

# A LATENT-STATE MODEL FOR TIME SERIES OF ANIMAL BEHAVIOUR

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# Outline

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2. Two-state Bernoulli hidden Markov model
3. Structure of the proposed model
4. Caterpillar feeding experiment
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  - Decoding, Runlengths, Model checking
5. Extensions to the model
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6. Summary



## Background and objective

- Animal behaviourists study causal factors that determine behaviour, such as drinking, locomoting, grooming and feeding
- Feeding behaviour results from the nervous system integrating information regarding
  - physiological factors: e.g. level of nutrients in the blood,
  - sensory inputs: e.g. perception of nutrients in food.
- The combined physiological and perceptual state of the animal is termed the **motivational state** (MacFarland, 1999).



## Background and objective

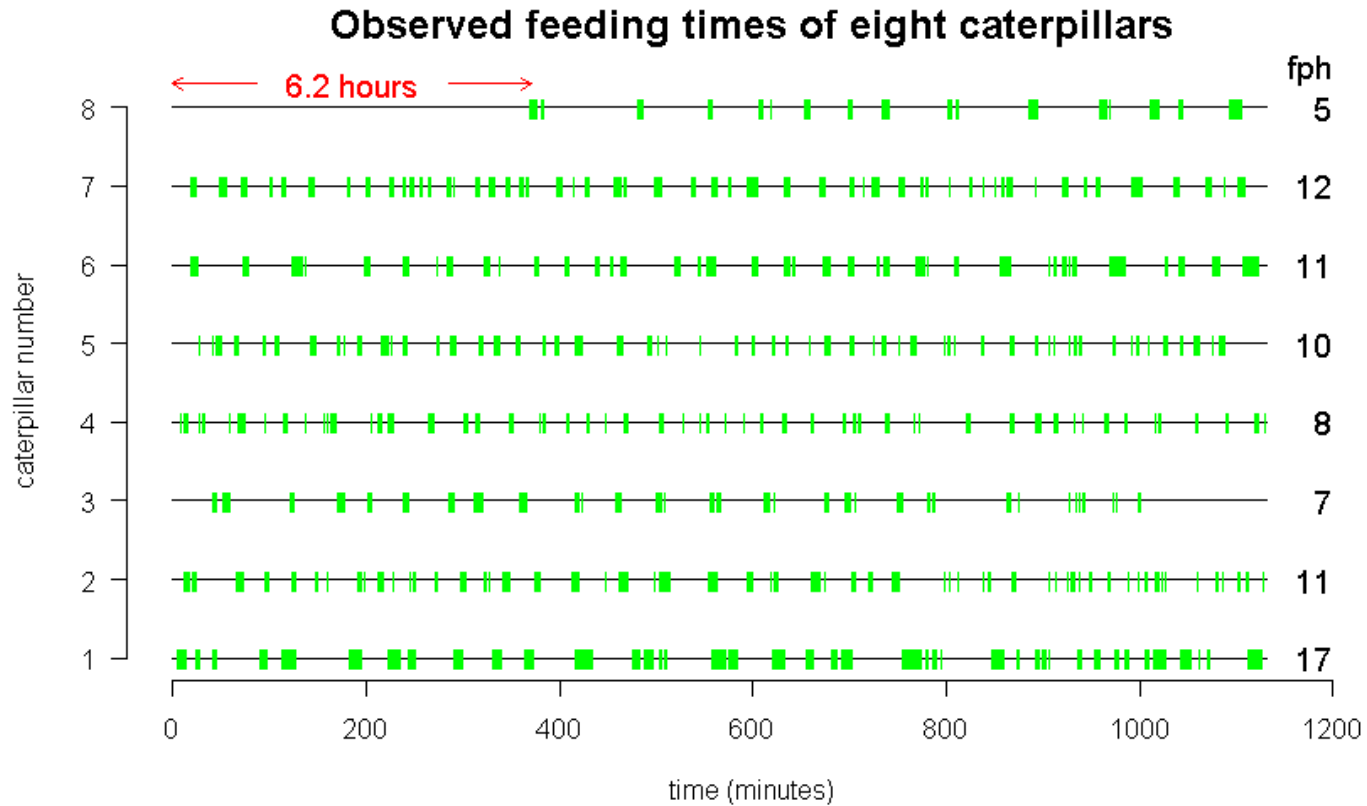
**Raubenheimer and Barton Browne (2000)**

observed eight caterpillars *Helicoverpa armigera*  
once per minute for 19 hours.

**Recordings:** feeding or not feeding

**Data:** 8 binary time series of length 1132

**Outlier:** One caterpillar was anomalous, and not modelled



## Background and objective

Assume there are two motivational states — **hungry** and **sated**.

### Notation:

$X_1, X_2, \dots, X_T$  sequence of observed (binary) feeding behaviour,  
 $C_1, C_2, \dots, C_T$  sequence of unobserved motivational states.

behavioural state	(observed)	motivational state	(unobserved)
feeding	$X_t = 1$	<b>hungry</b>	$C_t = 1$
not feeding	$X_t = 0$	<b>sated</b>	$C_t = 2$

The motivational state influences, but does not determine, behaviour.

A **hungry** animal doesn't always feed:  $\pi_1 = \Pr(X_t = 1 | C_t = 1) < 1$

A **sated** animal sometimes feeds:  $\pi_2 = \Pr(X_t = 1 | C_t = 2) > 0$

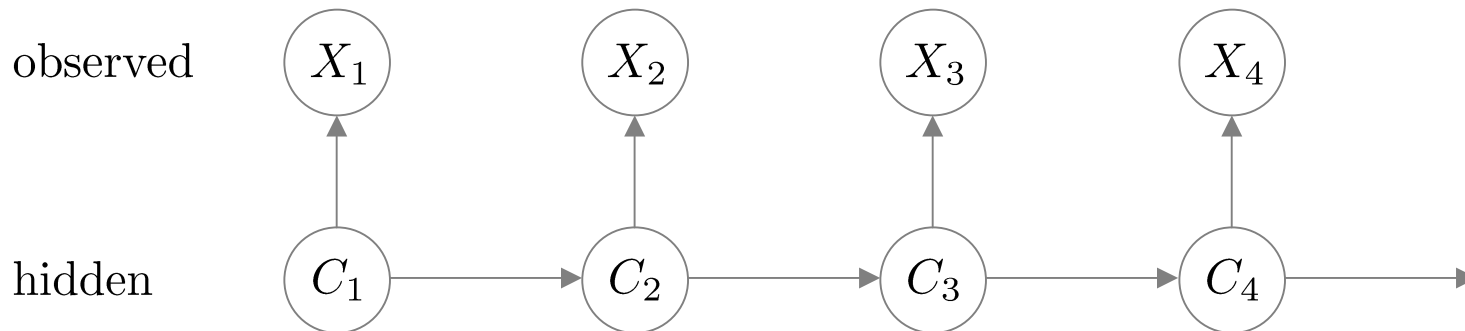
**Objective:** Infer the motivational states from the observed behaviour.

## Two-state Bernoulli HMM

### MacDonald and Raubenheimer (1995)

used a Bernoulli–hidden Markov model (HMM) to describe this phenomenon.

- motivation series:  $C_1, C_2, \dots$  homogeneous two-state Markov chain
- behaviour series:  $X_1, X_2, \dots$  mixture of two Bernoulli distributions
- assumption: conditional independence



### Definition of a HMM

Notation:  $X^{(t)}$  denotes the history up to time  $t$ , i.e.  $\{X_t, X_{t-1}, \dots, X_1\}$ .

$$\Pr(C_t | C^{(t-1)}) = \Pr(C_t | C_{t-1}) \quad \text{Markov property}$$

$$\Pr(X_t | X^{(t-1)}, C^{(t)}) = \Pr(X_t | C_t) \quad \text{Conditional independence}$$

## Two-state Bernoulli HMM

**Transition probability matrix** of the homogeneous Markov chain:

$$\mathbf{\Gamma} = \begin{pmatrix} \gamma_{11} & \gamma_{12} \\ \gamma_{21} & \gamma_{22} \end{pmatrix} = \begin{pmatrix} \Pr(C_{t+1} = 1 | C_t = 1) & \Pr(C_{t+1} = 2 | C_t = 1) \\ \Pr(C_{t+1} = 1 | C_t = 2) & \Pr(C_{t+1} = 2 | C_t = 2) \end{pmatrix}$$

$$\text{Note that } \begin{cases} \gamma_{11} + \gamma_{12} = 1 \\ \gamma_{21} + \gamma_{22} = 1 \end{cases}$$

**Initial state distribution:**  $\boldsymbol{\delta} = (\delta_1 \ \delta_2)$

If the chain is also stationary:  $\boldsymbol{\delta} = \frac{1}{\gamma_{12} + \gamma_{21}} (\gamma_{21} \ \gamma_{12})$

**State-dependent distributions**  $\begin{cases} X_t | C_t = 1 \sim \text{Bernoulli}(\pi_1) \\ X_t | C_t = 2 \sim \text{Bernoulli}(\pi_2) \end{cases}$

**Model parameters:**

State process (Markov chain):  $\gamma_{11} \ \gamma_{22}$  (and  $\delta_1$  unless stationary)

