proportion of these iterations ($i = 1000$) that generated a vector correlation less than or equal to c.

Species differences in the extent of sexual dimorphism may result from several combinations of male-specific divergence, female-specific divergence or both. To test for differences among species in sex-specific **P**, we performed pairwise comparisons, focusing on results from the CPCA analyses (i.e., using the aforementioned model building approach).

Comparing sexual dimorphism in means to sexual dimorphism in covariances

As a composite metric of multivariate sexual dimorphism in trait means, we used the Mahalanobis distance,

$$\boldsymbol{d}_i = [(m - f)^{\mathrm{T}}\ \boldsymbol{D}^{-1}\,(m - f)]^{0.5},$$

whereby, for the ith species, m and f represent the vector of trait means of male and females, respectively; **D** is the covariance matrix among trait means after pooling across sexes and species and $^{\mathrm{T}}$ indicates the matrix transpose. That is, $\boldsymbol{d}$ estimates multivariate divergence on the scale of the total phenotypic variance spanned by all species, while accounting for (among-species) trait covariance and scale differences among traits (Mahalanobis 1936). Accordingly, values of $\boldsymbol{d}$ were nearly identical, irrespective of whether m, f, and **D** were calculated at the raw scale or on the (pooled) mean-standardized scale; we present $\boldsymbol{d}$ calculated from the former.

Multivariate covariance structure is often represented by its eigenvectors and eigenvalues, corresponding to matrix "orientation" and "size," respectively (Hohenlohe and Arnold 2008). As the leading eigenvector (i.e., $\mathbf{P_{max}}$) of each sex- and species-specific **P**-matrix captured the majority (and comparable amounts of) variance (see Results), we used a geometric approach to summarize multivariate sexual dimorphism in the orientation of **P**. For each *i*th species, we calculated an angular measure (in degrees) of sex differences in **P**-matrix orientation as

$$\boldsymbol{\phi}_i = \cos^{-1}\left(v_{mi}^T\, v_{fi}\right)$$

whereby v_m and v_f correspond to $\mathbf{P_{max}}$ for males and females of the *i*th species, respectively.

To assess the relationship between the two metrics of multivariate sexual dimorphism, we calculated the Spearman rank correlation ($\mathbf{r_s}$) between $\boldsymbol{d}$ and $\boldsymbol{\phi}$. To accommodate the unknown degree of nonindependence among taxa, we used the approaches outlined by Martins (1996) and Stamps et al. (1997), using simulated trees to incorporate uncertain coancestry into a phylogenetic least squares (PGLS) model (Grafen 1989; Martins and Hansen 1997). We implemented the approach in R (http://www.R-project.org), simulating phylogenetic trees according to a "pure-birth" branching process, assuming constant speciation/extinction rates (Martins 1996), using the "pbtree" function in "phytools" version 0.4–21 (Revell 2012). Our models assumed that covariances due to coancestry accumulates according to a Brownian Motion model, equivalent to the independent contrasts method of Felsenstein (1985; see Rohlf 2006). Estimation of expected phylogenetic correlations and implementation of PGLS models were performed using the package "ape" version 3.1–4 (Paradis et al. 2004). From 10,000 simulated phylogenies, we estimated the regression coefficient, the associated standard error ($b \pm$ SE), as well as the estimated *P*-value corresponding to a test of significant covariance (i.e., $b > 0$) at each iteration. Uncertainty in the observed (nonphylogenetic) estimates was represented by the confidence intervals (CIs) associated with the observed *b*, calculated from the regression slopes and their errors, following (eq. 3C in Martins 1996). We also reported the proportion of iterations that generated *P*-values less than $\alpha = 0.05$ (Stamps et al. 1997).

We employed the same approach (i.e., observed correlation coefficients, complemented by simulated PGLS for each metric of sexual dimorphism regressed on latitude) to ask whether each of the multivariate measures of dimorphism, $\boldsymbol{d}$ and $\boldsymbol{\phi}$ varied systematically according to average species latitude. As composite multivariate metrics (e.g., based on total or principal directions of divergence) are not always easy to interpret, we also performed (simple) bivariate analyses to identify any associations between species trait means (for each sex and trait) and average species latitude.

