Comparative life-history responses of lacewings to changes in temperature

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Abstract

Insects play a crucial role in all ecosystems, and are increasingly exposed to higher in temperature extremes under climate change, which can have substantial effects on their abundances. However, the effects of temperature on changes in abundances or population fitness are filtered through differential responses of life-history components, such as survival, reproduction, and development, to their environment. Such differential responses, or trade-offs, have been widely studied in birds and mammals, but comparative studies on insects are largely lacking, limiting our understanding of key mechanisms that may buffer or exacerbate climate-change effects across insect species. Here, we performed a systematic literature review of the ecological studies of lacewings (Neuroptera), predatory insects that play a crucial role in ecosystem pest regulation, to investigate the impact of temperature on life-cycle dynamics across species. We found quantitative information, linking stage-specific survival, development, and reproduction to temperature variation, for 64 species from 39 locations. We then used multivariate generalized mixed models to assess how much temperature accounts for the covariation in the latter life-history processes. We found that developmental times consistently decreased with temperature for all species. Survival and reproduction however showed a weaker and nonlinear response to temperature, with highest survival and reproduction at optimal temperatures of 24-27 ºC. After accounting for temperature and species-specific effects on life-history processes, the latter covaried consistently across two main axes of variation related to development and reproductive output, suggesting the presence of intrinsic life-history tradeoffs. Such tradeoffs appear to differ to the ones observed in previous life-history analyses on vertebrates because, unlike in vertebrates, higher survival to adult stages is positively associated with faster developmental times. Our work highlights the importance of comparative studies of life-history responses of insects for climate-change and comparative demographic research and points to important knowledge gaps, such as a better assessment of adult survival and dormancy.

KEYWORDS: life cycle, Neuroptera, climate change, demography, life history.

INTRODUCTION

Insects represent the most diverse group of animals, with over a million described species, accounting for more than half of all known living organisms (Chapman, 2006), and potentially making up over 90% of the animal species on Earth (Wilson, 1999; Erwin, 1982). They inhabit a wide range of terrestrial biomes and play a crucial role in all ecosystems, performing various functions such as soil turnover and aeration, dung burial, pest control, pollination, and wildlife nutrition. However, despite their paramount importance to the overall functioning and stability of ecosystems worldwide, changes in abundances and extinctions of insects under global change drivers have only recently received widespread attention (Cardoso et al., 2019; Lampert et al., 2023; Gossner et al., 2023). Among the numerous factors contributing to declines in insect abundance, e.g., land-use changes (Sala et al., 2000; Settele et al., 2005; Sánchez-Bayo & Wyckhuys, 2019; Newbold et al., 2020; Seibold et al., 2019), pesticide use (Breuker, 2018; Gebert et al., 2022), or invasive species (Wagner & van Driesche 2009; Bates et al., 2020; Seebens et al., 2017), increases in temperature extremes under climate change play a particularly important role globally (Sánchez-Bayo, 2019; Jackson et al., 2022). This is because temperature is one of the most significant environmental factors influencing life-history processes including growth and development, reproductive biology, and the frequency of reproduction (Kobori and Hanboosong, 2017).

Temperature fluctuations can have both sublethal and lethal effects on the physiological processes of insects (Feder et al., 1997). However, how these effects translate to changes in abundances and population fitness can be complex due to the differential effects of temperature on different components of individual and population fitness, such as development, pupal mass, survival, and the accumulation of energetic compounds. For instance, caterpillars of the European grapevine month (*Lobesia botrana*) have been shown to respond positively to higher temperatures in the context of climate change, showing faster development, increased survival rates, and improved evasion of natural enemies through 'flee' behavior (Iltis et al., 2019). However, physiological tradeoffs mean that faster development comes at a cost of a depletion of lipid reserves (-26%) and a reduced total PO activity (-34%). This can ultimately have adverse effects on the survival of the native generation, as fat stores are essential for enduring extended periods of food scarcity (Sinclair & Marshall, 2018). It may also carry over into the adult stage, having a detrimental impact on the dispersal and reproductive capabilities of adults (Vande & Dyck, 2013).