State-dependent distributions:  $\pi_1 \ \pi_2$

# Two-state Bernoulli HMM

motivational state

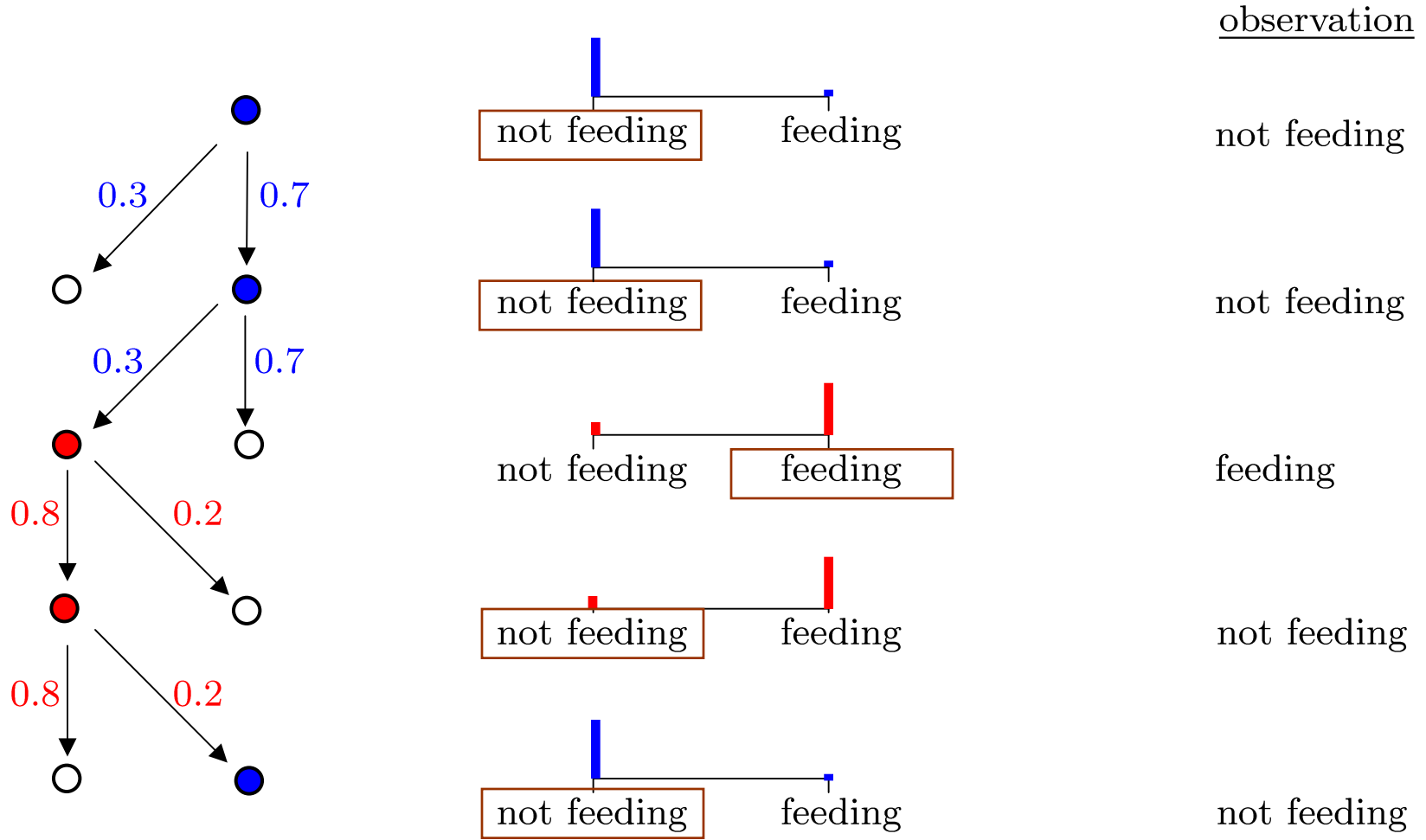
state-dependent distribution

transitional prob. matrix

state 1    state 2  
0.6        0.4

$\pi_1 = P(\text{feed} \mid \text{state 1}) = 0.8$   
 $\pi_2 = P(\text{feed} \mid \text{state 2}) = 0.1$

$$\Gamma = \begin{pmatrix} 0.8 & 0.2 \\ 0.3 & 0.7 \end{pmatrix}$$





hidden

observation

not feeding

not feeding

feeding

not feeding

not feeding

## Two-state Bernoulli HMM

**The likelihood** of an homogeneous HMM:

$$L_T = \delta P(x_1) \Gamma P(x_2) \Gamma P(x_3) \cdots \Gamma P(x_T) \mathbf{1}'$$

For a two-state Bernoulli-HMM:

$$P(x) = \begin{pmatrix} \pi_1^x (1 - \pi_1)^{1-x} & 0 \\ 0 & \pi_2^x (1 - \pi_2)^{1-x} \end{pmatrix}$$

**Parameter estimation** via:

- an EM algorithm (Baum-Welch algorithm),
- direct numerical maximization (e.g. `nlm` or `optim` in R).

**Global decoding:** estimating the most likely motivational state sequence.

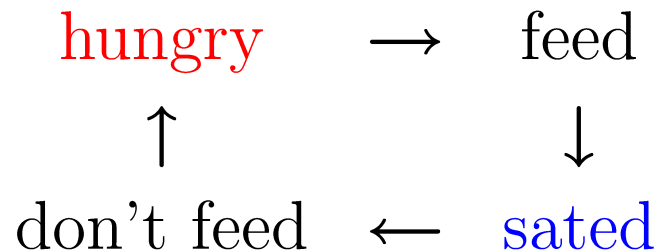
Maximize, w.r.t.  $c_1, c_2, \dots, c_T$ , the conditional probability:

$$\Pr(C^{(T)} = c^{(T)} \mid X^{(T)} = x^{(T)})$$

This solved using a dynamic programming method, the Viterbi algorithm.

### So what's the problem then?

1. The runlength distributions in each motivational state is (implicitly) assumed to be **geometric**. Alcroft *et al.* (2004) fitted a semi-Markov model to overcome this criticism.
2. The model does not account for **feedback** from behaviour to motivation:
  - feeding (eventually) leads to becoming sated;
  - non-feeding (eventually) leads to hunger.



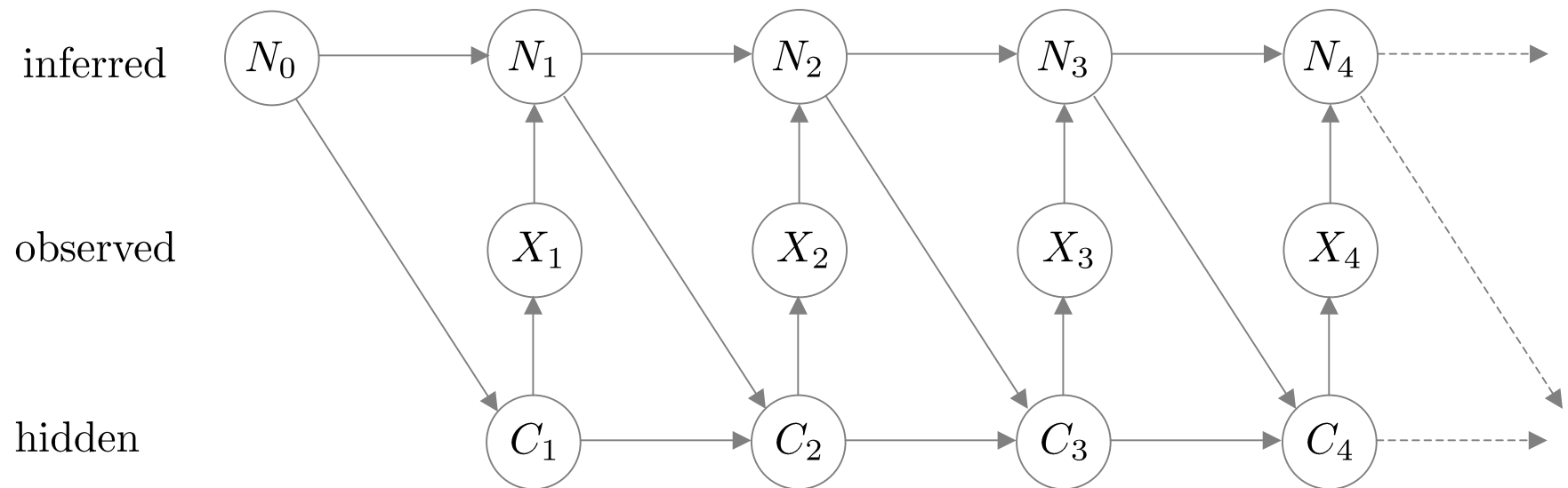
### Feedback loop:

motivation → behaviour → motivation → behaviour

## Structure of the proposed Model

### Components of proposed model:

- motivation series:  $C_t$  two-state process
- behaviour series:  $X_t$  mixture of two Bernoulli distributions
- nutritional level:  $N_t$  determined by feeding behaviour
- assumption: conditional independence

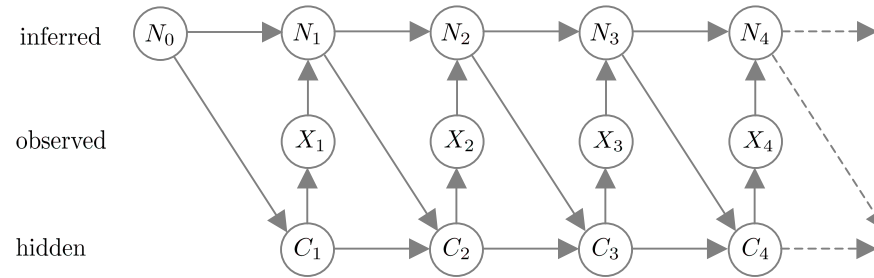


### General idea:

- The current state influences the feeding behaviour.
- Feeding behaviour determines the nutritional level.
- The nutritional level effects the probability of remaining in the current state.

## Structure of the proposed Model

### Model assumptions



1. The motivational state at time  $t$  depends **only** on the previous state and nutritional level.

$$Pr(C_t | C^{(t-1)}, N_0, N^{(t-1)}, X^{(t-1)}) = Pr(C_t | C_{t-1}, N_{t-1})$$

2. Feeding behaviour at time  $t$  depends only on motivational state.

$$\begin{aligned} Pr(X_t = 1 | C^{(t)}, N_0, N^{(t-1)}, X^{(t-1)}) &= Pr(X_t = 1 | C_t) \\ &= \begin{cases} \pi_1 & \text{if } C_t = 1 \\ \pi_2 & \text{if } C_t = 2 \end{cases} . \end{aligned}$$

3. Nutritional level is determined by feeding behaviour.

$$N_t = h(X^{(t)})$$

## Structure of the proposed Model

### State-transition behaviour

current state	nutritional level	probable reaction	corresponding transition
hungry	low	remain hungry	1 → 1
hungry	high	become sated	1 → 2
sated	low	become hungry	2 → 1
sated	high	remain sated	2 → 2

### A model for state transition behaviour

$$\Gamma(n_t) = \begin{pmatrix} \gamma_{11}(n_t) & \gamma_{12}(n_t) \\ \gamma_{21}(n_t) & \gamma_{22}(n_t) \end{pmatrix}$$

The state transition probabilities,  $\gamma_{ij}$  depend on  $n_t$  as follows:

$$\gamma_{11}(n_t) = \frac{\exp(\alpha_0 + \alpha_1 n_t)}{1 + \exp(\alpha_0 + \alpha_1 n_t)} \quad \text{i.e.} \quad \text{logit}(\gamma_{11}(n_t)) = \alpha_0 + \alpha_1 n_t$$

$$\gamma_{22}(n_t) = \frac{\exp(\beta_0 + \beta_1 n_t)}{1 + \exp(\beta_0 + \beta_1 n_t)} \quad \text{i.e.} \quad \text{logit}(\gamma_{22}(n_t)) = \beta_0 + \beta_1 n_t$$

$\alpha_1 = \beta_1 = 0 \implies$  no feedback from nutritional level to motivational state.

## Structure of the proposed Model

### A model for the nutritional level

The nutritional level is determined by the feeding behaviour as follows:

$$N_t = \lambda X_t + (1 - \lambda)N_{t-1}, \quad t = 1, 2, \dots, T. \quad (N_0 \text{ is regarded as a parameter.})$$

$\lambda \in (0, 1)$  determines the rate of decay.

Contribution of one feeding episode has **half-life** =  $\log(0.5)/\log(1 - \lambda)$ .

### Model parameters

$\alpha_0 \alpha_1$  determine how the nutritional level affects  $\Pr(\text{remaining hungry})$

$\beta_0 \beta_1$  determine how the nutritional level affects  $\Pr(\text{remaining sated})$

$\pi_1 \pi_2$   $\Pr(\text{feed} \mid \text{hungry})$   $\Pr(\text{feed} \mid \text{sated})$

$\lambda$  determines rate of nutrition depletion

$N_0$  initial nutritional level

$\delta_1$   $\Pr(C_1 = 1)$

## Structure of the proposed Model

**Likelihood** of the model:

$$L_T = \delta P(x_1) \Gamma(n_1) P(x_2) \Gamma(n_2) P(x_3) \cdots \Gamma(n_T) P(x_T) \mathbf{1}'$$

$$P(x) = \begin{pmatrix} \pi_1^x (1 - \pi_1)^{1-x} & 0 \\ 0 & \pi_2^x (1 - \pi_2)^{1-x} \end{pmatrix}$$

$$\Gamma(n) = \begin{pmatrix} \frac{\exp(\alpha_0 + \alpha_1 n)}{1 + \exp(\alpha_0 + \alpha_1 n)} & \frac{1}{1 + \exp(\alpha_0 + \alpha_1 n)} \\ \frac{1}{1 + \exp(\beta_0 + \beta_1 n)} & \frac{\exp(\beta_0 + \beta_1 n)}{1 + \exp(\beta_0 + \beta_1 n)} \end{pmatrix}$$

**Parameter estimation** by direct numerical maximization (e.g. `nlm` in R)  
(An EM algorithm would require numerical maximization in *each* M-step.)

