Divergence in life history and behaviour between hybridizing *Phymata* ambush bugs (Heteroptera: Reduviidae)

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Life-history variation plays a central role in evolutionary and ecological processes and might be especially pertinent to divergence in closely related species. We investigated differences in life history in a pair of parapatric species of ambush bugs (*Phymata*) and a putative hybrid population. Despite the evidence of gene flow among these species, we found clear divergence between these parapatric populations for a suite of juvenile and adult life-history traits, including components of fitness. The higher latitude species was also less active, suggestive of potential divergence in dispersal. Increased melanism was correlated with longevity in one species, although it was unclear whether this relationship was causal. Observed differences in the life history between species were consistent with expectations of high-latitude species putting a premium on early or rapid development and increased reproductive rates. However, these results were not consistent with 'pace-of-life syndromes' at the species level. Individuals from the putative hybrid zone exhibited intermediate values for most traits, although they had slower development and reduced mobility, consistent with some previous work suggesting natural selection via hybrid breakdown.

ADDITIONAL KEYWORDS: ageing – dispersal – hybridization – reinforcement – syndrome.

INTRODUCTION

At first glance, parapatry, where closely related species are geographically adjacent, presents an apparent paradox: how can local adaptation and divergence be maintained if there is potential gene flow between species? One resolution is that the resulting hybrids exhibit characteristics that confer a low probability of subsequent introgression of locally maladapted alleles between diverging populations (Barton & Hewitt, 1985). Although some empirical evidence supports the plausibility of this resolution (Coyne & Orr, 2004), it is challenging to demonstrate directly in natural populations, owing to the practical difficulties of studying the key processes of selection and gene flow. One prospect is the comparative study of key traits of parapatric populations and their hybrids.

Life-history characters are likely to be informative because of their intimate relationship to fitness (Schluter *et al.*, 1991; Stearns, 1992; Roff, 2002). Characters such

as developmental rates and reproductive timing might be especially important because these are exactly the characters that reinforce divergence between closely related populations. In some cases, local adaptation can generate systematic patterns at a geographical scale. For example, temperate ectothermic populations at higher latitudes often exhibit higher reproductive rates but shorter life expectancy (e.g. Blanckenhorn & Fairbairn, 1995). This is in line with classical life-history theory that predicts a high priority for rapid development and early reproduction at the expense of longevity in response to shorter breeding seasons (Williams, 1966).

Differences in life history are often associated with important behavioural characters, including those that mediate dispersal (e.g. activity levels and rates of movement; Duputié & Massol, 2013; Stevens *et al.*, 2013; Bonte & Dahirel, 2017). This, in turn, has consequences for the respective ranges of parapatric species, in addition to opportunities for hybridization (Barton & Hewitt, 1985; Goldberg & Lande, 2007). Some have argued that inherent time

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and energetic trade-offs will tend to generate negative relationships between movement and reproductive rates (Zera & Denno, 1997; Guerra, 2011), whereas proponents of the 'pace-of-life syndrome' hypothesis (a model largely invoking metabolic processes as the determinant of 'fast' or 'slow' lifestyles) predict that high reproductive rates will be associated with higher rates of individual activity and movement (Stamps, 2007; Wolf *et al.*, 2007; Réale *et al.*, 2010). In contrast, classical theory predicts trade-offs among costly characters but makes no explicit prediction regarding the sign of association between any given life-history trait and measures of behaviour. When considering the situation of parapatric species with hybridization, a priori predictions regarding patterns of spatial variation are more complicated. On the one hand, geographically intermediate populations (i.e. hybrids) might be expected also to exhibit intermediate phenotypic values, assuming polygenic and additive inheritance, and this might be the result of adaptation along a continuous cline (i.e. hybrids might be well adapted to intermediate conditions). On the other hand, matings between diverging 'parent' populations might result in negative epistasis for life-history characters (essentially revealing reduced fitness of hybrids), resulting in a pattern that does not resemble a cline.

In the present study, we evaluated differences in life history and behaviour in three populations of ambush bugs (*Phymata*) occurring in close proximity and in a manner consistent with parapatry with hybridization. Two of the populations correspond to separate 'parent' species: *Phymata americana*, which occurs more northerly, and *Phymata pennsylvanica*, which occurs more southerly (Masonick *et al.*, 2017; Masonick & Weirauch, 2020; Zhang *et al.*, 2020). The third population is a geographically intermediate population that appears to be composed of a hybrid swarm (Punzalan & Rowe, 2017). Given its occurrence at higher latitude, with its associated time constraints, we predicted that adult *P. americana* would exhibit a life-history strategy characterized by greater investment in rapid reproduction (oviposition rate) but reduced longevity, in comparison to *P. pennsylvanica*. Likewise, we expected more rapid development (hatching date and development time) in the higher latitude species. We quantified population differences in behavioural proxies for activity and short-term dispersal, and discuss the associations in light of the 'pace-of-life syndrome' hypothesis. It is important to note that classical life-history theory and 'pace-of-life syndrome' are not mutually exclusive, but one key difference is that the latter predicts positive relationships among life-history characters and activity levels or movement.