The above example shows that understanding the effects of temperatures throughout the entire life cycle, and not just for particular life cycle stages or overall abundances, is critical because most populations in natural communities are structured by genetic and phenotypic traits, and ages or stages. In such structured populations, mechanisms to buffer the effects of temperature extremes resulting from differential life-history responses to the environment or from intrinsic physiological tradeoffs in investment in different life-history processes is ubiquitous (Iltis et al., 2019; Villellas et al., 2015; Lloret et al., 2012). These mechanisms can help populations adapt to climate change (Kearney et al., 2009). At the same time, persistence may be particularly threatened when abiotic factors such as temperature simultaneously reduce the survival and reproduction of several life-cycle stages (Winkler et al., 2021; Mahmoud et al., 2020; Nakamura et al., 2016).

While research on the effects of temperature on the development and life-cycle dynamics of insects is not new, a comprehensive comparison of how temperatures affect life-history processes in different species is thus far lacking (Ma et al., 2020). Such a comparison would provide a valuable resource for life-cycle analyses, for instance eco-physiologically based life-cycle models (Rossini et al., 2023). Our main aim is therefore to bridge this substantial knowledge gap, focusing on Neuroptera, commonly known as lacewings. Neuroptera stand out among other taxa with relatively more available data, in particular in grey literature, but remain underrepresented in comparative studies (Eickermann et al., 2023). In addition, Neuroptera play a crucial role as effective predators of various insect pests (Koutsoula et al., 2023; Nair et al., 2020; Yayla et al., 2020) and are an indicator of environmental health and ecosystem quality. Here, we first perform a review of peer-reviewed and grey literature to generate a database with responses to temperature and other key environmental drivers across the life cycle for Neuroptera. Secondly, we use the information generated in the review to do assess the drivers of the covariation in life-history responses across species. We discuss our results in light of comparative life-history analyses in vertebrates and point to new research directions.

MATERIALS AND METHODS

Neuroptera life cycle

Neuroptera is an insect order with complete metamorphosis. The typical developmental cycle for Neuroptera, with only a few exceptions, encompasses stages of egg, three larval stages (with some exceptions in Ithonidae), a pre-pupa stage, pupa, and finally, the adult imago. The embryonic development in Neuroptera does not significantly differ from other taxa, with varying durations among species. Weight of egg decreases during embryogenesis. Hatching commences with embryonic moulting and is a precarious period where the newly born larva is highly vulnerable. The short period as adult imago signifies the second crucial stage in Neuroptera development. During this time, the insect moves slowly and remains highly vulnerable. Within a few days, under favourable conditions, the adult reaches sexual maturity, mating takes place, and the female initiates egg laying.

Literature review

We searched Web of Science and Scopus for literature for studies (published before March 31, 2023) that quantified the effects of temperature on different life-history processes in Neuroptera as described in previous section. Additionally, we employed Google Scholar to locate articles that may not have been indexed in the aforementioned databases. We used the following search terms:

"(Neuroptera AND life cycle)" OR "(Chrysopidae AND life cycle)" OR "(Hemerobiidae AND life cycle)" OR "(Myrmeleontidae AND life cycle)" OR "(Coniopterigydae AND life cycle)" OR "(Sisyridae AND life cycle)" OR "(Ascaphidae AND life cycle)" "(Dilaridae AND life cycle)" OR "(Polystoechotidae AND life cycle)" OR "(Psychopsidae AND life cycle)" OR "(Coniopterygidae AND life cycle)" OR "(Ithonioidea AND life cycle)" OR "(Berothidae AND life cycle)" OR "(Mantispidae AND life cycle)" OR "(Nemopteridae AND life cycle)" OR "(Ascalaphidae AND life cycle)" OR "(Nemopteridae AND life cycle)" OR "(Nymphidae AND life cycle)" OR "(Osmylidae AND life cycle)" OR "(Nevrorthidae AND life cycle)" OR "(Sisyridae AND life cycle)" OR "(Neuroptera life cycle AND temperature)" OR "(Temperature AND Neuroptera development)" OR "(Temperature AND Chrysopidae development)" OR "(Temperature AND Hemerobiidae development)" OR "(Temperature AND Neuroptera life history)" OR "(Neuroptera life history)" OR "(Neuroptera temperature adaptation)" OR "(Climate change AND Neuroptera)" OR "(Climate change impact AND insects)".

