

**A generalizable tool for predicting developmental phenology for  
wild poikilotherms.**

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## Abstract

Before exogenous feeding, poikilothermic organisms have a near mechanistic relationship between ambient temperature and developmental rates. As such, statistical models can be easily developed to predict when organisms develop. Until recently, most models only used non-variable developmental regimes making them difficult to apply to wild environments. However, the R package hatchR formalized an approach using effective values where each day is given a developmental unit, accurately predicting developmental phenology for wild poikilotherms. hatchR was developed specific to fish, however this manuscript broadens the tool's application showing how it can be used to predict developmental phenology for a broad range of taxa, including amphibians, reptiles, and invertebrates. Moreover, we provide numerous examples of how this approach informs scenarios from applied management to basic questions regarding ecological and evolutionary questions.

# Introduction

## MORE CITATIONS

Because poikilothermic organisms rely on the environment to determine their body temperature, the physiological processes that regulate their bodies is tightly linked with their ambient temperature. When these organisms are in their early life histories prior to exogenous feeding, developmental rates are solely determined by environmental and genetic and/or maternal effects, with the environmental responsible for most of the variation in phenotypes (West-Eberhard, 2003). In turn, while developmental rates may vary widely across species, they typically fit a consistent non-linear relationship with temperature which can be easily mathematically approximated using the power law.

Historically, predicting developmental rates for populations in the wild relied on thermal thresholds where degree days are summed from mating and phenology occurs once a thermal threshold is passed. However, these models can be error prone, especially for longer developing species, because of the non-linearity of development, where embryos developing at colder temperatures need far fewer degree days to hatch than those at warm temperatures. Similarly, when applied to wild environments models fail to account for diel variability, where daily (and hence developmental rates) may be highly different across early life history development. Finally, populations may be locally adapted with developmental rates varying across populations (Sparks, Westley, Falke, & Quinn, 2017).

To address these issues in fishes, *Sparks et al.* (XXX) developed hatchR, which leverages effective value models developed by Sparks et al. (2019). The models function using developmental curves fit from experiments where organisms are raised at different temperatures and reciprocating those models to provide daily development estimates and are readily applied to wild environments. hatchR is packaged as an available R package on CRAN, as well as a Shiny app presented as a graphical-user-interface. While hatchR was developed specifically for fishes, the approach functions equally well for any poikilotherm for which development roughly follows a power law relationship. Here, we demonstrate the wide applicability of hatchR to non-fish organisms providing numerous putative sources for parameterizing developmental models across broad taxa and three specific examples of how hatchR can be used to investigate questions regarding ecological and inter- and intraspecies relationships.

## Methods

### Effective value models

Effective value models function by leveraging the statistical relationship derived from raising poikilotherms at different temperatures and fitting that relationship with a non-linear model. The formulation of that relationship can then be reciprocated which provides the unit of development for a day's average temperature an effective value. Effective value models function then by cumulatively summing to one at which the organism achieves the development of the parameterized trait.

The model follows the general format of:

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

Where  $i$  is the daily value and a fish hatches or emerges when the cumulative sum reaches one:

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

As an example, we parameterize an effective value model for coastal tailed frogs (*Ascaphus truei*) common to western North America (Figure 1). Custom parameterized models use the `fit_model()` function in `hatchR`, which is built on model 2 using the power law from Beacham & Murray (1990). Alternatively, to predict phenology using `hatchR`, the `predict_phenology()` only requires a model expression as input and could assume other model formulations custom built outside of the package by the user.

### Data and data checks

`hatchR` requires two essential paired vectors of data, one of daily average temperature and the other the date for those temperatures. The software is designed to function around common field temperature loggers and provides users the ability to summarize temperatures with multiple daily recordings.

#### Data input

Maybe include the below:

