Modeling biological processes as stopped random walks

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EFI and Statistical Ecology Section Webinar

December 2, 2024

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Stopped Random Walks

Many biological processes can be modeled as stopped random walks

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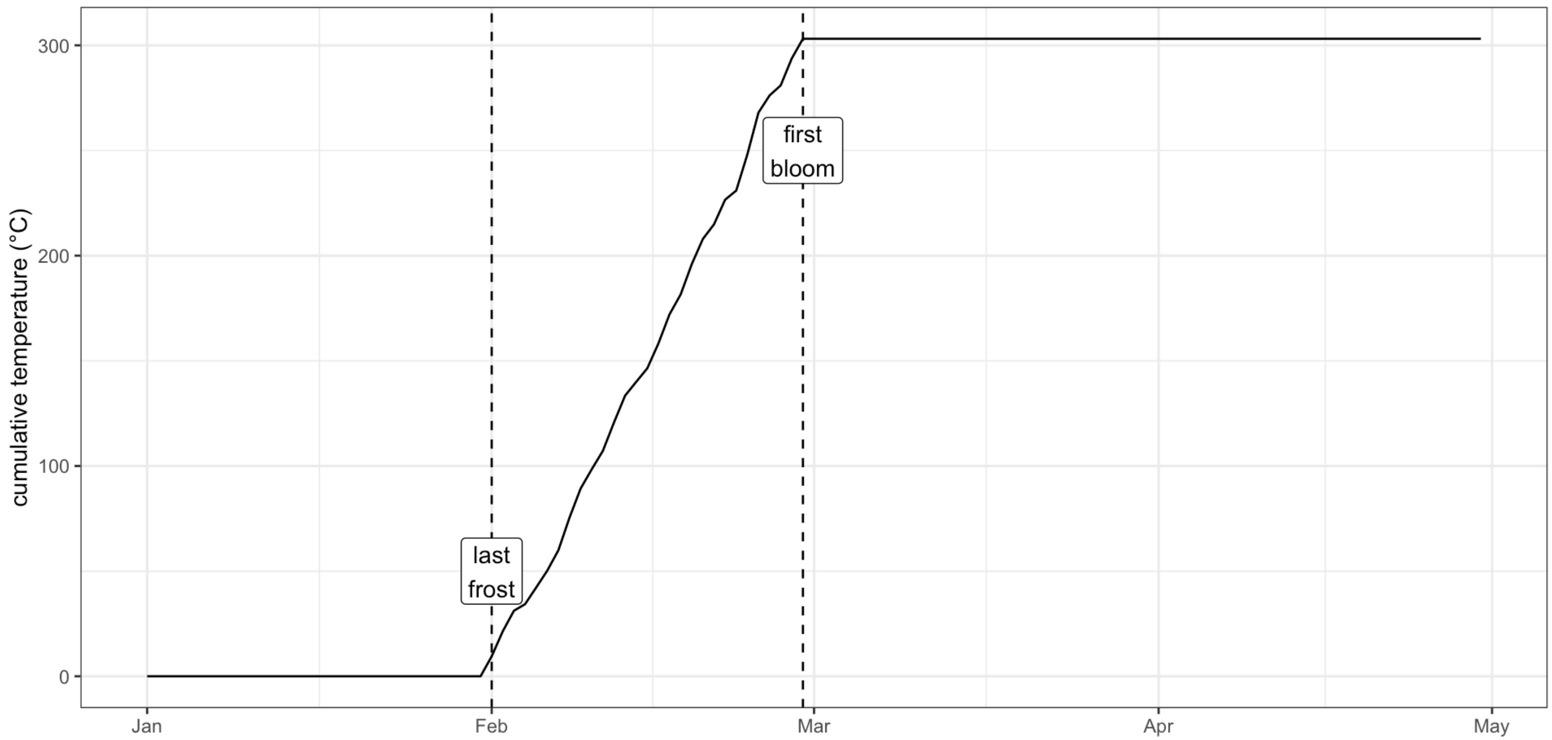
Simulation

▶ expand for R code



a simulation of the law of flowering plants: a flower first blooms in the spr
temperatures reach a threshold

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Two assumptions

Let $X_i > 0$ denote the force exerted on the plant on day i.

- Assume
  1. X_i have common mean μ (the ambient temperature).
  2. X_i are independent with common variance σ^2.

- Both assumptions can be relaxed.
  - e.g., 1. can be replaced with the assumption that X_i have mean μ_i, and $\sum \mu_i$ does not grow too quickly (regularly varying with index 1).

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CLT for stopped random walks

Let $S_a^i = \sum_{j=a}^{i} X_j$ denote the cumulative force from day a to i

Let n_γ denote the bloom date.

