

1 A generalizable tool for predicting developmental phenology for 2 wild poikilotherms.

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2 Abstract

Development in poikilothermic organisms is strongly temperature-dependent, particularly during early life stages prior to exogenous feeding. This thermally constrained physiology produces a near-mechanistic relationship between ambient temperature and development rate, allowing for predictive models of phenology. However, traditional models—often developed under constant laboratory temperatures—struggle to account for the variable thermal regimes experienced by wild populations. To address this, (Sparks et al., 2019) introduced the effective value model, a framework that integrates daily temperature data to predict developmental timing under fluctuating conditions. Building on this foundation, the R package **hatchR** was developed to operationalize the effective value model and enable its widespread application, initially focusing on fishes. In this paper, we expand the scope of **hatchR**, demonstrating its applicability across a broad range of poikilothermic taxa, including amphibians, reptiles, and aquatic invertebrates. We also illustrate how this framework supports both applied management goals—such as predicting hatching windows for conservation and monitoring—and basic research on ecological and evolutionary questions, including phenological plasticity, thermal adaptation, and life history strategies. By providing a generalizable, open-source tool, **hatchR** bridges the gap between physiological theory and real-world application, offering a robust platform for predicting developmental phenology in diverse and changing environments.

3 Introduction

Because poikilothermic organisms rely on external sources to regulate their body temperature, the physiological processes governing their growth and development are tightly coupled to ambient thermal conditions. This relationship is especially deterministic during early life stages prior to exogenous feeding, when metabolic rates are primarily governed by environmental temperatures, modulated by genetic and maternal effects (West-Eberhard, 2003). Although the absolute rate of development can vary widely among species and populations, most poikilotherms exhibit a consistent and often non-linear thermal performance curve that describes development as a function of temperature (Angilletta Jr, 2006; Schoolfield, Sharpe, & Magnuson, 1981). These relationships can be effectively approximated with power law or exponential models that capture increasing development rates with rising temperature, up to a physiological optimum beyond which performance declines.

Historically, models of developmental phenology in wild populations have relied on the accumulation of degree days (thermal sums) above a species-specific threshold. While widely used, degree-day models are fundamentally linear and fail to account for the non-linear nature of development, leading to biased predictions under fluctuating temperature regimes (Neuheimer & Taggart, 2007). This is particularly problematic for long-developing species or for organisms in variable climates, where embryos incubating at colder temperatures often require fewer thermal units to complete development than those incubating in warmer environments. Moreover, traditional models often assume temporally invariant development rates and do not incorporate diel temperature variability, which can significantly affect development in systems with large day–night thermal swings [CITATION needed, perhaps** <https://doi.org/10.1186/1472-6785-13-18> **...though I wonder why this is brought up, because hatchR doesn’t appear to address DTV?, since it auto-sums to daily averages? or am I misunderstanding? It seems like DTV might be better brought up in the discussion as a caveat?]. Finally, developmental reaction norms may vary across populations due to local adaptation or phenotypic plasticity, further complicating predictions (Angilletta Jr, 2009; Sparks, Westley, Falke, & Quinn, 2017).

To address these limitations in fishes, (Sparks et al., 2019) introduced the effective value model—an approach that captures the non-linear, temperature-dependent nature of development by integrating experimental data into a daily development rate function. Building on that work, the R package **hatchR** [CITE hatchR] was developed to operationalize the effective value framework and make it accessible to researchers and managers. **hatchR** uses temperature-performance curves generated from lab-based thermal rearing trials to estimate the proportion of development achieved each day under observed temperature conditions. These daily

contributions are summed until a cumulative threshold (typically 1.0) is reached, marking the completion of a developmental stage. The package includes both an R-based workflow and a user-friendly Shiny web interface to facilitate broad adoption across research and management communities.