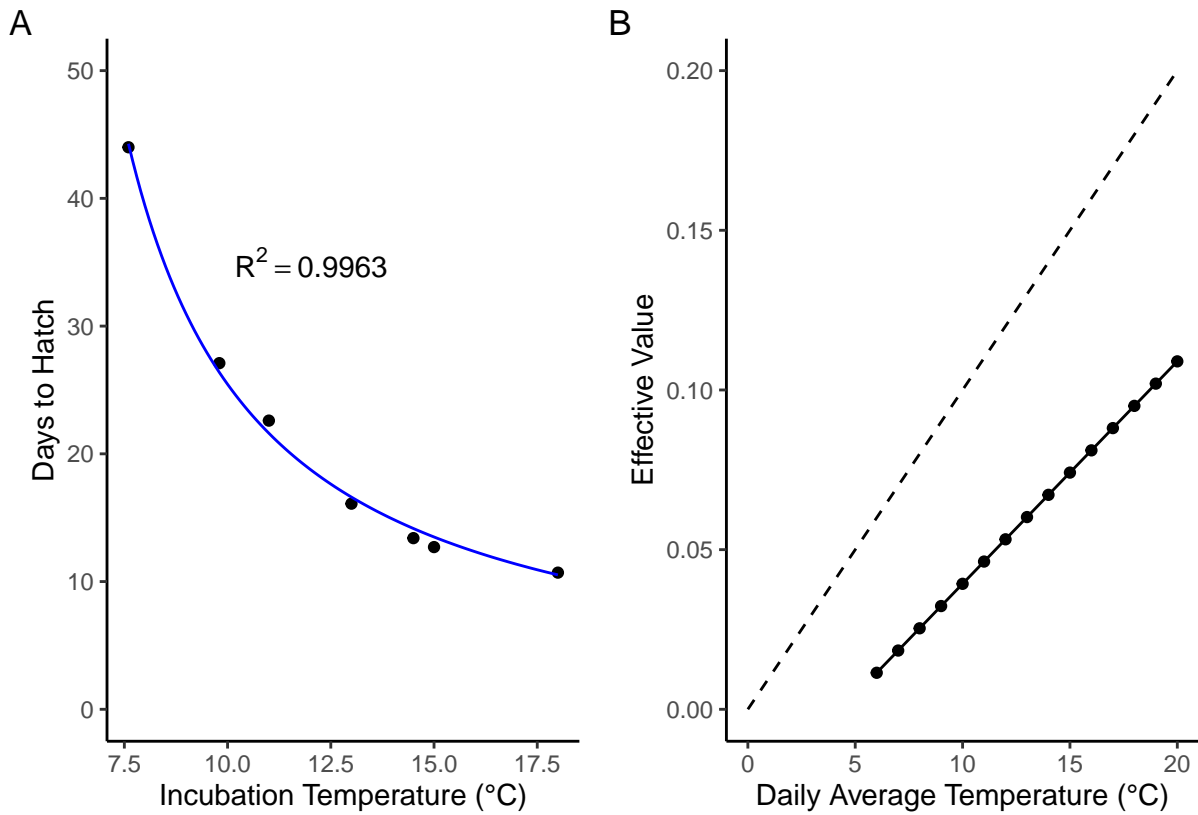


Figure 1: Custom hatching phenology model for coastal tailed frogs (*Ascaphus truei*). Panel A represents the model fit and raw data used to generate the effective value model and panel B are the effective values for daily temperatures between 6 and 20 °C. A dashed line with a 0.01 increase for every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

Table 1: Example temperature data for use in hatchR.

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

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.

## Predicting phenology

hatchR has two function to predict phenology. The first is `predict_phenology()` where users input date of reproductive event (`spawn.date`) along with their daily average temperature and corresponding dates. Alternatively, the function `predict_spawn()` leverages the effective value model framework but works backward from observed or expected development. For example, if a user observed one of the many frog or reptile parameterizations below in an area where they had accurate temperature measurements, they could easily estimate when those individuals' adults mated.

## Case studies

There are numerous applications for effective value models and poikilotherms that expand well beyond the bounds of this manuscript. We provide examples spanning four taxonomic classes of pikilotherms in the table below of studies that could liekly be used to parameterize custom models using the `fit_model()` function from hatchR. These are a non-exhaustive search of the both peer-reviewed and grey literature, but demonstrate the wide taxonomic breadth that could be paired with the effective value approach. We provide case studies of how these data may be used to address a variety of questions, but expect applications to extend far beyond what we demonstrate here.

Table 2: Sources for effective value parameterizations using `fit_model()` in `hatchR`. Represented are a broad range of taxa and some review studies which include numerous putative sources. While et al. (2018) and Pritchard & Leggott (1987) not vetted for full functionality and equations would need to be reciprocated.