- Assume the plant blooms when S_a^i first passes γ,

$$n_\gamma = \min\{i : S_a^i \geq \gamma\}$$

When γ is large,

$$n_\gamma \mathrel{\dot\sim} \text{Normal}\left(\gamma/\mu + a,\ \gamma\sigma^2/\mu^3\right)$$

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Simulation ($a = 32, \gamma = 300$)

▶ expand for R code

bloom_date	mean_temp
2024-03-25	5
2024-02-28	10

▶ expand for R code

term	estimate	std.error	statistic	p.value
a	31.62	0.37	86.36	0
γ	297.13	7.09	41.91	[illegible]

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Three takeaways from CLT

Recall bloom date $n_\gamma \dot\sim \text{Normal}\left(\gamma/\mu + a,\ \gamma\sigma^2/\mu^3\right)$. This imples:

1. $\mathbb{E}[n_\gamma - a] \propto 1/\mu$ and variance $\text{Var}\left(n_\gamma\right) \propto 1/\mu^3$
2. γ depends on the temperature scale (°C, °F, etc.) and is only identified if μ is known
3. When a unknown, we can count from any $b > 0$ since for $\delta = a - b$,

$$n_\gamma + \delta \dot\sim \text{Normal}\left(\gamma/\mu + \delta,\ \gamma\sigma^2/\mu^3\right)$$

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Experimental Data

Experiment (Charrier et al. 2011)

- 30 walnut trees (*Juglans* sp.), 6 genotypes at 2 locations.
  - Stems sampled in November from each tree and cut in 7-cm-long pieces with only one bud.
  - Stems chilled (4°C) and then forced (warmed) at different temperatures (5, 10, 15, 20 and 25°C).

- We examine the relationship between:
  - forcetemp: temperature during forcing
  - response.time: (day of budburst) when 50% of buds unfolded (stage 15 of BBCH scale)

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Experiment (Charrier et al. 2011)

▶ expand for R code

forcetemp	response.time
5	175.88
10	97.06
15	31.76
20	24.71
25	22.94

data from Charrier et al. (2011)

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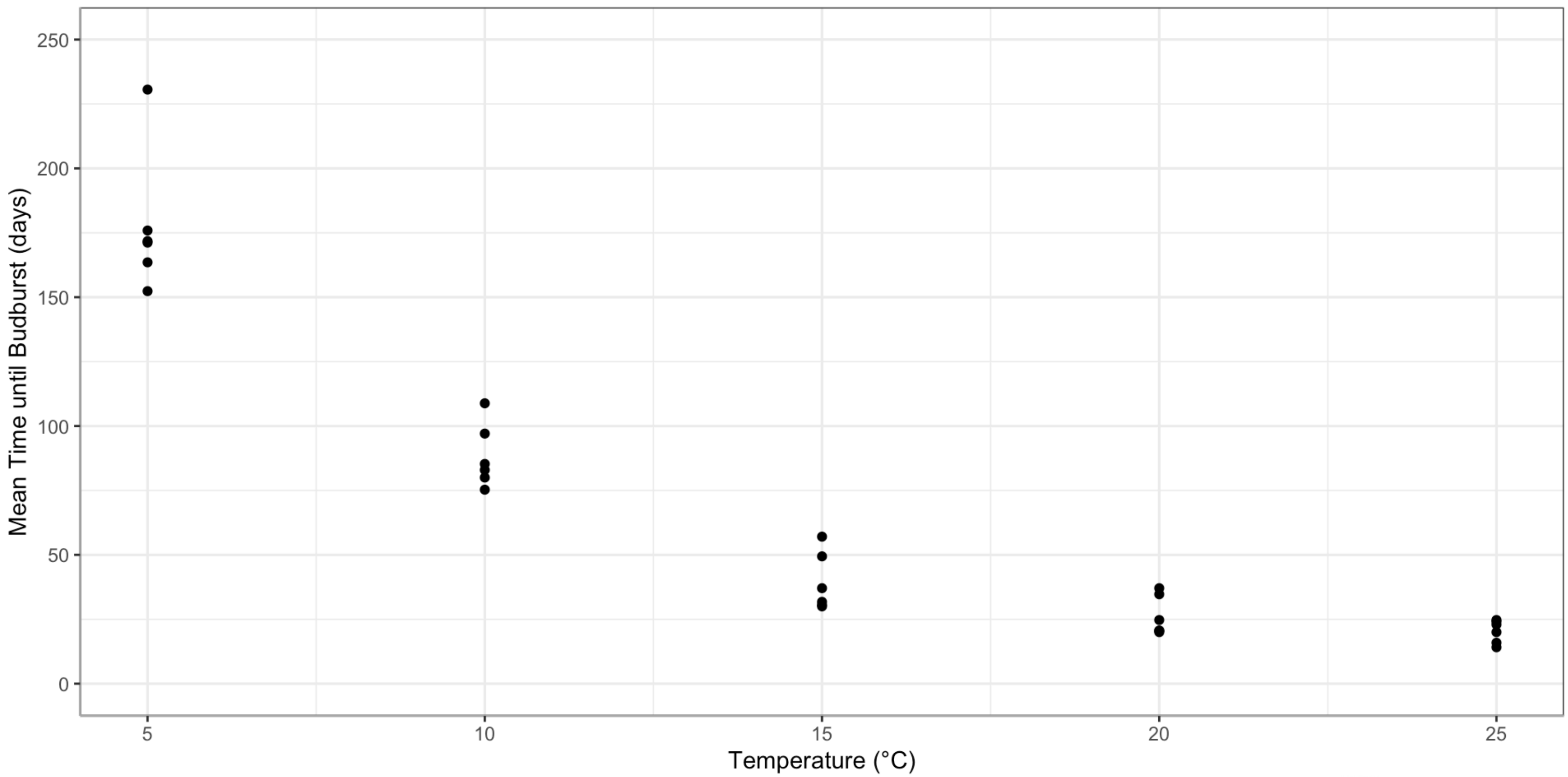
Experiment (Charrier et al. 2011)