MATERIAL AND METHODS

STUDY POPULATIONS AND MAINTENANCE IN THE LABORATORY

Within a 24 h period between 31 August and 1 September 2017, wild females and an excess number of males were collected by hand from three sites: *P. americana* from Koffler Scientific Reserve, King, ON, Canada (*N* = 55 females), *P. pennsylvanica* from Stevensville, ON, Canada (*N* = 70), and a population that appears to consist of a mixed swarm of hybrids from Pelham, ON, Canada (*N* = 45). These populations are referred to as Am, Pe and Mx, respectively, and previous work with bugs from the same sites (e.g. Punzalan & Rowe, 2015, 2017) suggests that these are ecologically persistent and relatively stable populations. Our designation of Mx as a population of putative hybrids is bolstered by previous work corroborating that F1 crosses between Pe and Am are viable and recover offspring phenotypes that bear a morphological resemblance to individuals collected in Mx (Punzalan & Rowe, 2017).

Females were held individually in 20 mL glass scintillation vials containing a 3 cm × 0.5 cm section of wooden stirring stick as an oviposition substrate and maintained in an environmental chamber (23 °C, 16 h light–8 h dark, 25% relative humidity). A random individual male from the corresponding population was introduced into each vial to permit mating and female oviposition. Vials were provisioned daily with ~20 live *Drosophila melanogaster*, and deaths were recorded (and insects preserved in ethanol). The oviposition substrate was checked daily and, if necessary (i.e. if eggs were laid), replaced. Approximately every 3 days, males were replaced or randomly re-allocated to vials (paired with different females of the same population) to reduce any effects of variation in male fertility. Beginning on 15 November 2017, eggs were placed in cheesecloth bags and moved outdoors to natural overwintering conditions (in Toronto, ON, Canada).

LONGEVITY, OVIPOSITION RATE AND MORPHOLOGICAL CORRELATES

For each wild-caught female, we recorded longevity as the number of days elapsed between the beginning of the study until death (in laboratory conditions) and fecundity as the total number of eggs laid during this period. The oviposition rate was calculated as fecundity divided by longevity. Preserved insects were photographed once each from the dorsal and lateral aspect, using a microscope-mounted digital camera, with length and greyscale standards for reference. For these images, we used IMAGEJ (https://imagej.nih.gov/ij/) to measure pronotum width (a proxy for body size, measured as the narrowest

portion between the lateral angle and the posterior angle; Mason, 1973). Given that other studies have implicated melanism as a mediator of fitness components and dispersal behaviour (Brakefield & Liebert, 2000; True, 2003; Dubovskiy *et al.*, 2013; Hegna *et al.*, 2013; Roff & Fairbairn, 2013), for each specimen we also measured lateral darkness (mean number of pixels converted such that higher values equate to 'darker') of a standardized region on the mesopleuron (see Punzalan & Rowe, 2017). Between-population differences in longevity were analysed using Cox proportional hazards, and between-population differences in oviposition rate were calculated using separate one-way ANOVAs. Given that the oviposition rate over the entire remaining lifespan potentially conflates reproductive senescence with longevity, we also re-analysed the oviposition rate (eggs per day), restricted to the first 49 days of the study (or less, for bugs that died before then). This interval was chosen because visual inspection of the data suggested that cumulative oviposition in all populations increased in an approximately linear manner up to 49 days, after which a slowing in the rate of oviposition was suggestive of the onset of reproductive senescence. The three populations exhibit substantial genetically based phenotypic differences in morphology and melanism (Punzalan & Rowe, 2015, 2017), which challenges meaningful interpretation of 'population' and 'population-by-trait interaction' effects in a full model (e.g. scores for lateral darkness do not even overlap in Pe and Am). Consequently, we analysed each population separately, using a Cox proportional hazards model to evaluate the relationship between longevity and traits (pronotum width and lateral melanism). In a similar manner, we evaluated whether pronotum width and lateral melanism were associated with oviposition rate, using linear regressions.

HATCHING AND DEVELOPMENT

On 3 May 2018, eggs were brought indoors into laboratory conditions identical to the adult regimen described above. Eggs and the oviposition substrate were kept in 177 mL plastic fly culture bottles, grouped by (maternal) family. Bottles were checked daily for hatching, which commenced 8 days later, continuing over a 3 day period, and the date of first sighting of a first instar nymph for each family was recorded. To simplify our notation, we refer to emergence dates as Days 1, 2 and 3, corresponding to 11, 12 and 13 May. For those families that hatched at least one nymph successfully ($N = 152$), we analysed population differences in hatching dates by means of a χ^2 contingency test, evaluating the association between the population of origin and whether first hatching occurred on Day 1 vs. first hatching on either Day 2 or Day 3. Classification of hatching according to these two mutually exclusive categories (rather than three, corresponding to the number of days) was warranted by the low observed/expected frequencies for Day 3. Approximately 7 days post-hatching, nymphs were transferred from bottles to plastic 37 mL shell vials (i.e. one family per vial), and the numbers of bugs in each vial ('family size') was recorded to calculate proportional hatching success. Vials were provisioned with a minimum of one *D. melanogaster* per nymph per day and were emptied of fruit fly carcasses as necessary. This regimen was continued for 56 days, after which bugs were housed individually in vials and provisioned with approximately four *Drosophila hydei* per day. Bugs were checked daily for deaths and emergence into adulthood. Proportional hatching success was square root-transformed before analyses of population differences, using a one-way ANOVA, and post-hoc comparisons performed using Tukey's honestly significant difference (HSD).

