

1 Linking thermal adaptation and life history theory explains latitudinal patterns of voltinism

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6 Abstract

7 Insect life cycles are adapted to a seasonal climate by expressing alternative voltinism
8 phenotypes - the number of generations in a year. Variation in voltinism phenotypes along
9 latitudinal gradients may be generated by developmental traits at critical life stages, such as
10 eggs. Both voltinism and egg development are thermally determined traits, yet independently
11 derived models of voltinism and thermal adaptation refer to the evolution of dormancy and
12 thermal sensitivity of development rate, respectively, as independent influences on life
13 history. To reconcile these models and test their respective predictions, we characterised
14 patterns of voltinism and thermal response of egg development rate along a latitudinal
15 temperature gradient using the matchstick grasshopper genus *Warramaba*. We found
16 remarkably strong variation in voltinism patterns, as well as corresponding egg dormancy
17 patterns and thermal responses of egg development. Our results show that the switch in
18 voltinism along the latitudinal gradient was explained by the combined predictions of the
19 evolution of voltinism and of thermal adaptation. We suggest that latitudinal patterns in
20 thermal responses and corresponding life histories need to consider the evolution of thermal
21 response curves within the context of seasonal temperature cycles rather than based solely on
22 optimality and trade-offs in performance.

25 Key words

26 Phenology, latitudinal variation, thermal adaptation, climate adaptation, life history

28 Introduction

29 Understanding how organisms are adapted to a variable climate is a fundamental problem in
30 ecology and evolutionary biology. Temperature is a major component of climate that has a

pervasive effect on biological rates [1]. Species have adapted their phenology and life cycle to seasonal and latitudinal gradients in temperature [2-4]. The seasonal timing of phenological events in turn influences subsequent biological interactions [5, 6], and these responses are predicted to be modified by climate change [7-9].

To predict how species will respond to future changes in temperature, we need to understand the genetic, phenotypic and environmental sources of variation which generate adaptive responses [10-13]. These sources of variation can be inferred from latitudinal patterns in thermally determined traits and thermal performance curves (TPCs), particularly when accompanied by breeding studies in controlled environments [14-16]. One key thermally determined trait that varies along a latitudinal gradient is voltinism - the number of generations each year [17]. Variation in voltinism is generated by variation in climatic factors or by variation in the life history traits which underpin it, such as egg hatching phenology, or their interaction [18, 19]. Egg hatching phenology is also a thermally determined trait that encompasses the thermal sensitivity of development rate and dormancy responses [20, 21]. Overall, hatching phenology can represent a developmental bottleneck in the life cycle and can strongly influence how life cycles are synchronised with current and future changes in climate [22].

Theoretical models of voltinism and thermal adaptation provide conceptual frameworks to understand patterns of variation along environmental gradients. However, models of thermal adaptation and the evolution of voltinism have developed independently and approach the problem of latitudinal gradients differently [7, 23]. Higher latitudes are typically associated with univoltine life cycles whereas lower latitudes are associated with multivoltine life cycles, although exceptions to the general pattern exist [24-26]. Lower latitudes are also associated with longer growing seasons and warmer climates, and vice versa at higher latitudes [27, 28]. Season length, as determined by photoperiod, is the main evolutionary driver of voltinism in many phenological models of voltinism because photoperiod is a reliable cue of changes in season [29, 30]. These models overlook the influence of temperature on development although both photoperiod and temperature co-vary along latitudinal gradients [31]. Models of voltinism patterns do not make explicit predictions about the evolution of TPCs. This is in contrast to models of thermal adaptation, which make several predictions for latitudinal gradients in TPCs of development rate depending on the

selection pressures involved and whether traits have evolved to compensate for latitudinal gradients in temperature [16, 32].

There are two general models of latitudinal compensation in TPCs [33]. The first is the optimality model of a TPC, where performance is maximised at the expense of thermal breadth of performance. This model predicts that the temperature where performance is optimal is predicted to shift according to local temperatures in cases when temperature is the main driver of selection. We would then predict that higher latitude populations will have a lower thermal optimum of performance and a shift in temperature limits of performance towards cooler temperatures (Figure 1A) [23]. Few empirical studies support this model of thermal adaptation along a latitudinal gradient [34-36]. The mixed support is likely because optimality models assume that thermal limits are free to vary and that there is a trade-off between performance and thermal breadth [37, 38]. Instead, thermal limits are conserved or have low plasticity along latitudinal gradients, and the thermal sensitivity of rates varies [32, 39].

TPCs that vary along the vertical axis, i.e. in thermal sensitivity, are predicted to arise when the length of the growing season is the main driver of selection. In this case, the second model of latitudinal compensation predicts that higher latitude populations will develop faster than lower latitude populations to compensate for a shorter growing season (Counter-gradient variation, Figure 1B) [40, 41]. In other words, genotype by environment interactions are negative [33]. Counter-gradient variation along temperature gradients are the most commonly reported latitudinal pattern of TPCs [32] and have been described in fish [27], frogs [42], butterflies [43], and damselflies [40].

A second case of seasonal constraints on TPCs is co-gradient variation, which predicts that higher latitude populations will develop slower than lower latitude populations (Figure 1C). Co-gradient variation is predicted to occur when genotype by environmental interactions are positive, and species may or may not compensate for latitudinal changes in temperature in other co-varying life history traits [33]. In these cases, other genetic or environmental selection pressures constrain the evolution of the TPC to compensate for temperature gradients [44, 45]. Co-gradient variation is not as widely reported as counter-gradient variation [41] but has been observed in damselflies [46], grasshoppers [18], butterflies [45, 47], beetles [48], snails [36], and crickets [10].