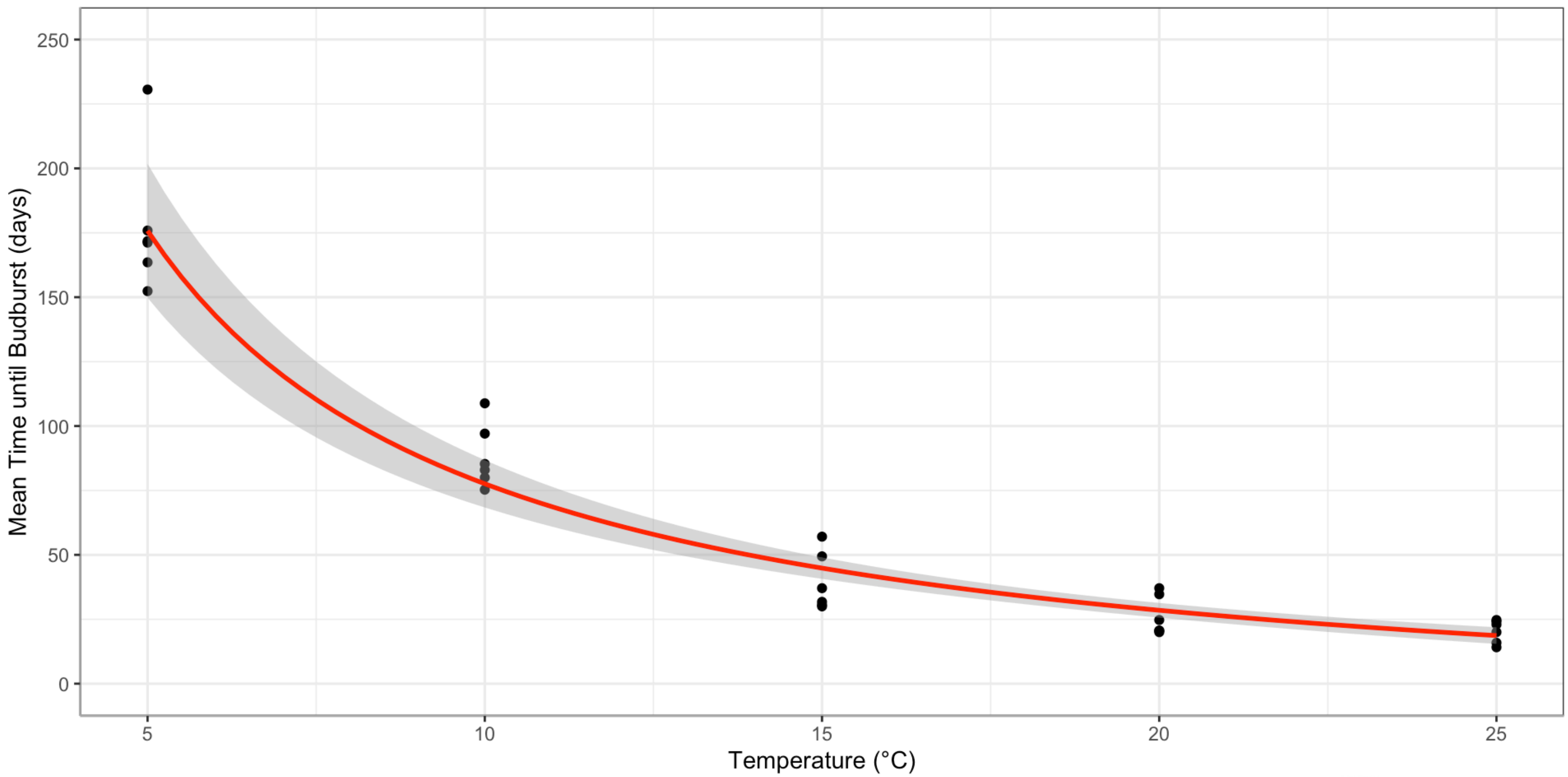
▶ expand for R code



data from Charrier et al. (2011)