We reared bugs to adulthood and noted the proportion of individuals that successfully emerged as adults, and their date of emergence. We are cautious about the interpretation of these data as precise estimates of juvenile viability; *Phymata* are difficult to rear to adulthood in the laboratory, likely due to the challenge of providing nutritionally diverse prey items (the bugs will only accept live, flying insects). The logistic necessity of rearing of bugs in (sometimes crowded) family groups also introduces the potential for density-dependent mortality (e.g. cannibalism and disease)—a possibility supported by our own data (Supporting Information, Fig. S1). Furthermore, the group-hatching/rearing protocol meant that the hatch date of any given individual was not precisely known. However, *Phymata* eggs are fully developed before winter diapause (Balduf, 1941), so hatching date can be viewed as a phenological 'decision'. Thus, the number of days elapsed since eggs were moved indoors (until emergence into adulthood) provides a measure of the rate of development during a specific interval (post-winter to adulthood) of the life cycle. These data, hereafter simply referred to as development time, were normally distributed and did not require transformation. We performed analyses for each sex separately, employing a mixed (Restricted Maximum Likelihood, or REML) model with population as a fixed effect and family (intentionally confounded with vial-specific mortality) as a random effect nested within population. Population differences were inferred from the least square means and post hoc comparisons were conducted using Tukey's honestly significant difference (HSD) test.

ADULT MOVEMENT: LOCOMOTOR PERFORMANCE

As a proxy for rates of movement and, potentially, short-range dispersal (e.g. leaving a patch), we devized a simple assay that uses the apparent compulsion of ambush bugs to climb vertical substrates (e.g. in nature, probably vegetation). We constructed a climbing apparatus from a wooden dowel (diameter = 0.8 cm) perpendicularly attached to a masonite pegboard base. The apparatus was placed in an environmental chamber maintained at ~28 °C and 40% relative humidity, conditions intended to emulate favourable mid-day summer conditions and expected to facilitate activity.

Each trial began by placing a haphazardly chosen (from one of the three populations) adult, between 8 and 34 days of age, at the base of the dowel and recording the time required to travel up the dowel to the top (distance of 30 cm). If a bug stopped moving for 3 s, it was gently prodded with a fine paintbrush, and the time spent stopped was later subtracted from the total time. A second trial was performed immediately after completion the first trial. Instances in which bugs did not climb after 5 min or flew off from the dowel before completing the distance were excluded from analysis. Likewise, data for individuals with visible deformities or injuries were not used. We also recorded instances in which an individual spread its wings and/or flew, which were referred to as 'flight behaviour'.

Population and sex differences in the ($\log_{10}$-transformed) average run time were analysed in a linear mixed (REML) model, with population and sex as fixed effects, family (nested in population) as a random effect, and age as a covariate. We observed significant sex differences in climbing speed (see Results), although our primary goal was to examine population differences; therefore, we repeated the analyses separately by sex. Tukey's HSD test was used to evaluate pairwise differences among population least squares means. The effect of population origin on the likelihood of performing flight behaviour at least once in any trial (as a binomial variable) was analysed using a χ^2 contingency test, ignoring family effects. All statistical analyses were performed in JMP v.10.0 (SAS Institute, Cary, NC, USA) or R (www.Rproject.org).

RESULTS

LONGEVITY AND OVIPOSITION RATE AND THEIR RELATIONSHIP TO MELANISM

Female longevity did not differ statistically among populations (χ^2 = 4.14, d.f. = 2, P = 0.1263), although longevity in the Mx population (67.5 days) was ~10% shorter than in the Am (74.0 days) and Pe (73.0 days) populations (Fig. 1). Populations differed significantly
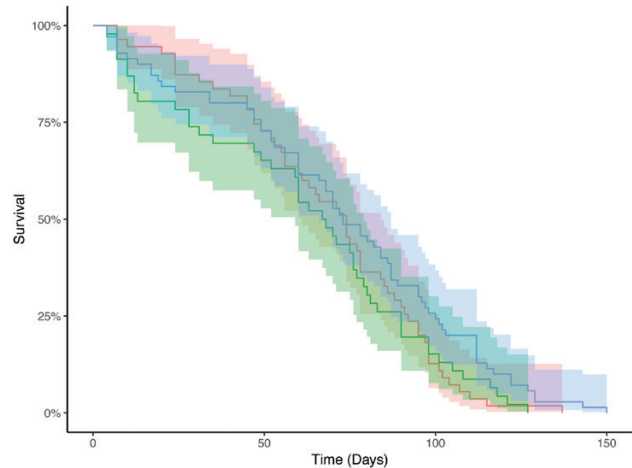
Figure 1. Survival curves corresponding to *Phymata americana* (Am; red lines), *Phymata pennsylvanica* (Pe; blue) and mixed (Mx; green) populations maintained in the laboratory. Shading indicates the 95% confidence intervals.

