

# Statistics for Ecologists

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Olivier Gimenez  
October 2020

**Who's that guy?!**

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# Olivier Gimenez

- Senior scientist at CNRS, in Montpellier - France.
- Trained as a statistician
- Soon attracted by the bright side of ecology
- Working at the interface of animal demography, statistical modelling and social sciences
- More on <https://oliviergimenez.github.io/>
- Twitter @oaggimenez

## Acknowledgments

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## Acknowledgments

- Sean Anderson, Ben Bolker, Jason Matthiopoulos, David Miller, Denis Réale and Francisco Rodriguez-Sánchez for sharing their courses material

## This Class

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## Slides, R codes, data and practicals

- I used R, and RStudio is your friend
- I also used R Markdown to write reproducible documents (slides/exercises)
- All material is available on GitHub  
<https://github.com/oliviergimenez/statistics-for-ecologists-Master-courses>
- Check out the files `gimenez_lectures.R` and `gimenez_practicals.R`
- You will need the following R packages: `arm`, `bbmle`, `broom`, `dplyr`, `effects`, `lme4`, `mgcv`, `MuMIn`, `R2jags`, `tibble`, `visreg`

## On our plate

- Distributions and likelihoods
- Hypothesis testing and multimodel inference
- Introduction to Bayesian inference
- Generalized Linear Models (GLMs)
- Generalized Additive Models (GAMs)
- Mixed Effect Models

## On our plate

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## Distributions and likelihoods

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# Distributions

- What for?
- Conceptual models, bearing in mind that:  
*All models are wrong, but some are useful (G.E.P. Cox, 1976)*
- Either represent how the world works
- Or capture the behavior of a statistic under some null hypothesis we'd like to test
- Discrete or continuous

## Discrete distributions

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## Bernoulli distribution

**Context:** A single trial with two outcomes, success/failure

$X \sim \text{Bern}(p)$  with  $p$  probability of having a success

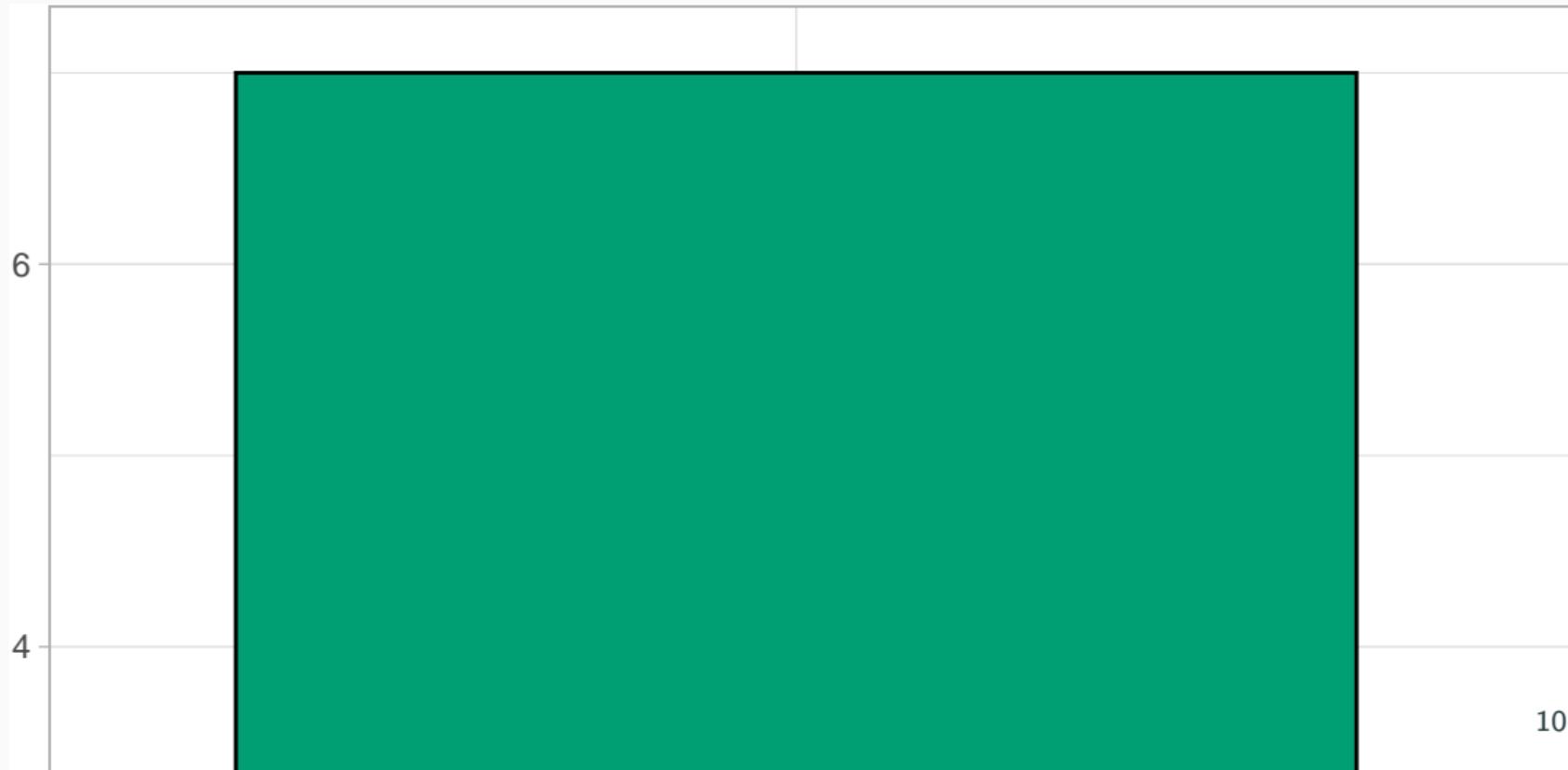
x	$P(X = x)$
1	$p$
0	$1 - p$

**Example:**  $X$  is the random variable *being born a female*

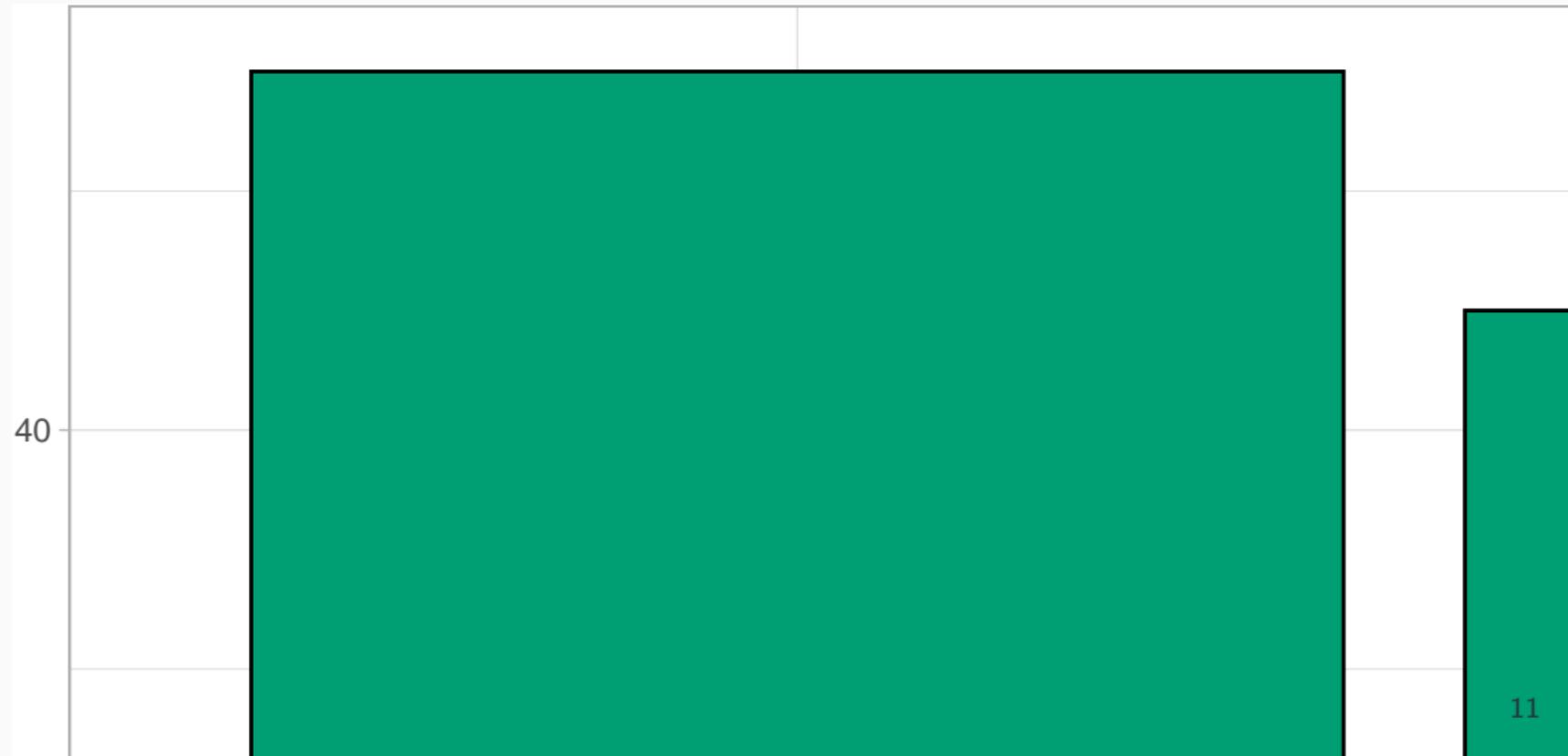
## Ten Bernoulli trials with $p = 0.5$



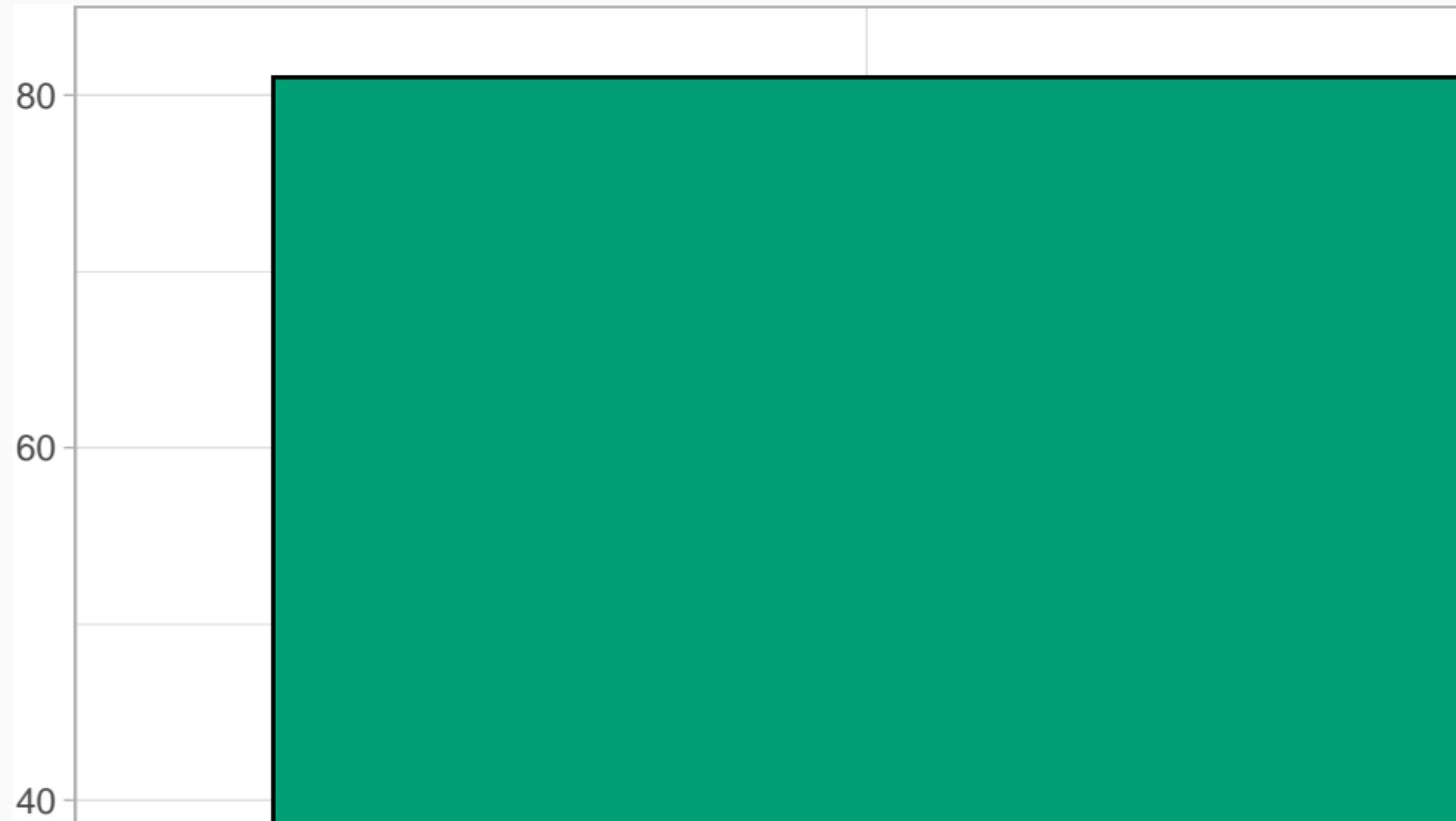
## Ten Bernoulli trials with $p = 0.5$ , again



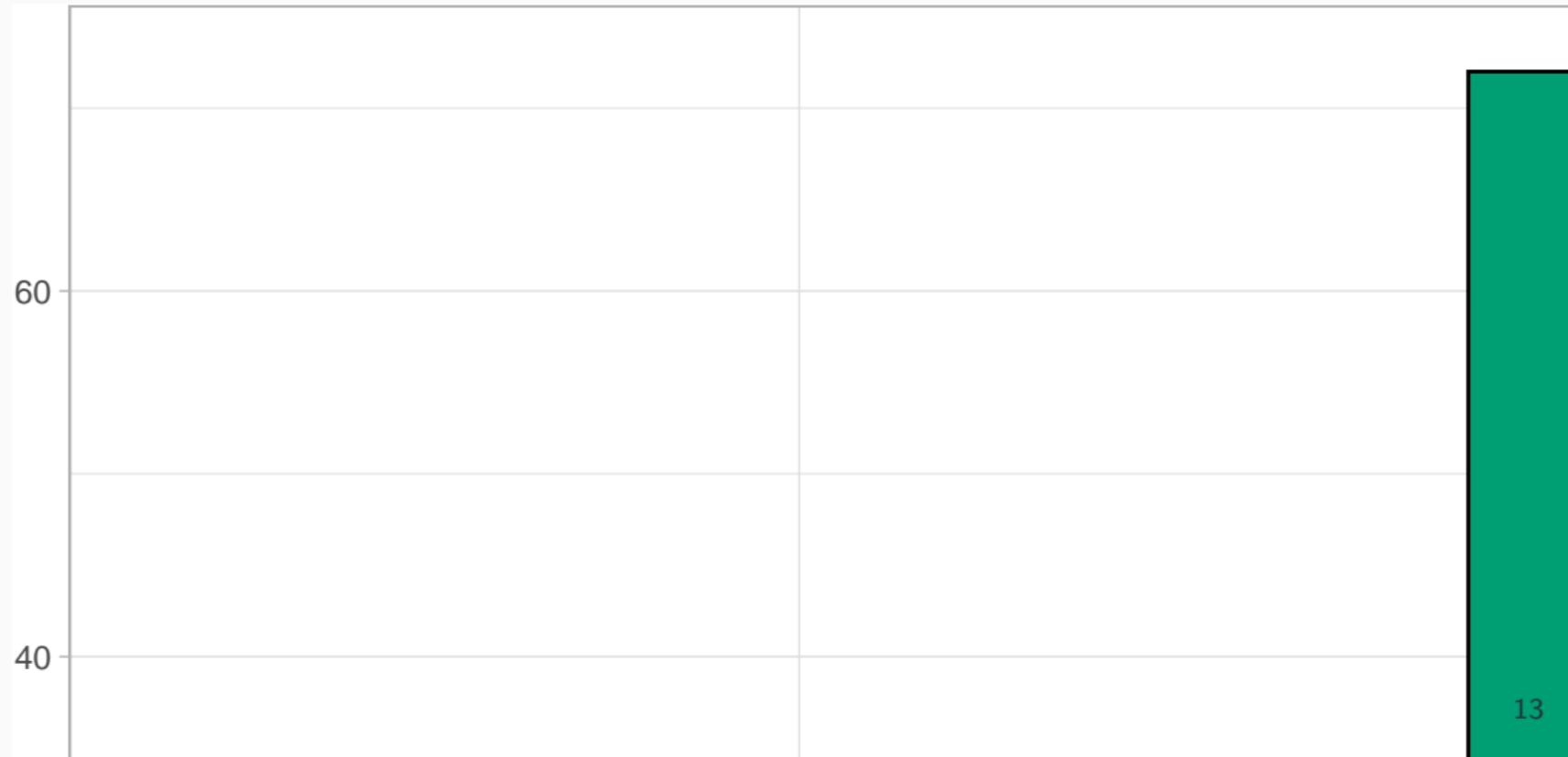
## Hundred Bernoulli trials with $p = 0.5$



## Hundred Bernoulli trials with $p = 0.2$



## Hundred Bernoulli trials with $p = 0.8$



## Summary: Bernoulli distribution

- **notation:**  $X \sim \text{Bern}(p)$
- **range:** discrete,  $x = 0, 1$
- **distribution:**  $P(X = x) = p^x(1 - p)^{1-x}$
- **parameters:**  $p$  is the probability of success
- **mean:**  $p$
- **variance:**  $p(1 - p)$

## Binomial distribution

**Context:** Total number of successes from a fixed number of independent Bernoulli trials, all with same probability of success

$X \sim \text{Bin}(N, p)$  with  $p$  probability of having a success and  $N$  number of trials

$$P(X = x) = \frac{N!}{x!(N-x)!} p^x (1-p)^{N-x} = \binom{N}{x} p^x (1-p)^{N-x}$$