Fit using lm

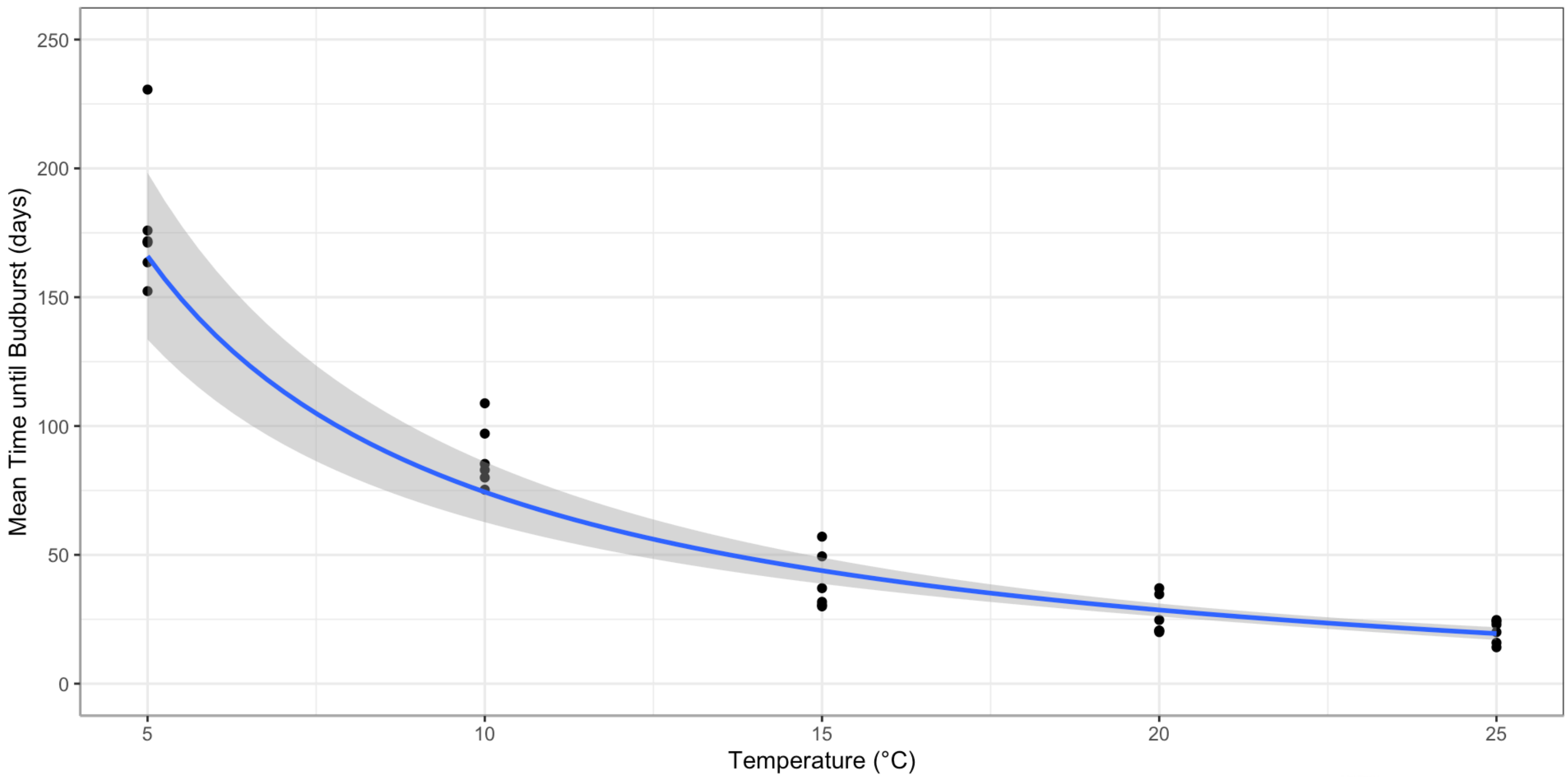
▶ expand R code



data from Charrier et al. (2011)

Fit using glm

▶ expand for R code

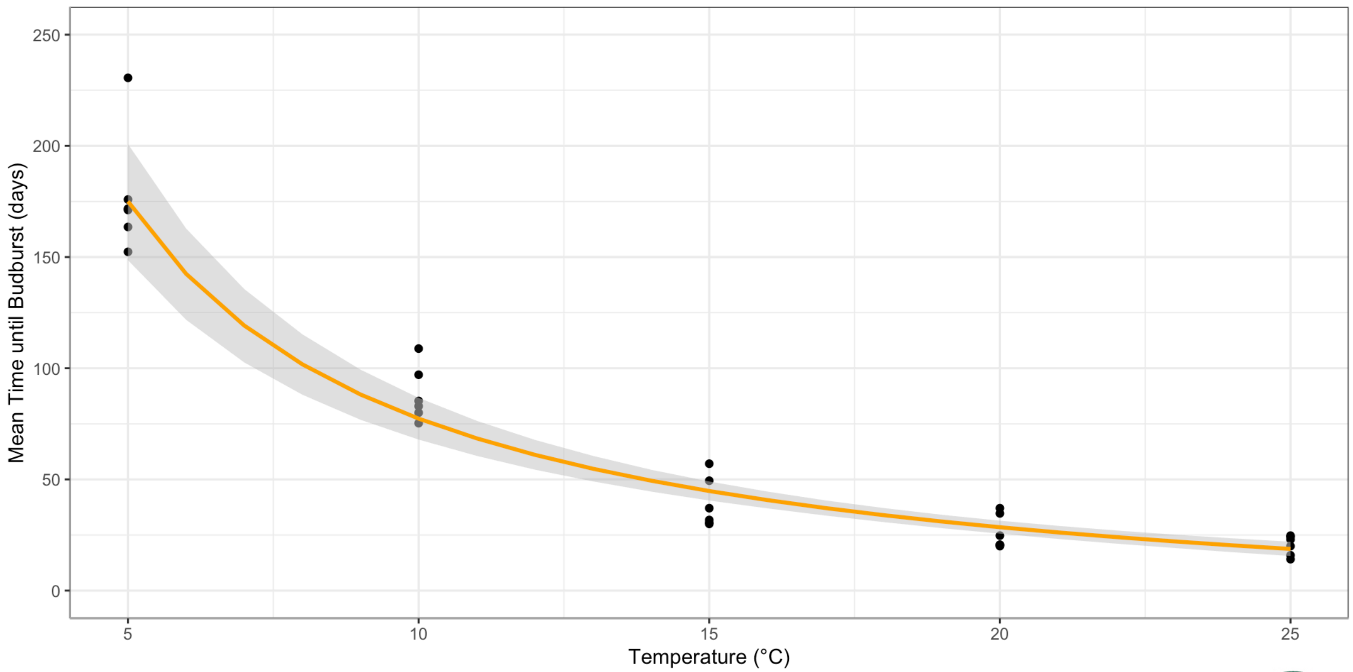


data from Charrier et al. (2011)