in oviposition rate ($F_{2,168}$ = 6.73, P = 0.0015), with Am ovipositing at significantly higher rates than Pe, and Mx ovipositing at an intermediate rate. These differences in rates reflected differences in the scheduling of oviposition, e.g. with Pe populations laying fewer eggs per day, but over a longer period of time (Fig. 2). The between-population differences in oviposition rate were not reflected in differences in total observed fecundity. Restricting the analysis of reproductive rate to oviposition within the first 49 days did not change our conclusions qualitatively regarding population differences ($F_{2,168}$ = 9.65, P = 0.0015) or post hoc contrasts (Supporting Information, Fig. S2), although the mean population oviposition rate was approximately double the average calculated from the entire lifespan.

We did not detect a significant relationship between pronotum width and longevity in any of the populations (all populations: χ^2 < 1.57, d.f. = 1, P > 0.2115), but we found a significant positive relationship between lateral melanism and longevity in population Pe (χ^2 = 4.71, d.f. = 1, P = 0.0299; for Am and Mx: χ^2 < 0.89, d.f. = 1, P > 0.3445; Fig. 3). Oviposition rate showed no significant relationship with either trait in the Am or Mx population (all $P \leq 0.2693$), but both traits were positively associated with oviposition rate in population Pe (partial regression coefficients for pronotum width: β = 0.482 ± 0.228, P = 0.0384; and for lateral melanism: β = 0.017 ± 0.008, P = 0.0337).

HATCHING AND DEVELOPMENT TIME

Populations differed significantly in the distribution of hatching dates (χ^2 = 22.57, d.f. = 2, P < 0.0001),
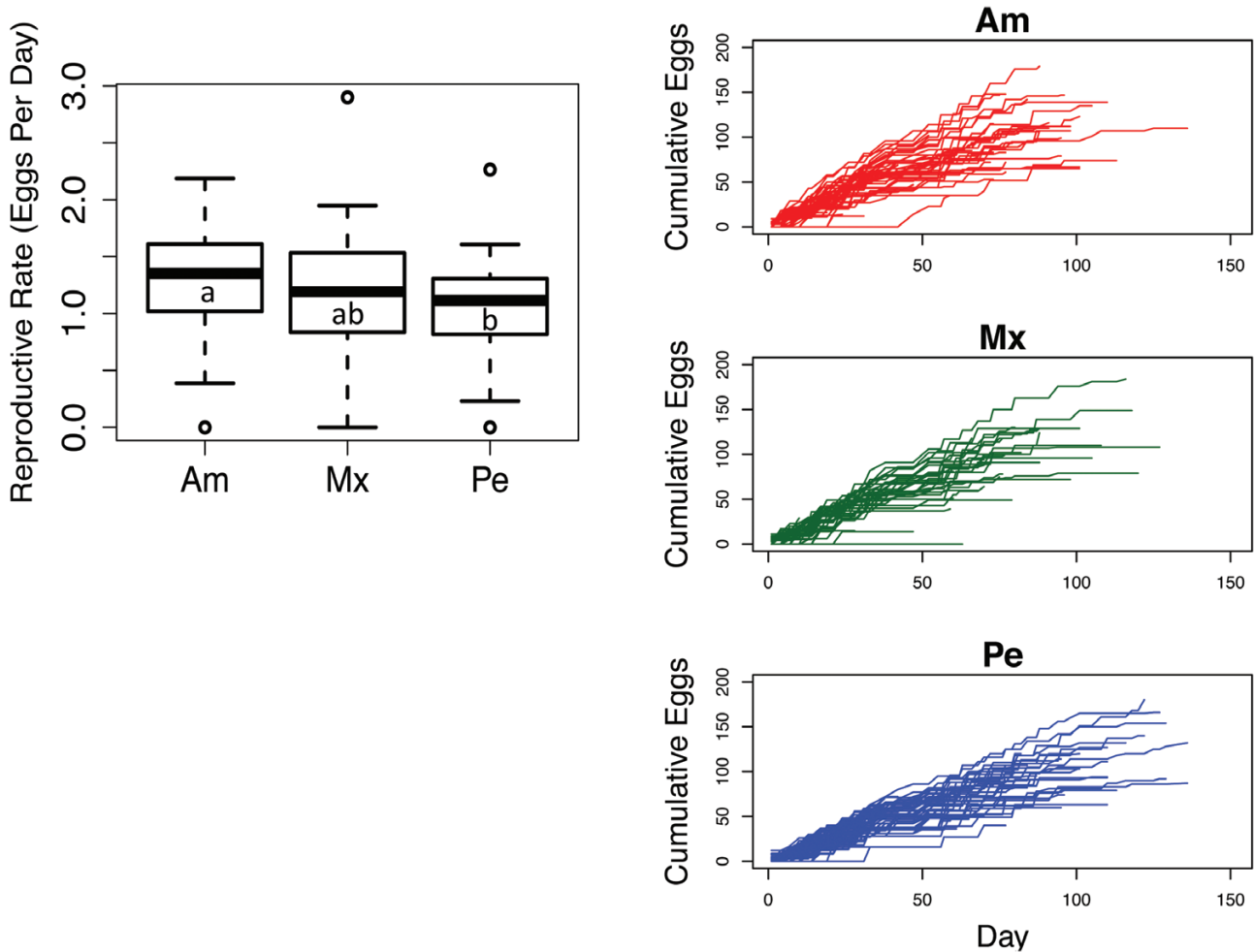
Figure 2. Population distributions for reproductive rate (left panel) and cumulative oviposition (right panels) for Am, Mx and Pe populations in the laboratory. Lower case letters indicate significant mean differences based on Tukey's HSD test.