While `hatchR` was originally developed for coldwater fishes, the approach is broadly applicable to any poikilothermic organism whose development conforms to a monotonic or unimodal temperature–rate relationship, including many amphibians, reptiles, and invertebrates. In this manuscript, we expand the taxonomic scope of **hatchR**, compiling thermal developmental data from the literature and demonstrating how effective value modeling can be applied to diverse taxa. We also present three case studies illustrating how **hatchR** can inform ecological, evolutionary, and management questions—ranging from understanding thermal adaptation and phenological mismatches to forecasting hatch timing in conservation planning. These applications are increasingly relevant as freshwater ecosystems face intensifying and interacting stressors, including climate change, habitat alteration, and invasive species, all of which can disrupt developmental timing and population dynamics [Craig et al. (2017); ADD ANOTHER BROAD PAPER; **also, seems unnecessary to limit to freshwater ecosystems?**].

4 Methods

4.1 Effective value models

Effective value models estimate developmental progress based on empirically derived relationships between temperature and development rate. These relationships are typically parameterized by raising organisms at constant temperatures in laboratory settings, then fitting a non-linear function that captures the temperature-dependence of development. This function can then be reciprocated to produce daily “effective values”—units of development—that accumulate over time.

Each day’s developmental contribution is calculated using the general power-law form:

$$EffectiveValue_i = 1/exp(\log_e a - \log_e(Temperature_i - b))$$

where i is the index for each day, a and b are empirically derived parameters, and temperature is the average for that day. Development is complete once the cumulative sum of daily effective values reaches one:

$$\sum_{i=1}^n EffectiveValue_i = 1$$

To illustrate this process, we developed a custom effective value model for the coastal tailed frog (*Ascaphus truei*), a cold-adapted amphibian widespread in forested streams of western North America (Figure 1). We used **hatchR**'s `fit_model()` function, which fits power-law models (specifically, Model 2 following Beacham & Murray (1990)) to thermal performance data (CITE). While **hatchR** defaults to the power-law framework, users may supply any model formulation via the `predict_phenology()` function, enabling flexibility for taxa or traits that require alternative temperature-development functions.

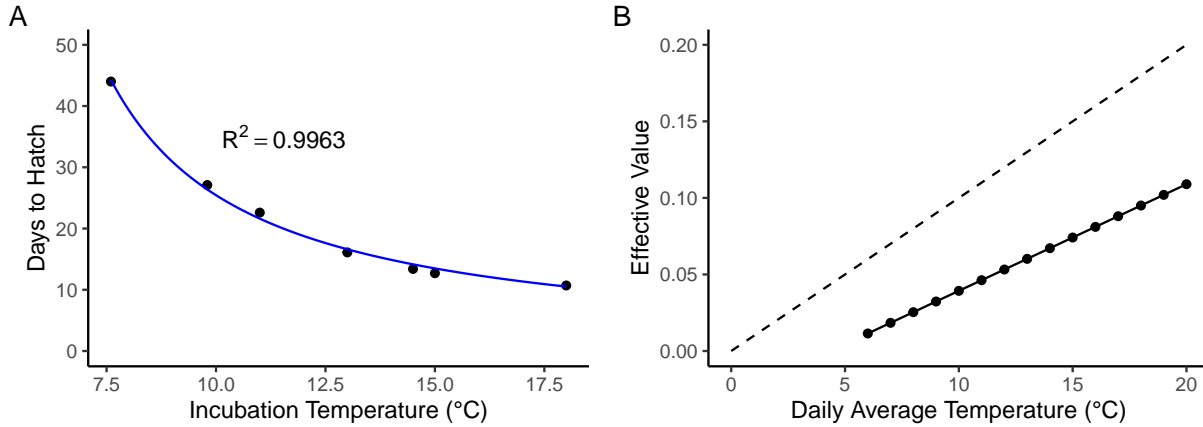


Figure 1: Custom hatching phenology model for coastal tailed frogs (*Ascaphus truei*). Panel A represents the model fit and raw data used to generate the effective value model and panel B are the effective values for daily temperatures between 6 and 20 °C. A dashed line with a 0.01 increase for every degree increase is included for reference.