Results

MULTIVARIATE DIVERGENCE, MEAN DIMORPHISM, AND INTRASPECIFIC LATITUDINAL CLINES

Overall, there were clear indications of multivariate divergence (whole model: $\lambda = 0.048, F_{42,\,2833.8} = 120.60, P < 0.0001$) among species ($\lambda = 0.193, F_{18,\,2701.6} = 118.45, P < 0.0001$) and between the sexes ($\lambda = 0.965, F_{3,\,955} = 307.04, P < 0.0001$) as well as species × sex interactions ($\lambda = 0.534, F_{18,\,2701.6} = 37.27, P < 0.0001$). Conducting analyses separately by species indicated sexual dimorphism (i.e., effect of "sex") for all seven species but also significant latitudinal and/or sex × latitude interactions in six of the species (Table 1). Univariate analyses of each species indicated that sex differences reflect females being generally larger in pronotum width (PN) (main effect of sex: $F_{1,\,77–252} > 29.61$ and $P < 0.0001$) for all except *vicina* ($F_{1,\,53} = 0.66, P = 0.4193$) and with males being darker in dorsal darkness, MD (i.e., sex: $F_{1,\,53–252} > 11.48, P < 0.0010$ for all). Male-biased sexual dimorphism in lateral darkness, ML, was also apparent in all species (sex: $F_{1,\,53–252} > 12.28, P < 0.0008$) except for *metcalfi* ($F_{1,\,111} = 0.063, P = 0.8019$). Relationships between trait expression and latitude varied widely among species and sex, including both positive and negative relationships as well as significant sex × trait interactions in some cases (Supporting Information S5 and S6).

Species exhibited considerable size variation, with the average PN of the largest (*coloradensis*) being about 77% larger for females, and 54% larger for males, than the smallest species (*vicina*). There were significant quantitative differences in darkness among males, with *americana*, *pennsylvanica*, and *vicina* being characteristically dark with respect to both MD and ML. In contrast, *metcalfi* had high values of MD but the lowest values of ML, corresponding to reduction in the expression of dark lateral coloration. These differences in rank order and/or associations between color pattern traits were not necessarily mirrored in females. For example, at the extremes, *pennsylvanica* exhibited very high—whereas *metcalfi* had very low—values of both MD and ML but *americana* had high values of MD but very low values of ML (Fig. 2).

SEXUAL DIMORPHISM AND DIVERGENCE IN P-MATRIX STRUCTURE

For all species, $\mathbf{P_{max}}$ summarized the majority of phenotypic covariation (63–78% in females, 73–91% in males) among the measured traits. Inspection of the trait loadings indicated that for most species, $\mathbf{P_{max}}$ represented an axis of positive covariance between color pattern traits and, in some cases, positive

Table 1. Intraspecific analyses of multivariate sexual dimorphism and effects of latitude on three traits (PN, MD, and ML) in seven *Phymata* spp., using MANCOVAs. DF denotes degrees of freedom and *N* refers to sample size.

Species		Value	*F*	Numerator DF	Error DF	*P*-value
americana	Intercept	1.95	144.38	3	222.0	<0.0001
($N = 228$)	Sex	2.63	194.82	3	222.0	<0.0001
	Latitude	0.17	12.37	3	222.0	<0.0001
	Sex × latitude	0.07	4.83	3	222.0	0.0028
coloradensis	Intercept	1.03	37.78	3	110.0	<0.0001
($N = 116$)	Sex	2.81	102.87	3	110.0	<0.0001
	Latitude	0.10	3.81	3	110.0	0.01201
	Sex × latitude	0.05	1.68	3	110.0	0.17450
fasciata	Intercept	0.91	22.77	3	75.0	<0.0001
($N = 81$)	Sex	1.21	30.15	3	75.0	<0.0001
	Latitude	0.15	3.79	3	75.0	0.0137
	Sex × latitude	0.03	0.79	3	75.0	0.5018
metcalfi	Intercept	0.75	27.21	3	109.0	<0.0001
($N = 115$)	Sex	3.76	136.53	3	109.0	<0.0001
	Latitude	0.05	1.69	3	109.0	0.1730
	Sex × latitude	0.08	2.76	3	109.0	0.0454
mystica	Intercept	1.62	61.18	3	113.0	<0.0001
($N = 119$)	Sex	0.77	29.13	3	113.0	<0.0001
	Latitude	0.05	1.88	3	113.0	0.1370
	Sex × latitude	0.05	1.83	3	113.0	0.1456
pennsylvanica	Intercept	0.78	64.99	3	250.0	<0.0001
($N = 256$)	Sex	1.66	138.62	3	250.0	<0.0001
	Latitude	0.03	2.71	3	250.0	0.0455
	Sex × latitude	0.02	1.54	3	250.0	0.2038
vicina	Intercept	4.94	84.00	3	51.0	<0.0001
($N = 57$)	Sex	1.31	22.23	3	51.0	<0.0001
	Latitude	0.18	3.11	3	51.0	0.0342
	Sex × latitude	0.06	1.05	3	51.0	0.3793