with ~94% of families from population Am hatching on Day 1, in contrast to only ~56% of families from Pe hatching on Day 1; families from the Mx population exhibited an intermediate pattern, with ~82% of hatching on Day 1 (Fig. 4). Populations differed in ($\log_{10}$-transformed) proportional hatching success, with the Pe population having significantly lower success than the Am and Mx populations ($F_{2,158}$ = 4.21, $P = 0.0166$; Fig. 5). Overall, females took longer to develop than males, and the development time was significantly shorter (~2 days based on least squares means) for females from Pe than those from Am and Mx populations (population effect: $F_{2,204.4}$ = 10.41, $P < 0.0001$, Fig. 6). Male development time was again shortest for Pe, although significantly different only from Mx, which required ~2.5 days longer ($F_{2,186.3}$ = 4.38, $P = 0.0139$; Fig. 6).
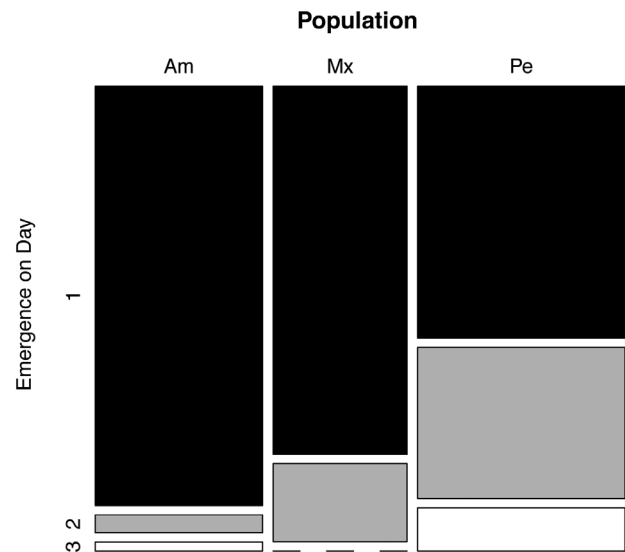
ADULT LOCOMOTOR PERFORMANCE

For those individuals that completed both trials ($N = 158$), 'run times' were highly repeatable (Spearman's $\rho = 0.77$, $P < 0.0001$), suggesting considerable individual-level variation in climbing ability. Subsequently, the average run time (after $\log_{10}$-transformation), including individuals that completed only one run, was used in statistical analyses. We detected significant population ($F_{2,63.8}$ = 8.98, $P = 0.0004$) and sex ($F_{2,147.1}$ = 64.88, $P < 0.0001$) differences in average run time, with no significant interaction ($F_{2,148.2}$ = 1.51, $P = 0.2229$), and a marginally non-significant effect of age ($F_{1,155.9}$ = 3.07, $P = 0.0819$).

In separate analyses by sex, for females, populations differed significantly in average run time in the climbing performance assay ($F_{2,49.9}$ = 3.78,
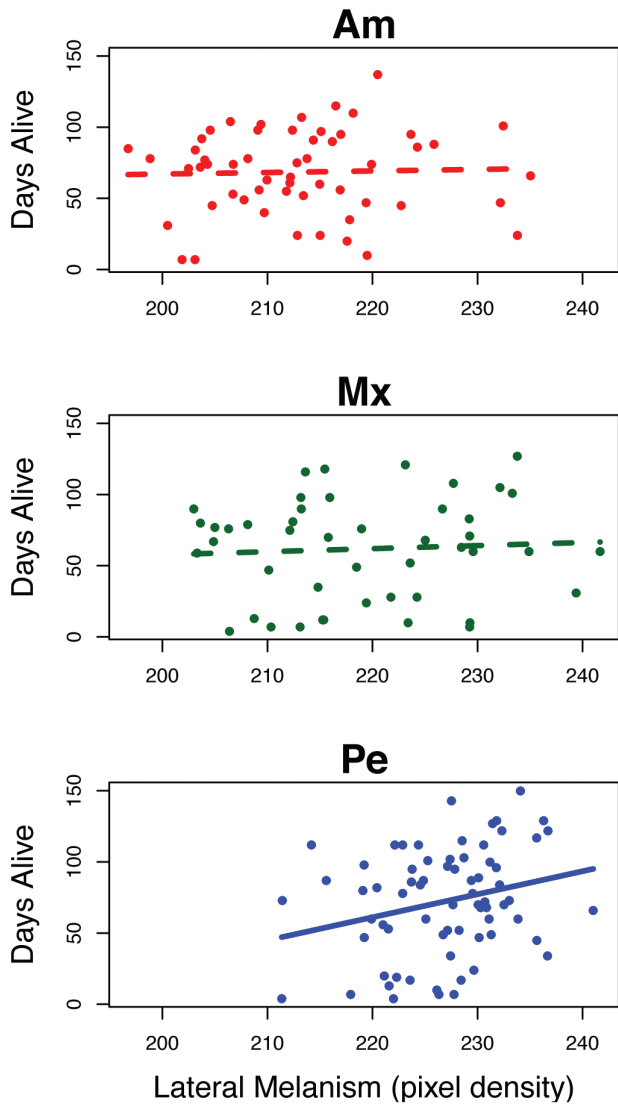
Figure 3. Scatterplots of the relationship between days remaining alive (in the laboratory) and scores of female lateral melanism (darkness in pixel density) for Am, Mx and Pe populations. Lines of best fit are from simple linear regressions, with the continuous line indicating a significant relationship based on Cox proportional hazards. Axes are on a common scale to facilitate comparisons.