Fit using Stan

- expand for Stan code

- expand for R code



data from Charrier et al. (2011)

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Observational Data

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Observations (Marsham 1746-1958)

- Robert Marsham recorded the first occurrence of 27 signs of spring each year.
  - Marsham family continued to collect the data after Robert's death in 1797

- We model the day leaves first appeared on his oak trees.
  - spring.temp: cumulative daily temperature (2/1 to 4/30)
  - response.time: number of days from January 1 to budburst

- The first day of temperature accumulation, a, ma

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Observations (Marsham 1746-1958)

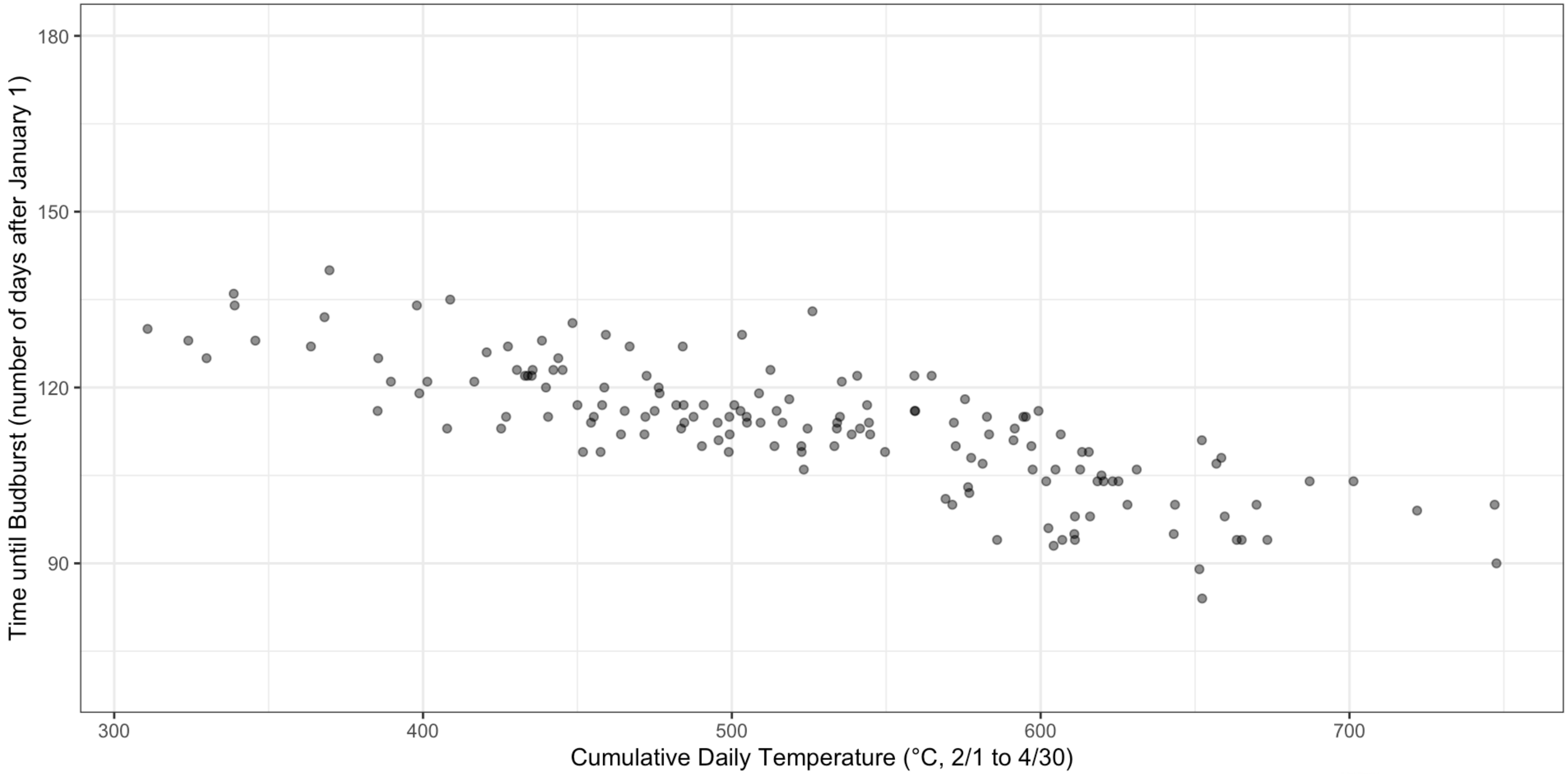
▶ expand for R code

year	response.time	spring.temp
1772	134	398.0
1773	113	541.5
1957	104	701.3
1958	122	472.4

data from Marsham (1746-1958)

Observations (Marsham 1746-1958)

