

**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

- P1: Poikilotherms and ambient temperatures
- P2: ATU models and effective value models
- P3: Examples with other species
- P4: Our approach here (R package and Shiny app)

## 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 western 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 actually predict phenology using `hatchR`, the `predict_phenology()` only expects a model expression as input and could assume other model formulations custom built outside of the package by the user.

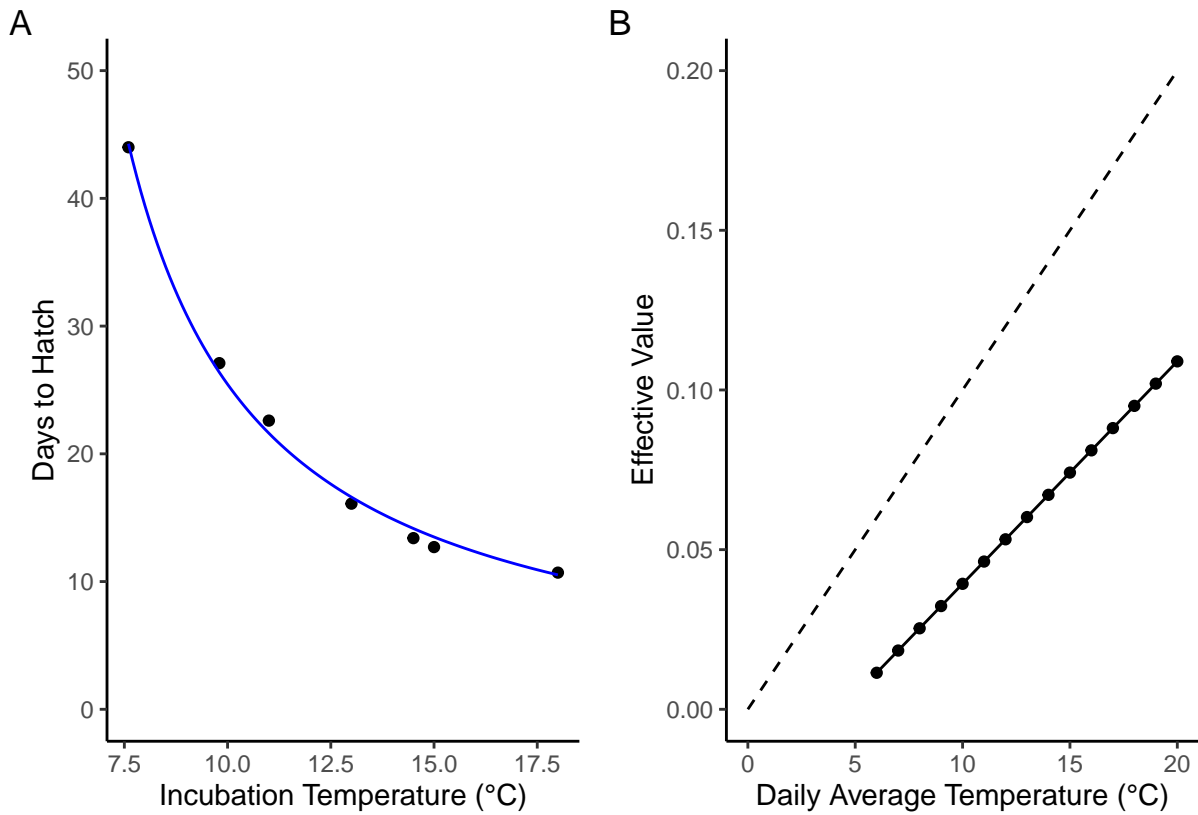


Figure 1: Custom hatching phenology model for western tailed frogs (*Ascaphus truei*). Panel A represents the model fit and raw data used to generate the effective value model and panel B are the effective values for daily temperatures between 6 and 20 °C. A dashed line with a 0.01 increase for every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

## 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:

Table 1: Example temperature data for use in hatchR.

date	temperature
2000-01-01	2.51
...	...
2000-07-01	16.32
...	...
2000-12-31	3.13

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 XXX examples in the table below of studies that could 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.

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.