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

Class	Order	Genera	Species	Study
		<i>Taeniopteryx</i>	<i>T. nebulosa</i>	J. E. Brittain (1977)
	Coleoptera	<i>Colaphellus</i>	<i>C. bowringi</i>	Tang, He, Chen, Fu, & Xue (2017)
			18 species	Developmental equations in Pritchard & Leggott (1987)
Malacostraca	Decapoda	<i>Pontastacus</i>	<i>P. leptodactylus</i>	Aydin & Dilek (2004)

## Ecological

To demonstrate an ecological application for hatchR, we used estimates for oviposition timing for *A. truei* from Karraker et al. (2006) (unpublished data). Using the parameterized coastal tailed frog model presented above (Figure 1) and assumed a fixed oviposition date based on the estimates from Karraker et al. (2006) we predicted days to hatch for populations in Washington and Oregon, where long-term temporal predictions of stream temperature were available (Siegel, Fullerton, FitzGerald, Holzer, & Jordan, 2023) at the COMID level. Our results indicate developmental 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 average days to hatch taking more than twice as long in Olympic National Park as in the Willapa Hills (32 days compared to 15 days). When broken down by site, there was a weak but significant relationship between year and days to hatch (Supplemental Data), with slight negative trend over the thirty year period, indicating temperatures at the sites were warming (Figure 2). Over the 30-year period, the site with the quickest average developmental period was in the Willapa Hills (15 days) and the site with the longest average developmental period was in Olympic National Park (44 days). Finally, the standard deviation at Willapa Hills, Siskiyou Mountains, and Cascade Mountains was much lower (<3) than that of the Olympic National Park sites (11.0) indicating much greater sensitivity to temperature change over the past 30-years in the park.



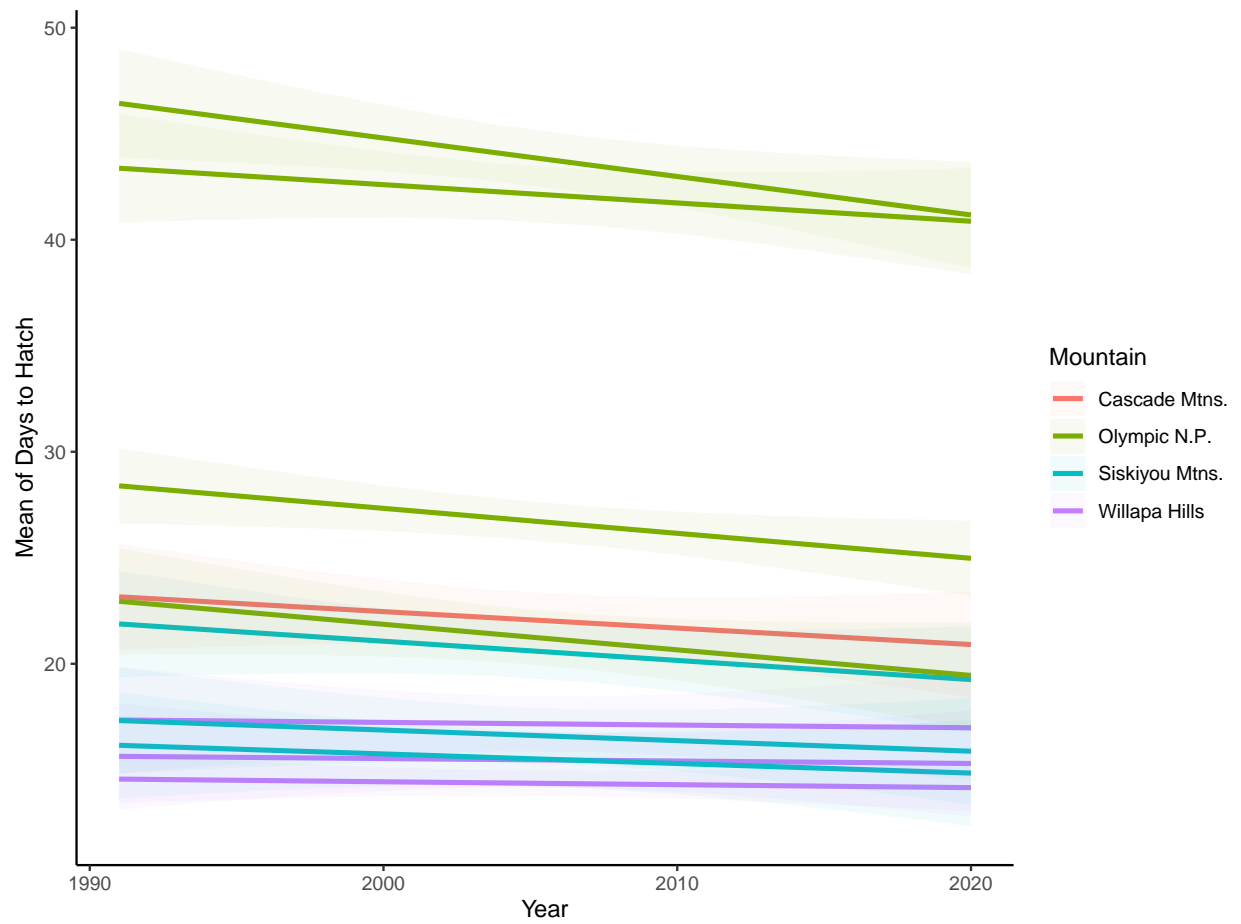


Figure 2: Estimated marginal means of days to hatch for coastal tailed frogs from various mountain ranges across their range.