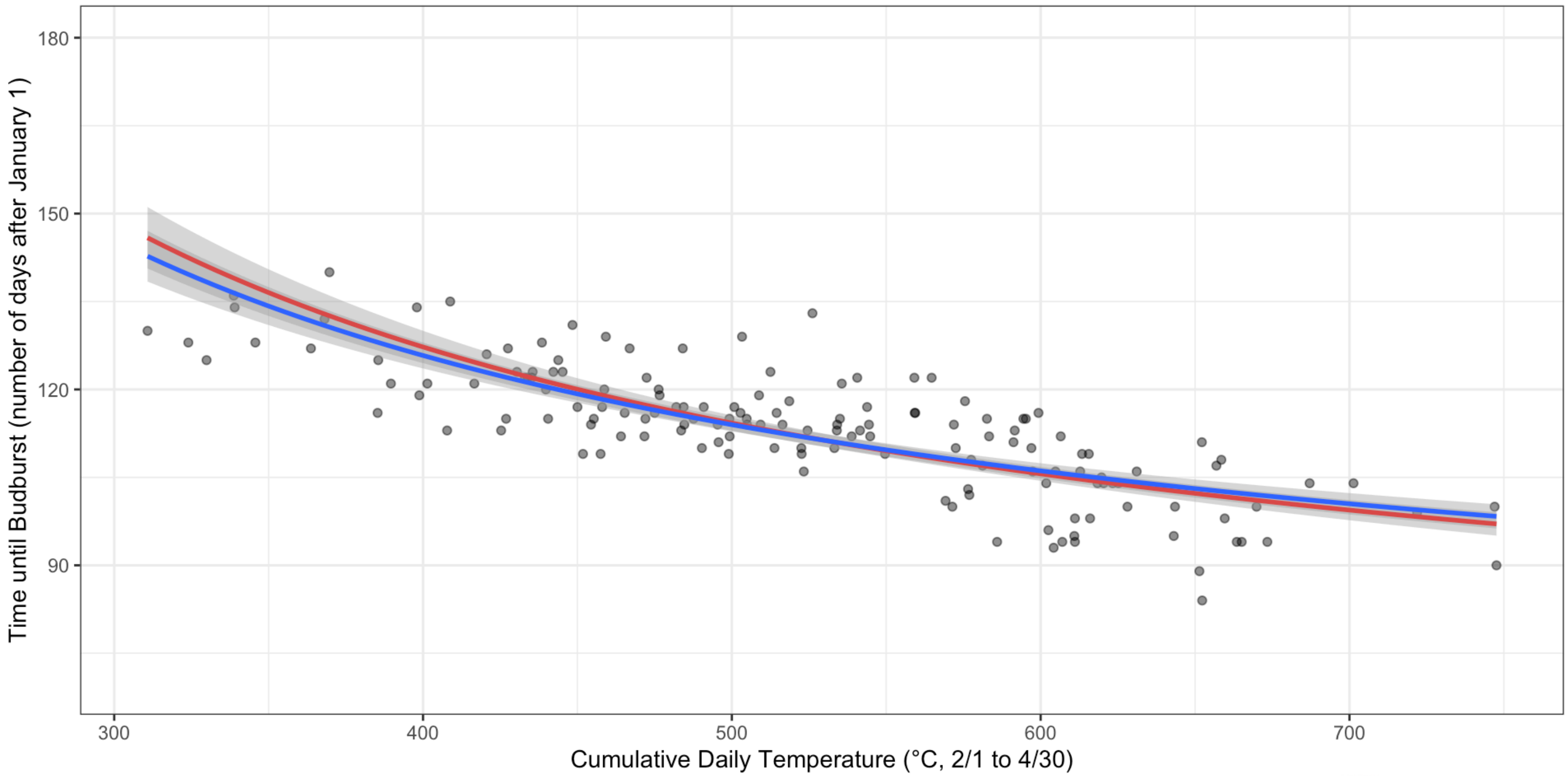
▶ expand for R code



data from Marsham (1746-1958)

Fit using lm/glm

- expand R code



data from Marsham (1746-1958)

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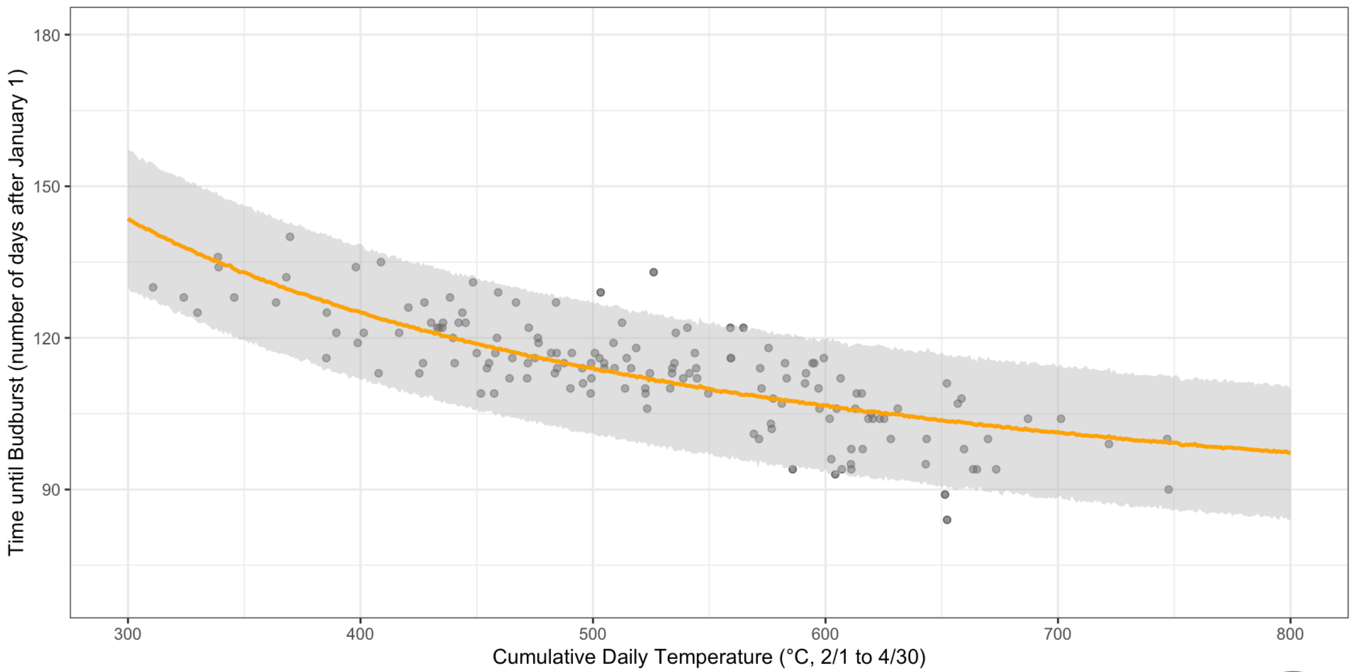
Fit using Stan