Intermediate responses between the two general thermal adaptation models of latitudinal compensation may also be generated because selection pressures acting on thermal breadth and thermal sensitivity are non-mutually exclusive [33]. We predict shifts in both thermal breadth and thermal sensitivity in these cases [49-51]. Co-gradient and intermediate responses of TPCs imply that other life history traits may also be influenced by the same selection pressures to compensate for these TPCs. The association between TPCs and life history traits is particularly relevant for traits related to development, such as development rate, as these are important traits which determine voltinism and are thermally determined in insects. Co-varying life history traits, such as size and growth rate, have been proposed to explain differences in TPCs of closely related species [45, 52]. The evolution of both voltinism and latitudinal compensation can thus shape TPCs of development but the role of voltinism patterns, or life history more generally, are absent in theoretical models of thermal adaptation [46, 53, 54].

Models of insect voltinism also infer the evolution of diapause and the expression of alternative developmental pathways. These models predict that a temperate insect with a switch in voltinism controlled by diapause should have a shorter development time in multivoltine populations than in univoltine ones [55, 56], as observed in many insects [10, 18, 57-59]. Levins [60] described a model that predicted that switches in developmental pathways, such as by the induction of diapause, are predicted to evolve under greater environmental heterogeneity in space and time. Models of insect phenology based on temperature show that hatching phenology can be generated by seasonal changes in temperature alone [19, 61, 62] and that voltinism patterns can be generated using dormancy responses other than diapause [63].

For a widely distributed insect where temperature is a major determinant of development or voltinism, the latitudinal pattern of TPCs will depend on the mechanism that generates voltinism and whether species have compensated for changes in temperature along a latitudinal gradient [46, 64]. If species express latitudinal compensation, we may predict a counter-gradient of TPCs. If voltinism imposes a genetic and environmental constraint on the evolution of the whole life cycle and species have not compensated for latitude in other life history traits, such as diapause, we would predict a co-gradient pattern of TPCs of development rate whereby multivoltine populations at low latitudes develop faster than

univoltine populations at high latitudes. At the extreme end, a diapause response can be considered an absence of temperature-dependent development.

Here we test these patterns in four species of matchstick grasshoppers (Orthoptera: Morabidae, sub-family Morabinae): *Warramaba picta*, *W. whitei*, *W. flavolineata* and *W. grandis* [65]. The genus *Warramaba* is an excellent system with which to examine the evolution of latitudinal adaptation of insect life cycles. Sexually reproducing *Warramaba* are widely distributed across more than 1000km along a latitudinal gradient in both aridity and temperature in arid and semi-arid Western Australia, and distributions overlap in some localities (Figure 2)[66-69]. We hypothesise that the egg is the primary stage for determining voltinism, as represented by hatching phenology. Because the Morabinae are flightless, have limited dispersal and have strong genetic structuring within taxa, we predict there is high potential for life cycle adaptation to local climates among lineages and species [65, 66] [70]. In this study, we provide the first comparative description of the life history, phenology and biology of *Warramaba* species from unpublished field diaries, as well as laboratory measurements on the thermal dependences of egg development and dormancy.

Methods

Inferring phenological timing of hatching

We define voltinism based on the phenological timing of hatching, as indicated by the presence of nymphs. Univoltine populations will have nymphs only during summer (Dec – Feb) and multivoltine populations will have nymphs present in summer and in winter (Jun – Aug). To infer the voltinism of *Warramaba*, we collated field observations made by M.J.D. White between 1967 and 1981, and by M.R. Kearney and colleagues between 2003 and 2018. These observations varied in their nature, ranging from presence/absence to breakdowns of instars. Most observations were made in spring (Sep – Nov) and summer and a targeted survey was undertaken in the winter of June 2017. Observations with no species or indication of stages recorded were excluded from the analysis for a total of 444 observations (Table S 1, Table S 2). To calculate sampling bias across different months of the year, we first determined whether a sampling locality had been surveyed for each month of the year. To

compare geographic variation in phenology we then assigned collection localities of *W. picta*, *W. whitei* and *W. flavolineata* to either a northern or southern region. Northern sites of *W. picta* were located at latitudes lower than -25° which was arbitrarily chosen because there was a large gap between sampling localities (Figure 2). Because sampling sites of *W. whitei* and *W. flavolineata* were continuously distributed from north to south, a boundary at -29.18° latitude was chosen based on strong separation in mitochondrial DNA [66](Figure 2). Geographic region was not assigned to *W. grandis* collection localities because we sampled along a latitudinal transect and there is no genetic evidence for lineage separation. To account for different sampling intensities across years at different sites, we calculated the proportion of years where grasshoppers were present, with 0 indicating no grasshoppers were observed in all visits and 1 indicating that grasshoppers were observed at each visit. The distribution of grasshoppers at the nymphal and adult stages was calculated separately for each geographical region.

Quantifying variation in developmental rates

To characterise the thermal dependence of egg development in *Warramaba*, we collected individuals of *W. picta*, *W. whitei*, *W. flavolineata* and *W. grandis* from Western Australia in the summer (Dec – Feb) of 2016 (Table S 3). To test for intraspecific variation in the thermal dependence of egg development and dormancy in *W. picta*, *W. whitei* and *W. flavolineata*, we sampled replicate populations in the northern and southern regions of their respective distribution. These geographical regions followed known mitochondrial lineages in *W. whitei* and *W. flavolineata* [66]. To test for latitudinal variation in developmental traits in *W. grandis*, we sampled 14 populations along a latitudinal northern to southern transect spanning 551 km.