4.2 Data input and quality checks

hatchR requires two core inputs: a vector of daily average water temperatures and a corresponding vector of calendar dates. These data are typically collected from field-deployed temperature loggers. For loggers that record sub-daily temperatures, **hatchR** includes the function `summarize_temp()` to compute daily means. Data completeness and consistency can be checked using `plot_check_temp()` and `check_continuous()` to ensure there are no gaps or anomalies in the temperature record (Table 1).

If you import data from raw files with multiple daily readings, the package allows you to summarize your with `summarize_temp()` and then check summarized data with the `plot_check_temp()` and `check_continuous()` functions.

Table 1: Example water temperature data. Temperature data are typically collected from field loggers and summarized to daily averages. Each row represents a date–temperature pair used to estimate daily effective values for phenology modeling.

date	temperature
2024-01-01	4.67
...	...
2024-07-01	22.31
...	...
2024-12-31	2.58

4.3 Predicting phenology

Developmental phenology can be predicted in two ways using `hatchR`. The `predict_phenology()` function estimates the date at which development completes, given a known reproductive event (e.g., oviposition or spawning; `spawn.date`) and daily temperature data. Alternatively, the `predict_spawn()` function works in reverse—estimating the likely date of a reproductive event based on a known or observed hatch/emergence date. This is especially useful for retrospective analyses or for estimating breeding windows from field observations.

BMM NOTE: Seems like we should include a figure of output here. Could just add a panel to figure 1 with days to develop plot.

5 Case studies

The effective value modeling framework is broadly applicable across poikilothermic taxa and can be used to address a wide array of ecological, evolutionary, and management questions. While this manuscript focuses on three illustrative case studies, many additional opportunities exist. Below, we provide a non-exhaustive compilation of species for which thermal developmental data are available in the peer-reviewed or grey literature. These sources can be used to parameterize custom models via the `fit_model()` function in **hatchR**, allowing users to build tailored effective value models for diverse taxa. The examples span four taxonomic classes—amphibians, reptiles, insects, and crustaceans—and demonstrate the breadth of systems to which this approach can be applied. While the case studies we present here are intended as proof-of-concept, we anticipate that applications will continue to expand alongside the growing availability of temperature–development datasets.

Table 2: Example sources for effective value parameterization using `fit_model()` in **hatchR**. This compilation spans amphibians, reptiles, aquatic and terrestrial insects, and decapod crustaceans. Some entries, such as While et al. (2018) and Pritchard & Leggott (1987), represent broader reviews with multiple species and are flagged as not yet vetted for full reciprocal model implementation. Users may need to extract or adapt published equations to align with the effective value framework.

Class	Order	Genera	Species	Study
Amphibia	Anura	<i>Lithobates</i>	<i>L.</i>	Moore (1939)
			<i>sylvaticus</i>	
			<i>L. pipiens</i>	
			<i>L.</i>	
			<i>clamitans</i>	
			<i>L. palustris</i>	
		<i>Ascaphus</i>	<i>A. truei</i>	Herbert A. Brown (1975)
	Urodela	<i>Ambystoma</i>	<i>A. gracile</i>	Herbert A. Brown (1976)
Reptilia	Squamata	<i>Sceloporus</i>	<i>S.</i>	Angilletta, Winters, & Dunham (2000)
			<i>undulatus</i>	
			<i>Podarcis</i>	<i>P. muralis</i> Van Damme, Bauwens, Braña, & Verheyen (1992)
	Testudines	<i>Mauremys</i>	<i>M. reevesii</i>	Du, Hu, Lu, & Zhu (2007)
			181 species	141 studies in While et al. (2018)
Insecta	Plecoptera	<i>Nemurella</i>	<i>N. pictetii</i>	John E. Brittain (1978), Elliott (1984)
		<i>Capnia</i>	<i>C. atra</i>	John E. Brittain & Mutch (1984)
		<i>Capnia</i>	<i>C. bifrons</i>	Elliott (1986)
		<i>Mesocapnia</i>	<i>M. oenone</i>	John E. Brittain & Mutch (1984)
		<i>Taeniopteryx</i>	<i>T.</i>	J. E. Brittain (1977)
			<i>nebulosa</i>	
		Coleoptera	<i>Colaphellus</i>	<i>C.</i> Tang, He, Chen, Fu, & Xue (2017)
			<i>bowringi</i>	
			18 species	Developmental equations in Pritchard & Leggott (1987)