associations among all three traits (Fig. 3, Supporting Information S4). Sexual differences in $\mathbf{P}_{\mathbf{max}}$ (i.e., $\boldsymbol{\phi}$) ranged between 7.2° to 25.4° and, with a few exceptions, the CPCA approach, random skewers analyses and the angular comparisons of $\mathbf{P}_{\mathbf{max}}$ were in qualitative agreement in their characterization of sexual dimorphism as well among-species divergence in **P** (Tables 2 and 3). Of the seven species, CPCA indicated some degree of dimorphism (i.e., not strict equality) between corresponding male and female **P**-matrices in five species, though even in these, the sexes shared some common eigenstructure (Table 2). Similarly, random skewers identified significant (at $P < 0.1$) **P**-matrix dimorphism in four of the species and monomorphism in two species, despite relatively strong matrix correlations (Table 2). The average vector correlation from the random skewers ($\boldsymbol{c}$) approach was negatively related to $\boldsymbol{\phi}$ ($r = -0.558$. $P = 0.193$; i.e., lower matrix correlations ~ larger angles between $\mathbf{P}_{\mathbf{max}}$), indicating some qualitative concordance between these as metrics of matrix dimorphism. The main disagreement between matrix comparison (and geometric) methods appeared to be with regard to one species (*metcalfi*) for which random skewers did not detect significant covariance dimorphism.

Considering the sexes separately, CPCA indicated unrelated matrices (the lowest degree of similarity in the Flury hierarchy) as the best model for 10 of 21 possible pairwise among-species comparisons for males but in only two (of 21) comparisons for females (Table 3). By contrast, matrix equality (the highest degree of similarity) was detected in seven cases for females but in only two cases for males (Table 3). Collectively, these results suggest that among-species variation in $\boldsymbol{\phi}$ is primarily attributable to divergence in male covariance structure.

TRENDS IN MULTIVARIATE SEXUAL DIMORPHISM AND TARGETS OF SELECTION

Values of $\boldsymbol{d}$ and $\boldsymbol{\phi}$ were significantly correlated ($\mathbf{r}_s = 0.821$, $P = 0.0341$), indicating that the degree of sexual dimorphism in multivariate means corresponded with the degree of dimorphism in (the principal direction of) phenotypic covariance structure (Fig. 4). Simulating phylogenetic trees combined with PGLS