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>	
		<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. undulatus</i>	Angilletta, Winters, & Dunham (2000)
		Podarcis	<i>P. muralis</i>	Van Damme, Bauwens, Braña, & Verheyen (1992)
	Testudines	Mauremys	M. reevesii	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)

Class	Order	Genera	Species	Study
		<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. nebulosa</i>	J. E. Brittain (1977)
Malacostraca	Decapoda	<i>Pontastacus</i>	<i>P. leptodactylus</i>	Aydin & Dilek (2004)

58 While et al. (2018) not vetted for completeness

59 Pritchard & Leggott (1987) contains examples of power equations for 18 insect species

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

## 61 Ecological

62 Tailed frog and westlope cutthroat example???

## 63 Phylogenetic

64 Frog example Moore 1939.

## 65 Local Adaptation

66 Need an example where multiple populations from the same species are parameterized. ideally not an  
67 amphibian

## 68 Discussion

69 P1: Summary of above

70 P2: Caveats

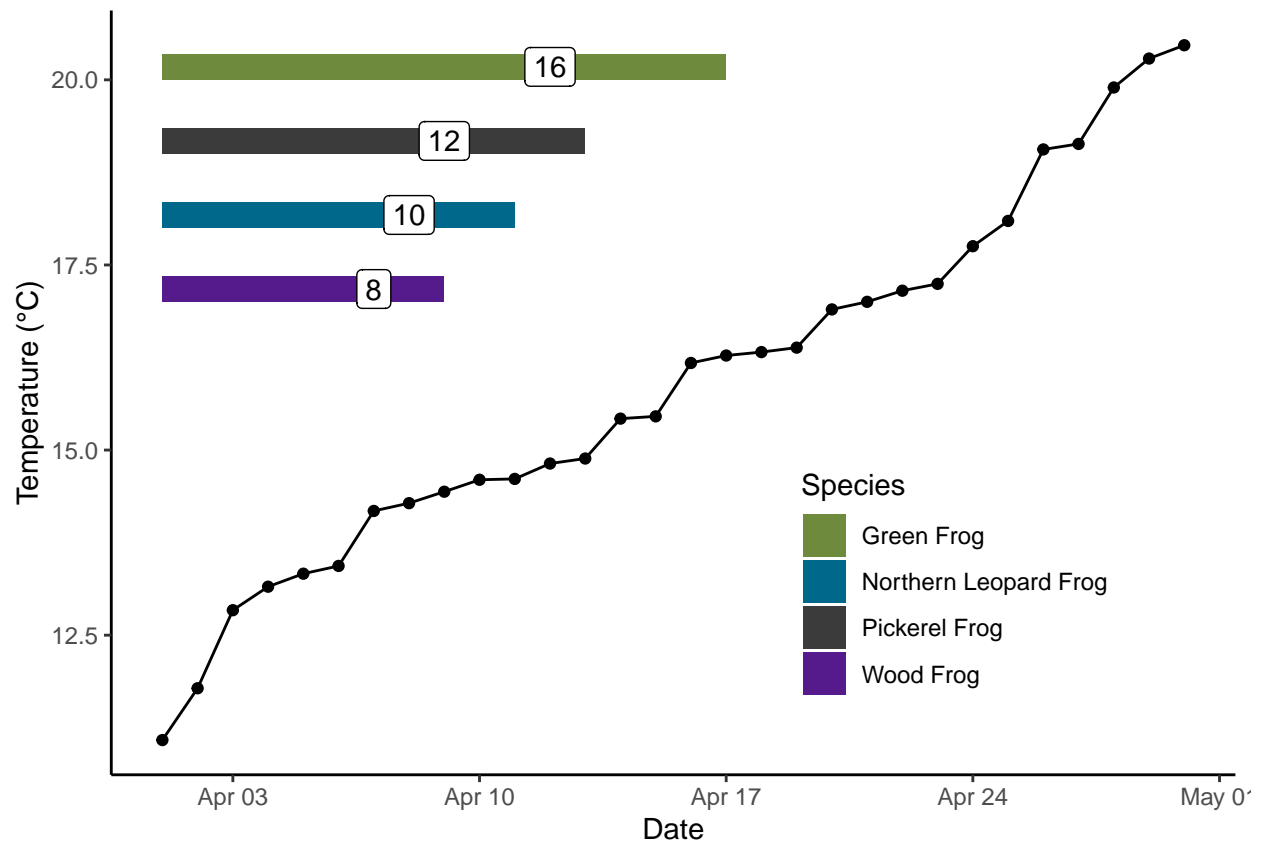


Figure 2: Custom hatch timing models developed for four North American frog species. Models are parameterized from Moore 1939 and phenology is predicted using a randomly generated temperature regime with mean 16 °C.



- namely that some taxa like insects and frogs are much more likely to bail on development when environmental cues suggest they need to

P3: Other considerations?

- easy to parameterize custom models for quick developing species

P4: ???

## Conclusion

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