Class	Order	Genera	Species	Study
		<i>Dendroctonus</i>	<i>D.</i>	Régnière et al. (2012) 10.1016/j.jinsphys.2012.01.010
			<i>ponderosae</i>	
	Lepidoptera	<i>Choristoneura</i>	<i>C. occidentalis</i>	Régnière et al. (2012) 10.1016/j.jinsphys.2012.01.010
		<i>Zeiraphera</i>	<i>Z.</i>	Régnière et al. (2012) 10.1016/j.jinsphys.2012.01.010
			<i>canadensis</i>	
	Diptera	<i>Bactrocera</i>	<i>B.</i>	Régnière et al. (2012) 10.1016/j.jinsphys.2012.01.010
			<i>cucurbitae</i>	
Malacostraca	Decapoda	<i>Pontastacus</i>	<i>P. leptodactylus</i>	Aydın & Dilek (2004)
Copepoda	Calanoida	11 genera		Forster et al. (2011) https://doi.org/10.1086/662174
	Cyclopoida	3 genera		Forster et al. (2011) https://doi.org/10.1086/662174
	Harpacticoida	2 genera		Forster et al. (2011) https://doi.org/10.1086/662174
Cephalopoda	Octopoda	<i>Octopus</i>	2 species	Márquez et al. (2021) https://doi.org/10.1111/raq.12495
	Myopsida	<i>Loligo</i>	2 species	Márquez et al. (2021) https://doi.org/10.1111/raq.12495
	Oegopsida	3 genera		Márquez et al. (2021) https://doi.org/10.1111/raq.12495
Asteroidea	Valvatida	3 genera		Hoegh-Guldberg & Pearse (1995) https://sci-hub.st/https://doi.org/10.1093/icb/35.4.415

5.1 Ecological Application: Spatial and Temporal Trends in Development

To demonstrate an ecological application for **hatchR**, we modeled variation in developmental timing for coastal tailed frogs (*A. truei*) across their range in the Pacific Northwest. Using oviposition estimates from Karraker et al. (2006) (unpublished data) and our earlier parameterized effective value model (Figure 1), we simulated daily development across 30 years (1991-2020) using modeled stream temperature data from Siegel, Fullerton, FitzGerald, Holzer, & Jordan (2023).

BCL NOTE: It feels like this section jumps into the methods a bit too quick, without providing context. At the start of this first paragraph, it would be worth providing a broad, 2-3 sen-

tence overview of the “what” and “why” of this specific ecological application... e.g. (rough idea), “Examining variation in development across space and time is critical to understand how organisms respond to ecological factors such as climate change [CITATION]. Here, we first demonstrate an application of hatchR to predict hatching times from a spatiotemporally extensive dataset. Using these predictions, we then show how one can examine putative drivers of variation in development and discuss their application in forecasting future responses.”

The dataset included r `nrow(model_data)` observations of predicted days to hatching, drawn from r `length(unique(model_data$comid))` stream reaches (labeled with Common Identifiers, i.e., COMIDs) nested within four mountain ranges: Olympic National Park, the Cascade Mountains, the Siskiyou Mountains, and the Willapa Hills. Each COMID had between 20 and 30 years of predictions.