From any study that matched our search terms, we extracted information on the relationship between temperature and life-history processes only when the latter was linked quantitatively to temperature fluctuations, that is, we discarded descriptive studies. We included studies performed in the field (in situ) as well as laboratory (in vivo) experiments. From the studies that matched our criteria, we recorded the species name, the location of their collection in as much detail as possible (continent, specific location, and coordinates if available). In cases where precise coordinates were absent but a specific location was indicated, we retrieved coordinates for the center of that location. We recorded the constant temperature used during the studies in degrees Celsius (°C) and, when available, the thermal constant 'K,' which represents the thermal requirement for development and is measured in degree-days (calculated by the equation $K = (1/y)\ (x — t)$, where y = mean developmental rate, and x = temperature (°C)). However, we also included data from studies that did not consider temperature but provided information on the life history of Neuroptera. If recorded in a study, we also noted how other abiotic and biotic factors affected life-history processes under different temperatures, e.g., food intake (see Supplementary Material S1 for details on all information collected).

For key life-cycle stages (as detailed above), we recorded developmental times, survival rates, and reproductive rates in response to temperature. Developmental times included the duration (in days) of egg development; the three instar, the pupae, and the adult stage after emerging from the pupa and before egg-laying; and of the reproductive period of females. We also recorded the average expected lifespan and generation time of adults in days. Reproduction included the percentage of females capable of reproducing and the total number of eggs laid by a single female. For survival, we recorded the percentage of successful larval emergence from eggs and the percentage of successful survival during the period from larva to adult. If articles provided minimum, maximum, and mean values, we also recorded these data as separate categories in our database.

Quantitative analyses

To explore the within-and among-species covariation in life-history processes (i.e., development times, survival, and reproduction) under different environmental regimes, we ran multivariate generalized linear mixed effect models (Brommer et al. 2019), using the MCMCglmm package in R (version 4.1.2) (Hadfield, 2010). These modeled the covariation in life-history processes as a function of mean temperature individuals were exposed to (in vivo or in situ). To improve convergence of the models, we standardized temperature values (mean=0, SD=1). No study we extracted information from recorded life-history processes across the entire life-cycle of Neuroptera. We therefore focused on response variables that were most consistently measured across studies (51 out of 274 records): developmental times of the three instar-stages and pupae, survival of pupae to adult, and number of eggs per female. We performed an arcsine transformation on survival rates and log-transformed the remaining response variables to ensure a Gaussian distribution of the model residuals (which improved model converge under the limited data). We also considered additional models in which we separately modeled developmental times (120 out of 291 records) and survival/reproduction (56 out of 291 records) as joint multivariate responses. The developmental times were mostly recorded under natural conditions (in situ; 114 out of the 120 records). We repeated the analyses removing the 8 in vivo records, but the results did not change (Supporting Material S2).

In all models, the multivariate response was accounted for using a covariance matrix in which life-history processes covaried within species. To incorporate the inherent non-independent relationships among species, we used a random species effect (variance term) on the mean of life-history responses. We did not use the animal term in the MCMCglmm package to correct for phylogeny because we the full analysis (51 records) consisted of 9 species, including 4 species for which the phylogeny is not well resolved; while the analysis using developmental times (120 records) used 23 species but included 10 species for which phylogeny is not fully resolved (see Supporting Material S2 for all *R* scripts that include the modelling workflows).

The MCMCglmm package uses a Bayesian framework to fit models. We thus ran three independent chains using 50,000 iterations after a burnin of 10,000 iterations. We used a thinning interval of 25 steps, resulting in 2000 posterior parameter samples per chain. We determined model convergence using standard Bayesian checks (i.e., traceplots and Gelman-Rubin diagnostic; Brooks and Gelman 1998). We considered differences in stage-specific developmental times between temperature regimes to be significant when the 95% credible interval (C.I.) of the respective parameters did not overlap 0.