**Example:**  $X$  is the random variable *number of heads in a series of coin flipping*

## Binomial distribution

$$P(X = x) = \binom{N}{x} p^x (1 - p)^{N-x}$$

x	$P(X = x)$
0	$(1 - p)^N$
1	$Np(1 - p)^{N-1}$
...	...
N	$p^N$

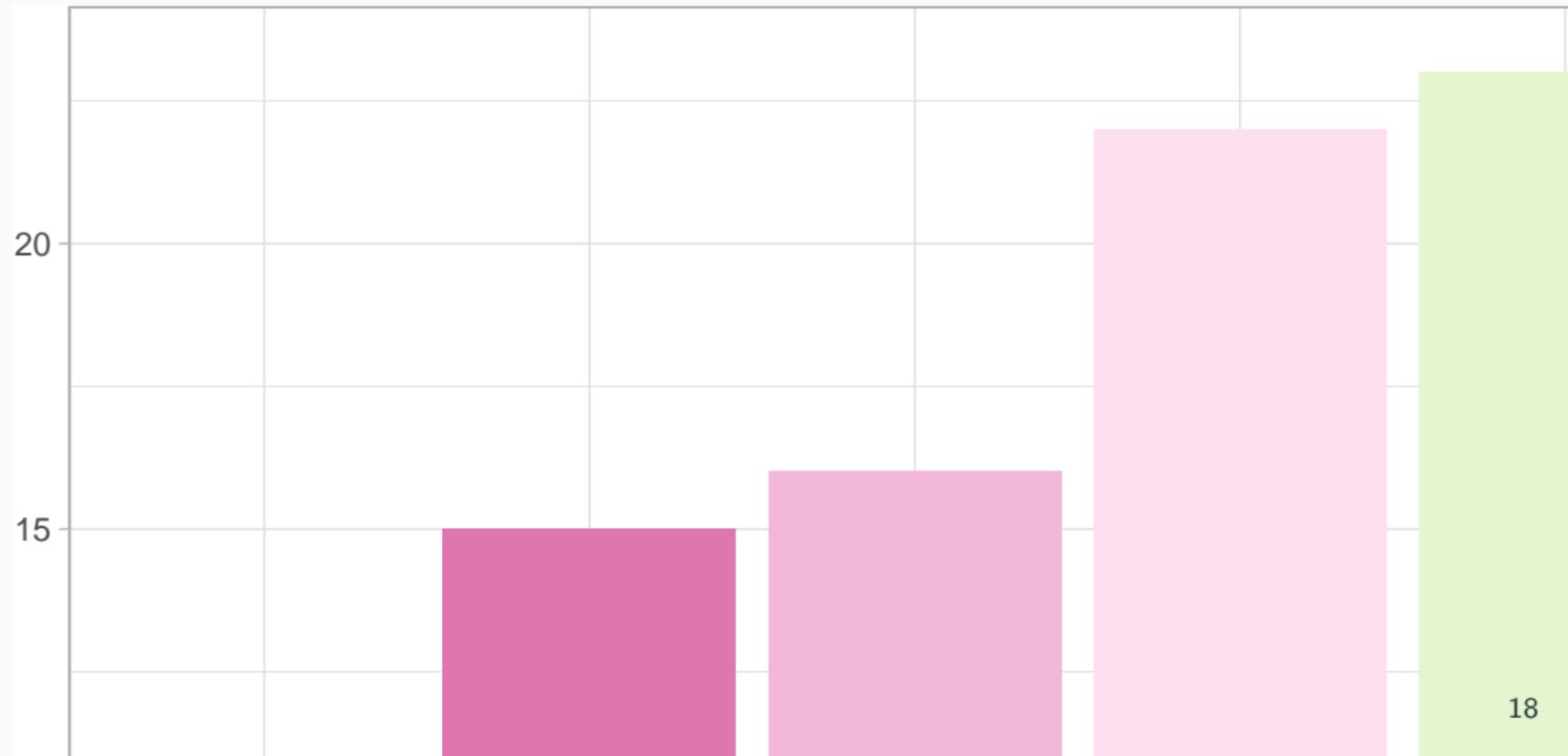
## Binomial distribution

$x$	$P(X = x)$
0	$(1 - p)^N$
1	$Np(1 - p)^{N-1}$
...	...
$N$	$p^N$

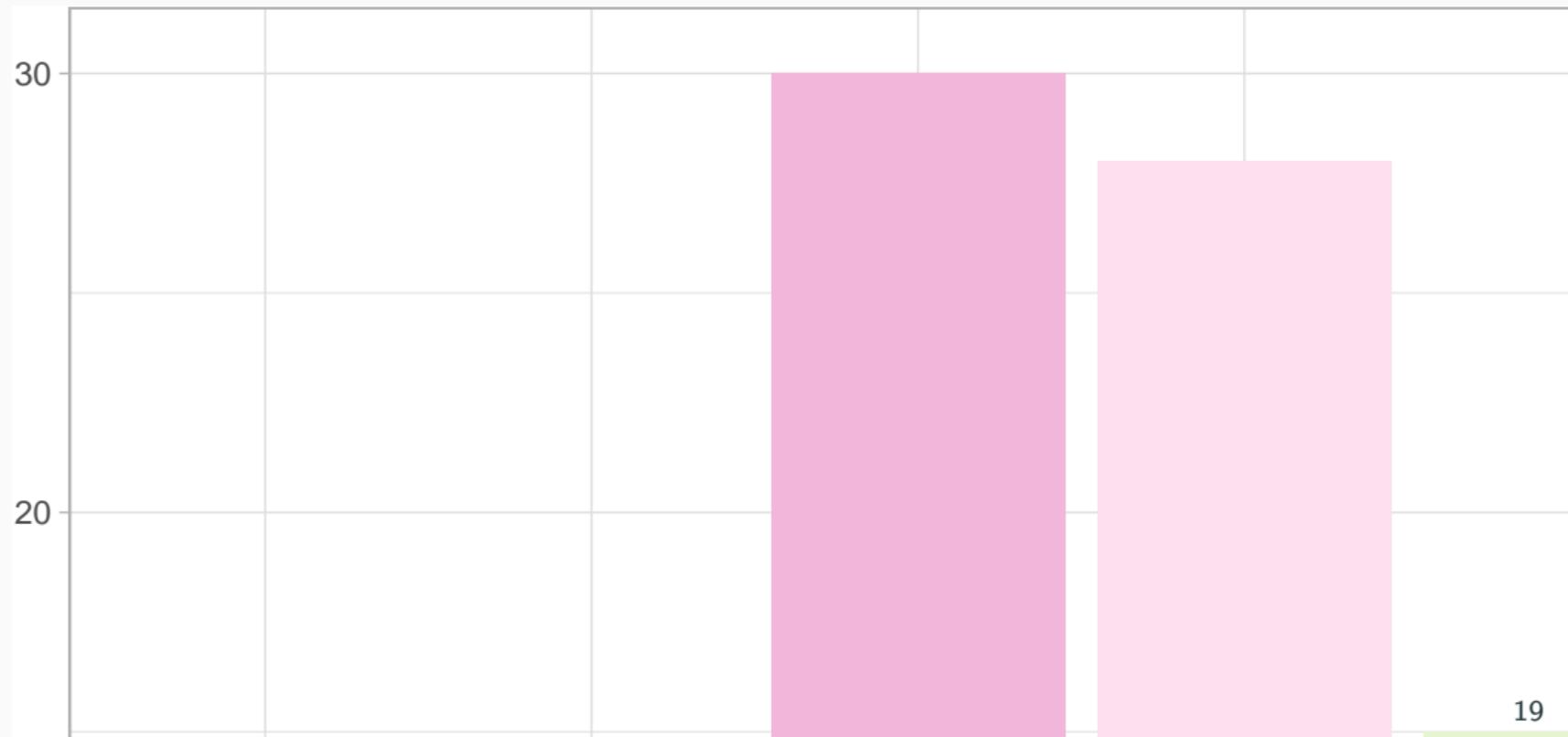
Fortunately, R has this pre-programmed

```
dbinom(x = 1, size = 10, prob = 0.5) # equals 10*0.5*(1-0.5)^(10-1)
#> [1] 0.009765625
```

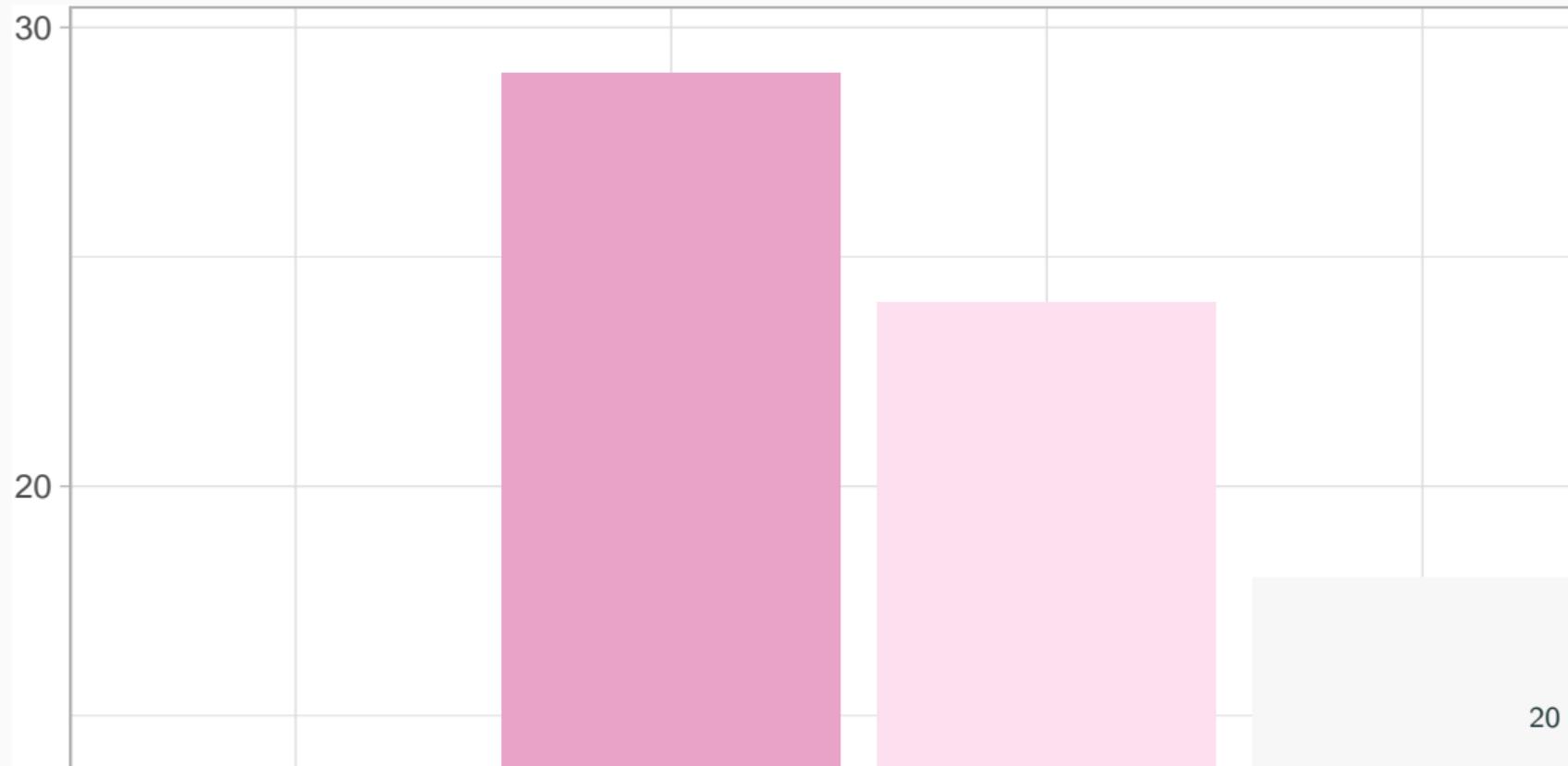
## Hundred Binomial trials with $N = 10$ and $p = 0.5$



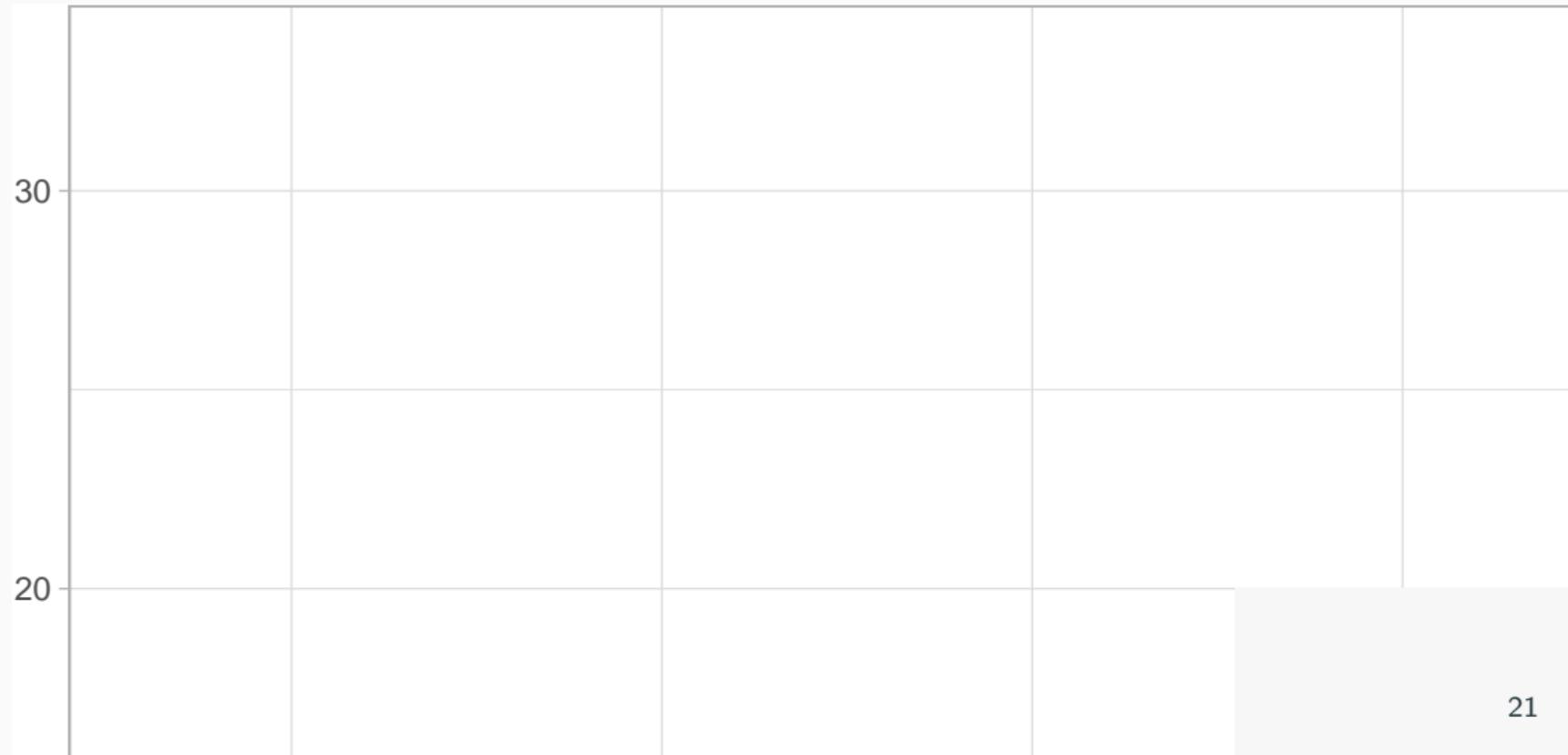
## Hundred Binomial trials with $N = 10$ and $p = 0.5$ , again



## Hundred Binomial trials with $N = 10$ and $p = 0.2$



## Hundred Binomial trials with $N = 10$ and $p = 0.8$



## Playing around with probabilities

- Let's say  $X \sim \text{Bin}(N = 10, p = 0.5)$  is a random variable counting the number of males

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## Playing around with probabilities

- Let's say  $X \sim \text{Bin}(N = 10, p = 0.5)$  is a random variable counting the number of males
- What is the probability of having at most 2 males?
- $P(X \leq 2) = P(X = 0) + P(X = 1)$
- How to compute this in R?

## Playing around with probabilities

- Let's say  $X \sim \text{Bin}(N = 10, p = 0.5)$  is a random variable counting the number of males
- What is the probability of having at most 2 males?
- $P(X \leq 2) = P(X = 0) + P(X = 1)$
- How to compute this in R?
- `dbinom(x=0,size=10,prob=0.5) + dbinom(x=1,size=10,prob=0.5)`

## Summary: Binomial distribution

- **notation:**  $X \sim \text{Bin}(N, p)$ 
  - **range:** discrete,  $0 \leq x \leq N$
  - **distribution:**  $P(X = x) = \binom{N}{x} p^x (1 - p)^{1-x}$
  - **parameters:**  $p$  the probability of success, and  $N$  the number of trials
- **mean:**  $Np$ 
  - **variance:**  $Np(1 - p)$
  - **in R:** `rbinom`, `dbinom`

## Poisson distribution

**Context:** Number of occurrences of an event over a given unit of space or time.

$X \sim \text{Poisson}(\lambda)$  with  $\lambda$  expected number of occurrences

$$P(X = x) = \frac{e^{-\lambda} \lambda^x}{x!}$$

**Example:**  $X$  is the random variable *number of birds counted on a colony during the breeding season*

## Poisson distribution

$$P(X = x) = \frac{e^{-\lambda} \lambda^x}{x!}$$

x	$P(X = x)$
0	$e^{-\lambda}$
1	$\lambda e^{-\lambda}$
...	...