**Global decoding:** estimating the most likely motivational state sequence.

The Viterbi algorithm is applicable.

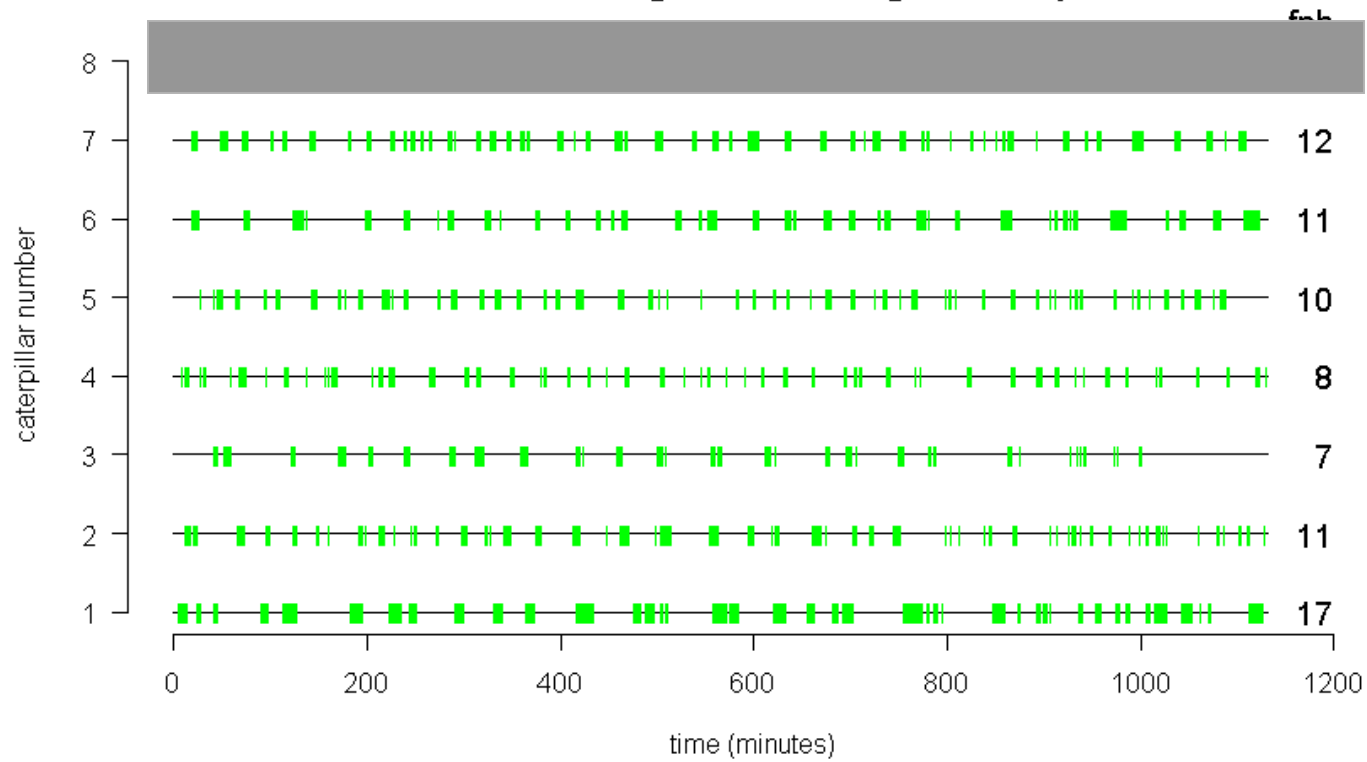


# Caterpillar feeding experiment -- Observations

Back to the data



Observed feeding times of eight caterpillars



## Estimates

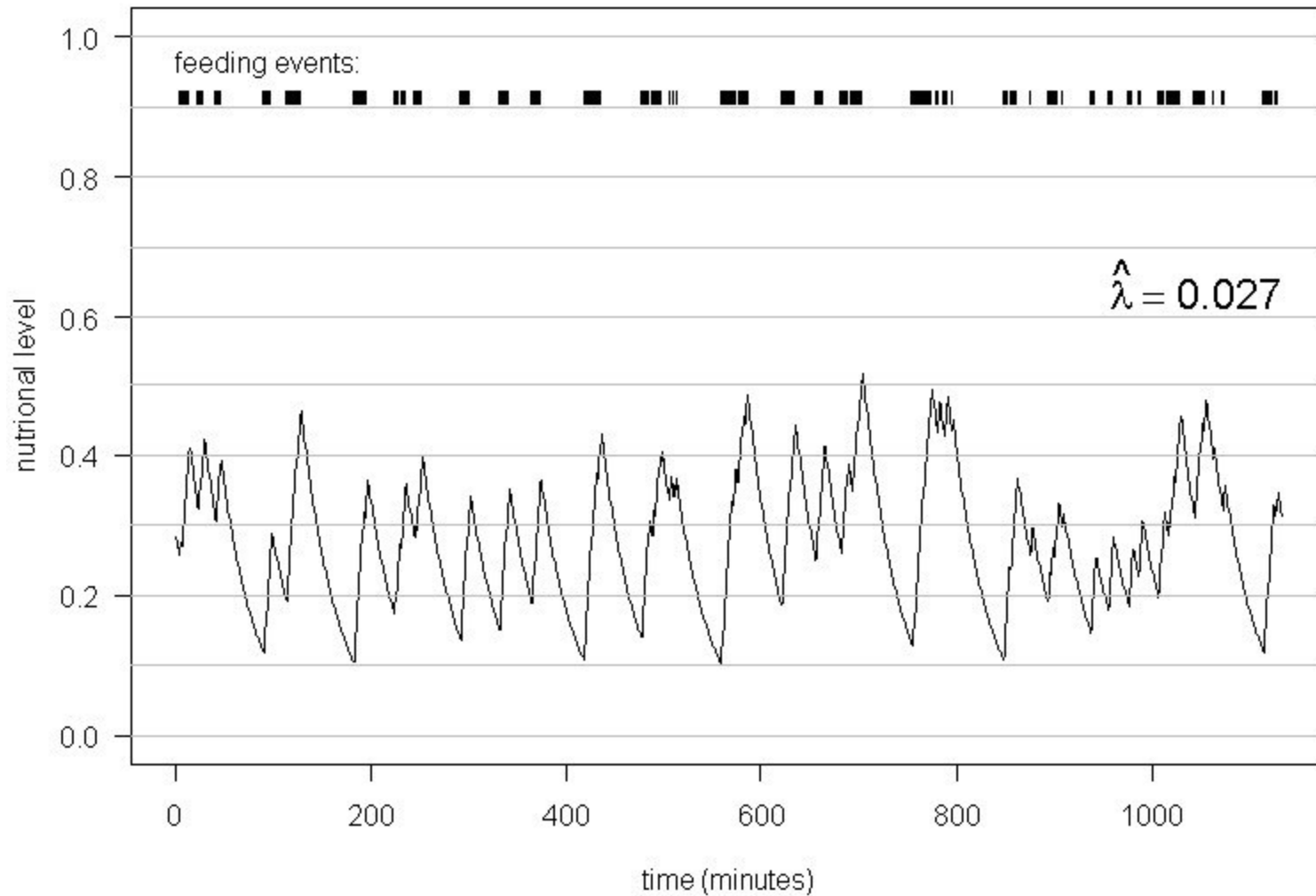
Parameter estimates for the seven caterpillars the seven

subj	$\hat{\alpha}_0$	$\hat{\alpha}_1$	$\hat{\beta}_0$	$\hat{\beta}_1$	$\hat{\pi}_1$	$\hat{\pi}_2$	$\hat{\lambda}$	$\hat{n}_0$	$-\log L$
1	5.80	-11.19	2.31	2.22	0.936	0.000	0.027	0.295	332.6
2	2.20	-5.16	-0.28	21.13	0.913	0.009	0.032	0.163	348.2
3	4.76	-10.12	3.00	15.91	0.794	0.004	0.080	0.740	225.2
4	2.19	-7.24	1.31	16.23	0.900	0.000	0.059	0.062	299.3
5	3.14	-7.27	1.68	10.91	0.901	0.006	0.097	0.999	332.5
6	3.08	-5.22	1.37	14.01	0.879	0.001	0.043	0.263	291.0
7	3.89	-9.05	0.62	13.34	0.976	0.003	0.054	0.379	315.2

- All  $\hat{\alpha}_1 < 0$  and all  $\hat{\beta}_1 > 0$ . (Expected).
- $(\hat{\alpha}_1, \hat{\alpha}_2)$ , and  $(\hat{\beta}_1, \hat{\beta}_2)$ , differ substantially between subjects, but the transition probabilities are not so different.
- All  $\hat{\pi}_1 \approx 1$  and all  $\hat{\pi}_2 \approx 0$ .
- The estimates  $\hat{n}_0$  differ substantially. (Expected)
- The estimates  $\hat{\lambda}$  differ substantially. (Interesting)