BCL NOTES: 1) It isn’t clear to me what the original data consists of and what was modeled. It sounds like the original data is just oviposition observation dates, effective values, and stream temps. But in the paragraph above, “The dataset included observations of predicted days to hatching” makes me question what was data and what was modeled. It seems like the model generated predicted days to hatching?, which would not be “observations” and would not be part of the “dataset”. (I think it is the “observations of predicted days” that is throwing me, as one doesn’t observe predictions... I mean, technical you could, but I don’t think that’s what is meant.) But below, it states that the “model explained X% of the variation in developmental timing”, suggesting that there was original hatching data to which the predicted hatching times were compared? Clearly, I’m confused. lol. Could just be me, but maybe worth being more specific and hand-holdy. 2) I explained “COMID” above, as not everyone will know what that means (especially if anticipating a broad readership). But please change if there’s a better way.

We evaluated eight candidate linear models that varied in the inclusion and interaction of year, COMID, and mountain range effects. Based on adjusted R^2 , AICc, and RMSE, the best-supported model included year and COMID as additive fixed effects: $\text{days_to_hatch} \sim \text{year} + \text{comid}$.

This model explained r `round(perf[1,4], 2)*100` % of the variation in developmental timing (adjusted $R^2 = r$ `round(perf[1,4], 3)`), with year having a significant weak and negative effect (r `round(params[2,2], 2)` days/year, $p = 0.001$), indicating an overall trend toward faster development consistent with regional warming (Figure ??A). COMID effects captured the persistent differences in thermal regimes among streams, with estimated marginal means ranging from ~15 to ~44 days to hatch across sites (Figure ??B).

BCL (minor) NOTE: *Ascaphus truei* needs italics in Fig. 2, but not sure how to edit

Our results indicate development rates were highly variable over different physical habitats (streams originating in lowland hills compared with those originating in mountain ranges with permanent snow fields), with sites in Olympic National Park consistently having the longest development times and the greatest interannual variability (SD ~ 11 days), while lowland streams in the Willapa Hills developed fastest with minimal variability (SD < 3 days). These results demonstrate the capacity of **hatchR** to detect spatiotemporal phenological variation and forecast responses to shifting climate patterns.

5.2 Phylogenetic Application: Species Differences in Development Rates / Reaction Norms

Closely related species often diverge in their thermal tolerances and developmental strategies as part of niche differentiation. These differences can be visualized through reaction norms that capture genotype-by-environment (G \times E) interactions, often derived from common garden or reciprocal transplant experiments. While such experiments are ideal for isolating genetic and plastic components of trait variation, they are logistically demanding and rarely available for many taxa.

hatchR offers a complementary approach by generating species-specific developmental models from published thermal rearing studies and applying them to shared temperature regimes. While this does not replace controlled experiments, it enables estimation of thermal reaction norms for development across species, even when the original experiments were conducted independently. By visualizing differences in effective value slopes and phenological outcomes under shared conditions, **hatchR** can highlight how developmental traits vary with phylogeny and ecological strategy.

To demonstrate this approach, we leveraged data from Moore (1939) to parameterize developmental models for four widely distributed North American frog species in the genus *Lithobates*: wood frog (*L. sylvaticus*), pickerel frog (*L. palustris*), northern leopard frog (*L. pipiens*), and green frog (*L. clamitans*). These species co-occur in parts of eastern North America but differ in their breeding phenology, habitat associations, and thermal niches. For example, wood frogs are early breeders in cold, ephemeral wetlands, while green frogs breed later in more permanent, warmer waters.

We applied the custom parameterized models to two hypothetical spring temperature regimes with mean daily temperatures of 16 °C (cool) and 24 °C (warm). Under the cool regime, wood frogs hatched earliest while green frogs lagged behind by up to eight days—nearly double the developmental duration (Figure 2A). However, under the warm regime, predicted hatch dates clustered tightly, with all species hatching

within one day of each other (Figure 2B). The effective value slopes (Figure 2C) reveal these underlying differences in developmental response curves, serving as species-specific linearized reaction norms. Notably, the rank order of developmental timing reverses across the two thermal regimes, a hallmark of strong G×E interaction.

BCL NOTE: Maybe I'm misunderstanding, but it doesn't appear to be a strong rank order reversal? From cold to hot, it kinda equalizes, but doesn't clearly reverse?