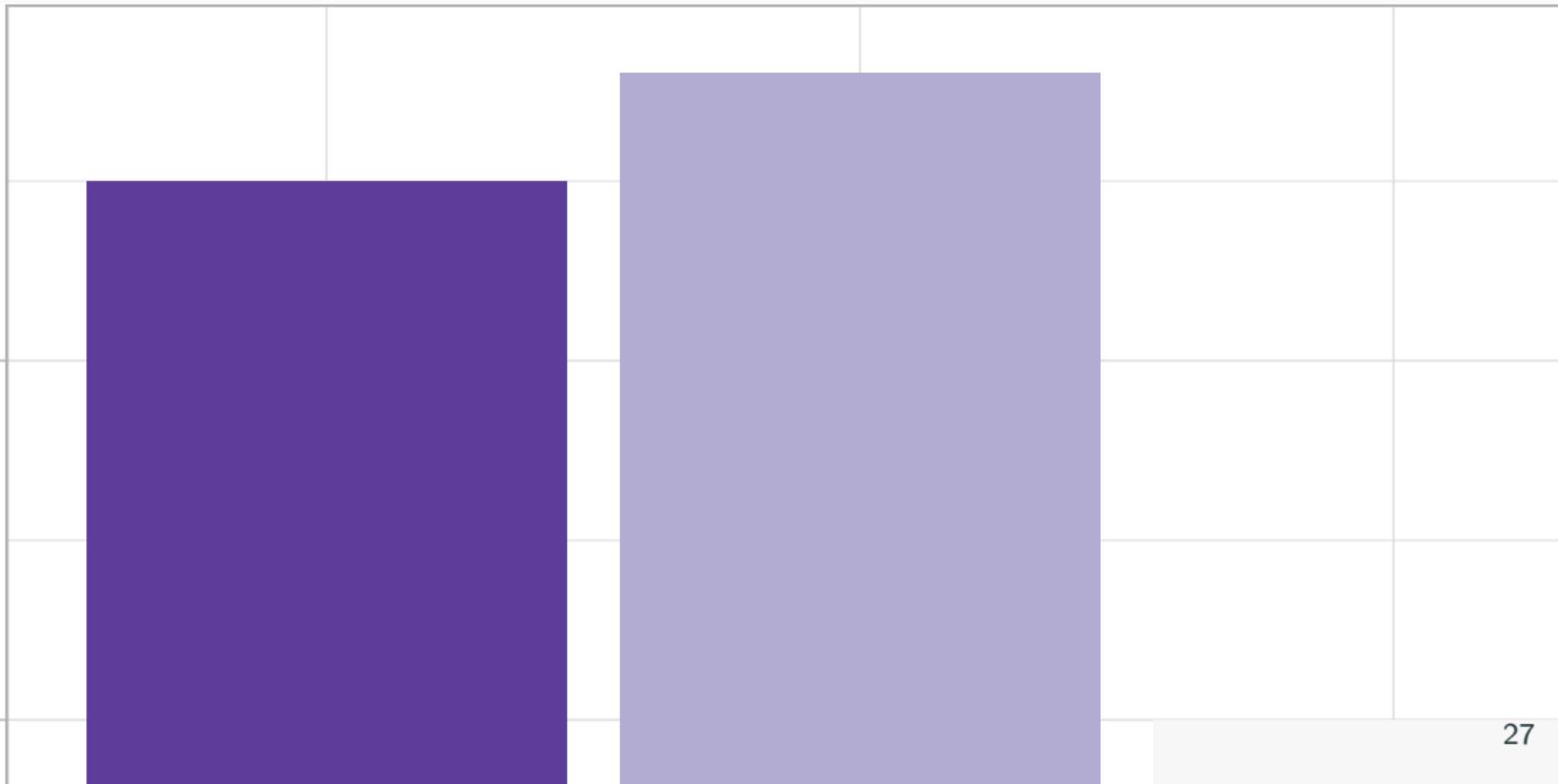
## Poisson distribution

$x$	$P(X = x)$
0	$e^{-\lambda}$
1	$\lambda e^{-\lambda}$
...	...

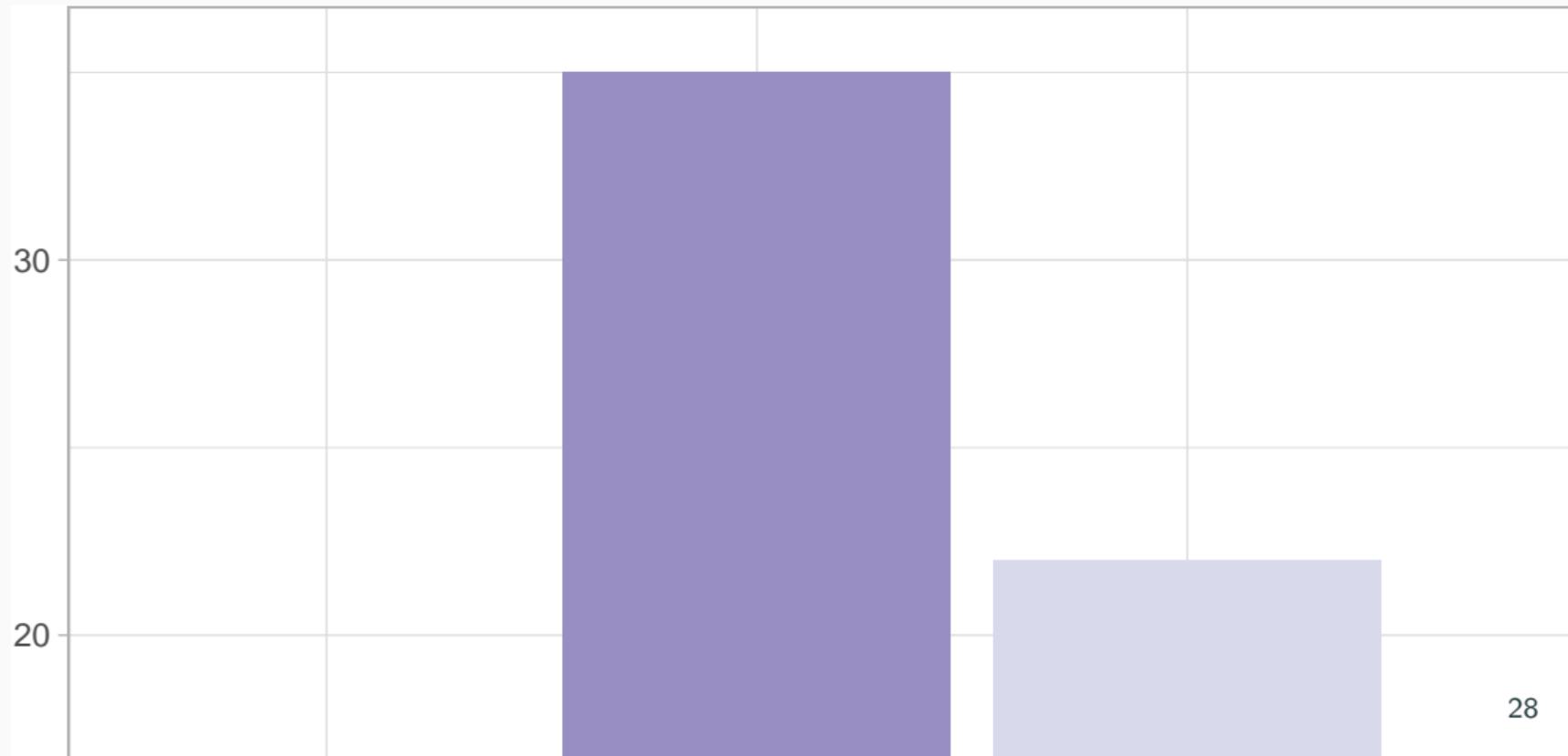
Fortunately, R has this pre-programmed

```
dpois(x=0,lambda=3) # equals exp(-3)  
#> [1] 0.04978707
```

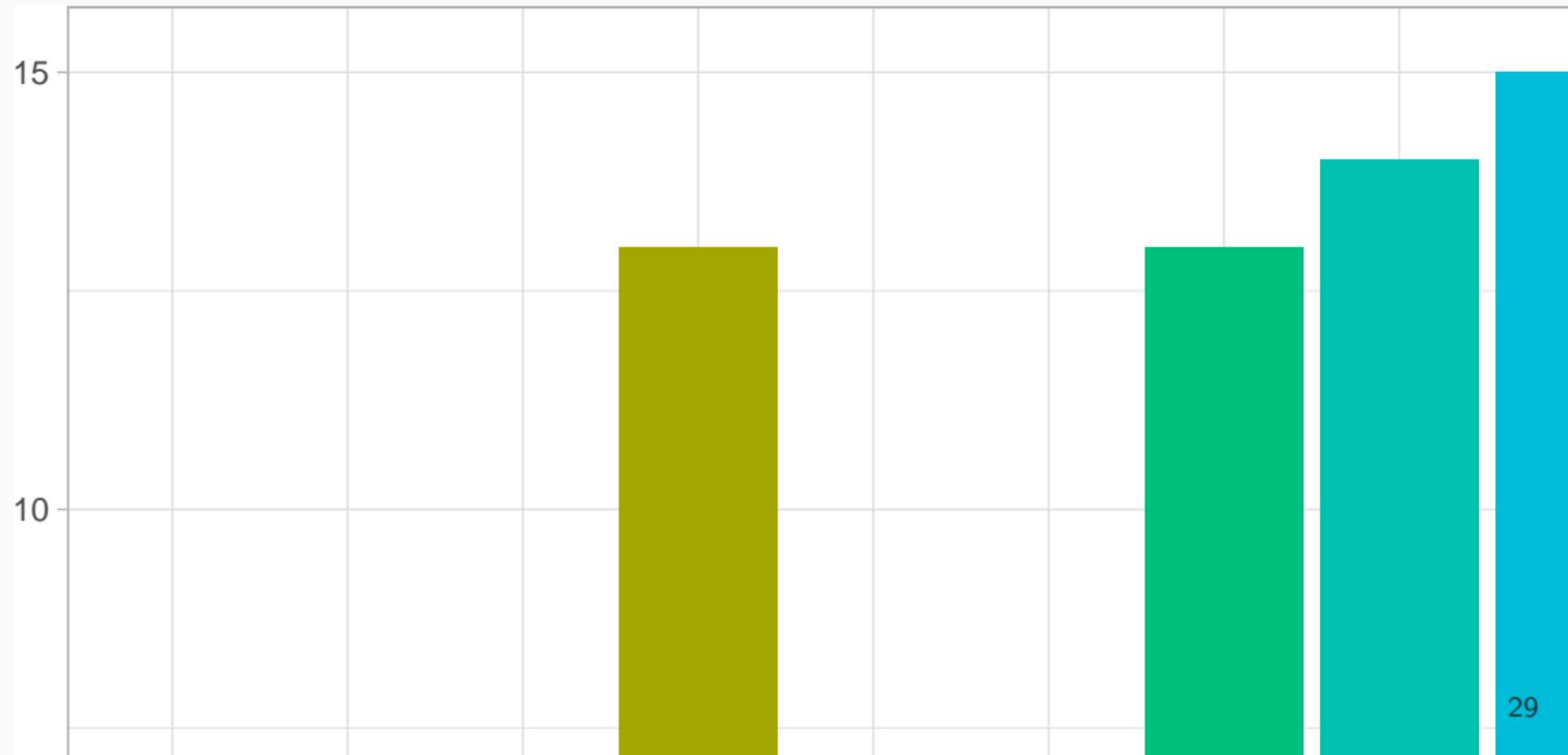
## Hundred Poisson trials with $\lambda = 1$



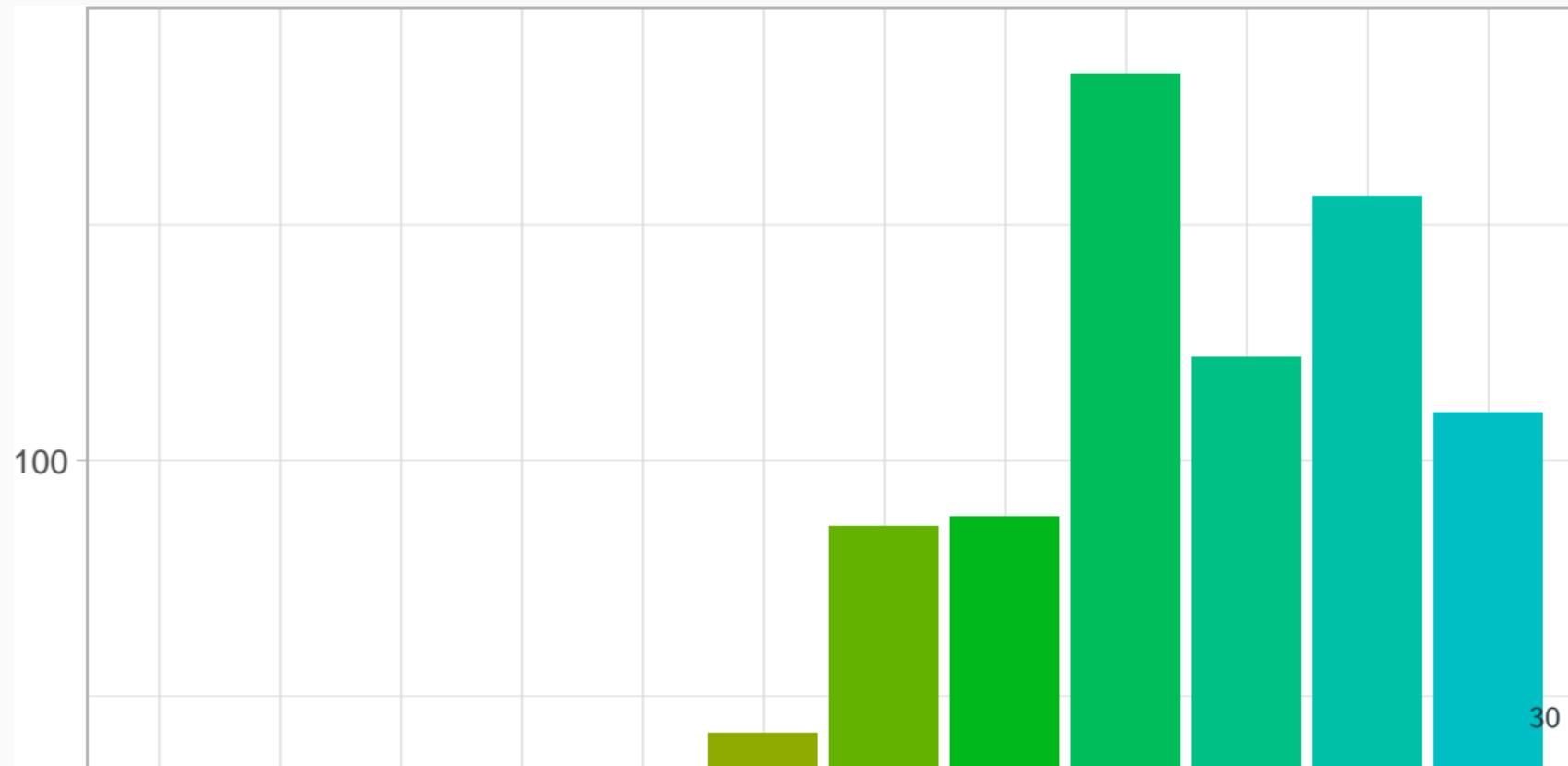
## Hundred Poisson trials with $\lambda = 2$



## Hundred Poisson trials with $\lambda = 10$



## Thousand Poisson trials with $\lambda = 10$



## Summary: Poisson distribution

- **notation:**  $X \sim \text{Poisson}(\lambda)$ 
  - **range:** discrete,  $x \geq 0$
  - **distribution:**  $P(X = x) = \frac{e^{-\lambda}\lambda^x}{x!}$
  - **parameters:**  $\lambda$  the rate or expected number per sample
- **mean:**  $\lambda$ 
  - **variance:**  $\lambda$
  - **in R:** rpois, dpois

## **Continuous distribution**

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## Normal (Gaussian) distribution

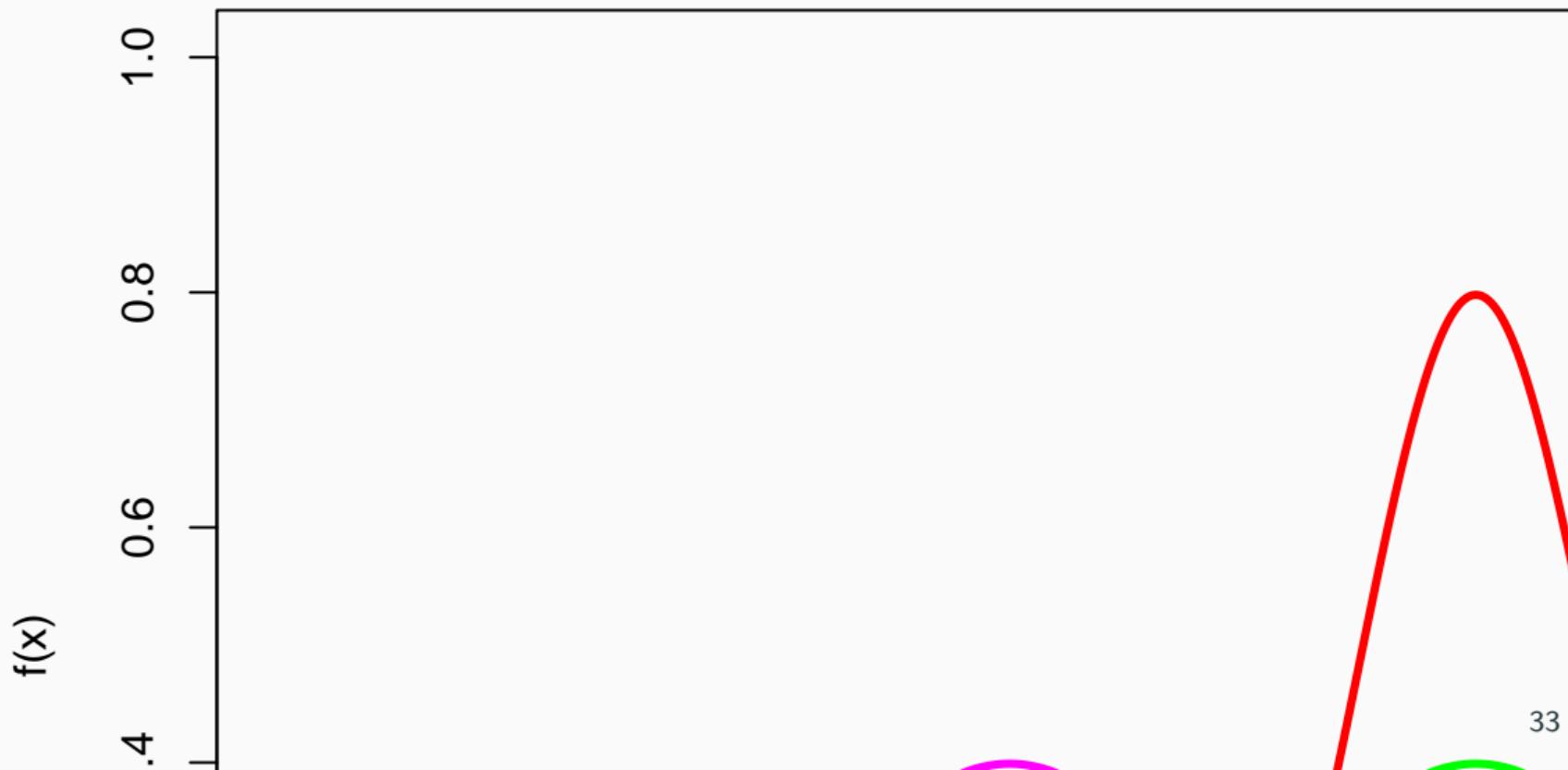
**Context:** Distribution of “adding lots of things together”. Derived from *Central Limit Theorem*, which says that if you add a large number of independent samples from the same distribution the distribution of the sum will be approximately normal.