## Phylogenetic

As species diverge from one another it is expected that phenotypes respond to different niche space which is part of that divergence. To assess those differences, one can execute experiments that test phenotypic divergence (common garden or reciprocal transplant) and display phenotypic data as reaction norms, showing the relative genetic and environmental contribution to phenotypes. hatchR is a unique tool for demonstrating these differences because the strong fits of developmental rates, either displayed as model fits or the linearized effective value model lines are forms of reaction norms, even if species did not experience the same developmental conditions. While not as precise as using controlled experiments, hatchR derived reaction norms can be used to demonstrate how genetic x environment interactions vary among species and how those phenotypes may fit the niche spaces occupied by phylogenetically close or divergent species.

To demonstrate this approach, we leverage custom time to hatch parameterizations for four *Lithobates* frog species developed by Moore (1939). We show large differences in developmental rates for common North American frogs which often overlap in their ranges—green frog, *L. clamitans*; northern leopard frog, *L. pipiens*; pickerel frog, *L. palustris*; and wood frog, *L. sylvaticus*. Specifically, when developmental models were fit to a randomly generated temperature regime of 16 and 24 C°, the species-specific effects of development are clear. Whereas at warm temperatures, all species hatch the same day or within one day of one another, at cold temperatures, wood frogs develop the quickest and green frogs the slowest (twice the rate of wood frogs). BRIAN ADD SOMETHING ABOUT THEIR ECOLOGY ABOVE TO FIT THIS INTO BROADER CONTEXT.

## Local Adaptation

As was the case with the phylogenetic example, developmental models may be parameterized for populations of the same species to better understand the effects of local adaptation. Here, we take data from a common garden experiment with Chinese cabbage beetles distributed across of a latitudinal cline of 3,440 kilometers (Tang et al., 2017). The beetles were raised at six temperatures ranging from 16 to 28 C° and while development rates for females were very similar for populations from northern latitudes, populations from the south developed faster, consistent with the cline variation (local adaptation) where the genetic and environmental effects on phenotypes are additive Sparks, Kraft, Blackstone, McNickle, & Christie (2022). We further demonstrated this phenomena by fitting custom developmental models for each population (Longnan was removed because values were the same as Xiushui), showing rank order changes in developmental rates at colder temperatures, indicating cline phenotypes may only be expressed in a subset of temperatures