This example demonstrates how **hatchR** can be used to explore evolutionary and ecological differences in thermal sensitivity across species. When combined with phylogenetic or trait-based analyses, such reaction norms can reveal how developmental strategies align with species' ecological niches, helping to explain the persistence of closely related species across thermal gradients.

5.3 Local Adaptation: Cogradient Variation in Development Rates

BCL Note: Not sure if it's a useful segue between these 2 case studies, but there's a cool paper on wood frog countergradient variation (Skelly 2004 <https://doi.org/10.1111/j.0014-3820.2004.tb01582.x>) that could be a useful eco-evo example of thinking species -> population?

As with interspecific comparisons, developmental models can be parameterized at the population level to examine local adaptation within species. In particular, **hatchR** allows researchers to compare how different populations respond to temperature, helping to reveal evolved differences in thermal sensitivity across environmental gradients.

Here, we used data from a common garden experiment on cabbage beetles (*Colaphellus bowringi*) reared at six constant temperatures (16–28 °C), spanning populations collected along a ~3,440 km latitudinal gradient in China (Tang et al., 2017). Although all beetles were reared under identical conditions, development rates differed among populations, particularly at cooler temperatures. Populations from southern latitudes—where temperatures are generally warmer—developed more quickly than northern populations, a pattern consistent with cogradient variation, where genetic and environmental effects on a phenotype act in the same direction (Conover, Duffy, & Hice, 2009; Sparks, Kraft, Blackstone, McNickle, & Christie, 2022).

To visualize these patterns, we fit custom effective value models for five of the six populations (excluding Longnan, which duplicated the values from Xiushui). The resulting linearized effective value curves (Figure 3) show that beetles from Xiushui County (southernmost) had consistently faster development rates across temperatures than their more northerly counterparts. These differences are especially pronounced at cooler temperatures, suggesting that local adaptation may only manifest under certain environmental conditions.