$X \sim \text{Normal}(\mu, \sigma^2)$  where  $\mu$  is the mean and  $\sigma^2$  the variance

$$f(x) = \frac{1}{\sqrt{2\pi}\sigma} \exp\left(-\frac{(x-\mu)^2}{2\sigma^2}\right)$$

**Example:** Practically everything.

## Normal probability density function



## Summary: Normal distribution

- **notation:**  $X \sim N(\mu, \sigma^2)$ 
  - **range:** continuous, all real values
- **distribution:**  $f(x) = \frac{1}{\sqrt{2\pi}\sigma} \exp\left(-\frac{(x-\mu)^2}{2\sigma^2}\right)$ 
  - **parameters:**  $\mu$  the mean and  $\sigma$  the standard deviation
- **mean:**  $\mu$ 
  - **variance:**  $\sigma^2$
  - **in R:** `rnorm`, `dnorm`

## Why do we love the Normal distribution

- If has nice properties, such as: if  $X \sim N(\mu, \sigma^2)$ , then  $Z = \frac{X - \mu}{\sigma} \sim N(0, 1)$
- It is a limiting distribution (*Central Limit Theorem*)
- It can be a good approximation for other distributions

## Example: Approximating Binomial by Normal (1)

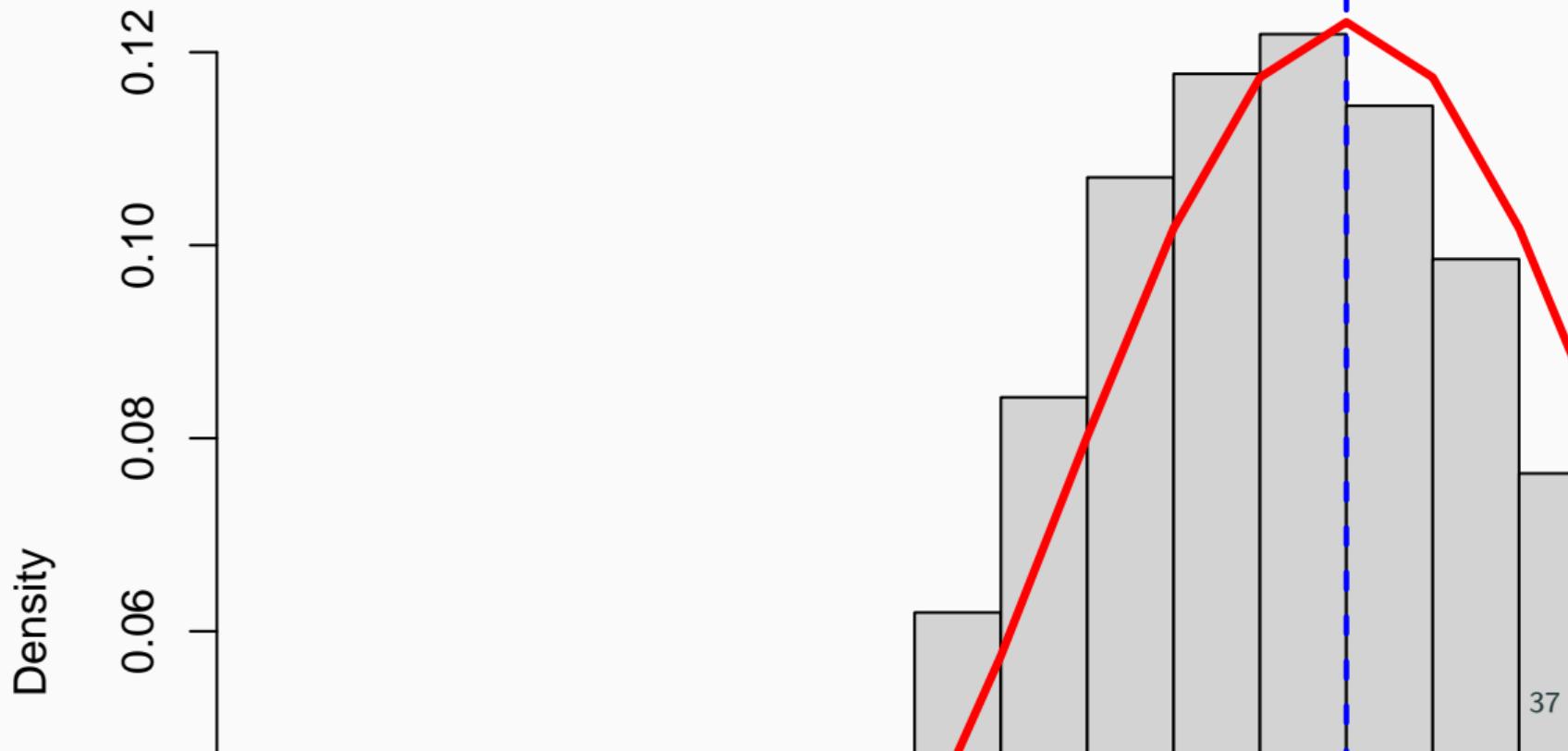
$X \sim \text{Bin}(N = 50, p = 0.3)$

Mean is  $Np = 50 \times 0.3 = 15$

Variance is  $Np(1 - p) = 50 \times 0.3 \times 0.7 = 10.5$

Therefore,  $X$  can be approximated by  $Y \sim N(15, \sigma = \sqrt{10.5})$

## Example: Approximating Binomial by Normal (2)



## Conclusions about distributions

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## Common Distributions - Discrete

- When we have something that is dichotomous (either 0 or 1, negative/positive, false/true, male/female, present/absent):

Binomial(number of trials, probability)

- When we have something that is a discrete count, with no theoretical maximum, but with a common average:

Poisson(lambda)

## Common Distributions - Discrete

- When we are recording the number of *failures* before a number of *successes*, or when we have something that is a discrete count with no theoretical maximum, and with more variation than Poisson:

NegativeBinomial(number of successes, probability of success)

NegativeBinomial(mean, overdispersion)

## Common Distributions - Continuous

- When we have something that is continuous, symmetrical about the mean and unbounded:  
Normal(mean, standard deviation)
- When we have something that is continuous, not symmetrical, and bounded at zero:  
Exponential(rate)  
Gamma(shape, rate)

## Common Distributions - Continuous

- When we have something that is continuous, not symmetrical, and bounded at zero:

$\text{Lognormal}(\text{logmean}, \text{logstdev})$

- When we have something that is continuous, and bounded between 0 and 1:

$\text{Beta}(\text{alpha}, \text{beta})$

- Simple bounded distribution:

$\text{Uniform}(\text{min}, \text{max})$

More? Check out in R:

?Distributions

## Likelihoods

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## Fitting distributions to data

- So far, when talking about probability distributions, we assumed that we knew the parameter values
- And we wanted to know what data we might get from these distributions
- In the real world, it is usually the other way around
- A more relevant question might be:  
*We have observed 3 births by a female during her 10 breeding attempts. What does this tell us about the true probability of getting a successful breeding attempt from this female? For the population?*

## Fitting distributions to data

We don't know what the probability of a birth is, but we can see what the probability of getting our data would be for different values:

```
dbinom(x = 3, size = 10, prob = 0.1)  
#> [1] 0.05739563
```

## Fitting distributions to data

We don't know what the probability of a birth is, but we can see what the probability of getting our data would be for different values:

```
dbinom(x=3,size=10,prob=0.9)  
#> [1] 8.748e-06
```

## Fitting distributions to data

We don't know what the probability of a birth is, but we can see what the probability of getting our data would be for different values:

```
dbinom(x=3, size=10, prob=0.25)  
#> [1] 0.2502823
```

So we would be more likely to observe 3 births if the probability is 0.25 than 0.1 or 0.9

## The likelihood

- This reasoning is so common in statistics that it has a special name:
- **The likelihood** is the probability of observing the data under a certain model
- The data are known, we usually consider the likelihood as a function of the model parameters  $\theta_1, \theta_2, \dots, \theta_p$

$$L = P(\theta_1, \theta_2, \dots, \theta_p \mid \text{data})$$

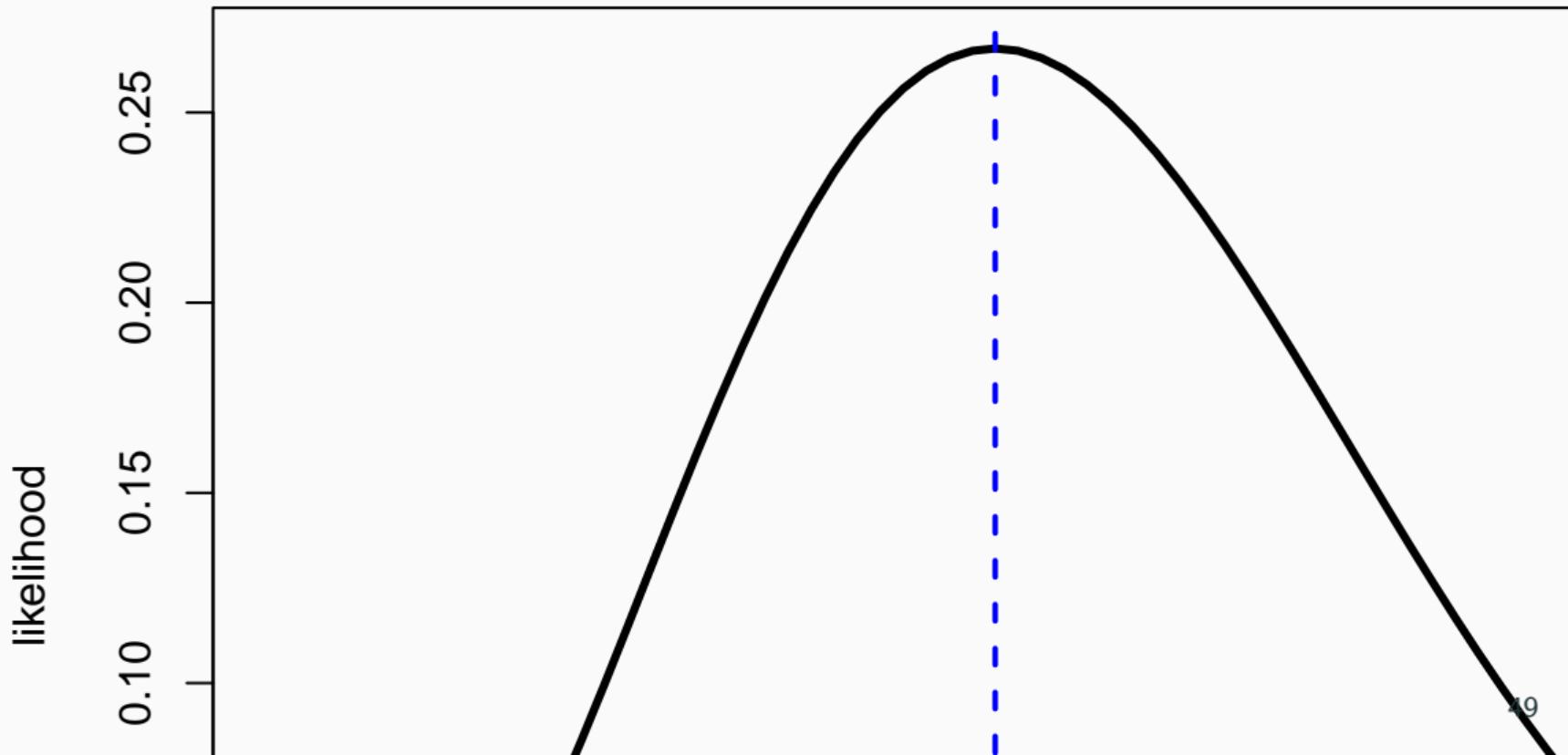
- This is a very important concept

## Likelihood functions

We may create a function to calculate a likelihood e.g.:

```
lik.fun <- function(parameter){  
  ll <- dbinom(x=3, size=10, prob=parameter)  
  return(ll)  
}  
  
lik.fun(0.3)  
#> [1] 0.2668279  
  
lik.fun(0.6)  
#> [1] 0.04246733
```

Maximize the likelihood (3 successes ot of 10 attempts)



## The Maximum Likelihood

- There is always a set of parameters that gives you the highest likelihood of observing the data: the Maximum Likelihood Estimate(s) [MLEs]
- This can be calculated using:
- Trial and error (not efficient!)
- Compute the maximum of a function by hand (rarely doable in practice)
- An iterative optimization algorithm: `?optimize` (1 parameter) and `?optim` ( $> 1$  parameter) in R

**By hand: compute MLE of  $p$  from  $Y \sim \text{Bin}(N = 10, p)$  with  $k = 3$  successes**

$$P(Y = k) = \binom{k}{N} p^k (1 - p)^{N - k} = L(p)$$

$$\log(L(p)) = \text{cte} + k \log(p) + (N - k) \log(1 - p)$$

We are searching for the maximum of  $L$ , or equivalently that of  $\log(L)$

Compute derivate w.r.t.  $p$ :  $\frac{d \log(L)}{dp} = \frac{k}{p} - \frac{(N - k)}{(1 - p)}$

Then solve  $\frac{d \log(L)}{dp} = 0$ ; the MLE is  $\hat{p} = \frac{k}{N} = \frac{3}{10} = 0.3$

Here, the MLE is the proportion of observed successes

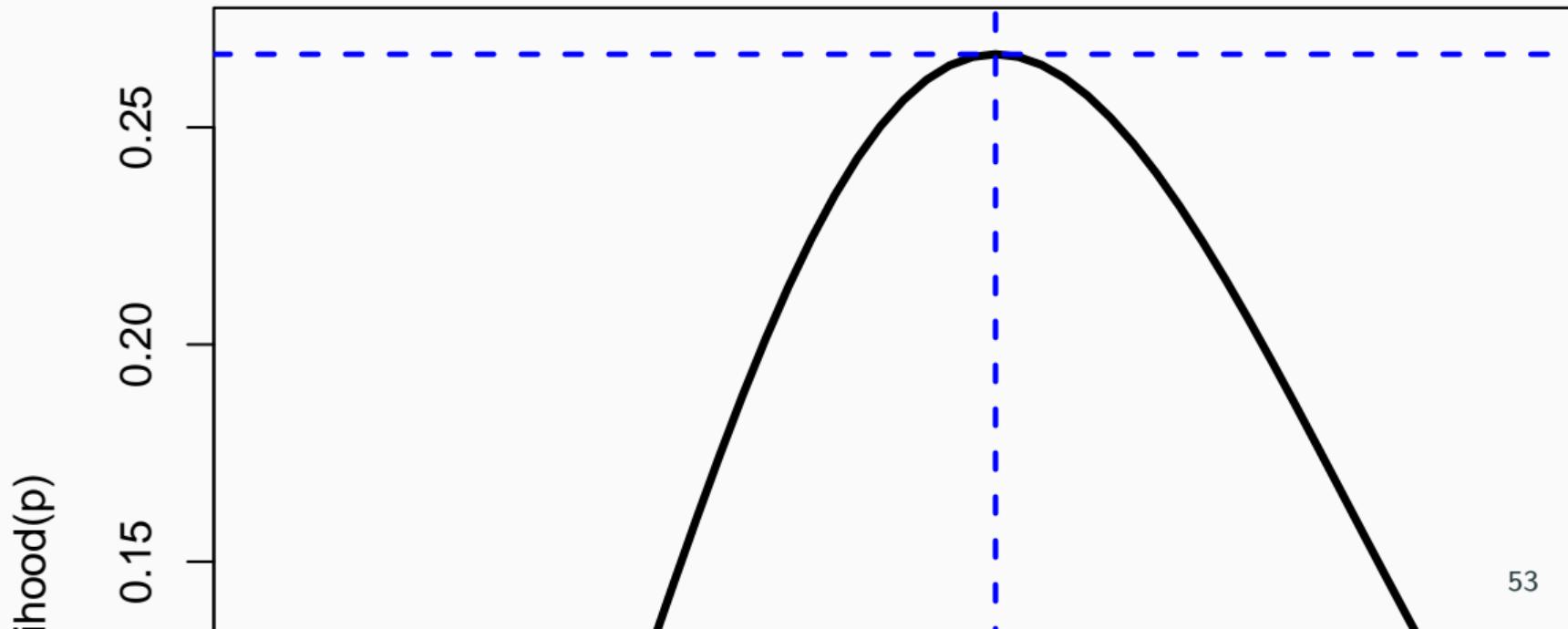
## Using a computer: MLE of $p$ from $Y \sim \text{Bin}(N = 10, p)$ with $k = 3$ successes

```
lik.fun <- function(parameter) dbinom(x=3, size=10, prob=parameter)
# ?optimize
optimize(lik.fun,c(0,1),maximum=TRUE)
#> $maximum
#> [1] 0.3000157
#>
#> $objective
#> [1] 0.2668279
```

Use optim when the number of parameters is  $> 1$ .