Initial egg mass was measured at the start of incubation to account for the effects of egg size on development rate (XS205DU, Mettler Toledo, Port Melbourne, Australia). In 2016, we incubated eggs from all populations, except southern *W. flavolineata* populations, at 16, 20 – 40 °C in increments of 2 °C, and 45 °C (Table S 4). Eggs incubated at 30 °C were held in cabinet incubators (Scientific Equipment Manufacturers Pty. Ltd., Magill, South Australia, Australia) and eggs at all other temperatures in thermocyclers (Biometra GmbH, Göttingen, Germany). The range of incubation temperatures chosen in 2016 captured the range which

they are likely to experience in the field [71]. Eggs from *W. flavolineata* were excluded from these experiments because unpublished observations of *W. flavolineata* egg development in 2005 indicated southern mitochondrial lineages of this species have an obligate diapause which requires chilling for its termination (supplementary material). In 2016, we investigated the conditions which would break the diapause in *W. flavolineata* eggs from southern populations (supplementary material).

Viable eggs, as determined by the opacity and colour of eggs after dry storage, were randomly allocated to experimental temperatures in the thermocycler. Clutches from individuals were randomised and eggs from individuals were split among incubation temperatures. All remaining viable eggs from the cohort were incubated in the cabinet incubator at 30 °C. Eggs incubated within the cabinet incubator were placed on filter paper on top of moist sand within petri dishes (see also supplementary material)[70].

The rate of egg development ($\%\cdot\text{day}^{-1}$) was calculated from the time between the start of incubation and the time the first instar nymph emerged in the glass vial. We identified eggs that did not hatch after at least 54 days as putatively dormant. Any such eggs were externally inspected for signs of embryonic development. To test whether these eggs had died or were dormant, we incubated the putatively dormant eggs at 34 °C in thermocyclers until they hatched. The lowest and highest temperatures at which continuous development and hatching was observed were taken as the lower and upper thresholds for development, respectively.

Data from the 30 °C incubator was pooled with the data from the thermocyclers for analysis. We are confident that there is no significant variation in the thermal response of egg development between eggs incubated in thermocyclers and in cabinet incubators [72].

Dormant and non-dormant eggs were analysed separately. We assessed variation in development rate across the range of experimental temperatures using Analysis of Covariance (ANCOVA), with incubation temperature, a quadratic term for temperature and \log_{10} initial egg mass as continuous predictor variables, species and geographical region as categorical predictor variables, as well as an interaction term between species and region to test for regional variation within species. Statistical analysis was conducted in R v. 3.4.4 [73].

226

227 Results

228 Field phenology of *Warramaba* in Western Australia

229 The hatching phenology of *Warramaba* observed in the field varied among species and
230 populations. Nymphs and adults of southern populations of *W. picta* were found in all
231 sampling months across their range, indicative of a multivoltine phenology (Figure 3). We
232 cannot conclude that northern *W. picta* were multivoltine based on our definition because we
233 did not observe nymphs in a northern population of *W. picta* during winter and only a single
234 locality was surveyed where adults were observed. Late instar nymphs and adults were found
235 in northern and southern populations of *W. whitei* during summer (Figure 3). In winter,
236 nymphs of *W. whitei* were found in northern populations and no nymphs were observed in
237 southern populations (Figure 3). Only one adult male grasshopper was found in one southern
238 population (Arrow Lake, WA, supplementary material, Table S 2). Adults and nymphs of *W.*
239 *flavolineata* were observed in northern and southern populations during summer but no
240 individuals of any stage were found in the winter, implying a univoltine phenology (Figure
241 3). Populations of *W. grandis* reliably yielded individuals in summer and individuals were not
242 found in winter in a southern population, suggesting *W. grandis* has a univoltine phenology
243 (Figure 3). A latitudinal gradient of *W. grandis* instars was observed during summer 2016
244 with earlier stage nymphs found in northern populations, and more mature, or adult,
245 individuals found in southern populations (Figure S 3).

246

247 Egg development and dormancy responses to temperature

248 Northern populations of *W. picta* did not develop below 24 °C, whereas southern populations
249 did not hatch below 20 °C (Figure 4, Table S 5). No eggs of *W. grandis* and northern *W.*
250 *flavolineata* hatched below 28 °C. Northern populations of *W. whitei* did not hatch below
251 22 °C, whereas southern populations did not hatch below 26 °C. The lower thresholds for
252 development (i.e. no development observed after 54–55 days) varied with species and region,
253 ranging in increasing order from 20 °C in southern *W. picta*, 22 °C in northern *W. whitei*,
254 24 °C in northern *W. picta*, 26 °C in southern *W. whitei*, and 28 °C for all populations of *W.*
255 *grandis* and *W. flavolineata*. The upper thermal limit of egg development for all species and
256 populations was 36 °C. Above 36 °C, eggs appeared to be dormant, but we were unable to
257 hatch any eggs which had not already started visible embryonic development. Most eggs

hatched between these thermal limits and were dormant below the lower thermal limit (Figure S 5). Non-dormant eggs ($n = 496$) hatched between 12 and 76 days (median 21 days) across all temperatures. Development rate of non-dormant eggs across all species and regions was best described with a quadratic term for temperature (Figure 4, ANCOVA $F_{1,487} = 106.400$, $P < 0.001$). The interaction between species and region was a significant source of variation in development rate (Figure 4, $F_{1,487} = 17.950$, $P < 0.001$). A winter diapause was observed in eggs from southern populations of *W. flavolineata* which required chilling to be broken (Figure S 8).