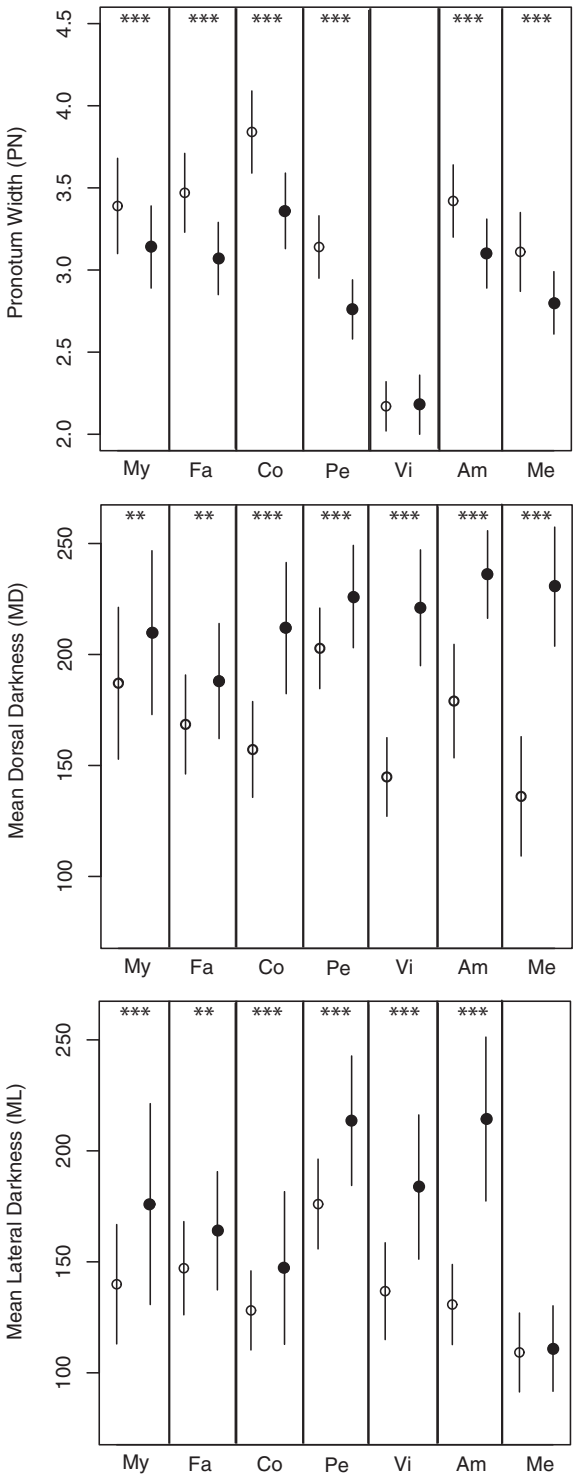

Figure 2. Mean trait values ± standard deviations for female (open) and male (closed) *americana* (Am), *coloradensis* (Co), *fasciata* (Fa), *metcalfi* (Me), *mystica* (My), *pennsylvanica* (Pe), and *vicina* (Vi) with respect to pronotum width (PN), mean dorsal darkness (MD), and mean lateral darkness (ML). Species are arranged, left to right, in order of increasing average latitude. Sexual dimorphism (i.e., significant effect of sex in species-specific ANCOVAs; see Methods) is indicated by single, double, and triple asterisks corresponding to alphas of 0.01, 0.001, and 0.0001, respectively.

indicated significant covariance ($P < 0.05$) between the two variables in 55.3% of iterations with CIs around the observed regression slope ($b = 7.20$) that did not overlap with zero (upper CI: 11.49, lower CI: 2.91). Thus, the positive association between the two types of sexual dimorphism was robust to phylogenetic uncertainty. Sexual dimorphism in the multivariate mean was significantly correlated with average species latitude ($\mathbf{r}_s = 0.929$, $P = 0.0067$) with a weaker positive trend seen between covariance dimorphism and latitude ($\mathbf{r}_s = 0.714$, $P = 0.0881$), whereby sexual dimorphism in both moments of the distribution generally increased with northerly distribution. Performing analyses using simulated phylogenies and PGLS for $\boldsymbol{d}$ ($b = 0.12$, upper CI: 0.30, lower CI: -0.07, $P < 0.05$ in 49.1% of iterations) and $\boldsymbol{\phi}$ ($b = 0.78$, upper CI: 1.58, lower CI: -0.02, $P < 0.05$ in 46.7% of iterations) indicated uncertainty in the relationship between sexual dimorphism and latitude, stemming from unknown phylogeny. Inspecting these trends in original (univariate) trait space (Fig. 2) suggests that the observed among-species cline for dimorphism in trait means was primarily due to increasing mean male dorsal darkness with increasing average latitude (MD: $\mathbf{r}_s = 0.892$, $P = 0.0068$) combined with female darkness being somewhat inversely related to species average latitude (MD: $\mathbf{r}_s = -0.500$, $P = 0.2532$; ML: $\mathbf{r}_s = -0.571$, $P = 0.1802$). Average male lateral darkness, ML exhibited virtually no relationship with latitude ($\mathbf{r}_s = 0.071$, $P = 0.8790$). Species mean size (PN) generally decreased with average species latitude and in a similar manner for both sexes (females: $\mathbf{r}_s = -0.500$, $P = 0.2532$, males: $\mathbf{r}_s = -0.464$, $P = 0.2939$; Fig. 2). Analogous univariate tests are not available to dissect the trend of $\boldsymbol{\phi}$ increasing with species latitude but inspection of the leading eigenvectors of the species- and sex-specific **P**-matrices (Supporting Information S7) did not reveal any obvious patterns.