Using a computer: MLE of  $p$  from  $Y \sim \text{Bin}(N = 10, p)$  with  $k = 3$  successes

### Binomial likelihood with 3 successes

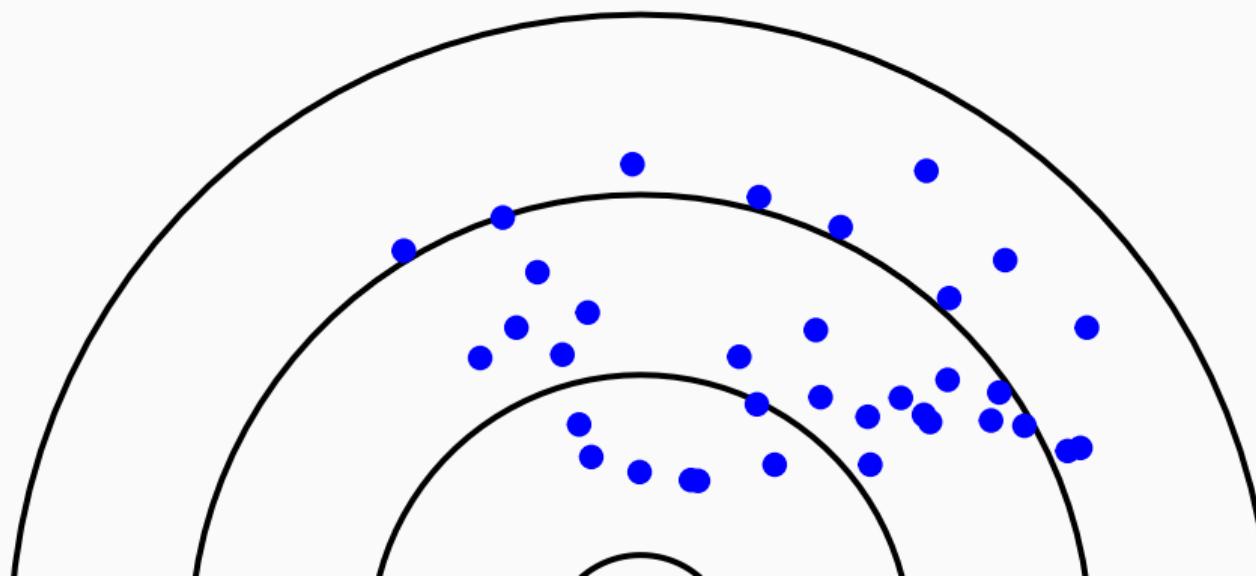


## The Maximum Likelihood Estimate (MLE)

- The MLE is the best guess set of parameter values for our given data

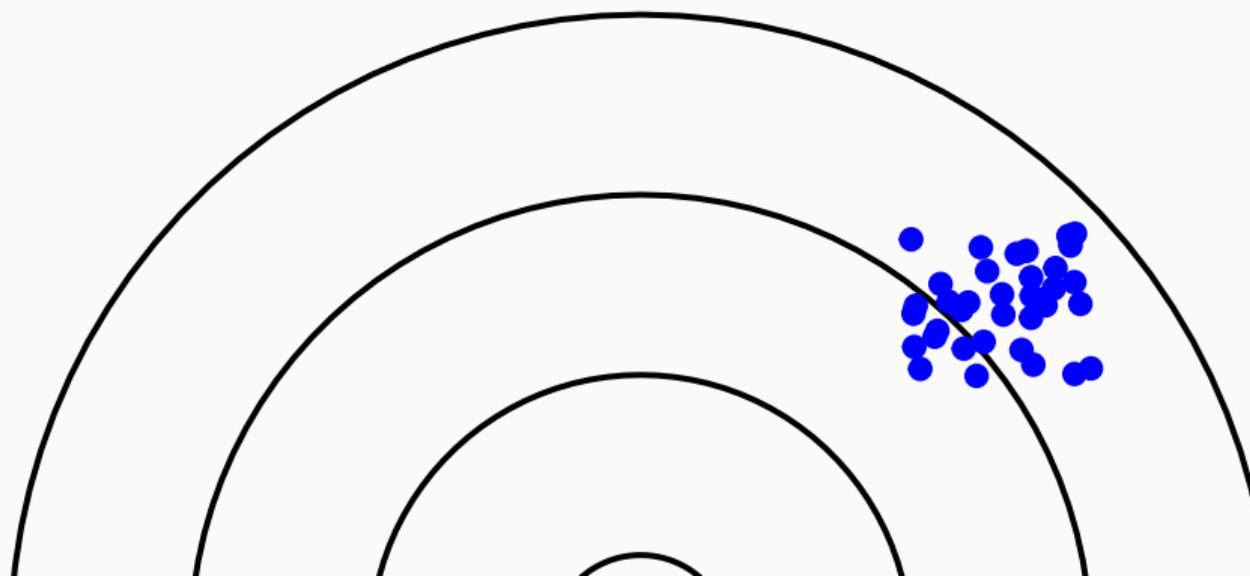
A dart target, with the red cross representing the true parameter value

## Imprecise and biased



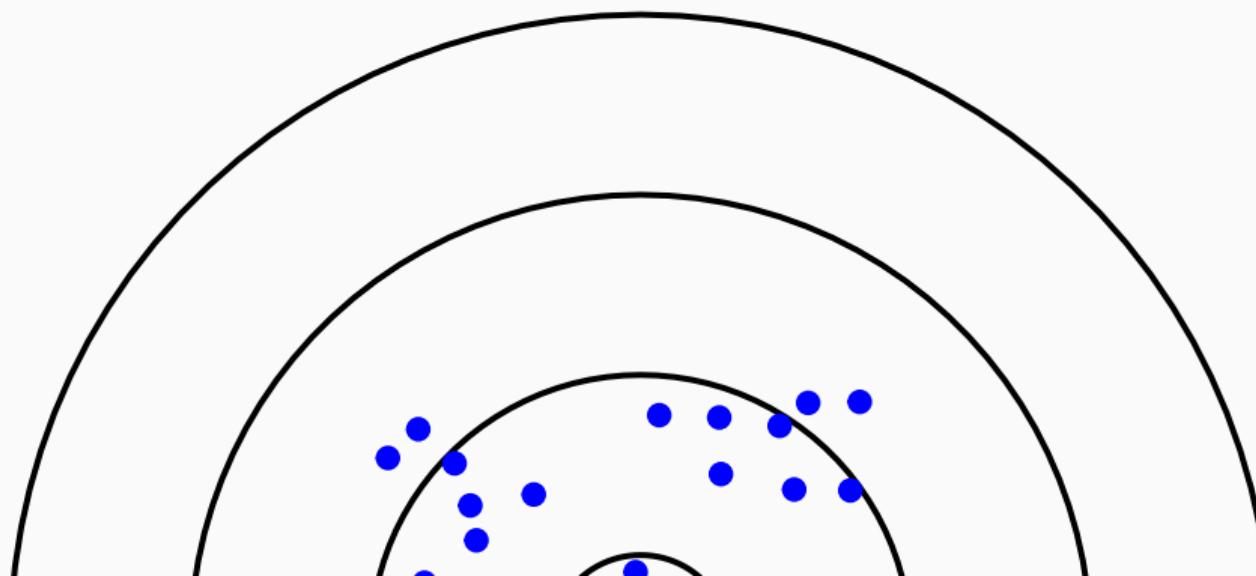
A dart target, with the red cross representing the true parameter value

Precise but biased



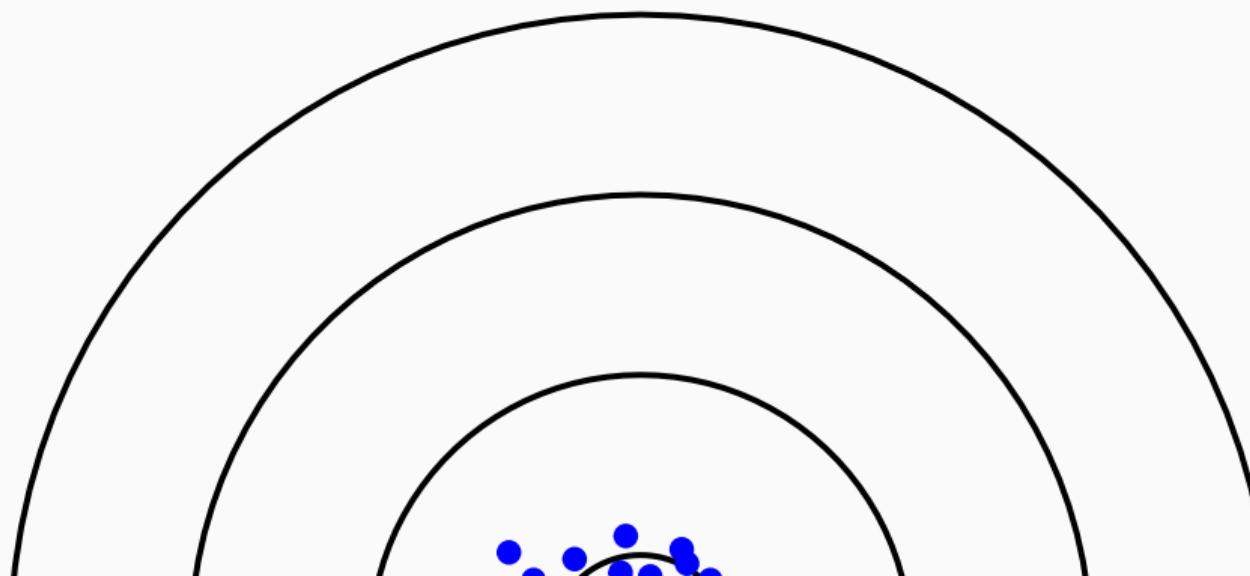
A dart target, with the red cross representing the true parameter value

**Unbiased but imprecise**



A dart target, with the red cross representing the true parameter value

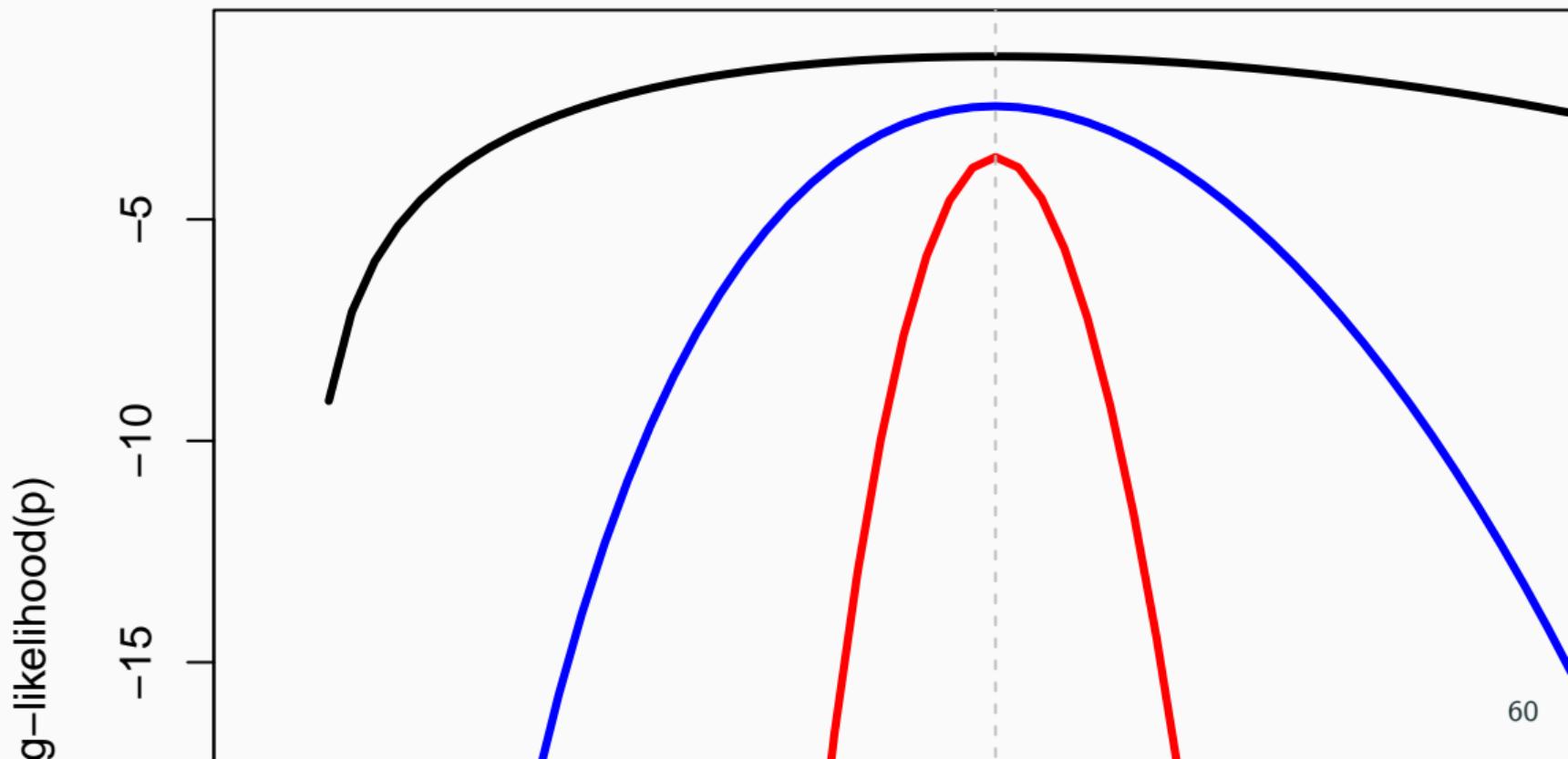
**Unbiased and precise!**



## The Maximum Likelihood Estimate (MLE)

- The MLE is the best guess set of parameter values for our given data
- But the chances of the true parameter values being close to the MLE is dependent on the amount of information in the data!

## Binomial likelihood with increasing sample size



## **Confidence intervals: A refresher**

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## Let's approach confidence intervals through simulations

Imagine you are measuring the temperature of a cup of water 10 times but you have an old really bad thermometer. The true temperature is 3 degrees Celsius and the standard deviation on the sampling error is 5.

```
# Simulate data:  
mu <- 3  
sigma <- 5  
n <- 10  
y <- rnorm(n = n, mean = mu, sd = sigma)  
y  
#> [1] 5.9276441 6.5473301 2.4534834 0.7325141 6.0294373 -6.0897798  
#> [7] 6.1504928 1.6190795 1.5792013 -1.5966100
```

## Apply linear regression

We will estimate a mean temperature by fitting an intercept only linear regression model:

```
m <- lm(y~1)
library(broom)
tidy(m)

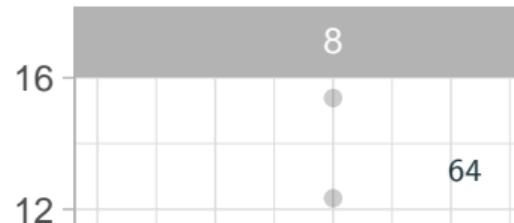
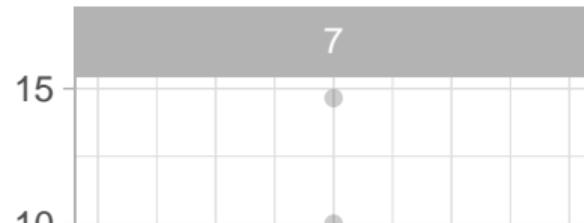
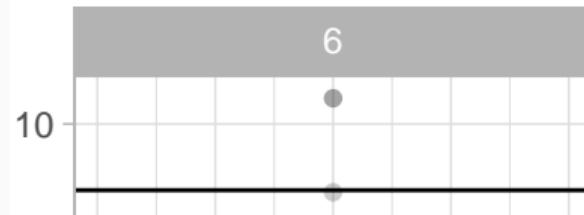
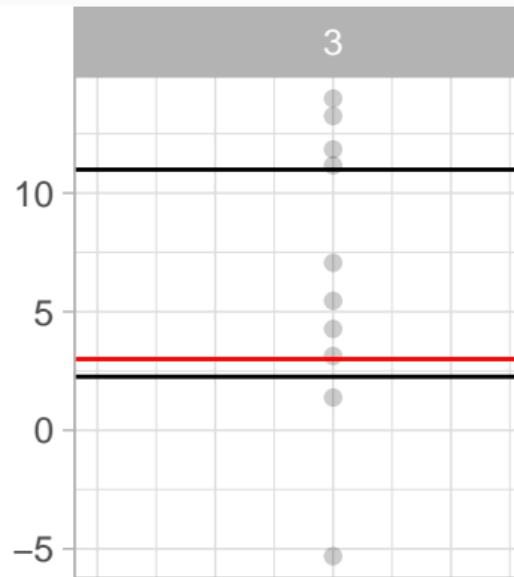
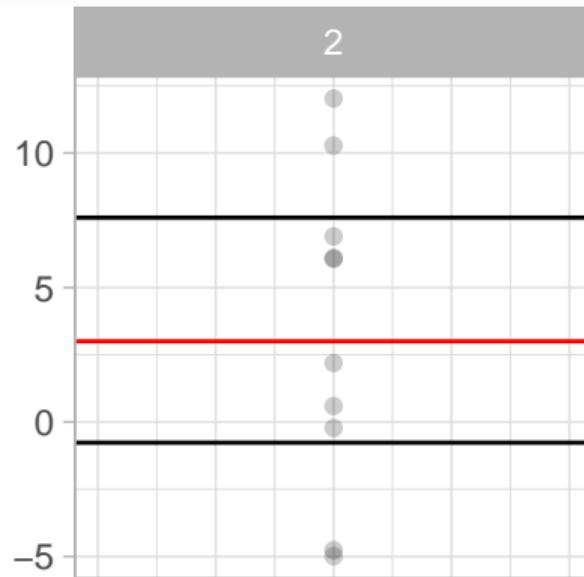
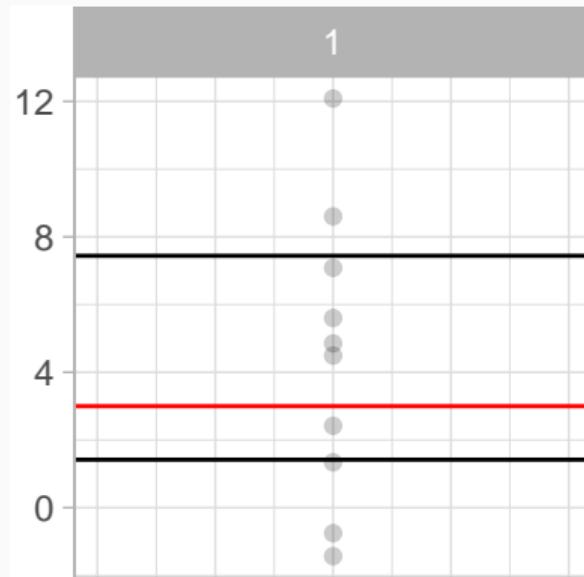
#> # A tibble: 1 x 5
#>   term      estimate std.error statistic p.value
#>   <chr>      <dbl>     <dbl>      <dbl>    <dbl>
#> 1 (Intercept)  2.34      1.29      1.82    0.103

confint(m)
#>                   2.5 %  97.5 %
#> (Intercept) -0.5749909 5.245549
```