# Estimates

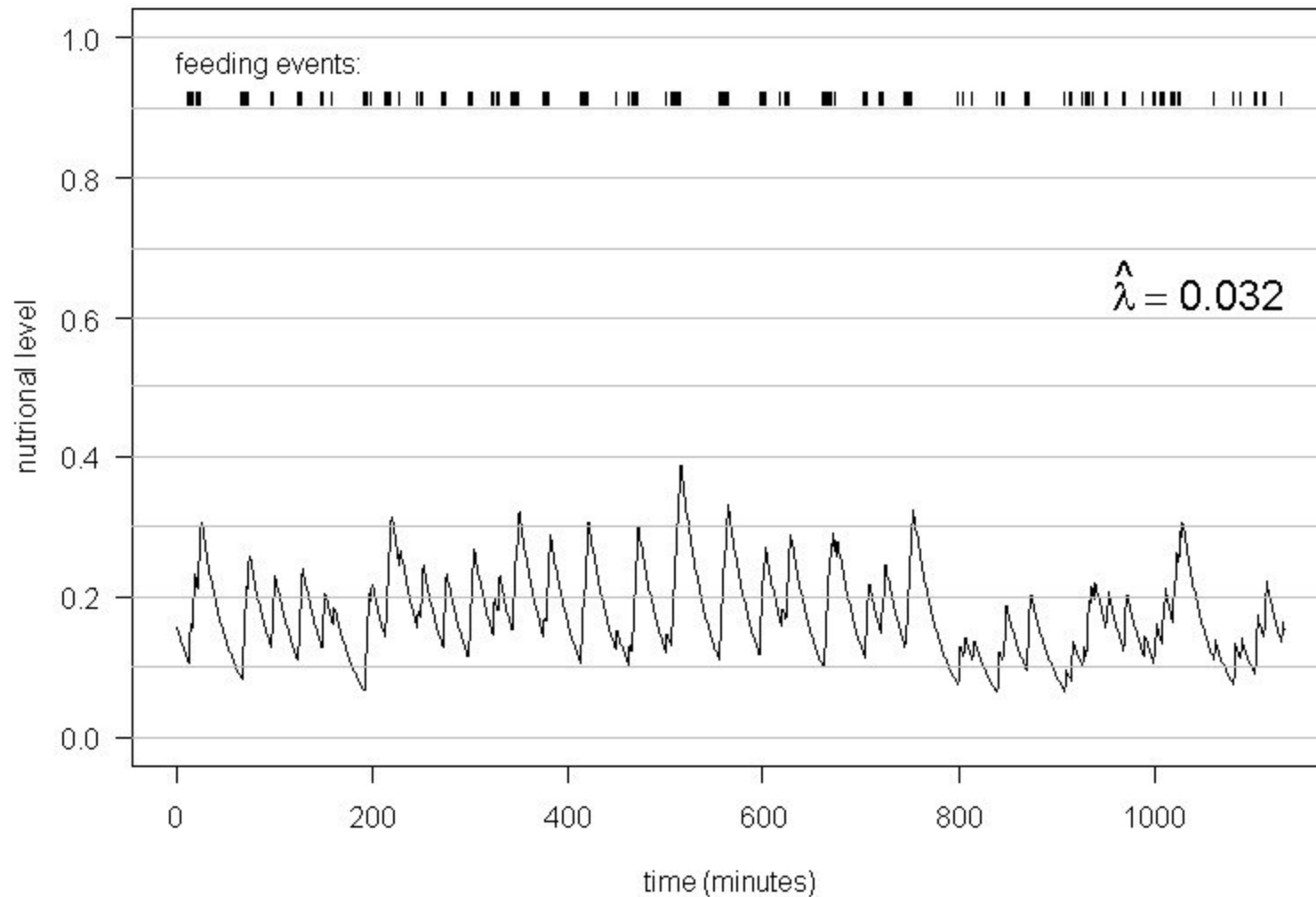
## The nutritional level: Subject 1



$$N_t = \lambda X_t + (1 - \lambda)N_{t-1}$$

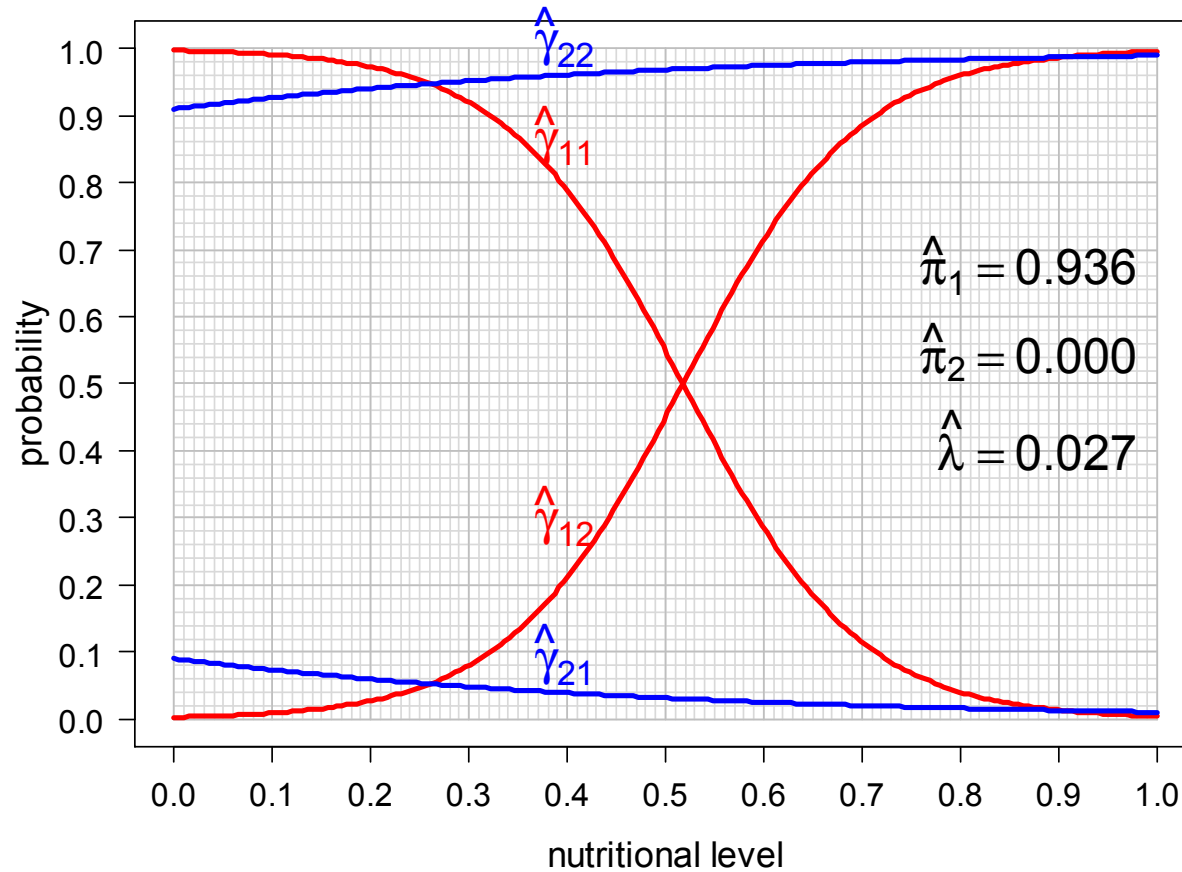
# Estimates

## The nutritional level: Subject 2



# Estimates

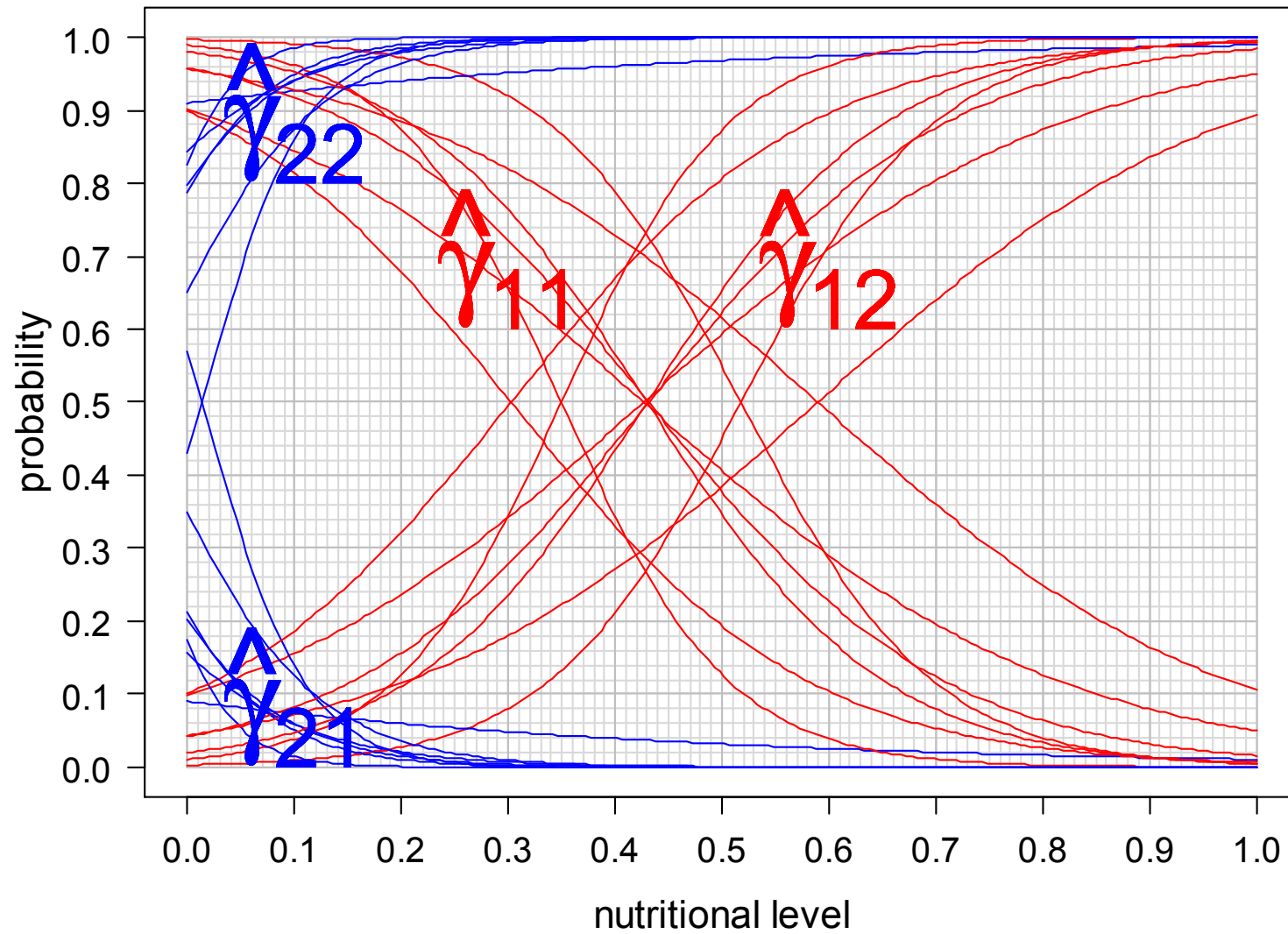
Transition probabilities and other estimates - caterpillar 1



$$\mathbf{\Gamma}(n_t) = \begin{pmatrix} \gamma_{11}(n_t) & \gamma_{12}(n_t) \\ \gamma_{21}(n_t) & \gamma_{22}(n_t) \end{pmatrix}$$