Lastly, we used the residuals of the multivariate model (observed – predicted mean value for each life-history process included as multivariate response variable) to investigate covariation among the processes not accounted for by temperature or species effect. For this, we performed a varimax rotated principal component analysis (PCA) on the residuals, following Healy et al. (2019) and Ozgul et al. (2023). The residual variation in life-history processes was scaled to I = 0 and SD = 1 to agree with PCA assumptions. After implementing the PCA, we used the Kaiser criterion (Legendre & Legendre 2012) to explore how many axes sufficiently explain the variation observed in the data. This criterion is based on keeping only principal component axes with associated eigenvalues > 1. We ran all analyses in R version 4.1.2 (R Core Team 2021).

RESULTS

Literature review

A considerable number of studies on life-history processes of Neuroptera did not include numerical data, rendering them unsuitable for our database. We retrieved 700 articles based on our search terms but were able to extract life-history information from only 9% of these articles (i.e., 63 studies). Of the 5,937 recognized species, inclusive of 469 fossilized species of Neuroptera in the world (Zhang, 2013), our data life-history information from 64 species distributed in 39 geographical locations (Fig. 1). Most of the data (90 % of studies) originated from laboratory experiments. In 75 % of cases, we recorded the temperature regime with which life-history processes were manipulated. Specifically, Neuroptera development was assessed within a temperature range of 9.5 to 15 °C (7.3% of records); 15.1 to 20 °C (12.1% of records); 20.1 to 25 °C (68.0% of all records); 25.1 to 30 °C (8.5 % of all records); 30 to 35 °C (3.0% of all records). The thermal constant was calculated in only 6.5% of cases. The photoperiod was indicated in 27 studies, and humidity in 18 studies. Information regarding the impact of food quantity on the development of Neuroptera was provided in only two laboratory experiments.

Figure 1: Locations from which we obtained data on life-history processes of Neuroptera. Locations show where experiments were conducted under natural conditions or the places from which Neuroptera were collected for in-vivo experiments.

In terms of life-history processes, developmental times across the instar and pupal stages were most consistently recorded across different studies (58.8 % of all studies). The range of duration for these periods was from 0 to 42 days for the first stage, from 0 to 81 days for the second stage, from 0 to 221 days for the third stage, and 0 to 69 for pupae (including cocoon). Fewer studies (30 %) recorded the survival of Neuroptera after all larval, pupal, and cocoon stages, and the number of eggs per female, ranging from 0-1264. Classic life-history traits, such as lifespan and generation time were recorded in fewer publications (see Supporting Material S1 for all life-history processes our review captured). Almost all the data on the duration of the development of pre-imaginal stages and their temperature influence pertain to representatives of the Chrysopidae and Hemerobiidae families. Species from these families are of particular interest to scientists due to their potential as a biological method of pest control.

Quantitative analyses

Across life-cycle stages, developmental times decreased significantly with temperature (Table 1, Fig. 2). Conversely, survival from pupae to adult and number of eggs per female peaked at an optimal temperature of ca. 25 ºC, but decreased at lower and higher temperatures. The effect of temperature on the latter two life-history processes was overall more uncertain than in the case of developmental times (Fig. 2). These patterns of temperature responses remained when we considering developmental times and reproduction/survival separately, although a slightly higher sample size when considering life-history processes separately decreased the uncertainty in survival responses to temperature (Supporting Material S2).

Table 1. Parameter estimates of fixed effects from multivariate GLMMs, modelling covariation of life-history processes as a function of temperature.