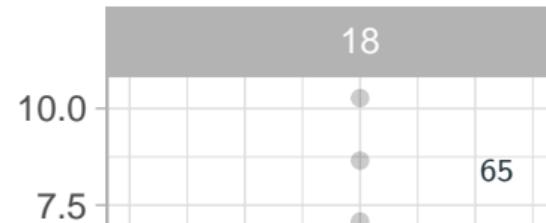
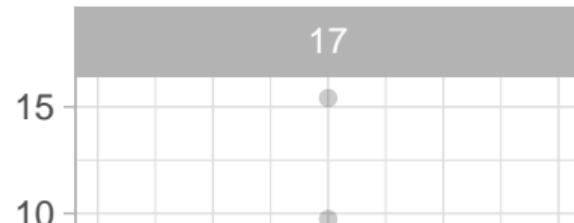
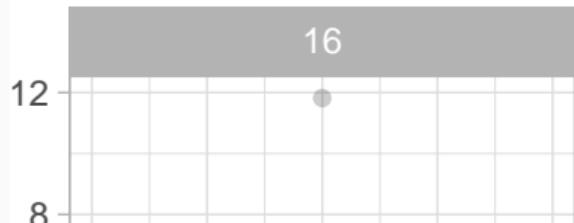
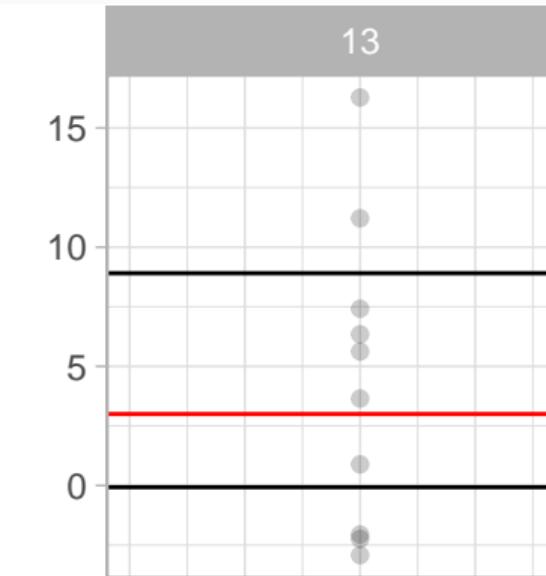
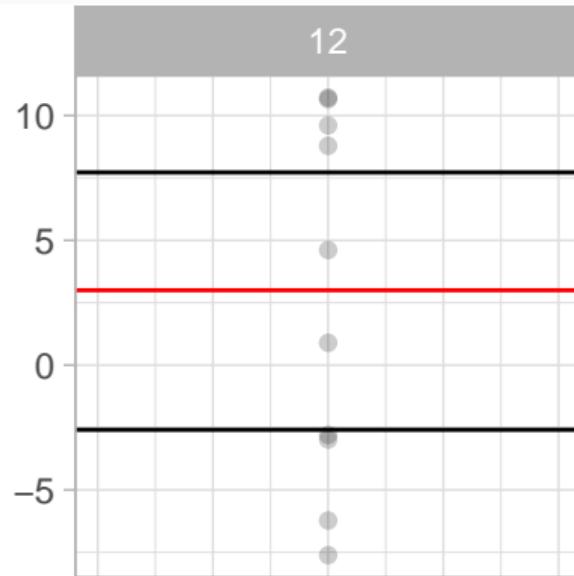
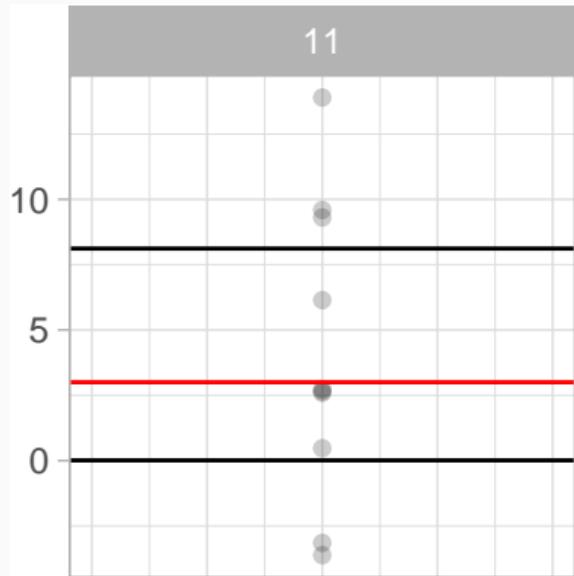
## Let's illustrate what those confidence intervals really represent.

- Imagine you went outside 20 times and each time you measured the cup of water 10 times. Then you fitted a linear regression model with an intercept only each time and plotted the confidence intervals.
- 19 times out 20 (95%) the 95% confidence intervals should contain the true value.

Does that look approximately correct?



Does that look approximately correct?



## Likelihood key facts

- The likelihood is the probability of observing a (fixed) dataset given a set of parameter values (to be estimated)
- Maximum likelihood theory provides estimates with optimal properties: unbiased, minimal variance and normally distributed (asymptotically)
- The rate of change of the likelihood around the MLE is an indication of our confidence in the estimated parameter values
- Use confidence intervals to capture uncertainty surrounding MLEs
- Likelihood functions can get very complicated!

## Textbooks



## This Class

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## On our plate

- Distributions and likelihoods
- Hypothesis testing and multimodel inference
- Introduction to Bayesian inference
- Generalized Linear Models (GLMs)
- Generalized Additive Models (GAMs)
- Mixed Effect Models

## Hypothesis testing: Rationale

The problem:

*Suppose a coin toss turns up  $k = 12$  heads out of  $N = 20$  trials. Can we say that the coin toss is fair? Do we get more heads than expected (assuming the coin toss is fair)?*

## Hypothesis testing: Rationale

1. Define the null and alternative hypotheses. The null hypothesis is usually the one that represents the less complicated explanation of the real world
  - $H_0$ : the coin toss is fair
  - $H_1$ : the coin toss is unfair, we get more heads or tails than expected

## Hypothesis testing: Rationale

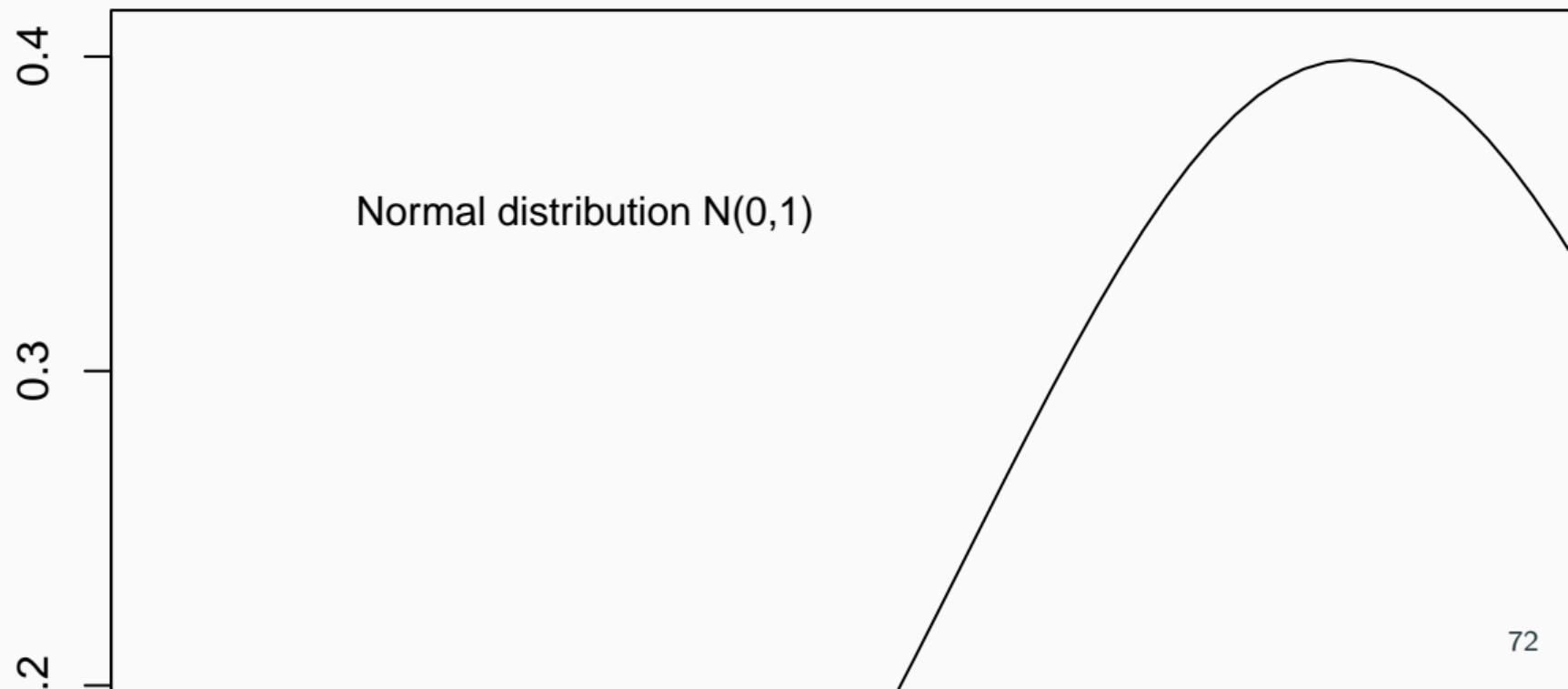
### 2. Construct a sampling distribution for the estimator under $H_0$

- The number of heads  $X$  is a Binomial distribution with parameter  $p$
- Under  $H_0$ , we have  $p = p_0$  with  $p_0 = 0.5$  if the coin toss is fair
- Under  $H_1$ , we have  $p \neq p_0$
- Remember that an estimator of  $p$  is the MLE  $\hat{p} = k/N$ , which is normally distributed with mean  $p$  and some variance; therefore, we have under  $H_0$ :

$$\frac{\hat{p} - p_0}{\sqrt{p_0(1 - p_0)/N}} \sim \text{Normal}(0, 1)$$

## Hypothesis testing: Rationale

2. Construct a sampling distribution for the estimator under  $H_0$



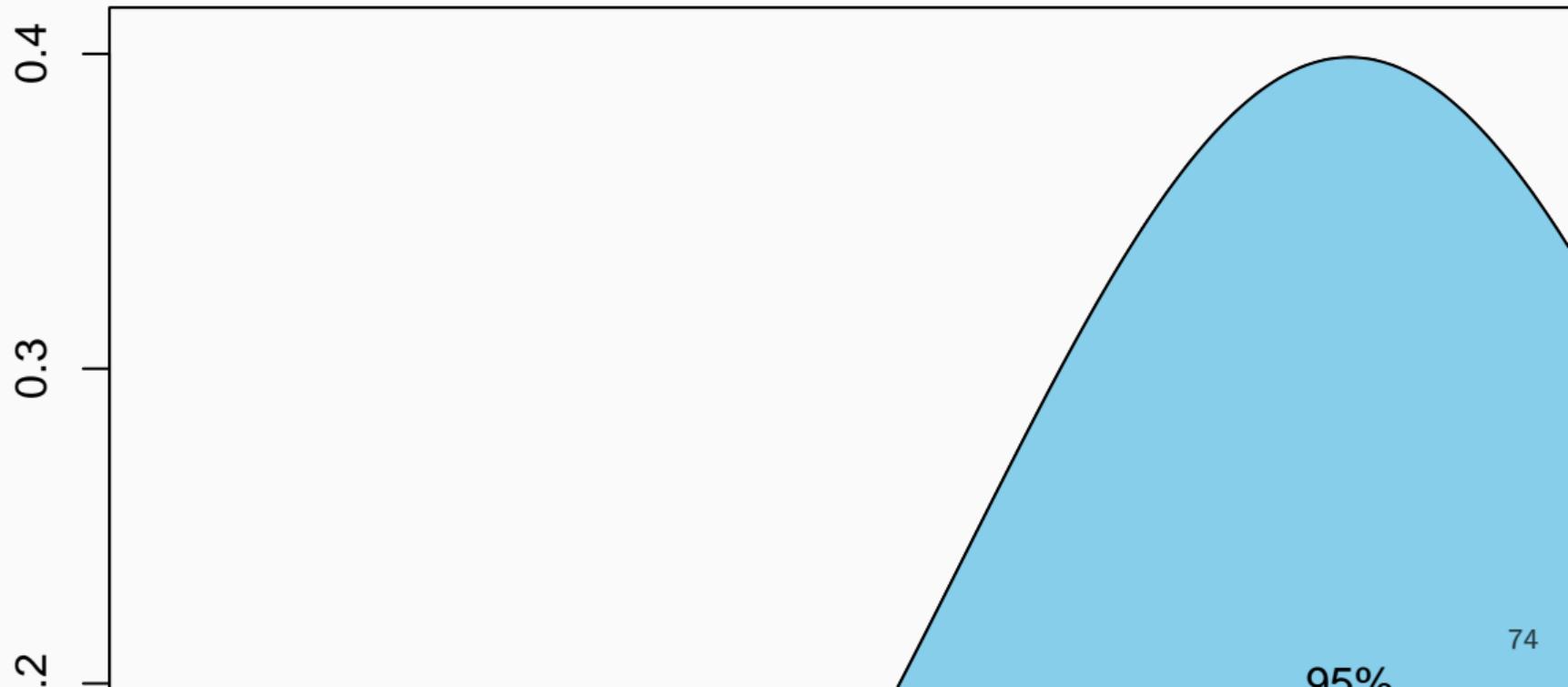
## Hypothesis testing: Rationale

3. The sampling distribution will assign a likelihood to every possible value of the estimator. Very small values of likelihood – at the extremes of the sampling distribution – can be taken as evidence that the population generating the data has a parameter different to the one postulated by  $H_0$ .

A probability value  $\alpha$  is chosen to represent the level of significance required of the result. For example  $\alpha = 0.05$  means that, under  $H_0$ , the estimator will be found in the extreme regions of parameter space only five times every one hundred samples.