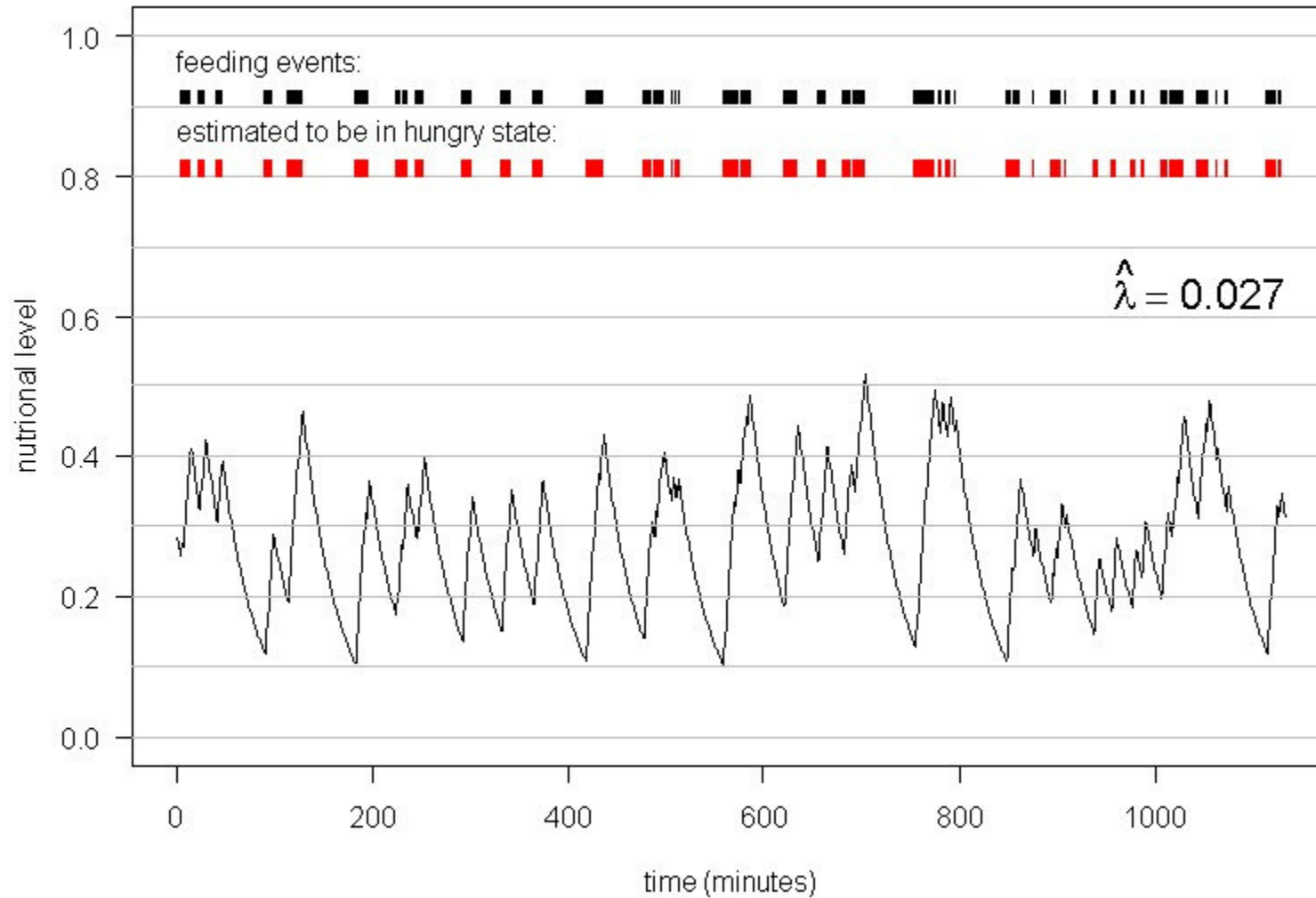
# Estimates

## Transition probabilities - all seven caterpillars



# Decoding

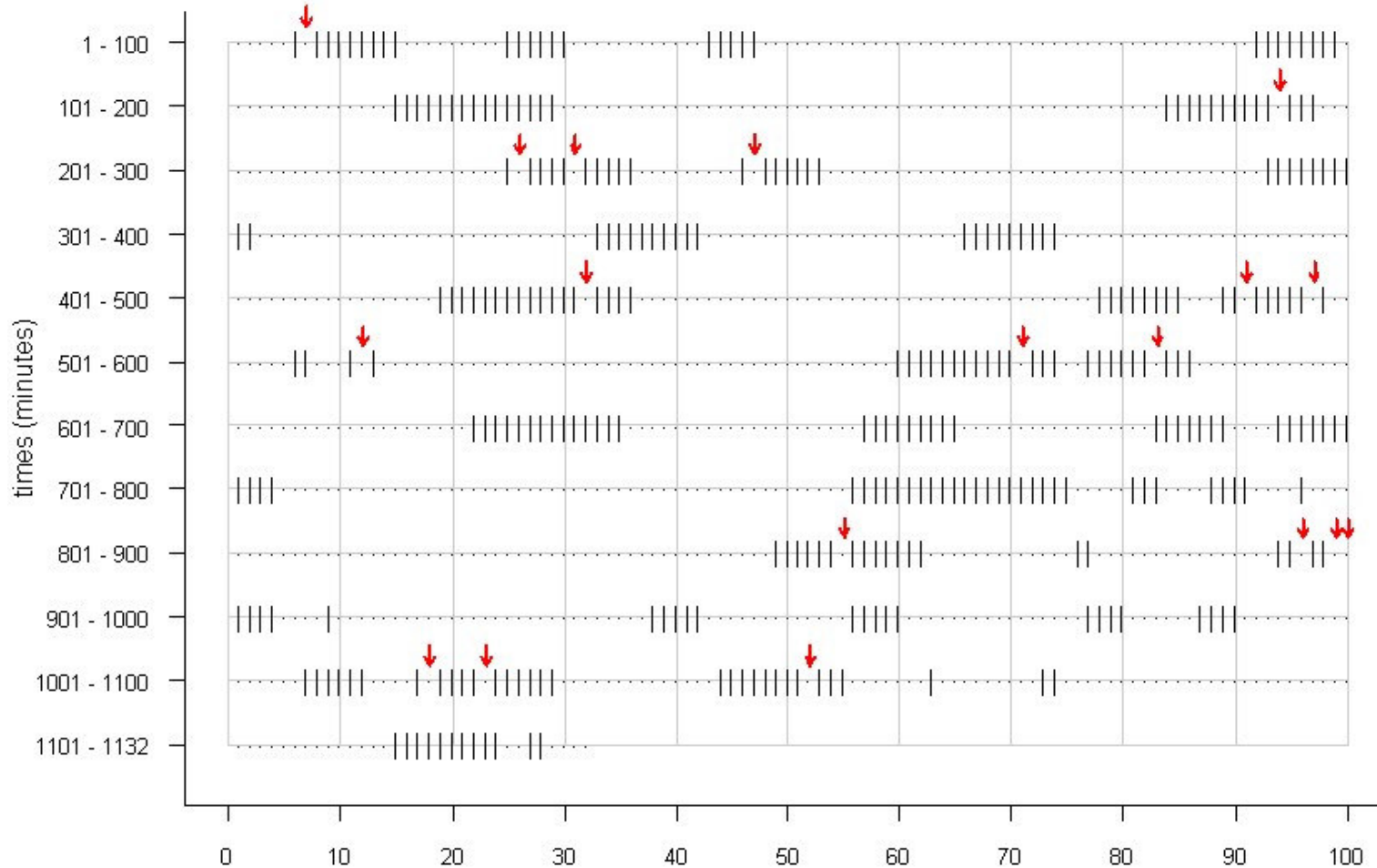
## Global decoding: Subject 1



# Decoding

## Global decoding: Subject 1

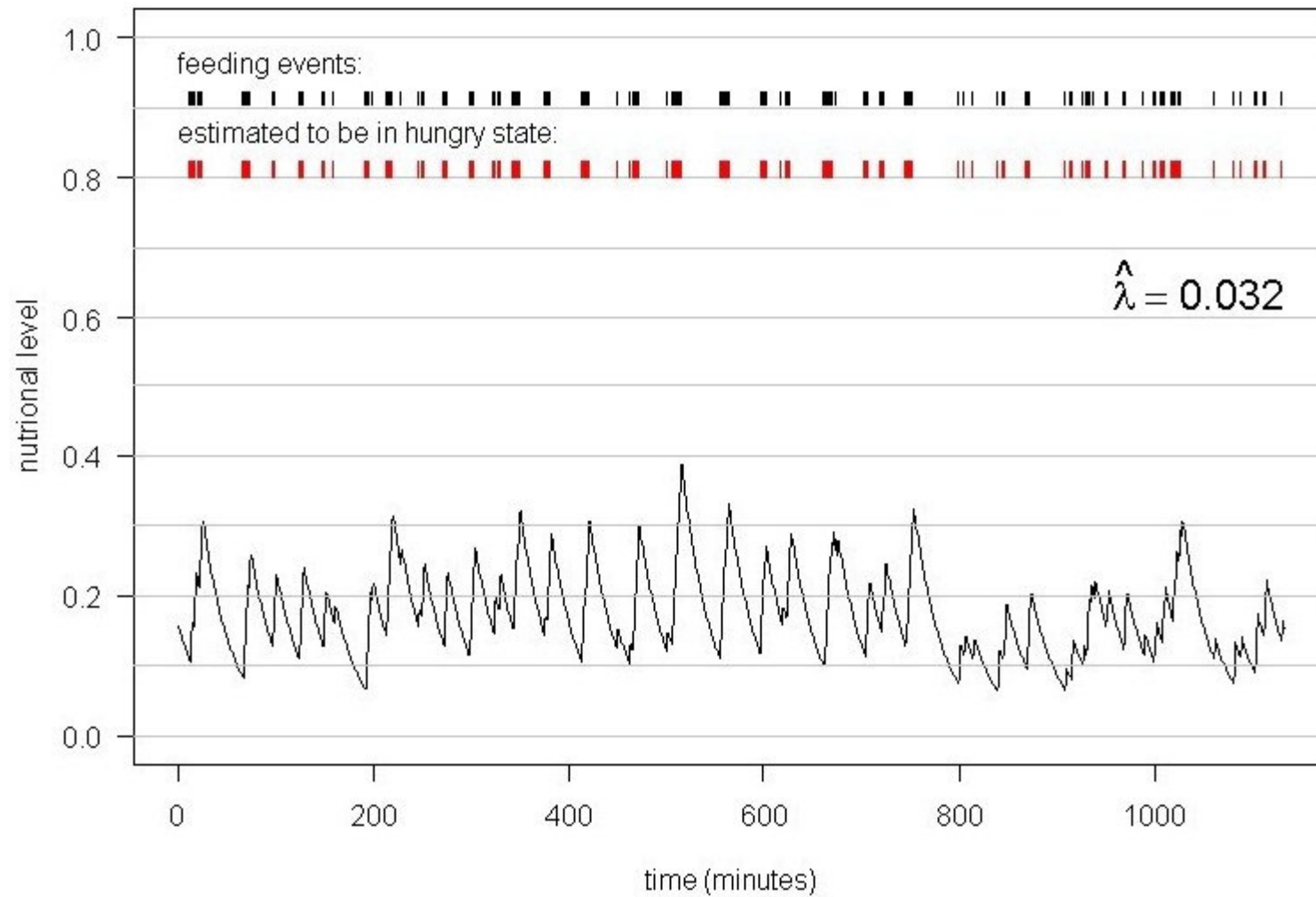
Down-arrows indicate non-feeding event while **hungry**,  
Up-arrows indicate feeding event while **sated**.