Figure 4. Mosaic plots depicting temporal patterns of hatching in Am, Mx and Pe populations. The height of bars indicates the proportion of families that hatched at least one egg on each day of the 3 day oviposition interval.
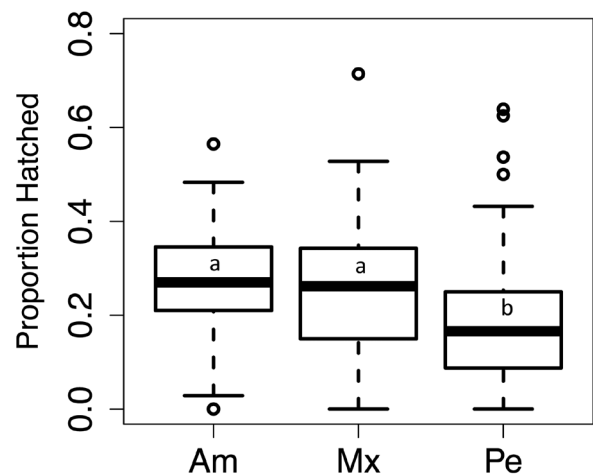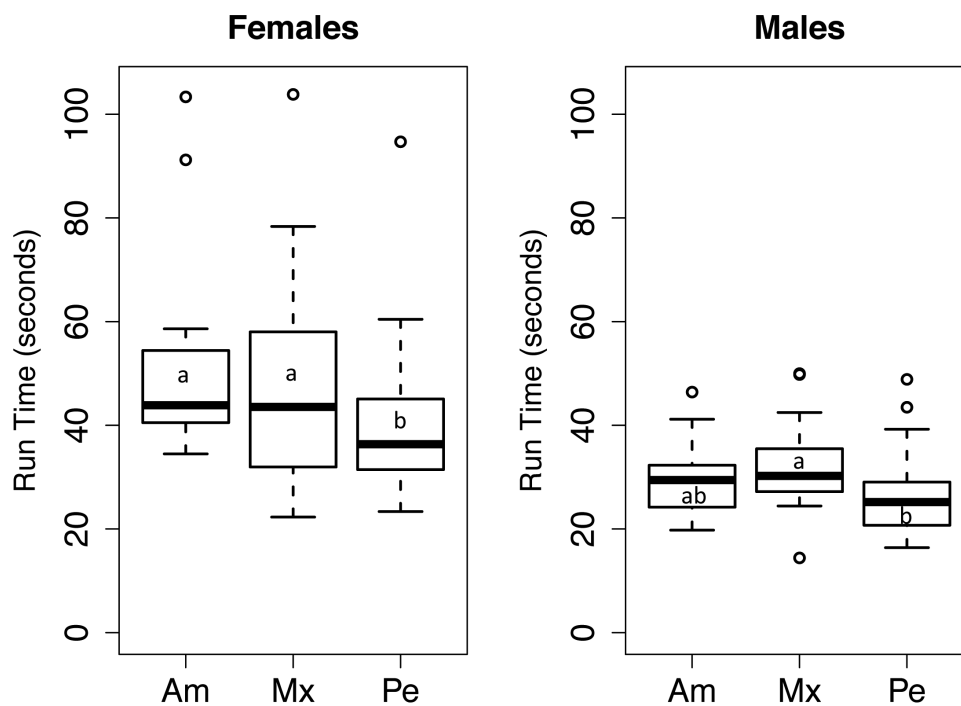

Figure 5. Variation in proportional hatching success among Am, Mx and Pe populations. Lower case letters indicate significant least squares mean differences based on Tukey's HSD test.