Life-history process	**Mean effect (at temp = 0)**	**Temperature slope**	**Temperature^2 slope**
Intercept (D 1st instar)	1.37[1.07,1.67]	-0.28[-0.35,-0.21]	0.04[0.01,0.09]
D 2nd instar	-0.10[-0.48,0.26]	-0.24[-0.32,-0.16]	0.09[0.04,0.13]
D 3rd instar	0.07[-0.32,0.47]	-0.28[-0.37,-0.19]	0.07[0.01,0.11]
D pupae	1.08[0.65,1.50]	-0.23[-0.34,-0.12]	-0.03[-0.08,0.03]
#eggs/female	4.47[3.83,5.14]	-0.29[-0.48,-0.09]	-0.30[-0.41,-0.19]
S pupae-adult	-0.32[-0.76,0.12]	-0.04[-0.11,0.03]	-0.04[-0.08,0.01]

Parameters show mean values and 95 % credible intervals in brackets. The model was parameterized using contrasts, so that the intercept represents the developmental times of the 1st instar and the subsequent terms represent differences from the intercept.

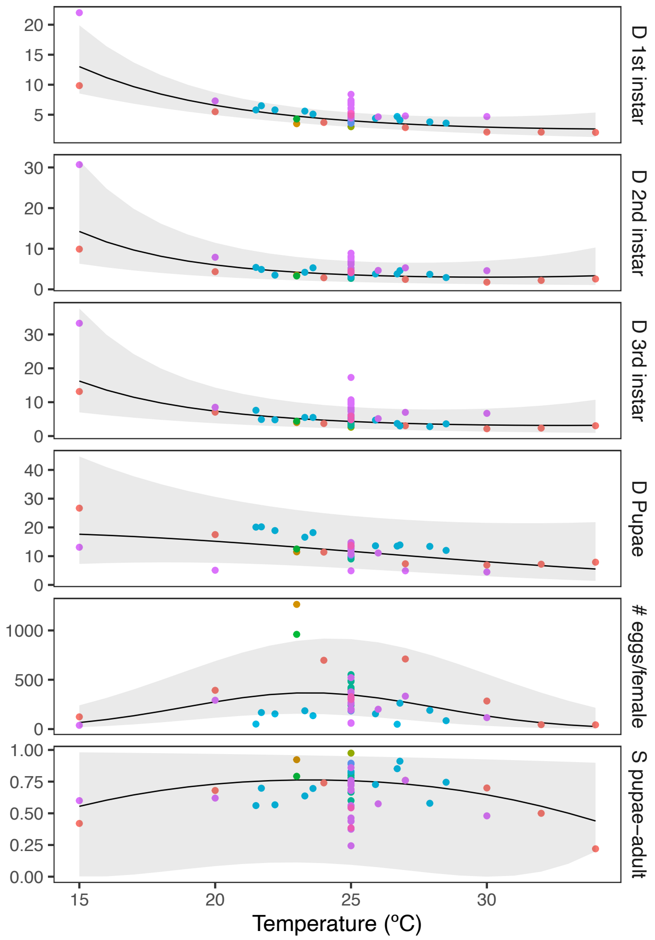

Figure 2. Covariation in life-history responses to temperature across 9 Neuroptera species (point colors; see Fig. S2.1 for species names). Points are observed values from the literature review. Lines are mean predictions of developmental (D) times (in days) for three instar and pupae stages, number of eggs per female, and proportion of pupae surviving (S) to adult stages from the multivariate MCMCglmm. Grey area are 95 % credible intervals of model predictions.

A substantial amount of variation in life-history processes not explained by temperature was captured by differences among species (random species effect in our models; Fig. 3a). On the other hand, covariation in developmental times and survival was driven largely by temperature responses (as random species-specific and residual-error covariation was relatively low; Fig. 3). However, independent of temperature responses, reproduction covaried strongly with the developmental time of the 3rd instar stage and pupae within species (high residual error covariation; Fig. 3b).