▶ expand for Stan code

▶ expand for R code



data from Marsham (1746-1958)

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Non-asymptotic model

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One last takeaway from CLT

- In experimental setting, day forcing begins known by design.
  - For observational, day forcing begins not known.
  - Cumulative temperature from 2/1 to 4/30 is a proxy for total force. Proxy is accurate when γ large. Why?

- Recall $n_\gamma \dot{\sim}$ Normal $\left(\gamma/\mu + a,\ \gamma\sigma^2/\mu^3\right)$ when γ is large.
  - When γ is large, n_γ is large, and $n\mu \approx \sum_{i=a}^{n} \mu_i \approx \sum_{i=b}^{n} \mu_i$ for any $a, b << n$. i.e., First few μ_i don't matter.
  - Argument fails when γ is not large.

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Non-asymptotic model

- Assume instead $X_i > 0$ is normal with mean μ_i and variance σ^2.
- Note that $\mathbb{P}\left(n_\gamma \leq m\right) = \mathbb{P}\left(S_a^m > \gamma\right) = \Phi\left(\frac{\sum_{i=a}^m \mu_i - \gamma}{\sqrt{m-a}\,\sigma}\right)$ so that the likelihood contribution of each observation is

$$\mathcal{L}\left(\gamma, \sigma, a; n_\gamma, \{\mu_i\}\right) = \Phi\left(\frac{\sum_{i=a}^{n_\gamma} \mu_i - \gamma}{\sqrt{n_\gamma - a}\,\sigma}\right) - \Phi\left(\frac{\sum_{i=a}^{n_\gamma - 1} \mu_i - \gamma}{\sqrt{n_\gamma - 1 - a}\,\sigma\right.$$

- n.b. $\sum_{i=a}^{n_\gamma} \mu_i = \sum_{i=1}^{n_\gamma} \mu_i \, 1_{i \geq a}$ and

$1_{i \geq a} \approx (1 + \exp(-b(i-a)))^{-1}$ when b is large.

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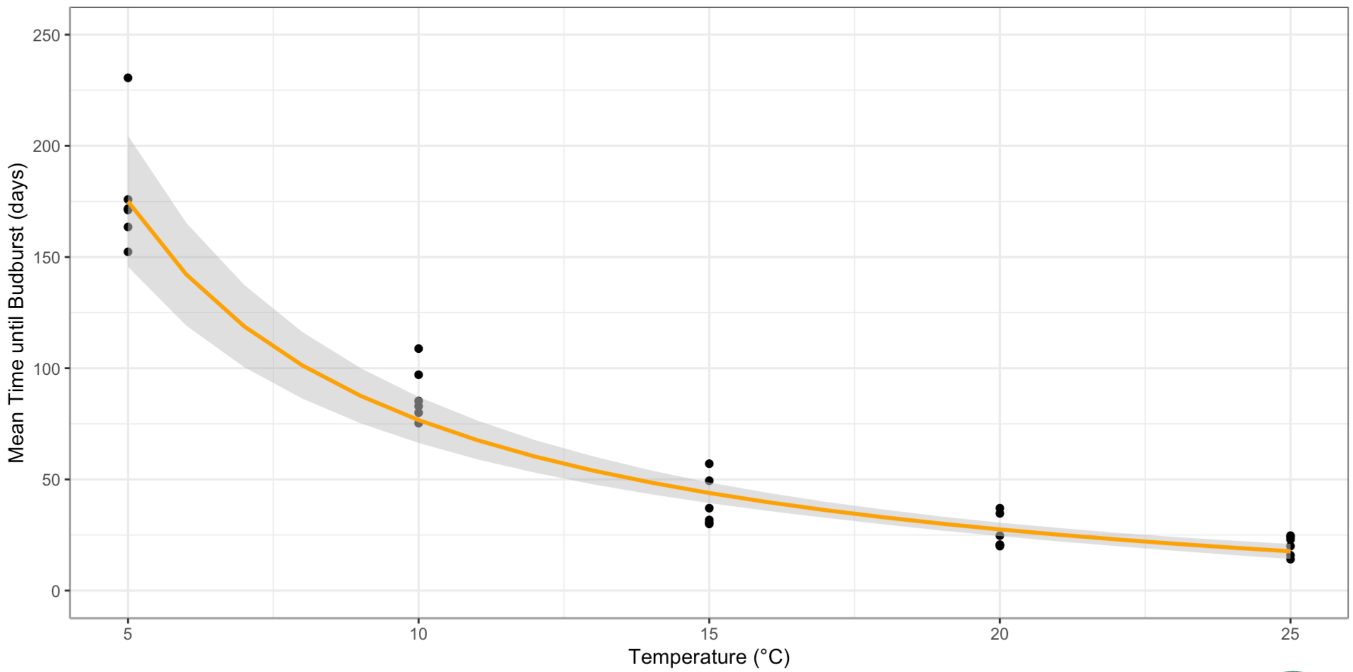
Experiment (Charrier et al. 2011)