Discussion

We evaluated multivariate sexual dimorphism in seven related insect species with respect to trait means as well as to trait (phenotypic) covariance structure. Our findings are consistent with sexual dimorphism having readily responded to sex-specific selection; we detected significant sexual dimorphism in the mean phenotype in all seven species and as well as dimorphism in trait covariance structure for five species using CPCA, and for four species when using the random skewers approach. In fact, the absence of detectable covariance dimorphism in the other two species might simply reflect lower statistical power for these two species with lower sample sizes (Phillips and Arnold 1999). Therefore, our treatment may provide a conservative perspective but suggests that sexual dimorphism in mean phenotype and covariance structure is equally pervasive in the genus.

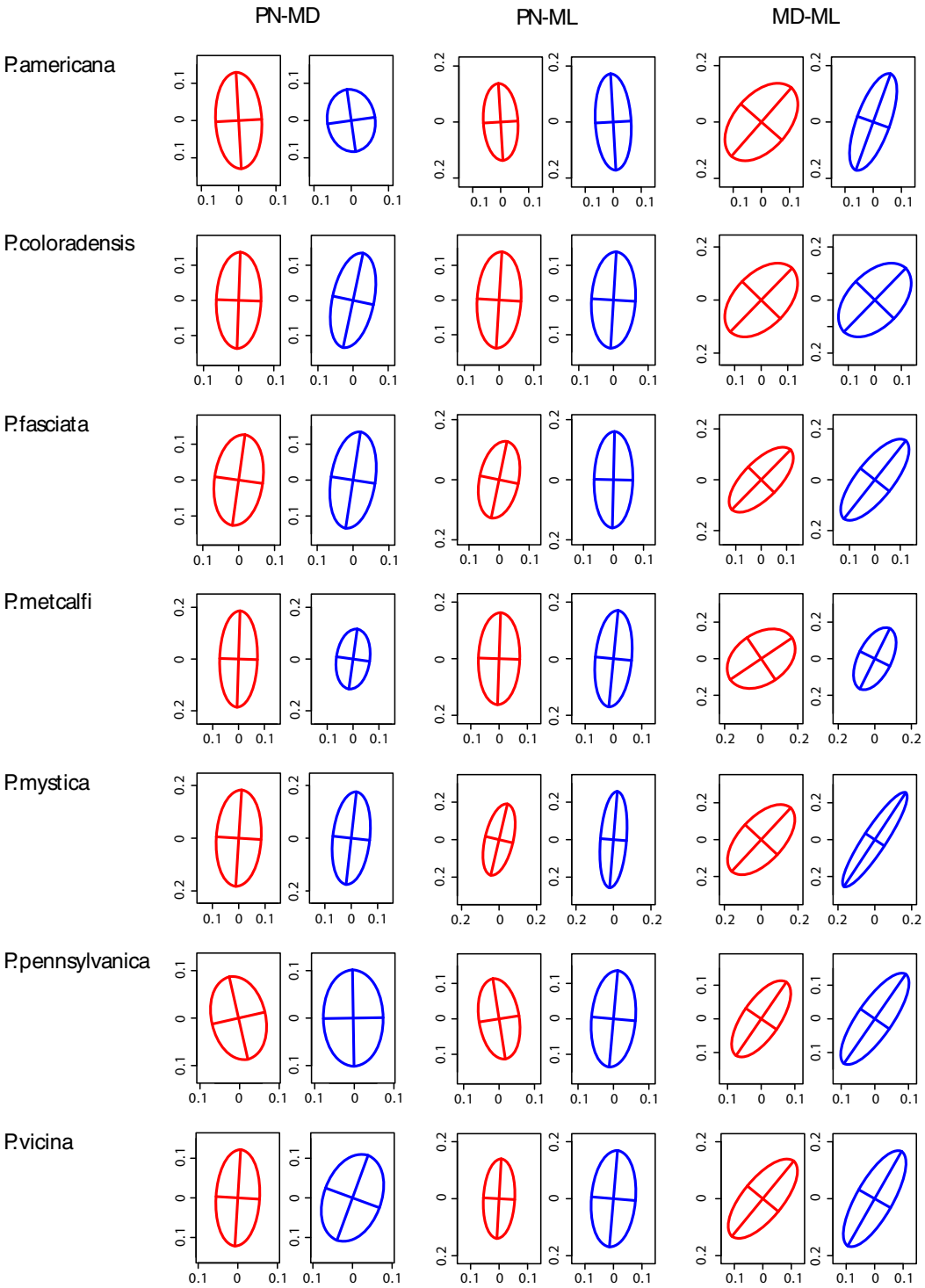

Figure 3. **Bivariate relationships between traits for the seven species of *Phymata*. Dimensions of each ellipse are based on twice the square root of respective eigenvectors (represented by solid lines within each ellipse). Female distributions are in red, males are indicated in blue. Pronotum width, mean dorsal darkness, and mean lateral darkness are denoted as PN, MD, and ML, respectively.**