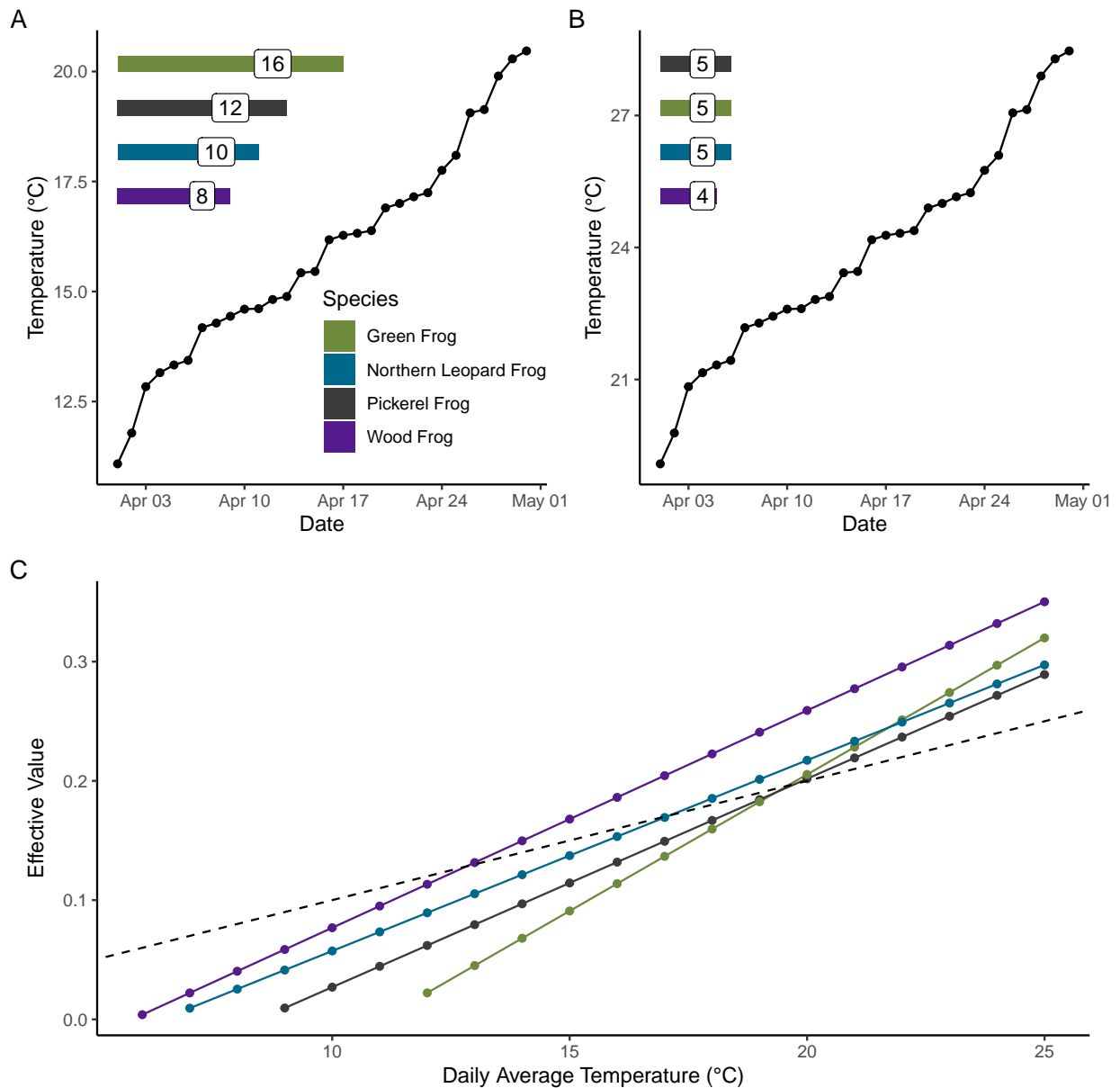


Figure 2: Custom hatch timing models developed for four North American *Lithobates* frog species. Models are parameterized from @moore1939 and phenology is predicted using two synthetic temperature regimes: Panel A shows predictions under a cooler regime (mean = 16 °C), while Panel B shows predictions under a warmer regime (mean = 24 °C). Panel C displays the effective value curves for each species—linearized approximations of thermal reaction norms. The crossover in rank order between Panels A and B illustrates genotype-by-environment interactions, reflecting species-specific thermal niches and breeding strategies.

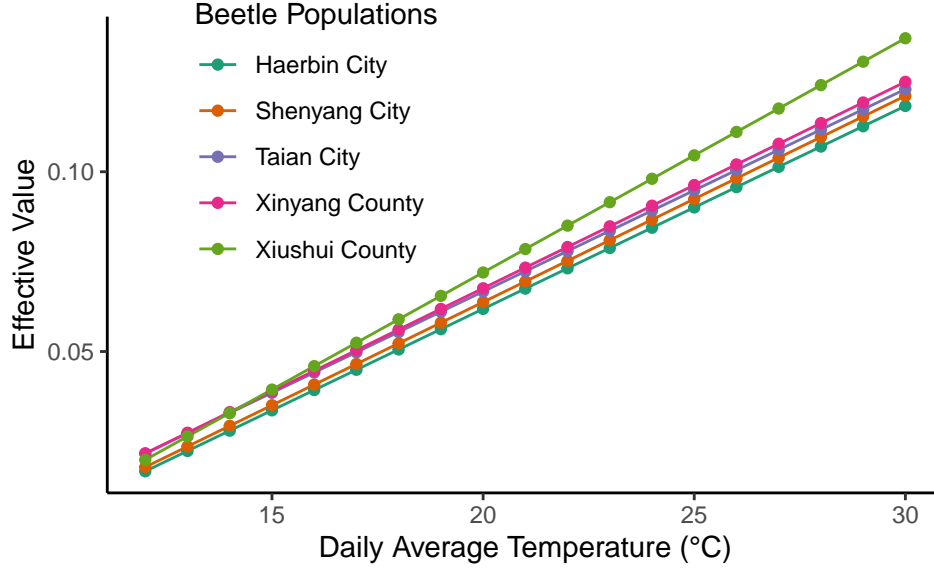


Figure 3: Effective value models for five populations of cabbage beetles (*Colaphellus bowringi*, females) along a latitudinal gradient in China [tang2017]. Models were parameterized from common garden experiments under constant temperatures. The southernmost population (Xiushui County) shows a consistently faster development rate than populations from more northerly sites, especially at colder temperatures. This pattern is indicative of cogradients variation, where both genetic and environmental effects reinforce the observed phenotypic trend.