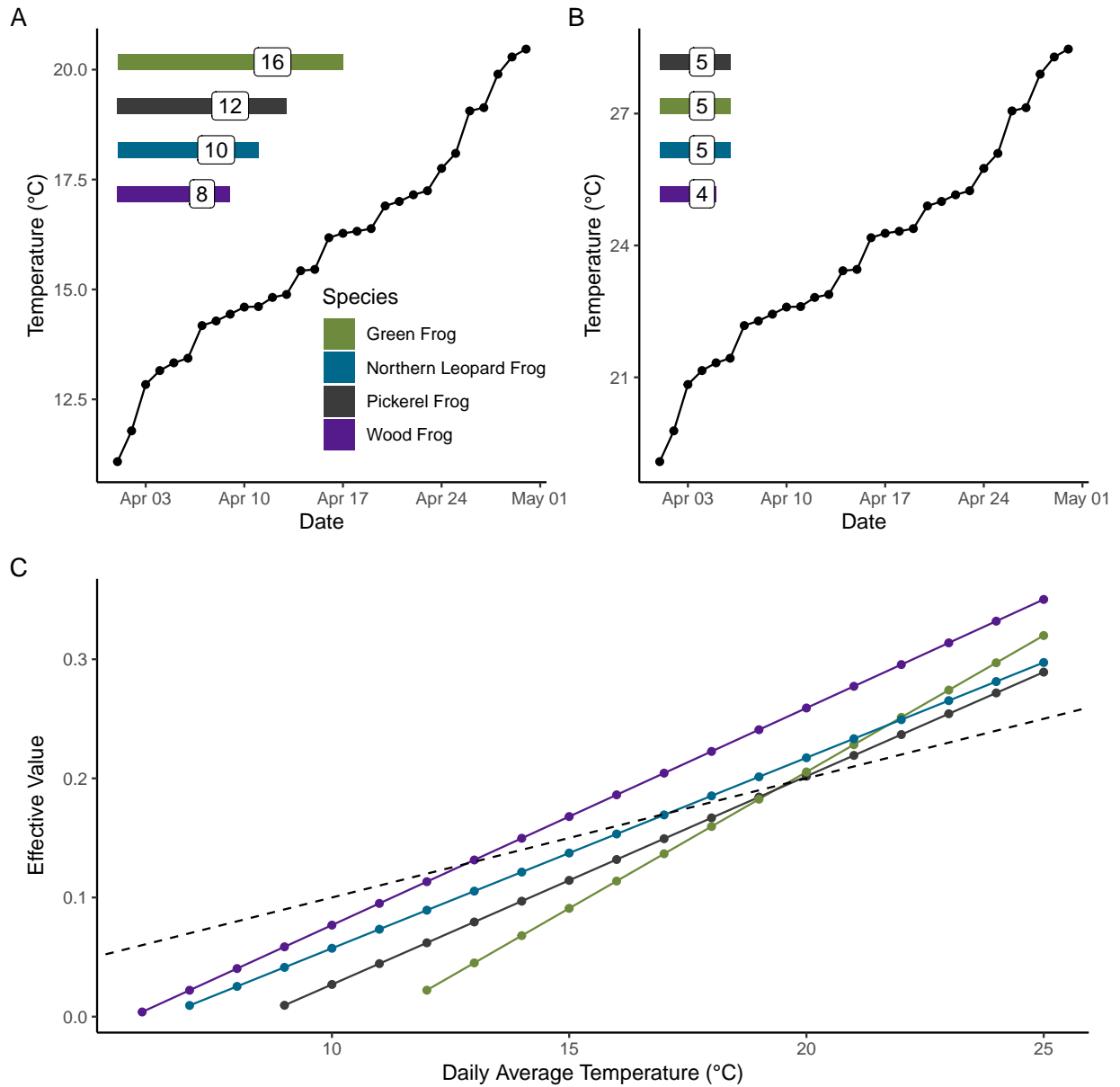


Figure 3: Custom hatch timing models developed for four North American frog species. Models are parameterized from Moore 1939 and phenology is predicted using a randomly generated temperature regime with mean 16 °C (Panel A) and mean 24 °C (Panel B). Panel C shows the effective values for different mean daily temperatures for each species, which are effectively species-specific linearized developmental reaction norms. Note the genetic x environment interactions in Panel C as temperatures warm and shown by the rank order change in species in Panel A compared with Panel B.

130 (Figure 4).