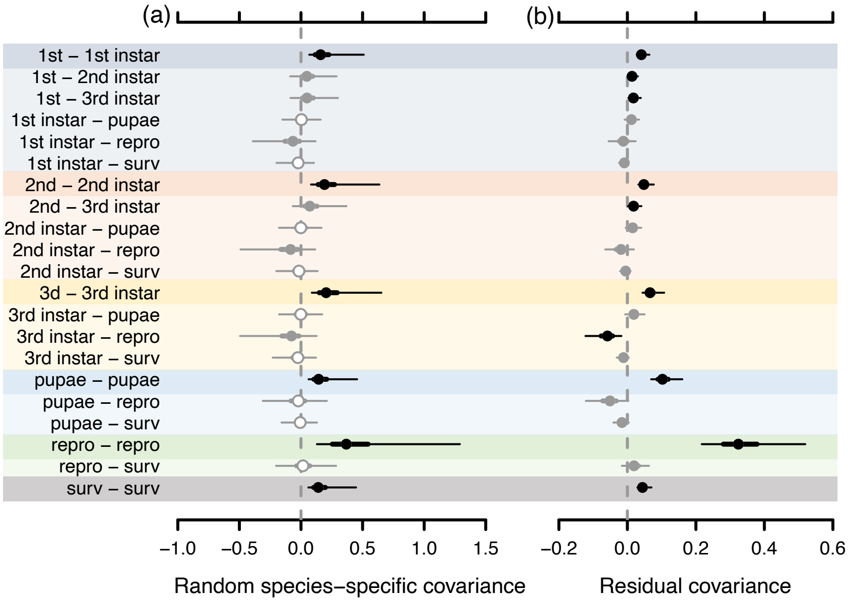

Figure 3. Caterpillar plots of the distribution of posterior parameters from the Bayesian multivariate mixed effect model describing the covariance of life-history processes in Neuroptera due to random among-species effect and residual (within-species) error. Life-history processes include: developmental times of 1st, 2nd, and 3rd instar and pupae stages; # eggs per female (repro); and survival rates (surv) from pupae to adult. Points represent posterior medians. Parameters where 50% credible intervals (C.I.) overlap 0 are indicated by open circles. Parameters where 50% C.I. do not but 95% C.I. do overlap 0 are indicated by closed gray circles. Parameters where 95% C.I. do overlap 0 are indicated by closed black circles. Thick lines represent 50% C.I.; thin lines represent 95% credible intervals.

The PCA analysis revealed that the residual covariation among the life-history processes was adequately captured by two main PCA axes that together explained 76 % of variation in life-history processes (Fig. 4). PCA axis 1 largely captured variation in instar development that traded off with survival to adult from pupae to adults, with positive loading of developmental times in the 3 instar stages and negative loading of survival to adult and number of eggs per females. PCA axis 2 largely captured variation in pupae development (positive loadings) that traded off mostly with the number of eggs produced (see Table S2.1 for loadings). These patterns suggest that separate physiological processes govern instar and pupae development, with faster development being associated with higher survival and reproductive output. These patterns of covariation remained when we modelling developmental times separately, thus increasing the sample size (Supporting Material S2).

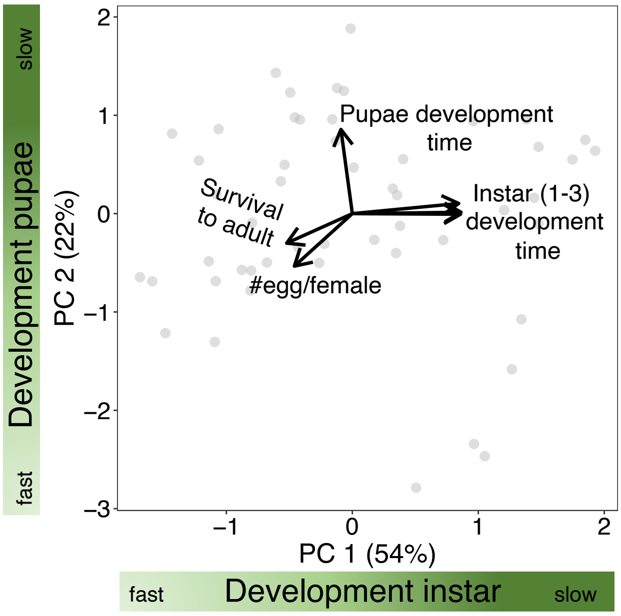

Figure 4. Life histories of study species' populations (points) are characterized by life-history processes representing developmental times in different life cycle stages. To characterize life histories, a PCA was performed on the residual variation of GLMMs modelling six life-history processes: development (in days) in 3 instar stages, development in pupae stage, survival from pupae to adult, and number of eggs produced per female. Arrow lengths are proportional to the loadings of each process onto the two axes.