# Decoding

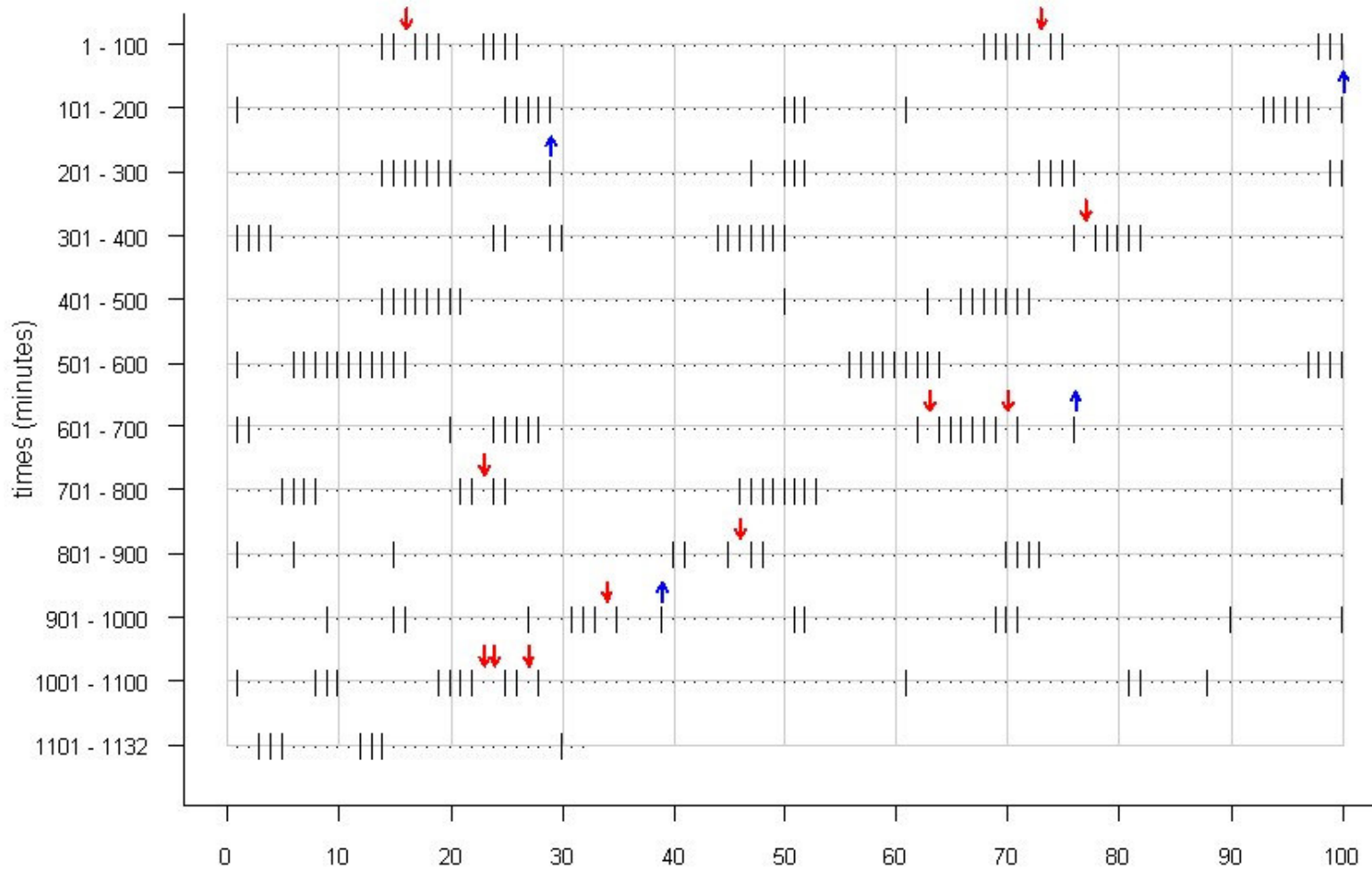
## Global decoding: Subject 2



# Decoding

## Global decoding: Subject 2

Down-arrows indicate non-feeding event while **hungry**,  
Up-arrows indicate feeding event while **sated**.

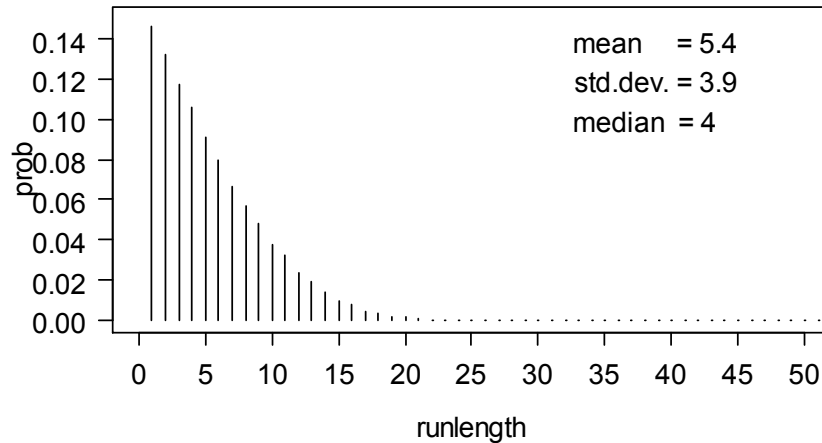


# Runlengths

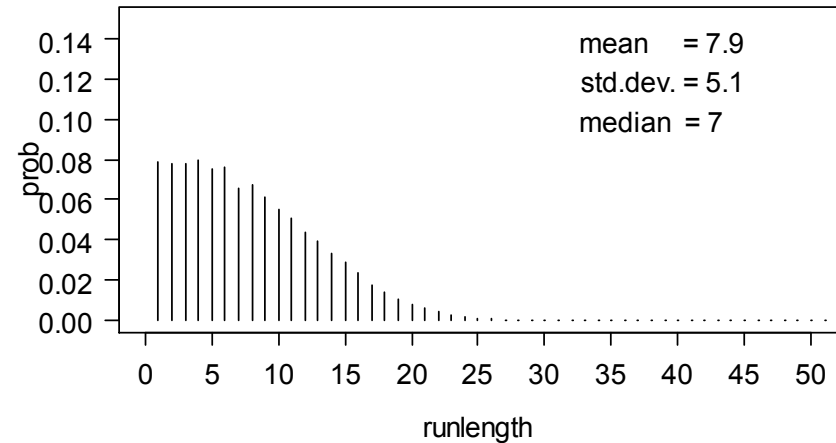
## Runlength distributions for caterpillar 1

Notice the difference between feeding runs and **hungry runs**,  
non-feeding runs and **sated runs**.

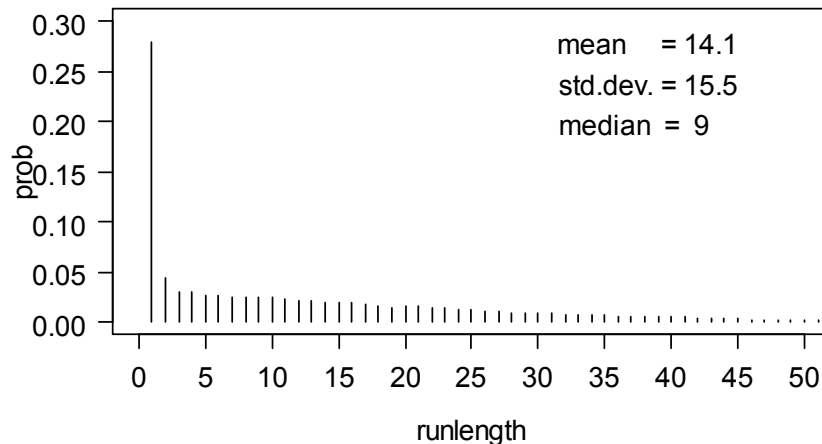
**feeding**



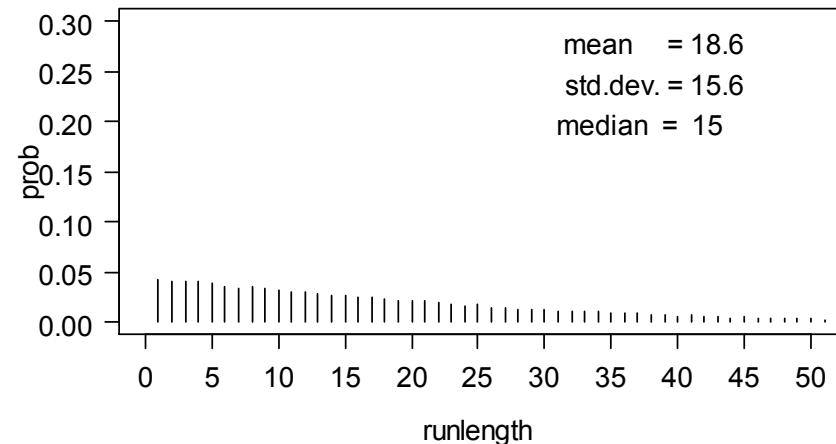
**hungry**



**not feeding**



**sated**



## Caterpillar feeding experiment -- Runlengths

### Runlength statistics

subject	feeding runs			estimated hungry runs		
	number	mean	s.d.	number	mean	s.d.
1	58	5.4	4.1	41	8.1	4.9
2	67	3.0	2.3	53	3.9	2.8
3	41	3.1	2.1	22	6.7	2.4
4	57	2.6	1.5	51	3.0	1.7
5	65	2.8	1.6	54	3.5	2.0
6	51	4.1	2.8	35	6.4	3.8
7	57	4.1	2.4	52	4.6	2.7

$$\text{Average} \left( \frac{\text{number of feeding runs}}{\text{number of hunger runs}} \right) = 1.35$$

$$\text{Average} \left( \frac{\text{mean feeding runlength}}{\text{mean hungry runlength}} \right) = 0.73$$

$$\text{Average} \left( \frac{\text{std. dev. feeding runlength}}{\text{std. dev. hungry runlength}} \right) = 0.83$$

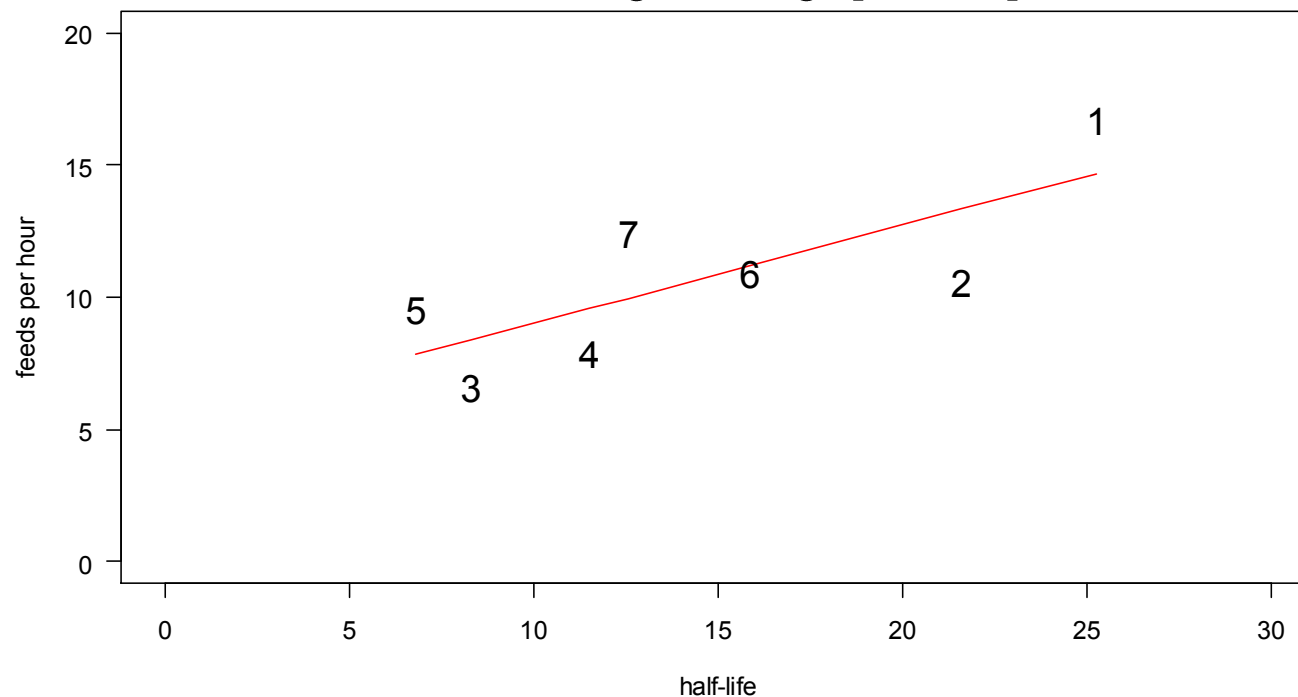
## Caterpillar feeding experiment -- Half-life

### Estimated half-life

$$\text{Half-life} = \log(0.5) / \log(1 - \lambda)$$

The time taken to halve the nutritional level when not feeding.

Half-life vs. average feeding episodes per hour



Half-life is related to the rate of feeding ( $\hat{\rho} = 0.77$ )

The rate of feeding differs substantially between subjects.

## Estimating standard errors

- either the “delta method” based on the estimated information matrix
- or parametric bootstrap (very computer intensive!)