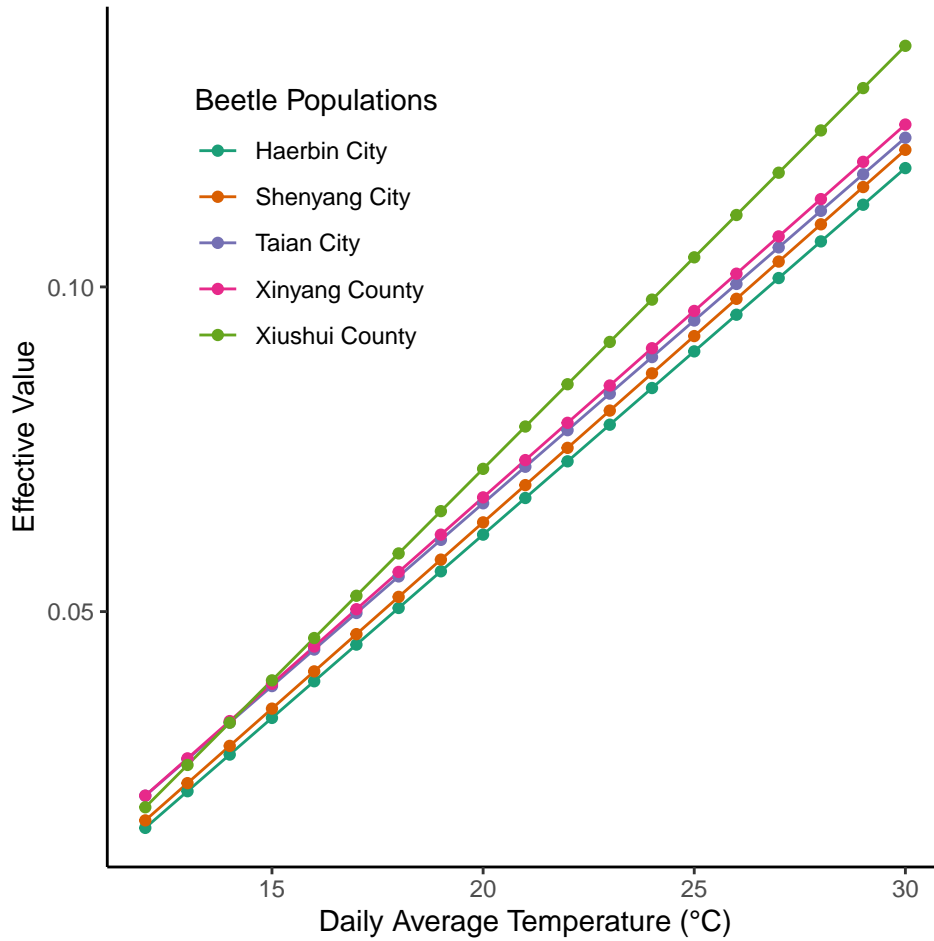


Figure 4: Effective value models developed for five populations of cabbage beetle (females) along a latitudinal cline in China from Tang et al. 2017. Note the large difference in developmental rate between Xiushui County and the other, more northerly populations, which is indicative of cline variation.

## 131 Discussion

132 hatchR, while originally designed specific to fishes, is a generalizeable tool to predict phenology for any  
 133 wild poikilotherm. Power law models can either be fit using the `fit_model()` function in the package or  
 134 users can build custom models and pass their expressions to `predict_phenology()` in the hatchR workflow.  
 135 hatchR also offers a graphical-user-interface which allows users to interact with the software without needing  
 136 programmatic aptitude. With this manuscript we demonstrate numerous putative sources of parameterization  
 137 for species spanning four taxonomic Classes and provide additional resources for many more species. We also  
 138 present three specific case studies to demonstrate the wide breadth of questions that may be answered with

parameterized effective value models.

As with fishes, it is important to recognize other environmental cues may impact when organisms hatch or achieve other developmental milestones. In particular, predator cues...BRIAN ADD HERE. Talk also about physical cues like salinity or metals etc.

Additionally, we encourage users to be especially cognizant of how models are parameterized (discussed at greater length in **hatch paper 1**). Specifically, when parameterizing models we recommend using a minimum of four temperature treatments with temperatures as disparate as reasonable. We similarly caution users to not heavily interpolate past the fits of their models. In the process of investigating potential sources for species parameterizations, we found many studies that only used two experimental temperatures to test developmental rates (*e.g.*, Kozák et al. (2009)). We explicitly recommend against using such data to parameterize these models because two treatments will result in a model that misses the non-linearity inherent to these relationships.

Given the broad applicability of this tool for wide range of species, we particularly highlight quick developing species such as the frogs presented in the phylogenetic case study. With all species, multiple treatments could reasonably be conducted in a month's time and could be used for a variety of questions or applications. For example, one could parameterize developmental models for a variety of populations of one species to investigate local adaptation and the response of populations to changing temperatures. Alternatively, models could be developed with *Daphnia* or insects in classrooms to introduce reaction norm concepts. Similar to bioenergetic models, if all individuals are assumed to be receiving the same energy input (*e.g.*, fed *ad libitum*,) models could potentially be extended for additional phenological events once individuals begin exogenous feeding (Lillehammer, 1986).

#### ... Outline Summary for Above...

P1: Summary of above

P2: Caveats

- namely that some taxa like insects and frogs are much more likely to bail on development when environmental cues suggest they need to
- more studies need to include more than 2 temperatures Qualls & Shine (1998) Kozák et al. (2009)

P3: Other considerations?

- easy to parameterize custom models for quick developing species

- examples where other stages could be modeled assuming constant feeding (Lillehammer, 1986)

P4: ???

## Conclusion

Despite being designed for fishes, hatchR is a generalizeable and simple tool for predicting developmental phenology across a wide array of poikilothermic organisms. Furthermore, the tool overcomes many of the limitations of other developmental models used for these species. Tools such as hatchR will be particularly useful for interrogating species and population responses to quickening changes to their thermal environments. While we provide numerous putative sources for parameterization and a handful of case studies, we expect the applications of hatchR far extend beyond what we envision here.

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