Discussion

Insect life cycles have evolved under both spatial and temporal changes in temperature along latitudinal gradients. In studies of northern hemisphere insects along latitudinal gradients, switches from multivoltine life cycles to univoltine life cycles are typically generated by varying the expression of diapause between lower latitudinal populations and higher latitudinal populations [28, 57, 74]. Voltinism patterns in the southern hemisphere are similar but fewer studies have explored the mechanisms which generate these patterns [18, 25, 75]. There have also been large scale studies of thermal response and adaptation along latitudinal gradients in the southern hemisphere [76-79], however, these studies have focused on mesic habitats.

Along a latitudinal gradient in arid and semi-arid Western Australia, the widely distributed matchstick grasshopper genus *Warramaba* showed an interspecific switch in voltinism (Figure 3). Southern populations of *W. picta* and northern populations of *W. whitei* at lower latitudes were multivoltine and *W. flavolineata* and southern populations of *W. whitei* at higher latitudes were univoltine. The exception to this pattern was *W. grandis*, which was univoltine despite having the second widest latitudinal distribution of the *Warramaba* and a parapatric distribution with the multivoltine *W. picta* (Figure 3). Conserved univoltine responses have also been observed in a high latitude damselfly [58]. The most striking latitudinal pattern was the difference in the TPC of egg development rate between voltinism phenotypes (Figure 5). Divergences in temperature-dependent developmental traits have been reported for different voltinism phenotypes in other insects [45, 46, 80, 81]. There were three characteristics which generated the divergent pattern of *Warramaba* TPCs through

interactions between voltinism, temperature and species identity. None of these characteristics were predicted by models of voltinism or thermal adaptation alone [33, 55, 82].

First, there was a co-gradient pattern in development rate where multivoltine *W. picta* and *W. whitei* developed faster than univoltine *W. flavolineata* and *W. grandis* (Figure 5). The same pattern was observed between geographic regions of *W. whitei*, with populations in the north developing faster than univoltine populations in the south (Figure 4). Co-gradient patterns of variation indicate that there are positive genetic by environmental interactions shaping the evolution of TPCs [41]. A potential environmental constraint on the evolution of egg TPCs is the length of the growing season along the latitudinal gradient [57]. If spatial changes in season length imposes a greater selection pressure than spatial changes in temperature per se, then the TPC for development would be expected to change more along the y-axis (development rate) than on the x-axis (position of thermal limits)[83].

The divergence of voltinism in *Warramaba* also follows patterns of genetic divergence in *Warramaba* based on the mtCO1 gene [66]. *Warramaba* are inferred to have rapidly expanded their distribution from climate refugia at low latitudes to higher latitudes during the glacial cycles of the Pleistocene [66]. This expansion is associated with patterns of chromosomal rearrangements and a latitudinal gradient in fecundity in *W. whitei* [67, 84]. The most ancestral karyotype in the genus is exhibited by the multivoltine *W. picta* [66], suggesting that this is the ancestral state and that univoltinism in southern *W. whitei*, *W. grandis* and *W. flavolineata* is a derived condition.

Second, there was a narrowing of the thermal breadth of egg development in univoltine populations that biased development towards higher temperatures (Figure 5). The narrow thermal breadths for development are unusual compared to other insects [21]. The variation of thermal breadth in *Warramaba* was primarily generated by the lower thermal limits of development, which are typically more plastic than upper thermal limits [28, 85]. Below the lower thermal limit, *Warramaba* eggs were dormant. We characterised two types of dormancy in *Warramaba* below the lower thermal limit: a non-diapause dormancy in all

species and a ‘winter’ diapause in *W. flavolineata* typical of northern hemisphere insects. One *W. whitei* egg hatched at 34 °C after remaining dormant at 38 °C (Table S 5) but we could not confirm whether sexually reproducing *Warramaba* had a ‘summer’ diapause like *W. virgo* [71]. This is likely because egg development in *Warramaba* is also dependent on soil moisture, and the incubation conditions within the thermocycler at these temperatures were confounded by a desiccating environment when water in the PCR tube evaporated between daily checks [71, 72].

Although most eggs from southern *W. flavolineata* did not hatch when we incubated them immediately after oviposition in 2005 and 2006, eggs incubated in 2016 developed continuously at 30 °C after they had been kept in storage at 22 – 24 °C for a considerable amount of time. This suggested that the threshold for diapause development is high enough to be broken at the storage temperature. Diapause in *W. flavolineata* is hypothesised to represent the opposite end of a spectrum of potential TPCs in response to a cooler and more seasonal climate [86]. In this case, the TPC can be viewed as a flat reaction norm of zero rate, in contrast to a high development rate in a multivoltine species like *W. picta*. Among the sexually reproducing species of *Warramaba*, diapause was only expressed in *W. flavolineata*, and most strongly in the highest-latitude populations where seasonal variation in temperature is greatest. This pattern of greater diapause expression at higher latitudes is consistent with the predictions of Levins [60].

The non-diapause dormancy below the lower thermal limit was characterised by an increase in egg mass but an absence of visible embryonic development when examined after 54 – 55 days of incubation. These eggs developed immediately after being transferred to 34 °C [87]. We also found an intermediate proportion of non-dormant and dormant eggs at the threshold temperature, which suggested a degree of developmental plasticity near this threshold; i.e. some eggs will continuously develop, whereas other eggs will remain dormant (Table S 5). There are fewer well-studied examples of insects whose life cycles are not regulated by a diapause compared to species with distinct diapause patterns and these patterns are likely under-represented in the literature [19, 56, 62, 88].