## Model checking – 1. forecasts

The forecast distribution:  $\hat{p}_t = \Pr(X_t = 1 | X^{(t-1)})$  is easy to compute. We test

$$\mathbf{H}_0 : g(\mathbf{E}(x_t)) = g(\hat{p}_t) \quad \text{vs.} \quad \mathbf{H}_A : g(\mathbf{E}(x_t)) = f(g(\hat{p}_t)),$$

where  $g$  is the logit function and  $f$  a smoothing spline.

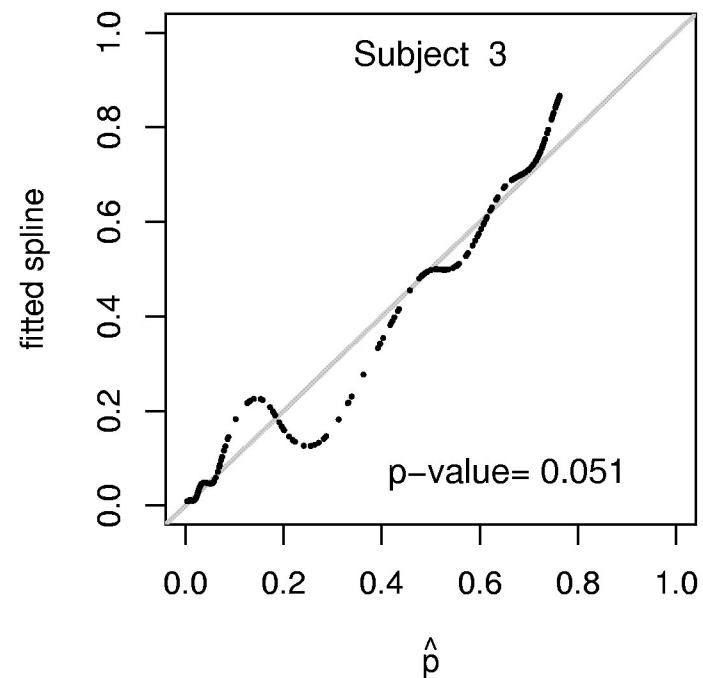
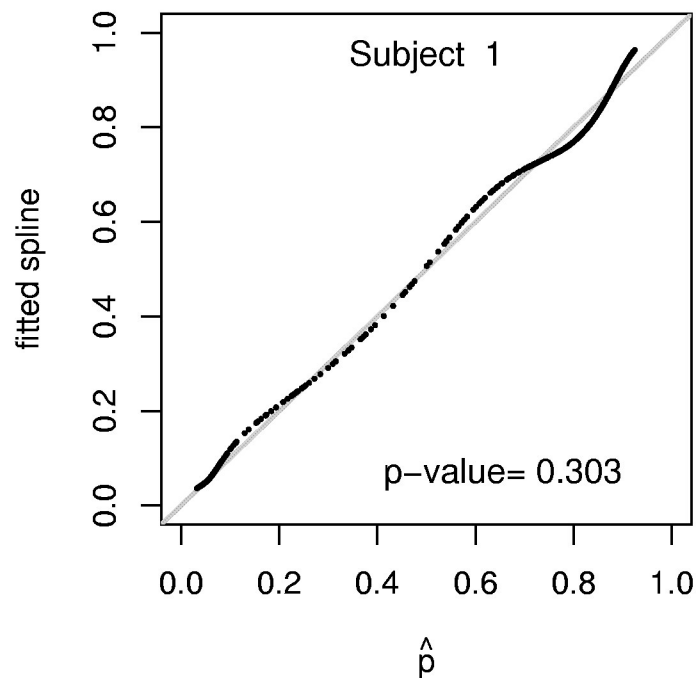
Departure of  $f$  from the identity function constitutes evidence of a poor fit.

## Model checking – 2. deviance residuals

# Caterpillar feeding experiment -- Model checking

## Model checking – 1. forecasts

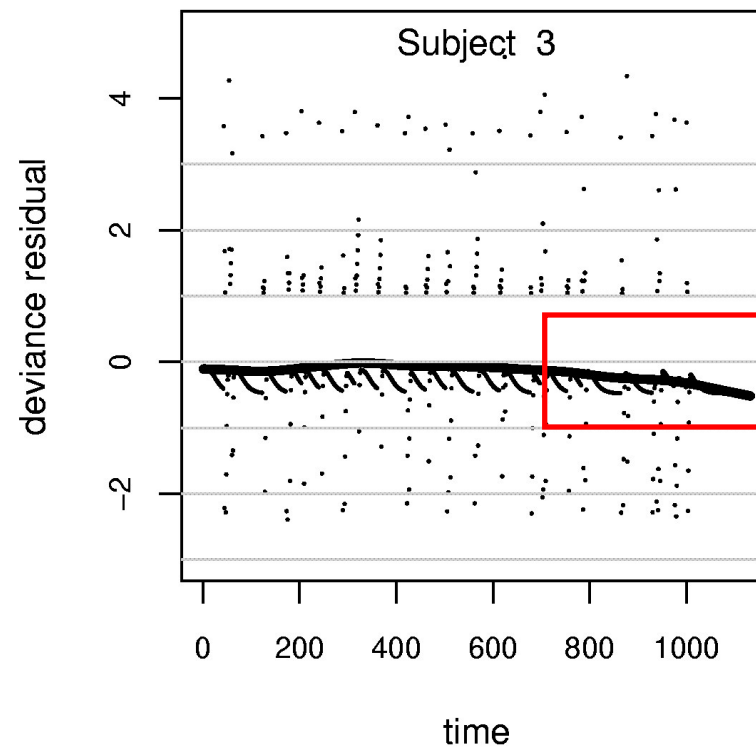
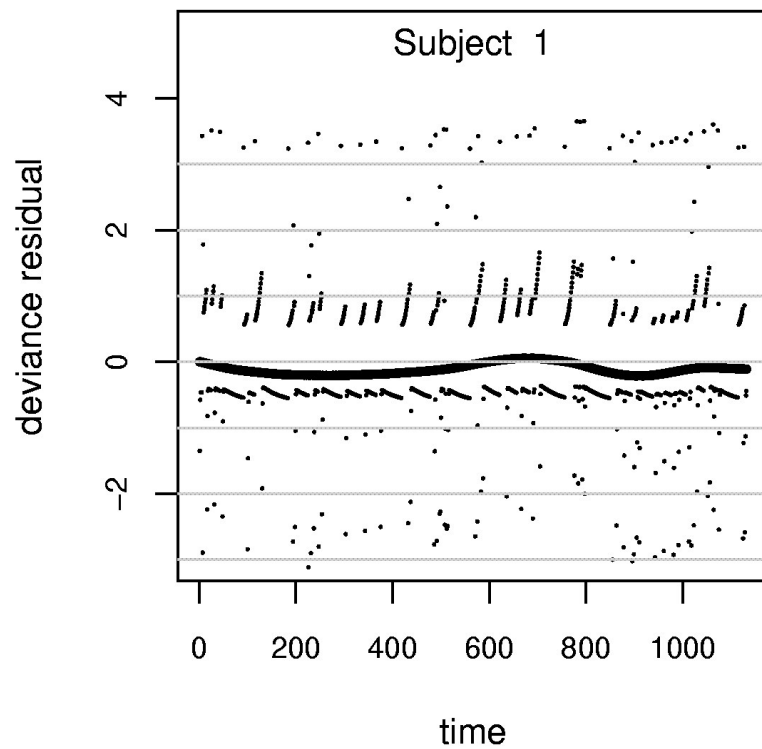
subject	1	2	3	4	5	6	7
$p$ -value	0.303	0.718	0.051	0.545	0.779	0.658	0.820



# Caterpillar feeding experiment -- Model checking

## Model checking – 2. deviance residuals

The solid line is a smooth of the deviance residuals.



Looking back at the data: **subject 3 stopped feeding over the last 2 hours.**



## Extensions of the model

1. **The number of states can be increased to  $m > 2$ .**

However, the number of parameters increases rapidly with increasing  $m$ .

2. **The definition of “nutritional level” can be changed.**

The definition  $N_t = \lambda X_t + (1 - \lambda)N_{t-1}$  is convenient but not essential.

3. **The state-dependent distribution can be changed.**

- discrete-valued, continuous-valued, circular-valued distributions
- multivariate, even mixed discrete-continuous, discrete-circular, etc.

The likelihood remains of the form:

$$\mathbf{L}_T = \delta \mathbf{P}(x_1) \Gamma(n_1) \mathbf{P}(x_2) \Gamma(n_2) \mathbf{P}(x_3) \cdots \Gamma(n_T) \mathbf{P}(x_T) \mathbf{1}'$$

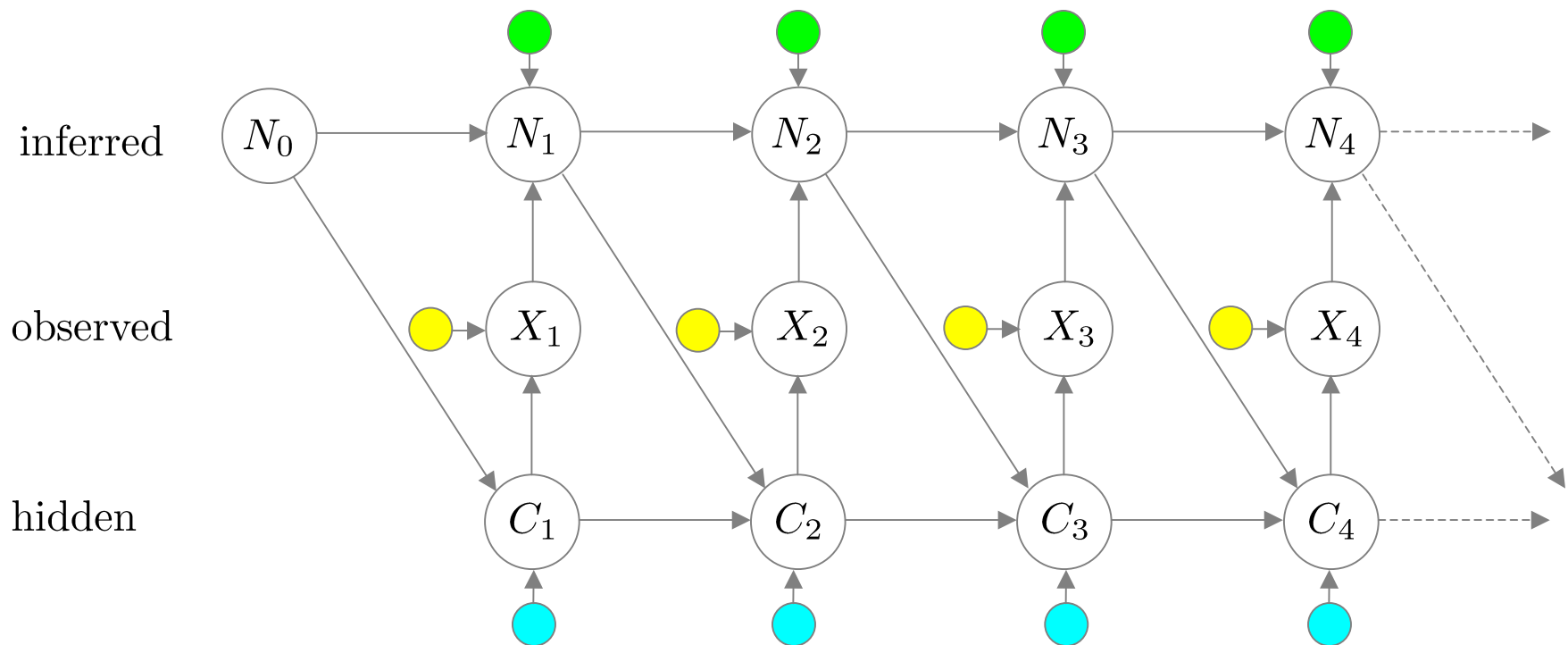
$$\text{with } \mathbf{P}(x) = \begin{pmatrix} p_1(x) & 0 \\ 0 & p_2(x) \end{pmatrix}$$

$$\text{instead of } \mathbf{P}(x) = \begin{pmatrix} \pi_1^x (1 - \pi_1)^{1-x} & 0 \\ 0 & \pi_2^x (1 - \pi_2)^{1-x} \end{pmatrix}$$