This example illustrates how **hatchR** can be used to explore the intersection of developmental plasticity and local adaptation using real-world data. Such applications are useful for disentangling the genetic basis of thermal sensitivity, anticipating geographic responses to climate change, and informing population-specific management strategies.

6 Discussion

Although originally developed for fishes, **hatchR** is a generalizable and flexible tool for predicting phenology across a broad diversity of poikilothermic organisms. The effective value framework accommodates nonlinear thermal sensitivity and allows researchers to estimate the timing of developmental milestones under realistic, fluctuating temperature regimes. In this manuscript, we demonstrate how power-law models can be fit using the `fit_model()` function, or defined externally and passed into the `predict_phenology()` function. For users without coding experience, a graphical user interface is also available via the **hatchR** Shiny app, expanding accessibility and encouraging broader adoption across disciplines.

We highlight the extensibility of **hatchR** through a compilation of parameterizable species across four taxonomic classes and through three case studies that illustrate ecological, evolutionary, and conservation

applications. These case studies span field data, phylogenetic comparisons, and experimental designs, demonstrating the tool’s flexibility across data types and biological questions.

As with any model of developmental timing, it is important to recognize that temperature is not the sole determinant of phenological events. For embryos, environmentally cued hatching is seen across taxa, wherein variation in hatch timing and developmental stage at hatching can result from myriad abiotic and biotic triggers apart from temperature [Warkentin 2011 <https://doi.org/10.1093/icb/ucr017>]. While **hatchR** focuses specifically on temperature-dependent development, it can be integrated with complementary datasets or experimental manipulations to investigate these more complex, context-dependent interactions.

We also encourage users to carefully consider how models are parameterized. As discussed in greater detail in Sparks et al. (2025), we recommend using experimental data with at least four distinct temperature treatments spanning a wide thermal range. This is critical for capturing the nonlinear shape of development rate curves and avoiding overfitting or extrapolation errors. Many studies we encountered—particularly older or gray literature—relied on only two temperature treatments (e.g., (Kozák et al., 2009; Qualls & Shine, 1998)), which we do not recommend for model fitting due to the inability to detect curvature.

Given the wide potential applicability of **hatchR**, we especially emphasize its utility for rapidly developing species. For example, as shown in our phylogenetic case study, frog species with short incubation periods can be reared across multiple treatments in a single month, making them ideal for both research and teaching applications. Researchers can use these models to investigate thermal adaptation, phenological mismatch, or range-wide trait variation. In educational settings, developmental models could be built for *Daphnia*, insects, or amphibians to introduce students to reaction norms, thermal performance, and evolutionary trade-offs. Moreover, while **hatchR** currently focuses on pre-feeding stages, the effective value approach could potentially be extended to post-hatch phenological events—particularly when energy input is standardized (e.g., individuals reared under *ad libitum* conditions) (Lillehammer, 1986).

7 Conclusion

Although initially developed for fishes, **hatchR** is a broadly applicable tool for modeling temperature-dependent development in poikilotherms. It addresses key limitations of traditional degree-day approaches by accounting for non-linear thermal response curves and enabling predictions under fluctuating thermal conditions. As global temperatures rise and the phenology of organisms shifts in response, tools like **hatchR** will be increasingly valuable for anticipating the ecological and evolutionary consequences of climate change. While we provide numerous species-level parameterizations and demonstrate a set of representative case

studies, the full range of possible applications—across taxa, ecosystems, and educational settings—extends far beyond what we present here.

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