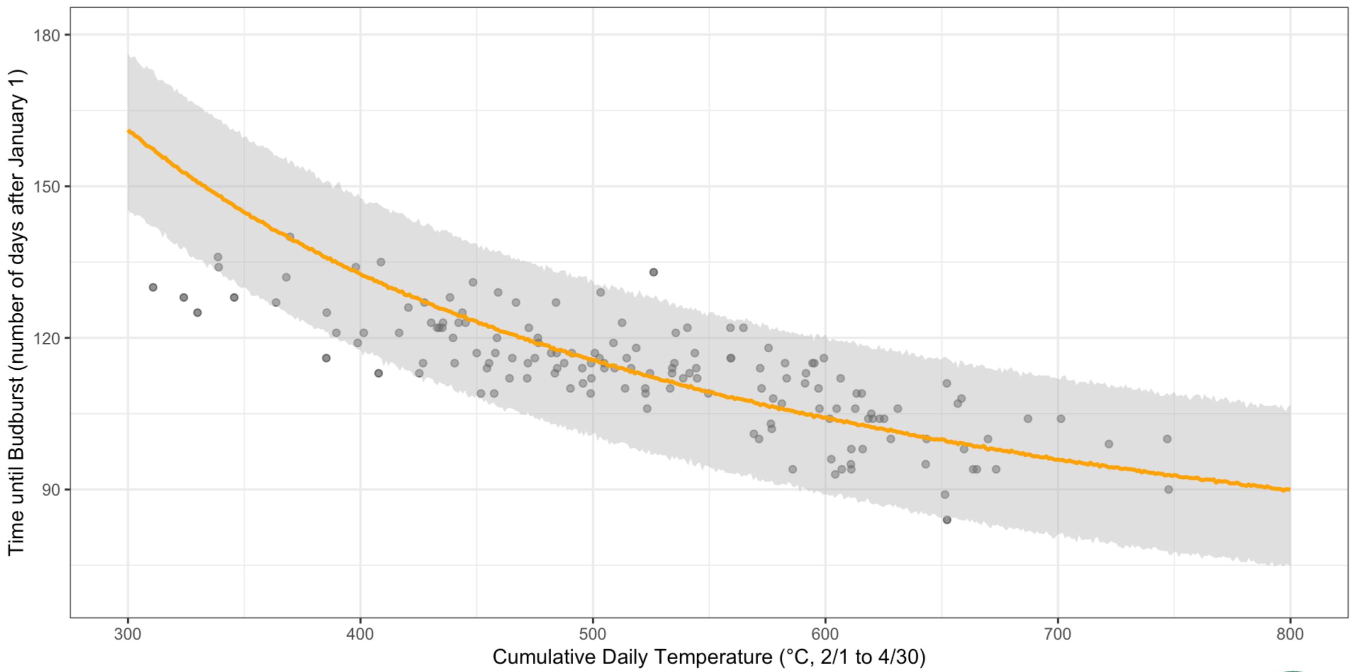
- ▶ expand for Stan code
- ▶ expand for R code (Experimental)



data from Charrier et al. (2011)

Observational (Marsham 1746-1958)

- expand for Stan code
- expand for R code (Observational)



data from Marsham (1746-1958)

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Conclusion

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Model comparison

- expand for R code

data	model	$\widehat{\gamma}$	$\widehat{\gamma}_{\text{lower}}$	$\widehat{\gamma}_{\text{upper}}$
Charrier	asymptotic	977	806	1144
Charrier	non-asymptotic	983	790	1175
Marsham	asymptotic	246	213	281
Marsham	non-asymptotic	380	344	415

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Summary

1. We justified modeling biological process as stopped random walks.
2. We reviewed the CLT for stopped random walks.
3. We applied the CLT to experimental and observational data.

- Found CLT approximation compared well to non-asymptotic model.
  - The model can be complicated to allow for more covariates or additional variation.

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References

1. Auerbach, Jonathan. (2023). A demonstration of the law of the flowering plants. Real World Data Science. https://realworlddatascience.net/ideas/tutorials/posts/2023/04/13/flowers.html

2. Charrier, G., Bonhomme, M., Lacointe, A., & Améglio, T. (2011). Are budburst dates, dormancy and cold acclimation in walnut trees (Juglans regia L.) under mainly genotypic or environmental control?. International journal of biometeorology, 55(6), 763-774. https://pubmed.ncbi.nlm.nih.gov/21805380/

3. Marsham, R. (1789). XIII. Indications of spring, observed by Robert Marsham, Esquire, FRS of Stratton in Norfolk. Latitude 52° 45'. Philosophical Transactions of the Royal Society of London, (79), 154-156.

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