The expression of both types of dormancy at low temperatures in *Warramaba* likely evolved to prevent hatching during winter. Eggs are small and unable to behaviourally avoid extreme environments, although soil microenvironments where they are oviposited may provide a degree of buffering against extremes [71, 89]. Dormancy synchronises life stages with conditions favourable for growth and reproduction, or by avoiding detrimental conditions [20]. Dormancy can provide increased desiccation tolerance during summer and prevent early emergence [87, 90]. This selection pressure would also explain the bias of egg TPCs in univoltine populations towards warmer temperatures as eggs from univoltine populations will enter dormancy when temperatures cool down, whereas multivoltine populations will continue to develop (Figure 5).

Third, the patterns of egg development TPCs showed mixed support for latitudinal compensation in nymphal mass and growth rate. We did not detect an overall change in hatching mass across incubation temperatures indicative of a temperature size rule but there were differences among species (Figure S 5A). As observed in other insects at high latitudes, univoltine *W. flavolineata* may compensate for a lower egg development rate by hatching at larger sizes. However, the small hatching sizes we observed in *W. grandis* were inconsistent with this prediction (Figure S 5A). Size may also be regulated by maternal investment or differential allocation of resources during development, which were not considered in this study [91, 92]. *Warramaba* may have compensated for latitude in their first instar growth rate (Figure S 5B); when nymphs were held at the same temperature until second instar, the magnitude of the difference between species in their growth rate decreased (Figure S 5B). The pattern of egg development in *W. grandis* does not explain the more mature demography of instars observed in higher latitude populations of *W. grandis* than in lower latitude populations (Figure S 3). This trend in demography could be generated by responses in other life stages, such as a prolonged adult stage or slower growth rate at higher latitudes. However, we did not find evidence that *W. grandis* from different populations grow slower at 30 °C in the laboratory (Figure S 4A). Overall, the variation in egg TPCs among species and region may be latitudinally compensated to various degrees in traits not considered here.

Our results highlight the significance of the egg stage for generating adaptive variation for insect life cycles in variable climates. In *Warramaba*, we could infer phenology based on

field observations and characterisation of egg TPCs in the laboratory. We have used hatching phenology as a proxy for voltinism, however, our field observations were limited during winter; further, intensive sampling during autumn, winter and spring are needed to refine our understanding of the phenology of *Warramaba*. Our results also demonstrated the utility of assessing thermal performance across the entire range of ecologically relevant temperatures. We did not detect a latitudinal gradient in development rate at 30 °C (Figure S 4A). When comparing development rates at 30 °C with mean soil temperatures simulated using a microclimate model, there was a counter-gradient pattern of variation; populations of *W. picta* were not associated with the highest soil temperature despite having the fastest rate (Figure S 4B). In this case, plastic or acclimatory responses may have masked the co-gradient variation we observed in the TPC across all experimental temperatures [59, 93-95]. Overall, the latitudinal patterns of egg TPCs in *Warramaba* were only explained by considering both the evolutionary constraints of voltinism and latitudinal changes in temperature [45, 46].

A growing number of studies have concluded that a holistic assessment of environmental and life history variation along latitudinal gradients is needed to understand the thermal adaptation of species and the potential evolutionary responses to climate change [16, 77, 96, 97]. Theoretical models can improve our understanding of the evolution of thermal performance curves under variable environments [60]. Climate change has generated renewed interest in thermal adaptation and evolutionary models of TPCs under variable environments [14, 98]. Continuous development and testing of TPC models will aid in our understanding and ability to predict potential climate change responses and explain exceptions to the patterns of thermal adaptation under current evolutionary frameworks.

Ethics

Grasshoppers were collected under a Licence to Take Fauna for Scientific Purposes (SF010681 & 08-00112-1) issued by the Department of Parks and Wildlife, Government of Western Australia to MRK.

Data, code and materials

The datasets supporting this article have been uploaded as part of the supplementary material.

415

416 Competing interests

417 We have no competing interests.

418

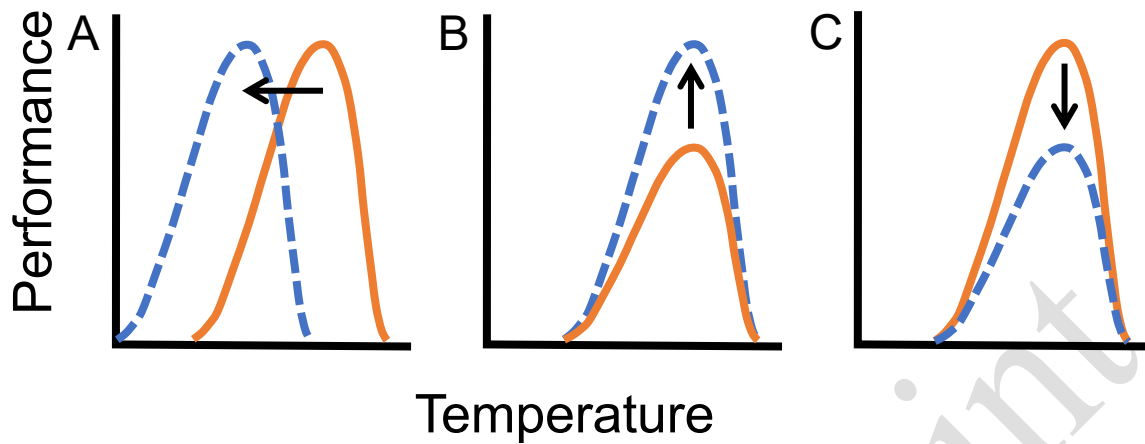
419 Authors' contributions

420 MRK and AAH conceived the study and helped edit the manuscript. JDK and MRK designed
421 the study. MRK collated the phenology data. JDK conducted the experimental work,
422 analysed the data and drafted the manuscript. All authors conducted the field work and gave
423 final approval for publication.