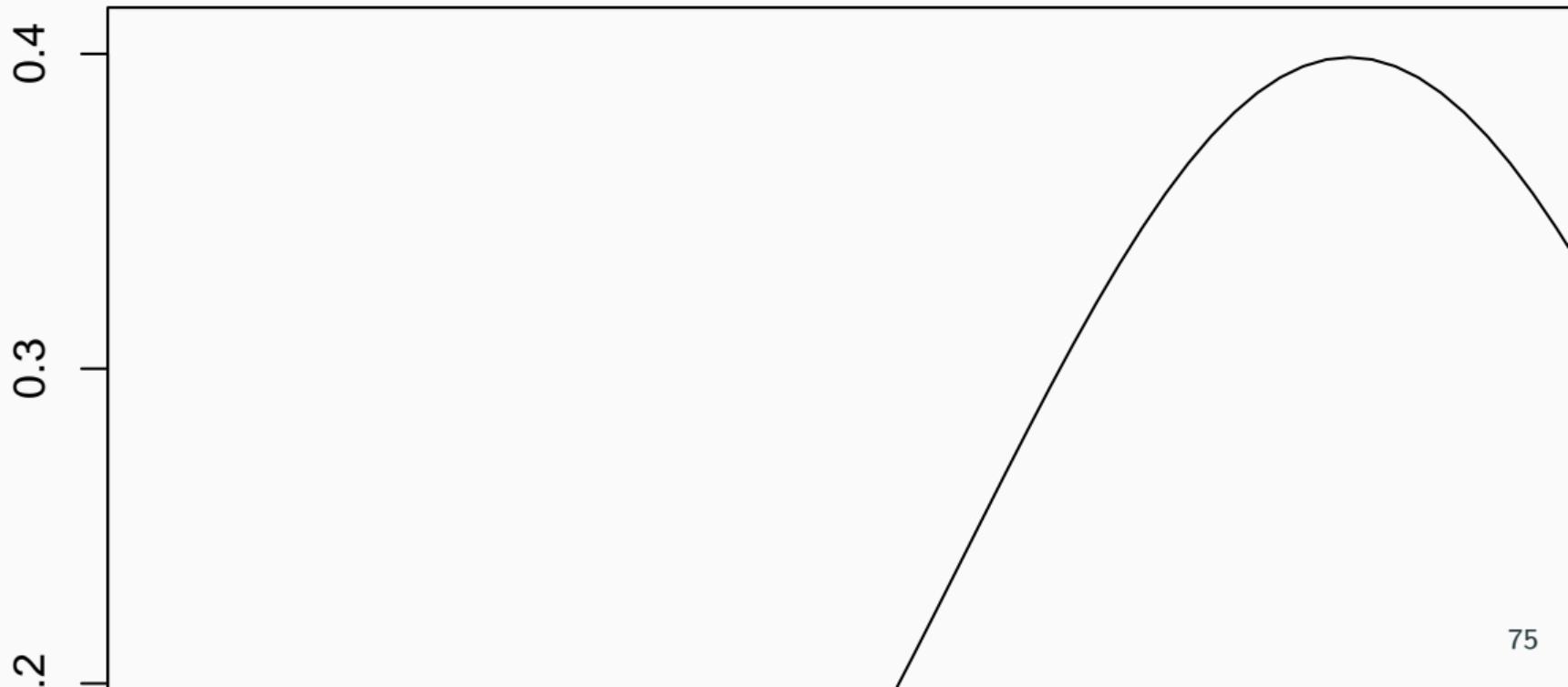
## Hypothesis testing: Rationale

3. For example, say the level of significance is  $\alpha = 0.05$



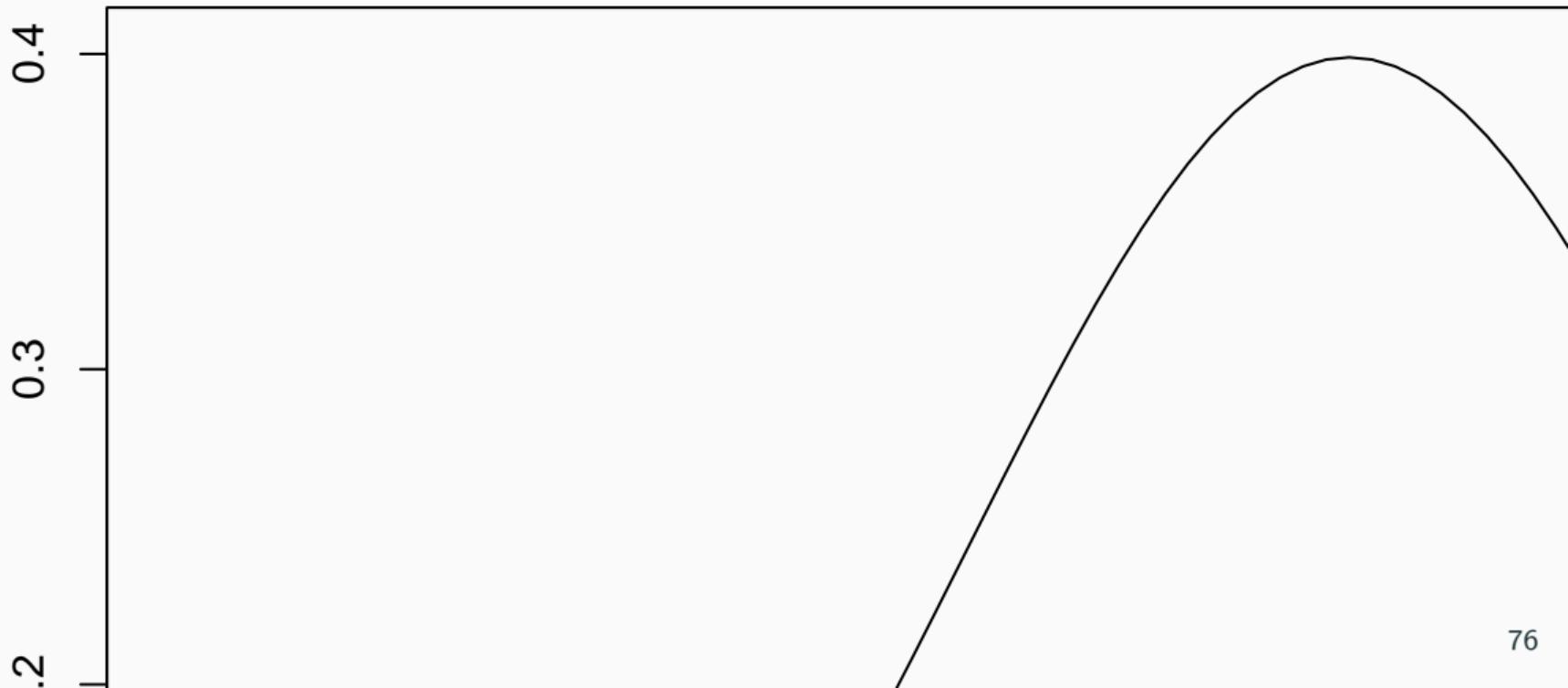
## Hypothesis testing: Rationale

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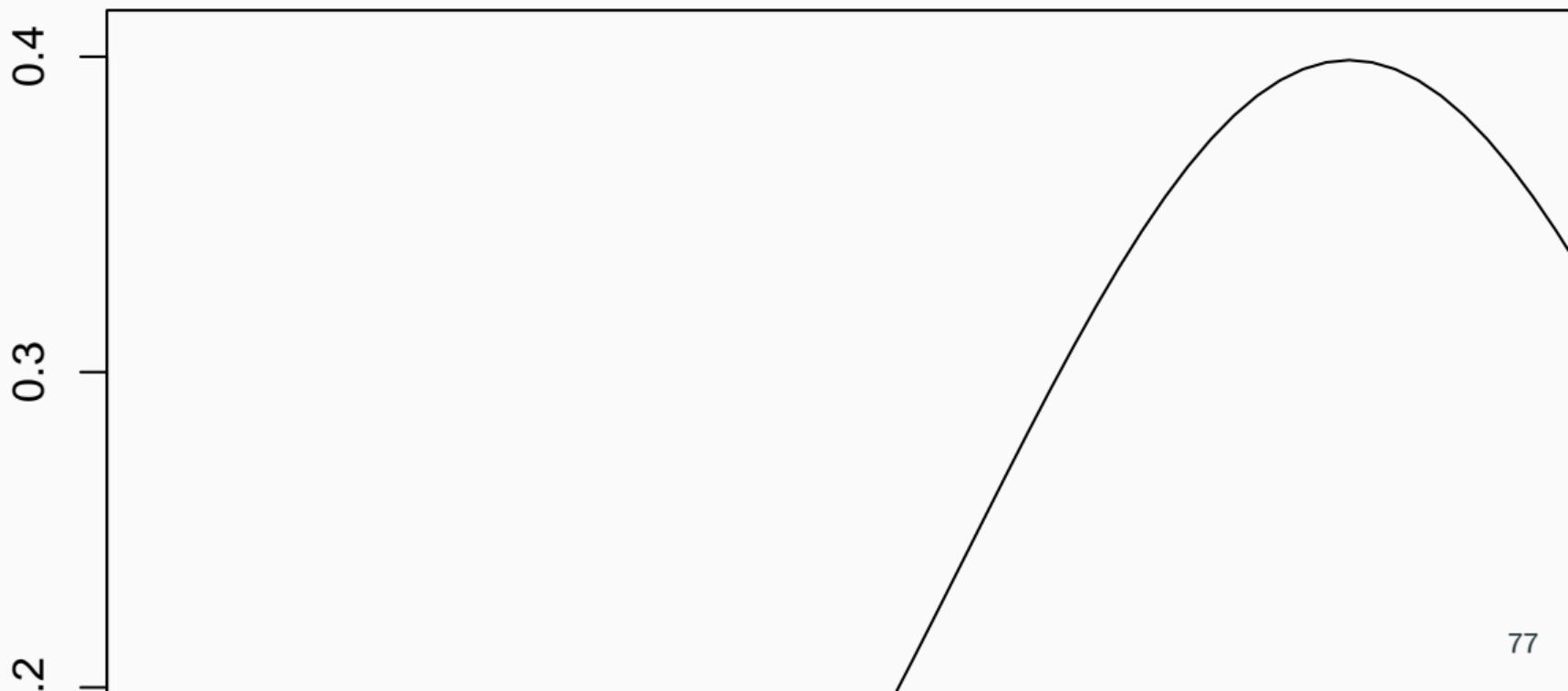
## Hypothesis testing: Rationale

4. Find the values that tell us if a particular estimate is extreme



## Hypothesis testing: Rationale

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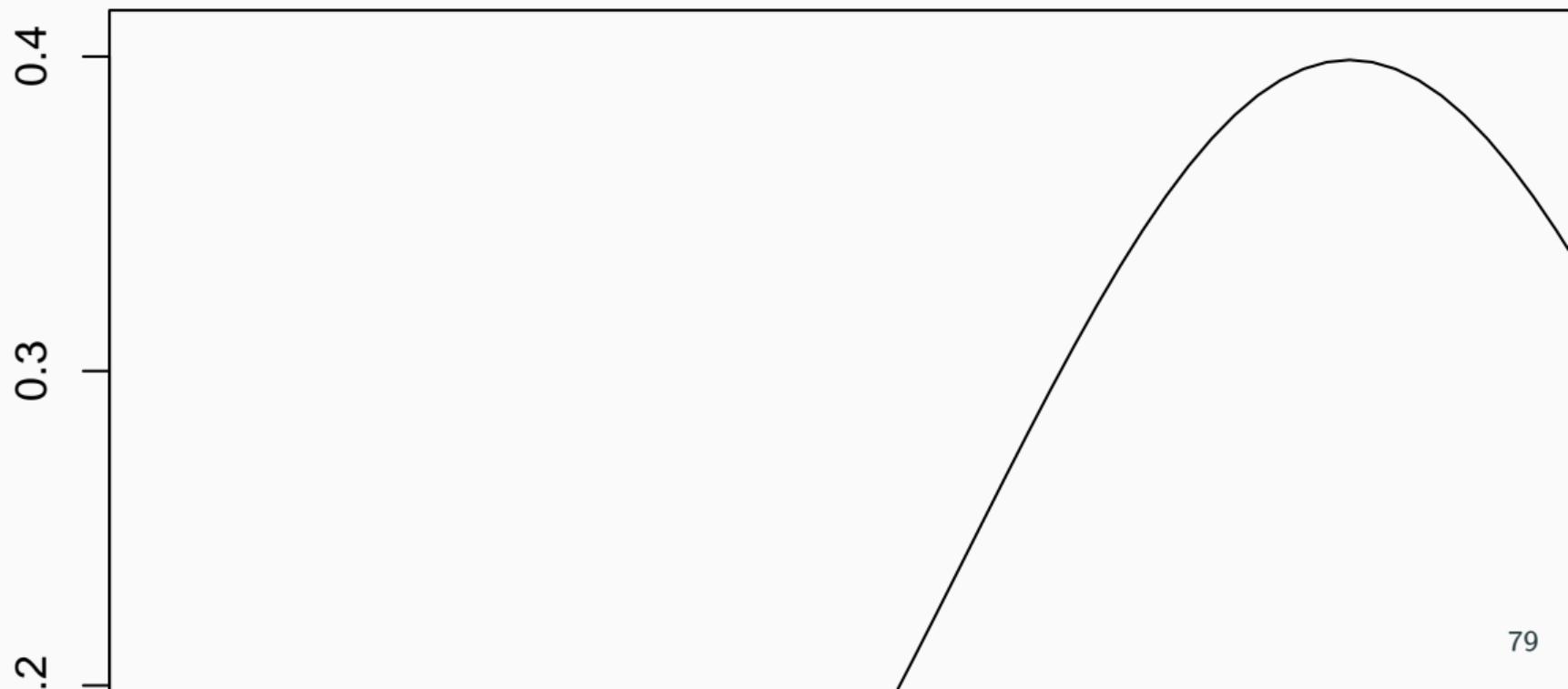
## Hypothesis testing: Rationale

4. Find the values that tell us if a particular estimate is significantly different from what would be expected under  $H_0$ 
  - Straightforward in R:

```
alpha <- 0.05
z.half.alpha <- qnorm(1 - alpha/2)
c(-z.half.alpha, z.half.alpha)
#> [1] -1.959964  1.959964
```

## Hypothesis testing: Rationale

4. Find the values that tell us if a particular estimate is extreme



## Hypothesis testing: Rationale

5. The estimate ( $\hat{q}$ ) is calculated from the data and compared with the critical value(s)

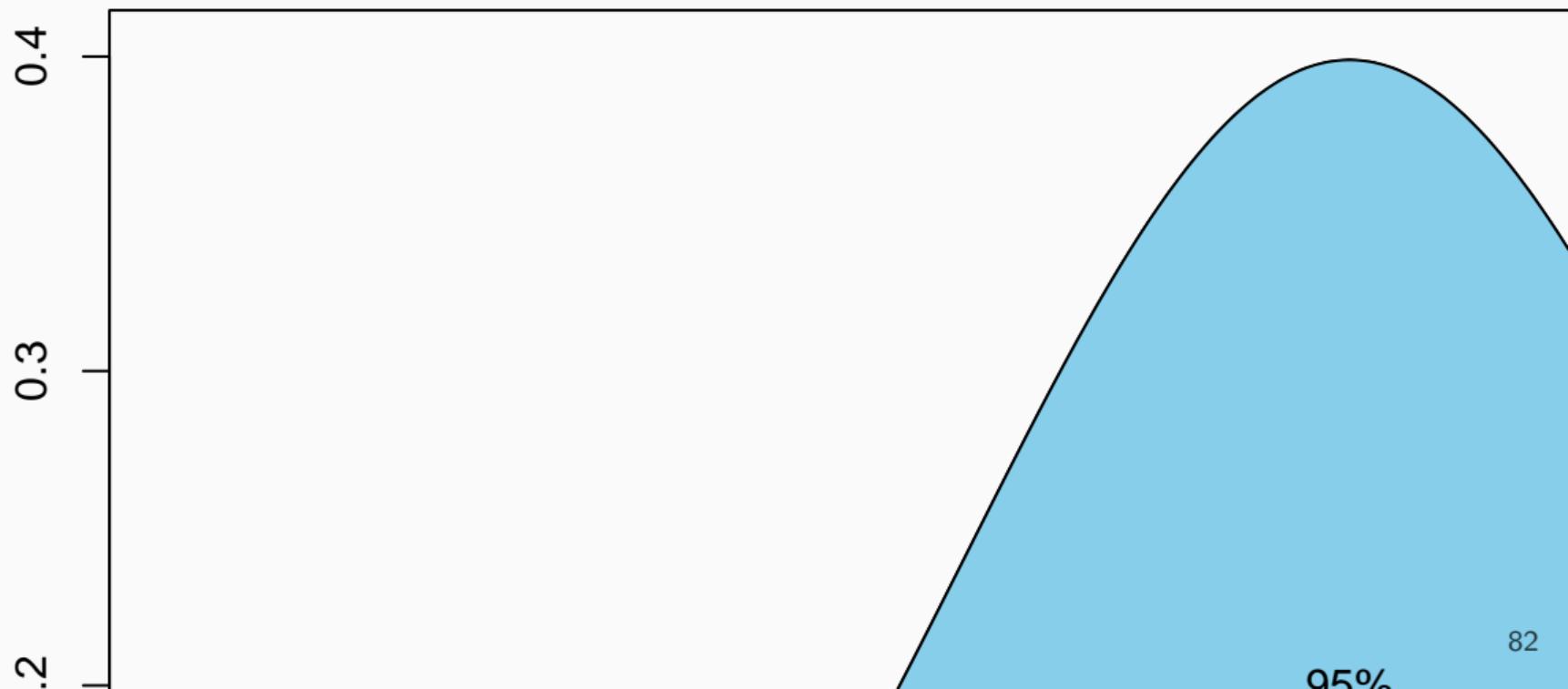
$$\frac{\hat{p} - p_0}{\sqrt{p_0(1 - p_0)/N}} = \frac{12/20 - 0.5}{\sqrt{0.5(1 - 0.5)/20}} = 0.89$$

## Hypothesis testing: Rationale

6. If the estimate falls in the region of extreme values, then  $H_0$  is rejected, otherwise we say that there is not enough evidence to reject it
  - The test statistic 0.89 lies between the critical values -1.96 and 1.96. Hence, at  $\alpha = 0.05$  significance level, we do not reject the null hypothesis that the coin toss is fair