$P = 0.0421$), with females from population Pe climbing the fastest and those from Am climbing the slowest (Fig. 7). Female performance was not correlated with age ($F_{1,73.5} = 0.038$, $P = 0.8460$). For males, we found significant population differences in run time ($F_{2,31.8} = 8.85$, $P = 0.0009$), with individuals from Mx climbing significantly slower than those from Pe, and with bugs from Am exhibiting intermediate climbing speeds (Fig. 7). Surprisingly, we found that male climbing speed was inversely related to age ($F_{1,80.9} = 4.54$, $P = 0.0362$), although this relationship was most prominent for males from the Pe population (Supporting Information, Fig. S3). There was some suggestion that populations differed in their propensity to perform flight behaviours when considering either females (Pe, 50%; Mx, 36%; Am, 25%) or males (Pe, 15%; Mx, 25%, Am; 7%), but none of these differences was statistically significant (females: $\chi^2 = 3.14$, d.f. = 2, $P = 0.2085$, $N = 78$; males: $\chi^2 = 2.00$, d.f. = 2, $P = 0.3671$, $N = 86$).
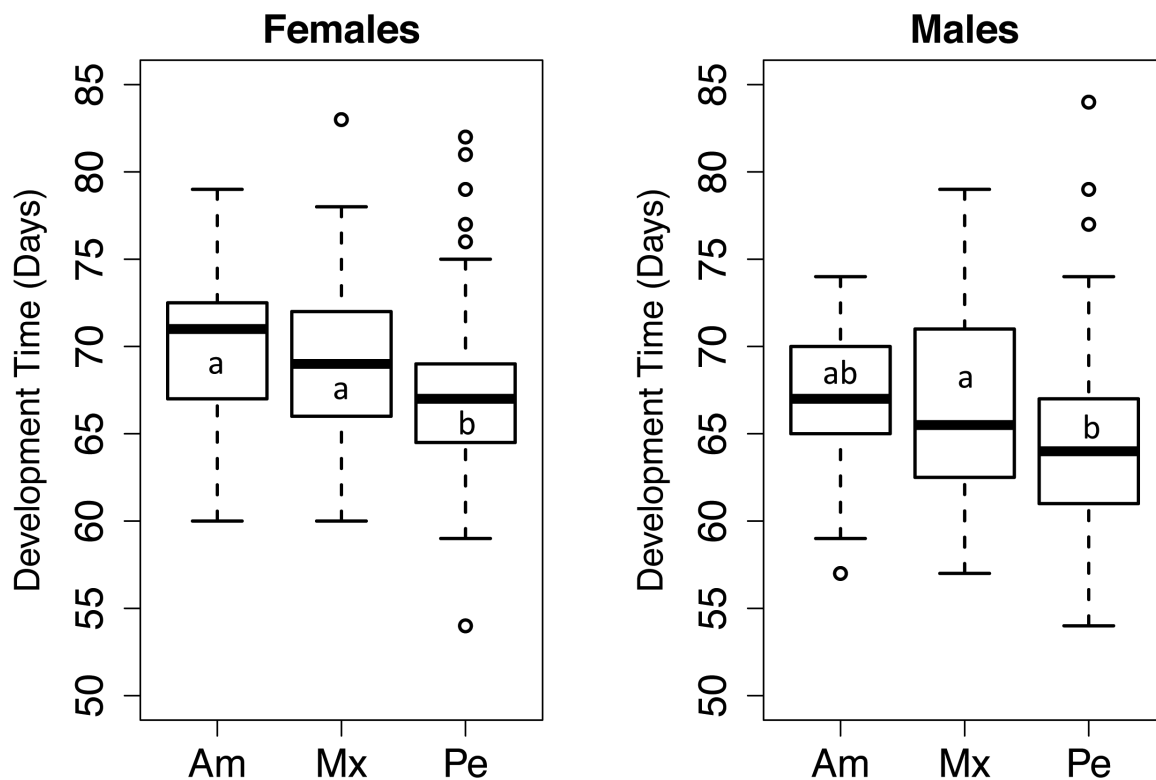
Figure 6. Juvenile developmental time (least squares mean days) for Am, Mx and Pe populations. Lower case letters indicate significant least squares mean (from a mixed model; see main text) differences based on Tukey's HSD test.

Figure 7. Variation among Am, Mx and Pe populations in adult locomotor performance (run time). Lower case letters indicate significant mean differences based on Tukey's HSD test.

DISCUSSION

Divergence between closely related species depends ultimately on a balance between local adaptation and gene flow, both of which are often tied closely to life-history traits. For example, species differences in the rate of development can have important consequences for the timing of reproduction and therefore, the possibility of heterospecific mating and hybridization. The frequency of such events will depend on the sheer number of interacting individuals, which itself depends on parameters tied closely to population size (e.g. female fecundity) and dispersal. If populations do interbreed, the extent of subsequent divergence, in turn, depends on the life-history attributes of hybrids.

We compared several key life-history traits in a parapatric pair of *Phymata* spp. and a population thought to be composed of hybrids. We found numerous differences in life-history characters, such as timing of hatch, juvenile development and female fecundity. We also found differences in behaviour that potentially relates to dispersal. Our results are illustrative of how adaptive divergence between parapatric populations may proceed despite the opposing force of hybridization. Our conclusions, which are elaborated upon below, are founded on two main lines of evidence: divergence consistent with adaptation to seasonal constraints, and reduced fitness and performance of suspected hybrids. We also speculate on the significance of female melanism, which appears to be an important covariate of aspects of *Phymata* life history.