DISCUSSION

Our research aimed to consolidate information regarding the influence of temperature on various stages of development of lacewings across species. Furthermore, we sought to address gaps in knowledge related to the impact of temperature on both the overall duration of the developmental cycle and the survival of Neuroptera at each stage. The ambient temperature represents a pivotal abiotic factor for insects that lack the ability to maintain a constant body temperature. Insects consistently grapple with temperature fluctuations to evade the detrimental consequences of heat stress. In order to mitigate these risks, insects have evolved an array of physiological and behavioral thermoregulation mechanisms, along with molecular responses that facilitate their survival and function across diverse temperature conditions. Elevated temperature sensitivity exerts an influence on the development and growth of insects and may result in phenological alterations (Kong et al., 2019; Chmura et al., 2018; Rebaudo & Rabhi, 2018). Established methodologies for evaluating and quantifying the temperature sensitivity of insect development and growth, in conjunction with a substantial body of existing data, present the potential for enhanced comprehension and forecasting of their phenological reactions (Jasrotia et al., 2022; von Schmalensee et al., 2021).

Clearly, temperature significantly influences the duration of Neuroptera development, as well as many other insect species. Within the viable temperature range, increasing temperatures are associated with an acceleration of growth and development in Neuroptera, along with increased metabolic activity, facilitating faster development of eggs, larvae, and pupae (Ranjbar & Nemati, 2020; Tauber & Tauber, 2015; Pappas et al., 2013; Syrett & Penman, 1981). Our results indicate that such faster development is not associated with inherent tradeoffs in survival and reproduction (typically found in vertebrates; e.g., Healy et al. 2019), providing an ideal setting for Neuroptera to profit from increased temperatures. However, our results also demonstrate that temperatures outside the optimal range of 20-30 ºC can substantially decrease survival and reproductive output and thus and overall viability (Aghdam & Nemati 2020; Pappas et al., 2013; Mantoanelli et al., 2006). For instance, high temperatures can induce stress and lead to moisture loss, increased evaporation, and overheating in females, which clearly has a negative impact on reproductive function (Aghdam & Nemati 2020; Samra et al., 2015; G.S. Albuquerque et al., 1994).

The lack of correlation between the development at the pupal stage and the development at the instar stages in Neuroptera may result from ecological and evolutionary adaptations that affect the different stages of their life cycle. Environmental conditions can vary significantly between the larval stage and the pupal and cocoon stages. Neuroptera larvae have an active metabolism and are predators adapted to specific environmental conditions where they live and hunt (Botti et al., 2022, Bolok et al., 2010, van Zyl et al., 1997; Breene et al., 1992; Boyden, 1983). All stages may undergo similar influences regarding food selection and predation. These stages involve similar physiological processes designed for growth and development. Meanwhile, the pupal and cocoon stages are subject to other influences, such as the impact of abiotic factors on metabolism and development. These stages usually do not interact with the external environment and may be less adapted to external conditions due to their quiescent stage (Aspöck et al., 1980). Their metabolic processes are significantly slowed down, and they expend energy on the transformation from the larval state to the adult insect (metamorphosis), involving restructuring and degradation of certain larval tissues (Zhao et al., 2022; Zhao et al., 2020).