Closer inspection reveals that species differences in multivariate sexual dimorphism reflect male–female divergence occurring in a number of ways (traits). For example, despite most species exhibiting the typical sexual size dimorphism (i.e., female > male; Fairbairn 1997), one species (*vicina*) was monomorphic in size. For other traits, such as lateral darkness, the variation in dimorphism was the result of an apparent suppression of melanism in one (*americana*) or both (*metcalfi*)

Table 2. Sexual dimorphism in P-matrix structure was inferred from CPCA using both the "jump-up" approach to test for matrix inequality as well as the Akaike's Information Criterion (AIC)/model building approach.

	"Jump-up" approach				Random skewers		$\mathbf{P}_{max}$
Species	χ^2	df	*P*	AIC approach	*c*	*P*	ϕ
americana	46.92	6	<0.0001	Unrelated	0.87	0.019	21.2
coloradensis	19.26	6	0.0037	Unrelated	0.90	0.049	25.4
fasciata	6.23	6	0.3984	Equal	0.97	0.234	7.2
metcalfi	17.90	6	0.0065	CPC	0.91	0.227	29.7
mystica	34.47	6	<0.0001	Unrelated	0.89	0.041	9.6
Pennsylvanica	17.53	6	0.0075	Unrelated	0.97	0.081	10.0
vicina	3.19	6	0.7848	Equal	0.94	0.368	10.0

In the present analyses, P-matrix similarity (in increasing order) ranges from unrelated, to common principal components (CPC), to equality. Sexual dimorphism in P-matrices is also described by the average vector correlation (*c*) from random skewers analyses and the angle, ϕ (in degrees) between the respective leading eigenvectors (P_{max}) of female and male P-matrices. Significance tests of *c* are against the null hypothesis of identical matrices (i.e., $c = 1$).

Table 3. Between-species pairwise comparisons of P-matrices for *Phymata americana* (Am), *coloradensis* (Co), *fasciata* (Fa), *metcalfi* (Me), *mystica* (My), *pennsylvanica* (Pe), and *vicina* (Vi) for females and males.

Females							
	Am	Co	Fa	Me	My	Pe	Vi
Am		Equal	Equal	Proportional	Unrelated	CPC	Equal
Co	6.2		Equal	Proportional	Proportional	CPC	Equal
Fa	10.6	4.8		CPC	CPC	Unrelated	Equal
Me	15.6	11.8	12.9		Equal	CPC	Proportional
My	10.4	5.3	2.0	14.8		Unrelated	Proportional
Pe	7.9	13.8	17.6	23.2	16.7		Unrelated
Vi	5.6	4.7	6.9	16.5	5.7	10.9	
Males							
Am		Unrelated	Unrelated	Unrelated	Unrelated	Unrelated	Unrelated
Co	10.1		Unrelated	CPC	Unrelated	Unrelated	Unrelated
Fa	19.5	19.9		Equal	CPC	CPC	Equal
Me	10.5	7.6	12.3		CPC	CPC1	CPC1
My	15.0	14.7	5.2	7.1		CPC	CPC
Pe	15.8	16.2	3.9	8.6	1.6		CPC1
Vi	13.0	10.9	8.9	3.4	3.9	5.5	

Results of the CPCA model building approach appear above the diagonal and those using the geometric approach (angle in degrees) appear below the diagonal.

sexes, whereas in other species, melanism was quite pronounced in both sexes (e.g., *pennsylvanica*). Similarly, the direction of covariance dimorphism was highly variable, often with **P** oriented quite differently in each species and particularly so, when considering male **P**-matrices. This male-biased variability in **P**-matrix divergence is analogous to some empirical patterns of variability in (univariate) sexual dimorphism. For example, within-clade diversity in sexual dimorphism is attributable to divergence in (mean) male secondary sex characters in some taxa (Darwin 1871) and sometimes apparent as male-divergent allometry (e.g., Fairbairn 1997, but see De Lisle and Rowe 2013).