ADAPTIVE HYPOTHESES FOR LIFE-HISTORY DIVERGENCE

Our findings are generally consistent with previous observations (e.g. Armbruster *et al.*, 2007; Nilsson-Örtman *et al.*, 2013; Sniegula *et al.*, 2015) and expectations based on seasonal constraints: the higher latitude and more time-constrained species, *P. americana*, hatched earlier than *P. pennsylvanica* and oviposited at a higher rate in common garden conditions. However, the head start in *P. americana* afforded by faster egg hatch and greater early reproduction was offset by their longer development times, requiring ≥ 2 days longer, probably to accommodate the larger adult body size in *P. americana* (Punzalan & Rowe, 2017). We did not detect significant differences in longevity in the laboratory, although we acknowledge that we did not have complete measures of lifespan, because we monitored the longevity of wild-caught bugs of unknown age. It is also important to note that precise estimation of the age of the wild-caught bugs is complicated further by the possibility of phenological differences at different geographical locations.

We also found significant genetically based differences in movement rates, with *P. pennsylvanica* being, on average, more active in common-garden conditions. At this point, we can only speculate on ultimate causes, but given that foraging success in *Phymata* relies on finding attractive but short-lived inflorescences (Elliott & Elliott, 1991; Greco & Kevan, 1995; Yong, 2005), one possibility is that our results reflect selection on the ability of *P. pennsylvanica* to find new patches. In addition, we observed that movement in male *P. pennsylvanica* was an increasing function of age. This was unexpected, but might reflect age-dependent reproductive investment (Gross, 1996; Kokko, 1997; Kemp, 2006), whereby older males preferentially allocate resources to mate searching at the expense of (sit-and-wait) hunting.

Collectively, our results indicate contrasting adult life-history strategies in these two *Phymata* species but are inconsistent with simple predictions of divergence along a so-called 'pace of life' continuum across the life history. For example, *P. pennsylvanica* hatched later but reached adulthood sooner; as adults, they were 'fast' with respect to measures of adult movement but 'slow' in reproduction. We note that our study was concerned with trait associations at the population level, and our findings do not negate the possibility of positive covariances at the individual level (see Santostefano *et al.*, 2017). Nonetheless, this underscores the potential for complex relationships among life-history traits at different levels of organization; classical theory has long recognized that the sign of covariance depends ultimately on the relative variance in both acquisition and allocation at each level (van Noordwijk & de Jong, 1986)

COVARIATES OF LIFE-HISTORY VARIATION

Differences in climate associated with latitude might also have contributed directly to the observed differences in hatching success in the present study (i.e. lowest in *P. pennsylvanica*). Diapaused eggs from all populations were subjected to natural winter conditions characteristic of *P. americana*, because the minimum temperature during the winter months (corresponding to the egg stage) is a main predictor of habitat suitability for *P. pennsylvanica*, apparently confining it to lower latitudes (Zhang *et al.*, 2020).

Interestingly, we found that female melanism and longevity were positively correlated (only) in *P. pennsylvanica*, a species characterized by relatively dark females. Given that our methodology used post-mortem measurement of phenotypic traits, we cannot rule out the effects of age-related melanization, in which darkening typically occurs within the first 7–14 days of adulthood in *P. americana* (Punzalan *et al.*, 2008a) and even earlier in *P. pennsylvanica* (D. Punzalan, unpublished data). The fact that bugs in the present study were collected relatively late in the season casts some doubt on the effects being purely

age related. Although previous work has implicated intra- and interspecific variation in melanism as an important target of natural selection in male *Phymata* (Punzalan *et al.*, 2008b; Punzalan & Rowe, 2015), the adaptive significance of female melanism is not yet understood, and studies are underway to evaluate possible links with other components of female fitness.

LIFE-HISTORY TRAITS OF PUTATIVE HYBRIDS

Individuals representative of the putative hybrid zone had intermediate values for the majority of measured traits, consistent with an additive genetic basis to those life-history characters and mirroring previous findings for morphological characters (Punzalan & Rowe, 2017). However, there was also some evidence of hybrid breakdown in the putative hybrid population, including a suggestion of reduced female longevity, longer juvenile development times in males and reduced adult mobility. These results complement a previous study suggesting hybrid breakdown of juvenile viability in the same population (Punzalan & Rowe, 2017) and are consistent with the often sex- and stage-specific nature of reductions in hybrid fitness (Veen *et al.*, 2001). If our findings extend to reduced fitness and dispersal in wild *Phymata*, they provide several mechanisms that might contribute to adaptive divergence despite what seems likely to be ongoing gene flow between *P. americana* and *P. pennsylvanica*.

ACKNOWLEDGEMENTS

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SUPPORTING INFORMATION

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

Figure S1. The number of offspring reared successfully to adulthood as a function of family size, in Am, Mx and Pe populations.
Figure S2. Population distributions for reproductive rate, based on the first 49 days (or less) in the laboratory, for Am, Mx and Pe populations.
Figure S3. Locomotor (climbing) performance as a function of age in laboratory males corresponding to Am (open circles), Mx (triangles) and Pe (filled circles) populations.

SHARED DATA

The data from this study are available to download from the Dryad Digital Repository (http://doi.org/doi:10.5061/dryad.t4b8gtj19; Punzalan, 2021).