424

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429 Equity Trustees Charitable Foundation & the Ecological Society of Australia awarded to
430 JDK.



432

433 Figure 1 Theoretical models of latitudinal variation in thermal reaction norms between high
 434 latitude populations (blue, dotted) and low latitude populations (orange, solid). Arrows
 435 indicate the direction of selection. (A) Optimality model: reaction norm is horizontally
 436 shifted to adapt optimal performance to environmental temperature. (B) Counter-gradient
 437 variation: high latitude populations compensate for a shorter season length by increasing
 438 thermal sensitivity without increasing thermal breadth. (C) Co-gradient variation: thermal
 439 sensitivity of high latitude populations decreases without increasing thermal breadth with or
 440 without compensation in other traits.

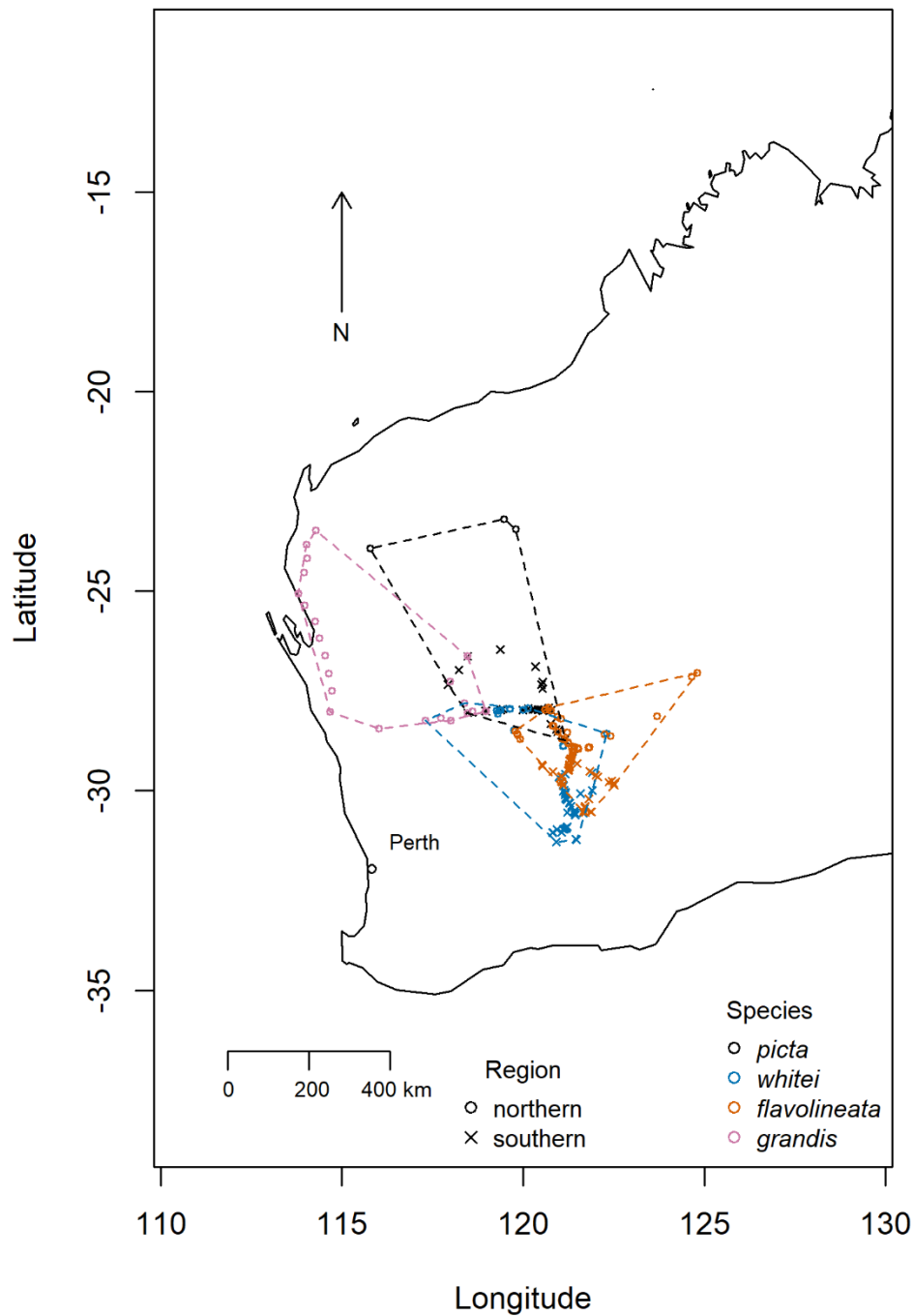
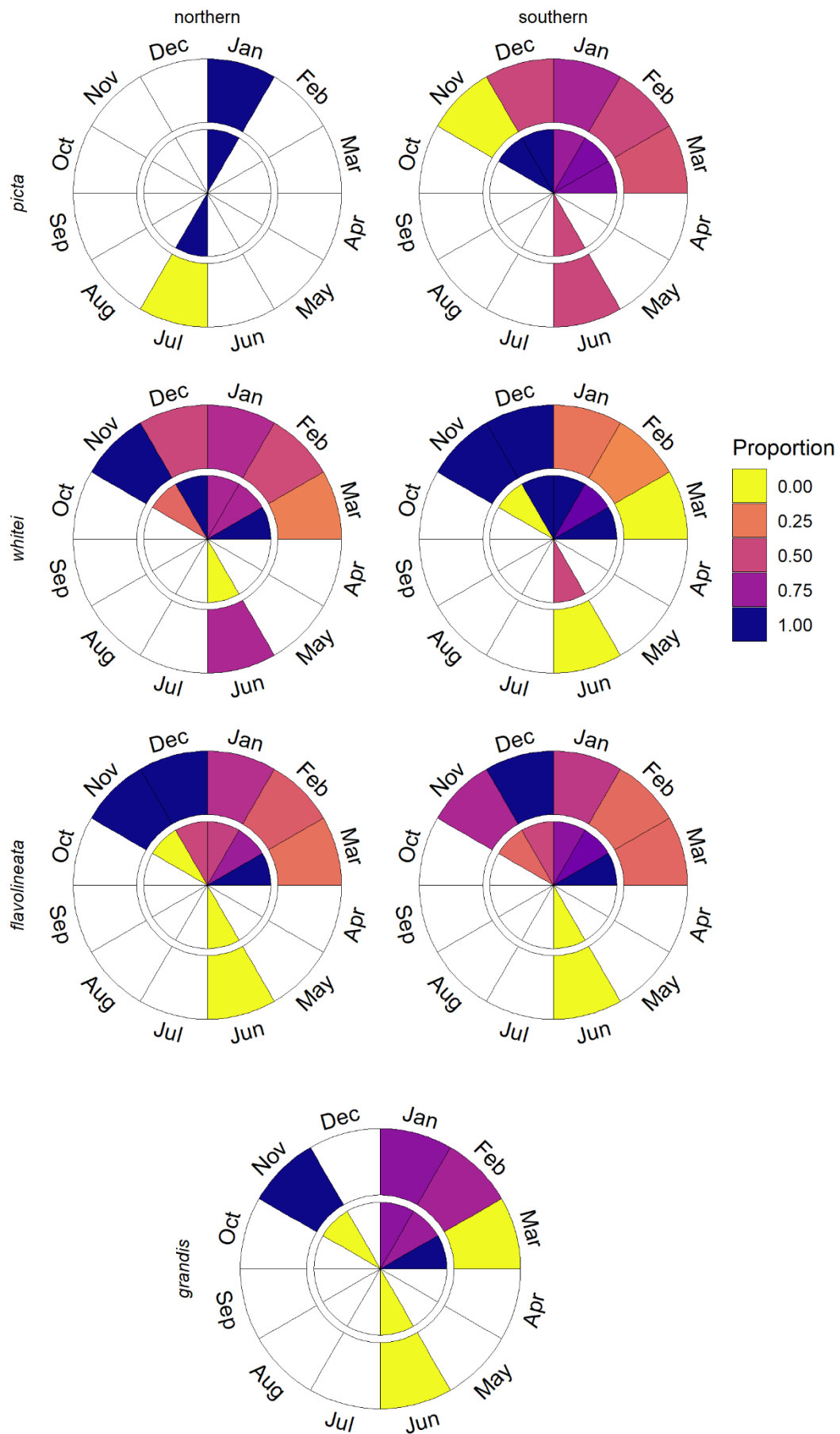