The ubiquity of sexual dimorphism, as well as the diversity in how it is manifested, suggests high evolvability and relatively weak constraints on sexual dimorphism at the macroevolutionary time scale. Yet despite significant among-species and between-sex differences, we found some evidence of conservatism. For example, males of all species exhibited relatively high levels of average dorsal melanism, with females showing much more interspecific variability in this regard. **P**-matrices, too showed signs of conservatism; CPCA indicated that even when covariance matrices were not equal, they sometimes still shared common eigenstructure—a result consistent with a recent review (Arnold et al. 2008). Some

degree of similarity in covariance structure is generally expected among closely related species (Steppan et al. 2002), though the challenge is to determine whether these affinities are simply a consequence of neutral evolution from a common ancestor (Lande 1979; Schluter 1996) or the result of patterns of nonlinear selection that are conserved over time (Zeng 1988; Arnold et al. 2001). These alternatives can be distinguished, to some degree, when equipped with phylogenetic data (e.g., Hohenlohe and Arnold 2008). In the present article, however, this was not possible due to lack of phylogenetic resolution of *Phymata*.

Remarkably, we found that the two types of sexual dimorphism (represented by $\boldsymbol{d}$ and $\boldsymbol{\phi}$) were positively correlated. The result is not a numerical artifact of trait scaling (i.e., the association between trait means and variances was accounted for) nor is it an inevitable result, predicted by theory. Our results have similarities with a study by Gosden and Chenoweth (2014) that found evidence of increasingly divergent sex-specific **G**-matrices (and a corresponding decrease in shared genetic architecture) with increasing population genetic divergence in the fruit fly, *Drosophila serrata*. These results are consistent with the ecology of sexes often diverging to the extent that selection acts on altogether different trait combinations in males and females. This further implies that, not only do sexes evolve toward separate adaptive peaks but, as they do so, their genetic architecture readily conforms to essentially different (local) adaptive topographies.

The correlated evolution of the two types of sexual dimorphism is unlikely to be simply a consequence of neutral divergence from a sexually dimorphic ancestor, nor an artifact of a single evolutionary event. Although sexual dimorphism can exhibit phylogenetic signal (e.g., Cheverud et al. 1985; Baker and Wilkinson 2001), coancestry does not predict a necessary association between the extent of dimorphism in trait means and in their covariances, after removing the effects of trait size/scaling. We accommodated possible nonindependence among taxa by simulating phylogenies (following Martins 1996) and found support for a positive association between the two types of sexual dimorphism, robust to a large sample of possible evolutionary histories. Although the simulation-based approach was accompanied by lower statistical power, these analyses did not qualitatively alter our conclusions.

Nonetheless, the ideal studies—directly incorporating phylogenetic information—would have great utility for additional hypothesis tests. For example, one could test whether $\boldsymbol{d}$ and/or $\boldsymbol{\phi}$ increases with phylogenetic distance from a common ancestor as might be expected from the breakdown of intersex genetic covariances over time (Lande 1980; Baker and Wilkinson 2001, Reeve and Fairbairn 2001), which is a fundamental question and subject of debate (e.g., Schluter 1996; Hohenlohe and Arnold 2008; Barker et al. 2010; Gosden and Chenoweth 2014).

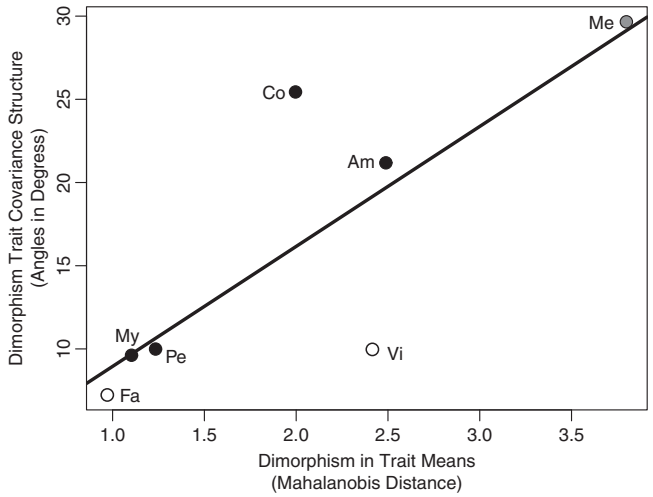

Figure 4. Sexual dimorphism in the multivariate mean (*d*) and in trait covariance structure (ϕ) for seven species of *Phymata*. Matrix similarity estimated from the CPCA model building approach is indicated by shade of points (white = equality, gray = common principal components, black = unrelated). Line of best fit is from ordinary least squares regression. Species and their abbreviations are *americana* (Am), *coloradensis* (Co), *fasciata* (Fa), *metcalfi* (Me), *mystica* (My), *pennsylvanica* (Pe), and *vicina* (Vi).