## Extensions of the model

### 4. Covariate information can be included almost anywhere.

- — to influence the feedback state (nutritional level)
- — to influence the state transition probabilities
- — to influence the state-dependent distributions



## Extensions of the model

### 5. Mixed models for multiple time series.

Analogous to the mixed hidden Markov models introduced by Altman (2007)

Some of the original parameters in the “caterpillar” model can be regarded as

**fixed effects** — the same for all caterpillars, or as

**random effects** — specific to individual caterpillars in a population.

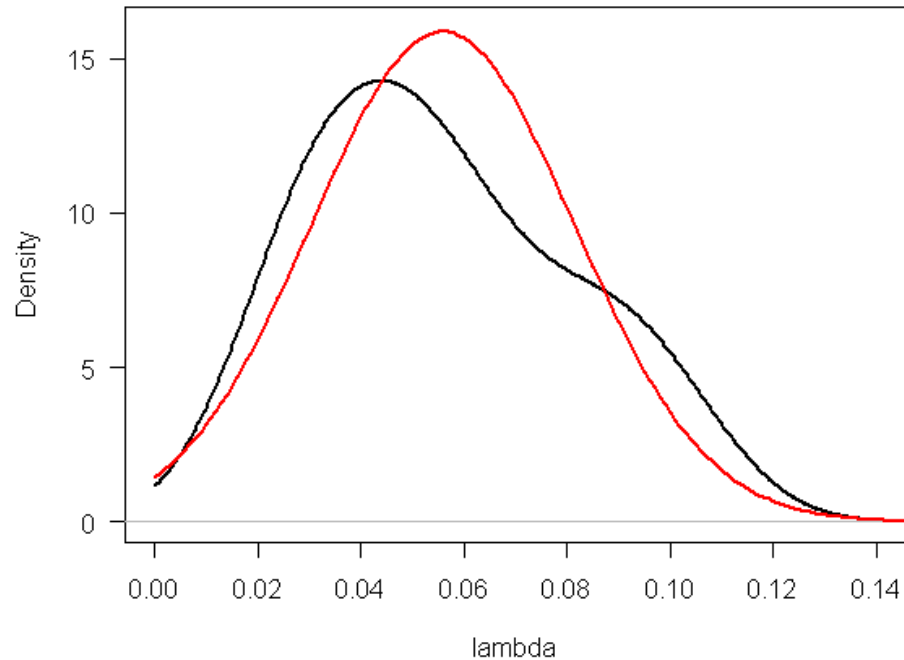
#### Example based on the parameters of caterpillar model

The assumptions below are only approximately applicable for our data. We make them to illustrate the technique.

effect	fixed or random, i.e. the same for all individuals, or different?
$\alpha_0$ $\alpha_1$	fixed
$\beta_0$ $\beta_1$	fixed
$\pi_1$ $\pi_2$	fixed
$\lambda$	random
$N_0$	random, but it's distribution is not of interest.
$\delta_1$	random, but can be approximately determined via the other parameters, and will not be regarded as a free parameter.

## Distribution for $\lambda$

Estimates of  $f(\lambda)$ ;  
truncated normal and truncated kernel



**Model:**  $\lambda \sim (0,1)$ -truncated  $N(\lambda; \mu, \sigma^2)$

$$f(\lambda; \mu, \sigma^2) = \frac{\phi\left(\frac{\lambda - \mu}{\sigma}\right)}{\Phi\left(\frac{1 - \mu}{\sigma}\right) - \Phi\left(\frac{0 - \mu}{\sigma}\right)}, \quad \lambda \in (0, 1)$$

# Caterpillar feeding experiment -- Mixed model

## Notation

For  $T$  observations on each of  $I$  subjects, let

$x_{it}$  be the observation on subject  $i$  at time  $t$

$n_{it}$  be the nutrition level of subject  $i$  at time  $t$

## The likelihood

$$\mathbf{L} = (\alpha_0, \alpha_1, \beta_0, \beta_1, \pi_1, \pi_2, N_0, \mu, \sigma^2; x_{it}, i = 1, 2, \dots, I, t = 1, 2, \dots, T)$$

$$= \prod_{i=1}^I \int_0^1 (\underbrace{\delta \mathbf{P}(x_{i1}) \Gamma(n_{i1}) \mathbf{P}(x_{i2}) \cdots \Gamma(n_{iT}) \mathbf{P}(x_{iT}) \mathbf{1}'}_{\text{previous likelihood for subject } i}) f(\lambda; \mu, \sigma^2) d\lambda$$

The likelihood can be maximized numerically with respect to the parameters.

- The numerical integration at each iteration makes this slow.
- Parameter constraints need to be respected, e.g. by reparameterization.
- Rescaling is needed to avoid numerical underflow.

## Caterpillar feeding experiment -- Mixed model

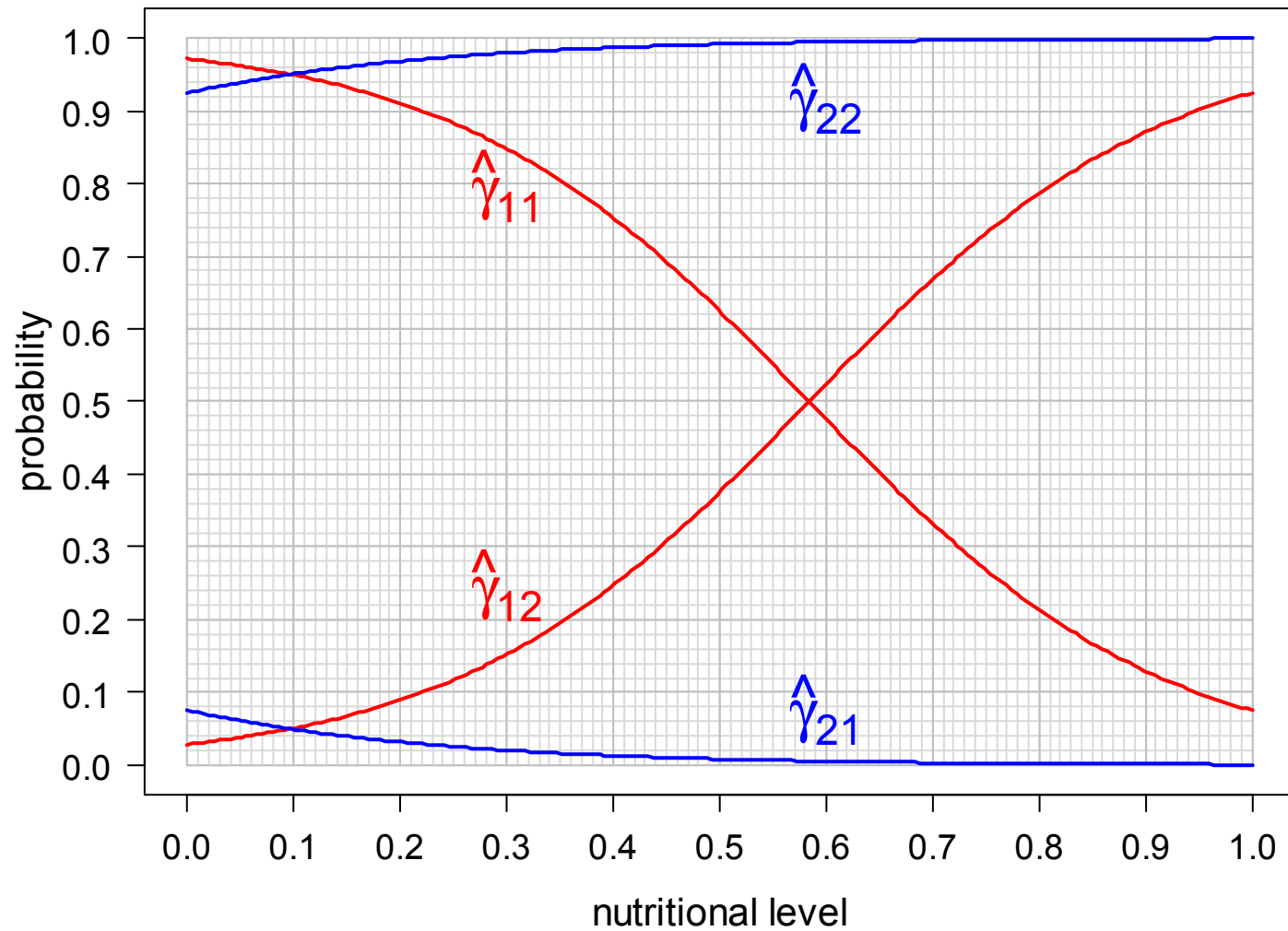
Parameter estimates for the original and the mixed model (**brown**).

subj	$\hat{\alpha}_0$	$\hat{\alpha}_1$	$\hat{\beta}_0$	$\hat{\beta}_1$	$\hat{\pi}_1$	$\hat{\pi}_2$	$\hat{n}_0$	$\hat{n}_0$
1	5.80	-11.19	2.31	2.22	0.936	0.000	0.295	<b>0.101</b>
2	2.20	-5.16	-0.28	21.13	0.913	0.009	0.163	<b>0.317</b>
3	4.76	-10.12	3.00	15.91	0.794	0.004	0.740	<b>0.999</b>
4	2.19	-7.24	1.31	16.23	0.900	0.000	0.062	<b>0.488</b>
5	3.14	-7.27	1.68	10.91	0.901	0.006	0.999	<b>0.996</b>
6	3.08	-5.22	1.37	14.01	0.879	0.001	0.263	<b>0.381</b>
7	3.89	-9.05	0.62	13.34	0.976	0.003	0.379	<b>0.698</b>
<b>1-7</b>	<b>3.53</b>	<b>-6.04</b>	<b>2.50</b>	<b>4.55</b>	<b>0.921</b>	<b>0.006</b>		

Parameter estimates for the random effect :  $\hat{\mu} = 0.094$        $\hat{\sigma} = 0.058$

# Caterpillar feeding experiment -- Mixed model

## Transition probabilities - all seven caterpillars



## Caterpillar feeding experiment -- Mixed model

### Model selection criteria

The estimates of the mixed model *look* reasonable *but* the model fits worse than the original "full model".

Model	number of parameters	Akaike Information criterion
Full	56	4400
(*) Common $\pi_1, \pi_2$	44	4398
Mixed effects	15	4499

\*The model with common values of  $\pi_1, \pi_2$  for all subjects (and everything else different) achieved the best AIC of the models investigated.

Models with more than a single random effect were not investigated.  
They take too long to fit (in **R**)!



### Positive aspects

- The proposed models generalize the class of **hidden Markov models**, in that they allow for **feedback behaviour**.
- Like HMMs they are satisfyingly flexible.
- They differ from the class of **Markov switching models**, which are applied to model econometric time series and financial time series.

### Still needed:

- Asymptotic properties of estimators need to be established.
- More efficient methods for estimating standard errors.
- More efficient methods for fitting mixed models. (It took 8 hours to fit the model with **one random effect** using **R**.)

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