Figure 2 Map of sampling localities for each species of *Warramaba* used in this study and their relative distributions. Distribution limits (dashed lines) were estimated using minimum convex polygons. Grasshoppers were sampled between 1967 – 2018. Northern populations (open circles) of *W. whitei* and *W. flavolineata* were located at latitudes lower than -29.18° based on a major divergence in mitochondrial DNA. Region was not assigned to *W. grandis*.



448 Figure 3 Proportion of years with observed presence of adult (inner ring) and nymphs (outer
449 ring) for *Warramaba picta*, *W. whitei* and *W. flavolineata* in northern and southern regions of
450 their respective distributions and for *W. grandis* across their distribution. Region was not
451 assigned to *W. grandis*. Grasshoppers were surveyed at intermittent periods in the field
452 between 1967 – 2018 (444 observations). 0 (yellow) indicates that localities were sampled,
453 and species were absent. Blank segments were not surveyed that month for any year. Most
454 surveys were conducted during spring (Sep – Nov), summer (Dec – Feb) and a targeted
455 survey in winter (Jun – Aug).

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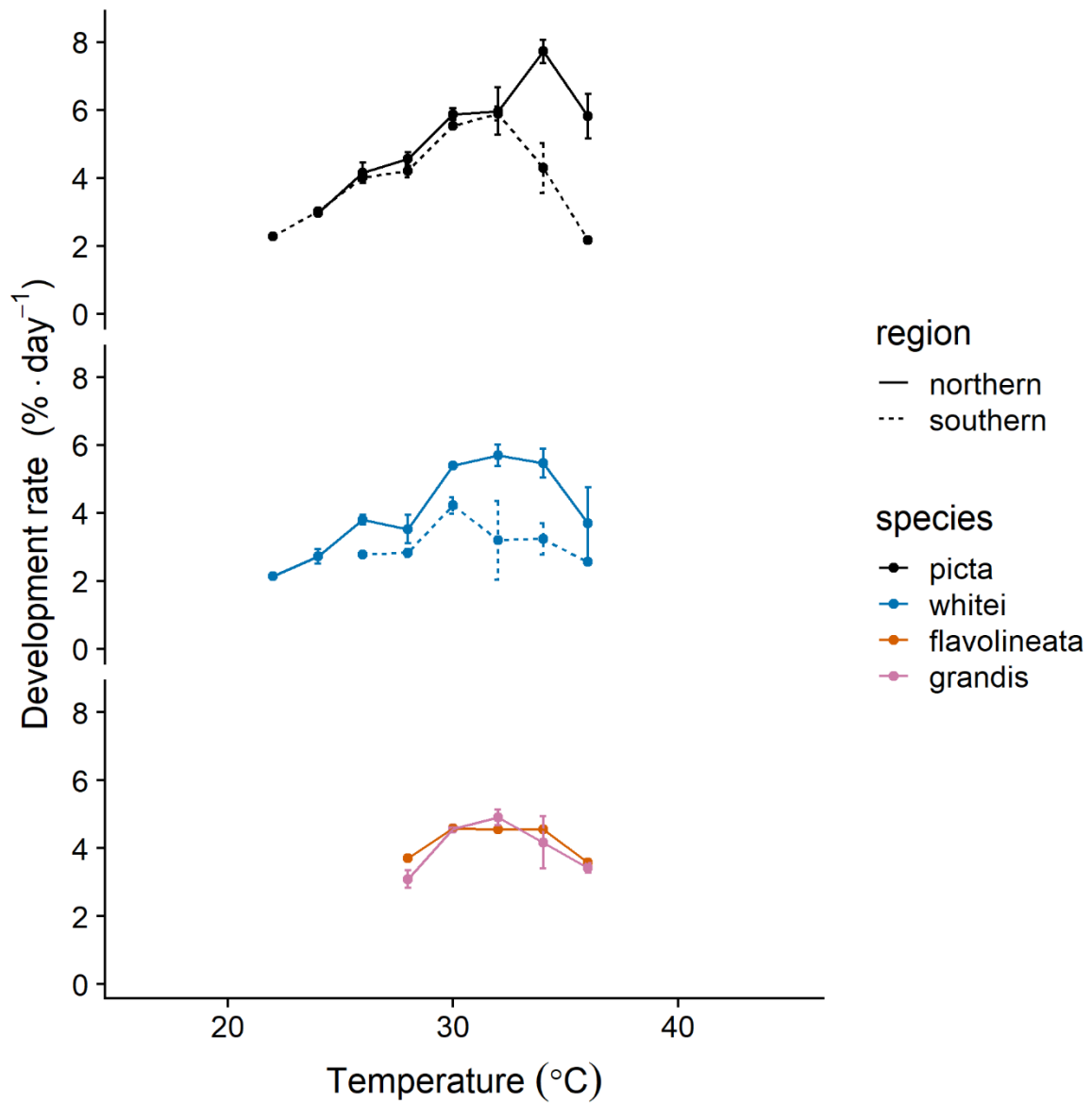


Figure 4 Mean development rate (%·day⁻¹ ± standard error) of non-dormant eggs for each species of *Warramaba* at constant temperatures between 16 and 45 °C (n = 496). Thermal response curves were characterised for northern (solid lines) and southern (dashed lines) populations of *Warramaba* in 2016 experiments. Eggs were kept in dry storage (22 – 24 °C, 30 % R.H.) until used in experiments.

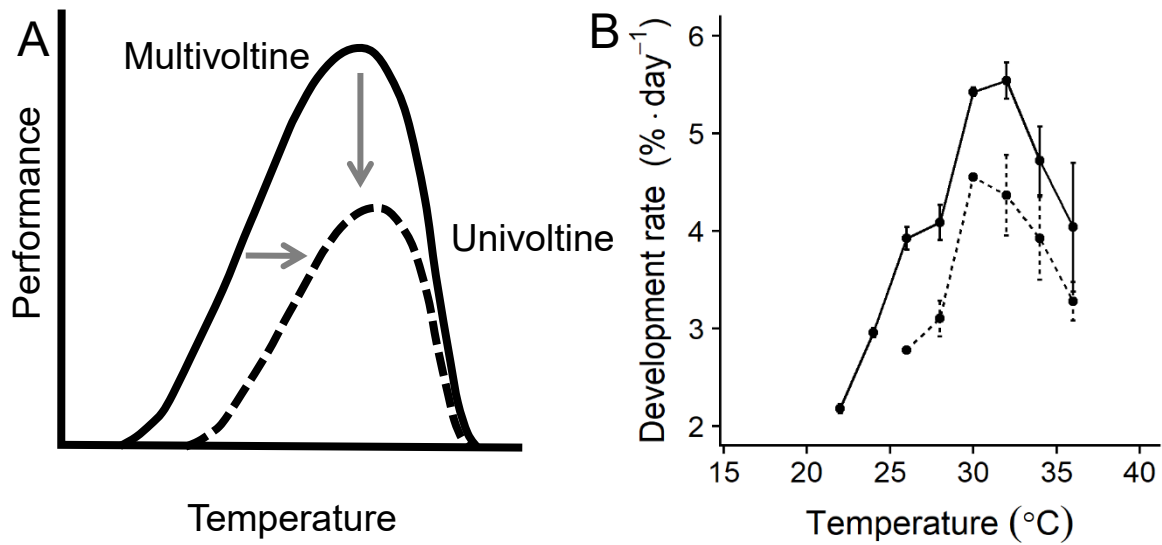


Figure 5 (A) Voltinism-shaped variation: Multivoltine populations (solid lines) at low latitudes develop faster and over a wider temperature range than univoltine populations (dashed lines) at low temperatures. Dormancy is represented by an absence of a thermal response curve. Arrows indicate the direction of selection by seasonal and latitudinal gradients in temperature. (B) Mean development rate ($\% \cdot \text{day}^{-1} \pm \text{standard error}$) of non-dormant eggs from multivoltine populations (solid lines) and univoltine populations (dashed lines) of *Warramaba* spp. at constant temperatures between 16 and 45 °C. Data collected in 2016 from species and regions were pooled into their respective voltinism pattern inferred from hatching phenology in the field between 1967 - 2018. Eggs were kept in dry storage (22 – 24 °C, 30 % R.H.) until used in experiments.

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