SELECTIVE CAUSES OF SEXUAL DIMORPHISM

Biogeographic trends observed at the macroscale (i.e., across-species) revealed some systematic patterns that point to putative selective agents to explain the observed sexual dimorphism. Notably, male dorsal melanism was prevalent in all species and became increasingly prominent toward the north, consistent with the trait serving a thermal function in males (Punzalan et al. 2008b). Sex differences in body size did not vary systematically across species; rather, size typically decreased with latitude in both males and females. This reduction in size at high latitudes is consistent with some predictions of seasonal constraints on development time resulting in smaller adult size at emergence (e.g., Rowe and Ludwig 1991; Blanckenhorn and Demont 2004).

In contrast, intraspecific patterns in latitudinal variation were highly variable and often not consistent with interspecific patterns. For example, body size (in one or both sexes) decreased with latitude in three species but exhibited the opposite latitudinal cline in two. Latitudinal patterns of intraspecific variation in color pattern traits were equally variable, with every possible relationship with latitude observed. Moreover, significant statistical interactions were observed for some species and traits, indicating that the covariance between latitude and the expression of sexually homologous traits was not necessarily consistent between males and females of the same species. Although we intentionally removed these latitudinal effects in our analyses of sexual dimorphism in **P**, we should point out that the failure to do so (i.e., analyses using

the uncorrected variation; data not shown) results in considerably different matrices as well as a different relationship (i.e., no pattern) between and $\boldsymbol{d}$ and $\boldsymbol{\phi}$ ($r = -0.441$, $P = 0.322$). Given the presence of significant latitudinal effects, this is not surprising.

The mismatch between latitudinal patterns observed within versus between species also highlights the difficulties in drawing universal conclusions regarding processes that occur at different evolutionary scales. Despite interspecific differences almost certainly being a reflection of genetic divergence, intraspecific variation in secondary sex traits may exhibit a large environmental component, which in turn, might covary with latitude. Indeed, there are alternative (and not necessarily adaptive) explanations for intraspecific latitudinal variation in size and color pattern. Adult body size and coloration of ambush bugs have been shown to depend on conditions (e.g., temperature, Mason 1975; food resources, Punzalan et al. 2008a) during development. Thus, intraspecific covariation between traits and latitude could partially reflect species- and sex-specific gradients in the acquisition of resources and its allocation.

Conclusions

Overall, the present data indicated that sexual dimorphism in covariance structure is common—nearly as prevalent as multivariate mean dimorphism in the species examined here. The diversity of trait directions in which species and sexes differed suggests that covariance dimorphism evolves readily and in proportion to the disparity between sex-specific optima. This was evident as significant correlation between sexual dimorphism in trait (multivariate) mean and in dimorphism in **P**. Latitudinal variation (at the level of species means) were consistent with predictions of divergence being primarily limited by life-history constraints on development time, as well as selective constraints on sex-specific thermal performance. Although these findings do not rule out genetic constraints stemming from sexes sharing a common genome, collectively, they point to an evolutionarily labile genetic architecture underlying sexually homologous traits while underscoring the primacy of selection in dictating the mode of evolution.

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DATA ARCHIVING

The doi for our data is 10.5061/dryad.0g98k.

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Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Supporting Information S1. Background information on *Phymata* and specimens.
Supporting Information S2. *Phymata* spp. sexual color pattern dimorphism.
Supporting Information S3. Detailed methods for image data collection and analysis.
Supporting Information S4. Phenotypic variance–covariance matrices (**P**) and corresponding jackknife standard errors (parentheses), estimated separately by sex and species (see Methods).
Supporting Information S5. Effects of sex, latitude, and their interaction on trait expression.
Supporting Information S6. Intraspecific latitudinal variation in trait expression.
Supporting Information S7. Leading eigenvectors ($\mathbf{P_{max}}$) and percent variance explained for females (F) and males (M) of the seven *Phymata* spp.