Our comparative analyses also confirmed previous studies supporting the idea that early and reproductive stages are more sensitive to extremely high temperatures compared to the mature larval stage (Ma et al., 2021; Zhao et al., 2017). For instance, Chun-Sen Ma and colleagues (2021) suggest that the varying impact of extremely high temperatures might be due to the different thermal environments inhabited by various stages, thus leading to their adaptation (Ma et al., 2021; Pincebourde & Casas, 2015; Woods, 2013; Kingsolver et al., 2011). Furthermore, they suggest that body size explains why larger larvae are more heat-tolerant than smaller early life stages (Ma et al., 2021; Kingsolver et al., 2011; Ma et al., 2004; Zhao et al., 2017), as smaller larvae are more prone to rapid increases in body temperature and water loss, a view with which we fully agree. At the same time, our results contradict the hypothesis that immobile stages of insects (eggs and pupae) should be more resistant to heat compared to mobile adult stages and larval stages due to their lower ability for behavioral thermoregulation (Huey et al., 2003). We found that across, species, the pupal stage of Neuroptera is also sensitive to high temperatures. We believe that at this stage, the insect is unable to regulate its body temperature through mechanical means, unlike a mobile larva that can seek shade. Most Neuroptera species seek shaded places, such as cracks in tree bark, leaf litter, and other hidden locations, for pupation (Canard & Volkovich, 2001). Under optimal conditions, as demonstrated in the study by Canard & Principi in 1984, *C. regalis* only experiences a minimal weight loss due to dehydration and respiration during the pupal stage, less than 7% of its initial weight by the end of diapause (Canard & Principi, 1984). However, there are few studies on the impact of extreme temperatures during the pupal stage, and we are unaware of the potential harm caused by overheating and significant water loss at this stage.

Our work also points to important knowledge gaps in studies on insect population responses to their environment. We found no studies that assessed the survival of the imago stages and few studies that assessed the effects of various environmental drivers on life-history processes. Predicting the effects of warming on the population size or density of a specific species is challenging, as local climatic or habitat conditions may mask such effects. Experimental data are scarce, and there are limited models. For instance, a UK study from 1974 to 1992 suggested an increase in common butterfly species, potentially influenced by factors beyond climate (Pollard et al., 1995). Further analysis using the same dataset revealed a clear correlation between population fluctuations and weather conditions in 28 of 31 species (Roy et al., 2001). These findings informed a model describing population dynamics for 8 species under a UK climate warming scenario until 2080. Five of these species saw population increases, one decreased, and two showed no clear trend. Consequently, species dependent on weather conditions may respond differently to further climate warming (Musolin & Saulich, 2012).

Neuroptera provides an excellent example of how our understanding of climate-induced changes is limited. While each species in this order has a critical temperature maximum, they also possess apparent mechanisms to mitigate adverse effects. For instance, many Neuroptera species are active during twilight or at night, cover themselves with chitin remnants after molting, use plant fragments for camouflage, and seek shaded habitats. Larvae of Myrmeleontidae can burrow deeper into the sand or move to shaded areas when the upper layer becomes excessively heated. All these behavioral adaptations reduce the risk of overheating. Additionally, many Neuroptera species exhibit adaptive abilities regarding diapause duration. Lastly, all Neuroptera larvae and the majority of species are active predators, and their population size correlates with that of their prey. This includes the dynamics of correlations influenced by seasonality or phenological adaptations of Aphidoidea with Chysopidae, Hemerobiidae, Coniopterygidae, or Formicidae with Myrmeleontidae. A comprehensive approach understanding these factors is required to predict population dynamics and the consequences of climate change.

Despite remaining knowledge gaps, our results on the covariation of life-history processes in Neuroptera and how much of this covariation is explained by temperature paints a nuanced picture of potential population dynamics under climate change. They demonstrate that predicting responses to future thermal conditions requires a mechanistic understanding of how organisms react to a wide range of temperatures experienced throughout their life cycle, not just at specific phases of the life cycle (Sinclair et al., 2016). Faster developmental times may not necessarily lead to higher abundances due to differential temperature responses across the life cycle. Such buffering effects across the life cycle are commonly investigated in mammals and birds (Jackson et al. 2022; Paniw et al. 2018) and provide an exciting new area of research for insects (Lackey et al. 2023), which cover different ecological and evolutionary niches and are thus governed by different physiological tradeoffs and adaptations.

DATA AVAILABILITY

All data and R scripts to run the comparative analyses can be found here: https://github.com/MariaPaniw/lacewings_life_histories

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SUPPORTING MATERIALS

Supporting Material S1 – Review protocol and data extracted

Supporting Material S2 – Additional results of quantitative analyses

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