## Hypothesis testing: Rationale

6. If the estimate falls in the region of extreme values, then  $H_0$  is rejected

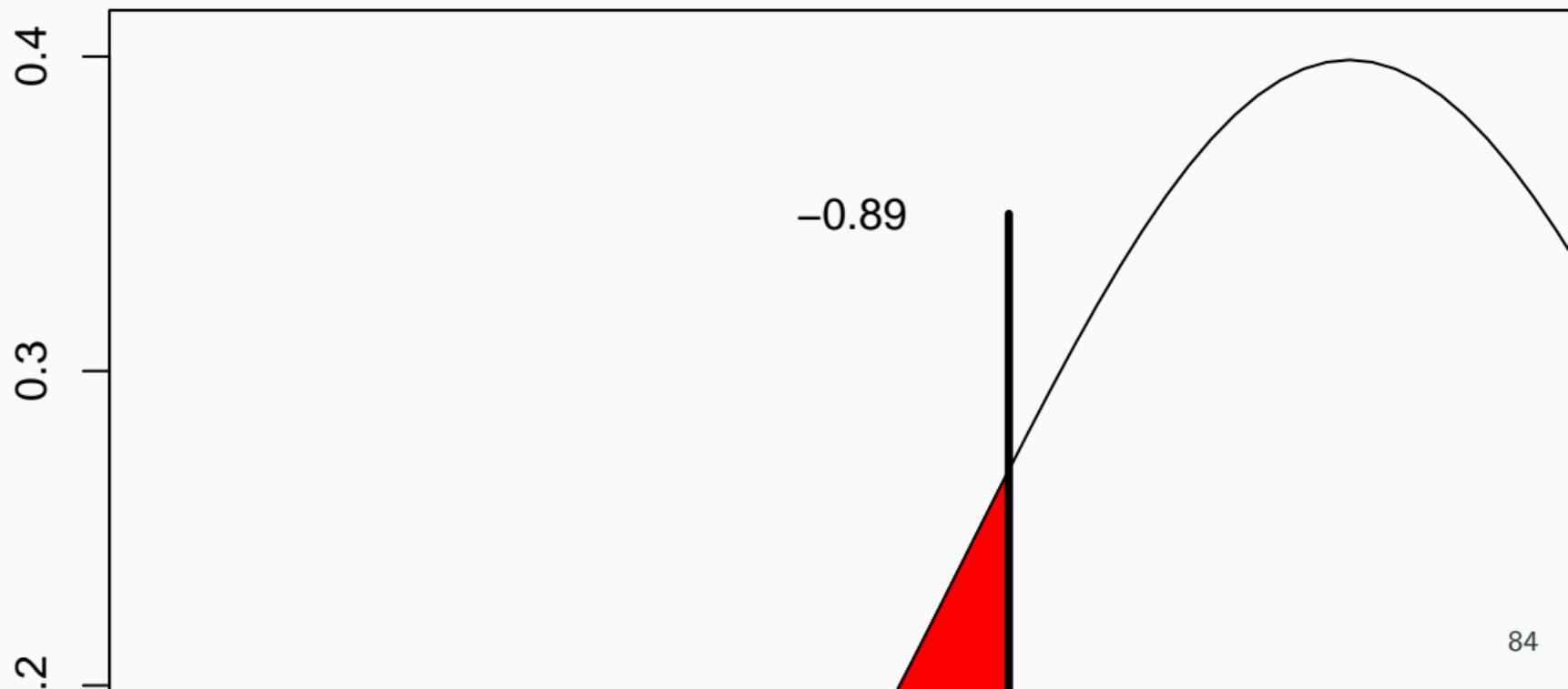


## Hypothesis testing: Rationale

- Another way to test significance is to use the p-value
- Probability that, when  $H_0$  is true, the value of the test statistics would be the same as or more extreme than the actual observed results
- If the p-value is  $< \alpha$ , then reject  $H_0$

## Hypothesis testing: Rationale

- The p-value is the red area

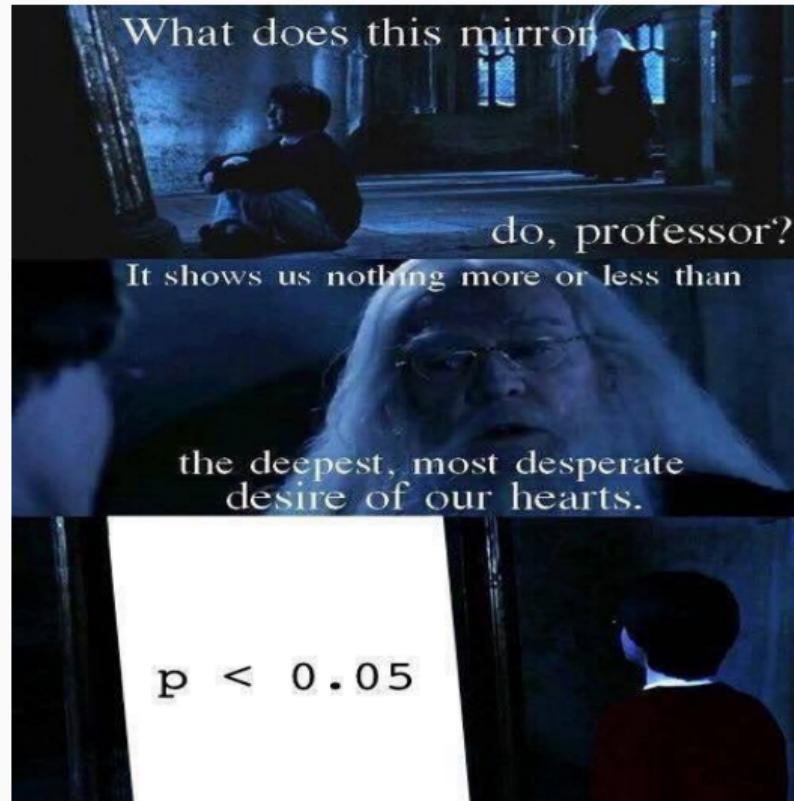


## Hypothesis testing: Rationale

- To compute the p-value, we need  $P(X \geq 0.89) + P(X \leq -0.89)$
- This can be obtained in R as follows:

```
pval <- 2 * (1 - pnorm(0.89)) # pnorm(x) = P(X <= x)
pval # twotailed pvalue
#> [1] 0.3734659
```

## Problems with hypothesis testing



## Problems with hypothesis testing

- **Significance levels are arbitrary:** Changing  $\alpha$  magically turns an ordinary result into something worth reporting.

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- **A significant result is guaranteed if the sample size is large enough:**  $\alpha$  must be appropriately chosen in relation to sample size. There are methods for doing this, known as power analyses.

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- **A significant result is guaranteed if the sample size is large enough:**  $\alpha$  must be appropriately chosen in relation to sample size. There are methods for doing this, known as power analyses.
- **The dichotomy between a null/alternative hypotheses is limiting:** Why not look at several candidate values at the same time?

## Multimodel inference

---

## Linear regression example

Impact of climatic conditions on white stork breeding success



manglat

## Linear regression example

Impact of climatic conditions on white stork breeding success

```
nb_young <- c(2.55,1.85,2.05,2.88,3.13,2.21,2.43,2.69,2.55,2.84,2.47,2.69,  
              2.52,2.31,2.07,2.35,2.98,1.98,2.53,2.21,2.62,1.78,2.30)  
temperature <- c(15.1,13.3,15.3,13.3,14.6,15.6,13.1,13.1,15.0,11.7,15.3,  
                  14.4,14.4,12.7,11.7,11.9,15.9,13.4,14.0,13.9,12.9,15.1,  
                  13.0)  
rainfall <- c(67,52,88,61,32,36,72,43,92,32,86,28,57,55,66,26,28,96,48,90,  
                 86,78,87)  
lin_reg <- lm(nb_young ~ temperature + rainfall)
```

## Linear regression example

Impact of climatic conditions on white stork breeding success

```
library(broom)

tidy(lin_reg) # elegant summary using broom package
#> # A tibble: 3 x 5
#>   term      estimate std.error statistic p.value
#>   <chr>      <dbl>     <dbl>      <dbl>    <dbl>
#> 1 (Intercept)  2.45      0.765      3.20    0.00446
#> 2 temperature  0.0311    0.0547      0.568   0.576
#> 3 rainfall     -0.00732   0.00290     -2.53   0.0201
```

## How to select a best model?

- The proportion of explained variance  $R^2$  is problematic, because the more variables you have, the bigger  $R^2$  is
- Idea: **penalize models with too many parameters**

## Akaike information criterion (AIC)

$$AIC = -2 \log(L(\hat{\theta}_1, \dots, \hat{\theta}_K)) + 2K$$

with  $L$  the likelihood and  $K$  the number of parameters  $\theta_i$

## Akaike information criterion (AIC)

$$AIC = -2 \log(L(\hat{\theta}_1, \dots, \hat{\theta}_K)) + 2K$$

A measure of goodness-of-fit of the model to the data: the more parameters you have, the smaller the deviance is (or the bigger the likelihood is)

## Akaike information criterion (AIC)

$$AIC = -2 \log(L(\hat{\theta}_1, \dots, \hat{\theta}_K)) + 2K$$

A **penalty**: twice the number of parameters  $K$

## Akaike information criterion (AIC)

- $AIC$  makes the balance between *quality of fit* and *complexity* of a model
- Best model is the one with lowest  $AIC$  value
- Two models are difficult to distinguish if  $\Delta AIC < 2$

## Back to the linear regression example

Fit all candidate models on white stork data and get their AIC

```
linreg_temp_rain <- lm(nb_young ~ temperature + rainfall)
linreg_temp <- lm(nb_young ~ temperature)
linreg_rain <- lm(nb_young ~ rainfall)
linreg_null <- lm(nb_young ~ 1)

c(AIC(linreg_temp_rain),AIC(linreg_temp),AIC(linreg_rain),AIC(linreg_null))
#> [1] 17.97668 22.34309 16.34487 20.44140
```

Looks as though model with rainfall has the lowest AIC

However, the model with both covariates has an AIC value within 2 units

Where to go from there?! **Multimodel inference**

## Multimodel inference

---

## AIC weights

- Let  $\Delta\text{AIC}_i$  be the difference between  $\text{AIC}$  of model  $i$  and the lowest  $\text{AIC}$  (corresponding to the best model)
- Akaike weight  $w_i$  for model  $i$  gives the probability that model  $i$  is the best model

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta\text{AIC}_i\right)}{\sum_{n=1}^N \exp\left(-\frac{1}{2}\Delta\text{AIC}_i\right)}$$

## AIC weights with R: Back to the stork example

Compute the weights:

```
library(bbmle)
AICtab(linreg_temp_rain,linreg_temp,linreg_rain,linreg_null,
       base = T, weights = T)

#>           AIC  dAIC df weight
#> linreg_rain     16.3  0.0 3  0.617
#> linreg_temp_rain 18.0  1.6 4  0.273
#> linreg_null      20.4  4.1 2  0.080
#> linreg_temp      22.3  6.0 3  0.031
```

## Model averaging

- Model-averaged estimates are weighted averages (by the  $w_i$ ) of the parameters from each of the models

$$\bar{\hat{\theta}}_j = \sum_{i=1}^K w_i \hat{\theta}_j(\text{model}_i)$$

## Model-averaged estimate of rainfall effect, by hand (1)

```
tidy(linreg_temp_rain)
#> # A tibble: 3 x 5
#>   term      estimate std.error statistic p.value
#>   <chr>      <dbl>     <dbl>      <dbl>    <dbl>
#> 1 (Intercept)  2.45      0.765      3.20    0.00446
#> 2 temperature  0.0311    0.0547     0.568   0.576
#> 3 rainfall     -0.00732   0.00290    -2.53   0.0201
```

$$0.273 * (-0.007315652)$$

## Model-averaged estimate of rainfall effect, by hand (2)

```
tidy(linreg_temp)
#> # A tibble: 2 x 5
#>   term      estimate std.error statistic p.value
#>   <chr>      <dbl>     <dbl>     <dbl>    <dbl>
#> 1 (Intercept)  2.18      0.849     2.57    0.0179
#> 2 temperature  0.0183    0.0610    0.300    0.767
```

$$0.273 * (-0.007315652) + 0.031 * 0$$

## Model-averaged estimate of rainfall effect, by hand (3)

```
tidy(linreg_rain)
#> # A tibble: 2 x 5
#>   term      estimate std.error statistic p.value
#>   <chr>      <dbl>     <dbl>     <dbl>    <dbl>
#> 1 (Intercept)  2.87     0.186     15.5  5.90e-13
#> 2 rainfall     -0.00716   0.00284    -2.52 1.97e- 2
```

$$0.273 * (-0.007315652) + 0.031 * 0 + 0.617 * (-0.007163572)$$

## Model-averaged estimate of rainfall effect, by hand (4)

```
tidy(linreg_null)
#> # A tibble: 1 x 5
#>   term      estimate std.error statistic p.value
#>   <chr>      <dbl>     <dbl>     <dbl>    <dbl>
#> 1 (Intercept)  2.43     0.0738     33.0 3.10e-20
```

$$0.273 * (-0.007315652) + 0.031 * 0 + 0.617 * (-0.007163572) + 0.080 * 0 \\ = -0.006417097$$

## Model-averaging with R: Back to the stork example

Perform model averaging

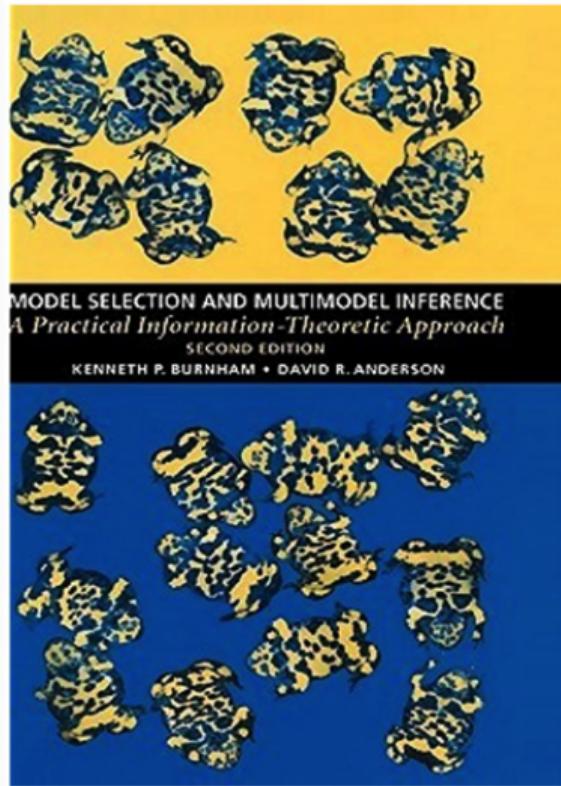
```
library(MuMIn)
m.ave <- model.avg(linreg_temp_rain, linreg_temp, linreg_rain,
                     linreg_null, rank = "AIC")
m.ave$coefficients
#>      (Intercept) rainfall temperature
#> full     2.701251 -0.006414962 0.009038803
#> subset   2.701251 -0.007210205 0.029776596
```

- The **full** average assumes that a variable is included in every model, but in some models the corresponding coefficient is set to zero.
- The **subset** (or **conditional**) average only averages over the models where the parameter appears.

## Conclusions about multimodel inference

- Several models can be ranked and weighted to provide a quantitative measure of relative support for each competing hypothesis
- If there are two or more models with similarly high levels of support, model averaging of this 'top model set' provides a robust means of obtaining parameter estimates
- Acknowledge uncertainty in the selection of a single best model

## Textbooks



## This Class

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## On our plate

- Distributions and likelihoods
- Hypothesis testing and multimodel inference
- **Introduction to Bayesian inference**
- Generalized Linear Models (GLMs)
- Generalized Additive Models (GAMs)
- Mixed Effect Models

## Bayesian inference

---

## Introduction

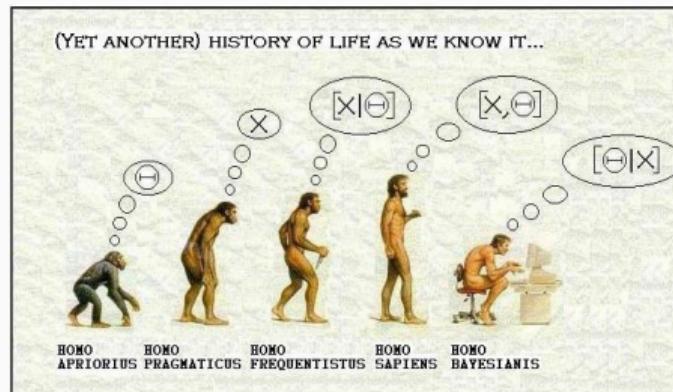
- The Bayesian approach dates back to 18th century to Reverend Thomas Bayes.



- However, due to practical problems of implementing the Bayesian approach, little advance was made for over two centuries.
- Recent advances in **computational power** coupled with the development of new methodology have led to a great increase in the application of Bayesian methods within the last two decades.

# Classical versus Bayesian

- Typical stats problems involve estimating parameter  $\theta$  with available data.
- The frequentist approach (maximum likelihood estimation – MLE) assumes that **the parameters are fixed, but have unknown values to be estimated.**
- Classical estimates generally provide a **point estimate** of the parameter of interest.
- The Bayesian approach assumes that **the parameters are not fixed but have some fixed unknown distribution** - a distribution for the parameter.



## What is the Bayesian Approach?

- The approach is based upon the idea that the experimenter begins with **some prior beliefs** about the system.
- And then **updates** these beliefs on the basis of observed data.
- This updating procedure is based upon what is known as Bayes' Theorem:

$$\Pr(A | B) = \frac{\Pr(B | A) \Pr(A)}{\Pr(B)}$$

## What is the Bayesian Approach?

- Schematically, if  $A = \theta$  and  $B = \text{data}$
- The Bayes' Theorem

$$\Pr(A | B) = \frac{\Pr(B | A) \Pr(A)}{\Pr(B)}$$

- Translates into:

$$\Pr(\theta | \text{data}) = \frac{\Pr(\text{data} | \theta) \Pr(\theta)}{\Pr(\text{data})}$$

## Bayes formula

$$\Pr(\theta \mid \text{data}) = \frac{\Pr(\text{data} \mid \theta) \Pr(\theta)}{\Pr(\text{data})}$$

- **Posterior distribution:** the basis for inference, a distribution, possibly multivariate if more than one parameter ( $\theta$ )
- **Likelihood:** we know that guy from before, same as in the MLE approach
- **Prior distribution:** the source of much discussion about the Bayesian approach
- $\Pr(\text{data}) = \int L(\text{data} \mid \theta) \Pr(\theta) d\theta$ : possibly high-dimensional integral, difficult if not impossible to calculate. This is one of the reasons why we need simulation (MCMC) methods - more soon.

## A Simple Example

- Let us take a simple example to fix ideas
- 120 deer were radio-tracked over winter
- 61 close to a plant, 59 far from any human activity
- Question: is there a treatment effect on survival?

	Released	Alive	Dead	Other
treatment	61	19	38	4
control	59	21	38	0

## A Simple Example

- So,  $n = 57$  deer were assigned to the treatment group of which  $k = 19$  survived the winter.
- Of interest is the probability of **over-winter survival**, call it  $\theta$ , for the general population within the treatment area.
- The obvious estimate is simply to take the ratio  $k/n = 19/57$ .
- How would the classical statistician justify this estimate?

## A Simple Example

- Our model is that we have a Binomial experiment (assuming independent and identically distributed draws from the population)
- $K$  the number of alive individuals at the end of the winter, so that  
$$P(K = k) = \binom{n}{k} \theta^k (1 - \theta)^{n-k}$$
- The classical approach is to maximise the corresponding likelihood with respect to  $\theta$  to obtain the entirely plausible MLE:

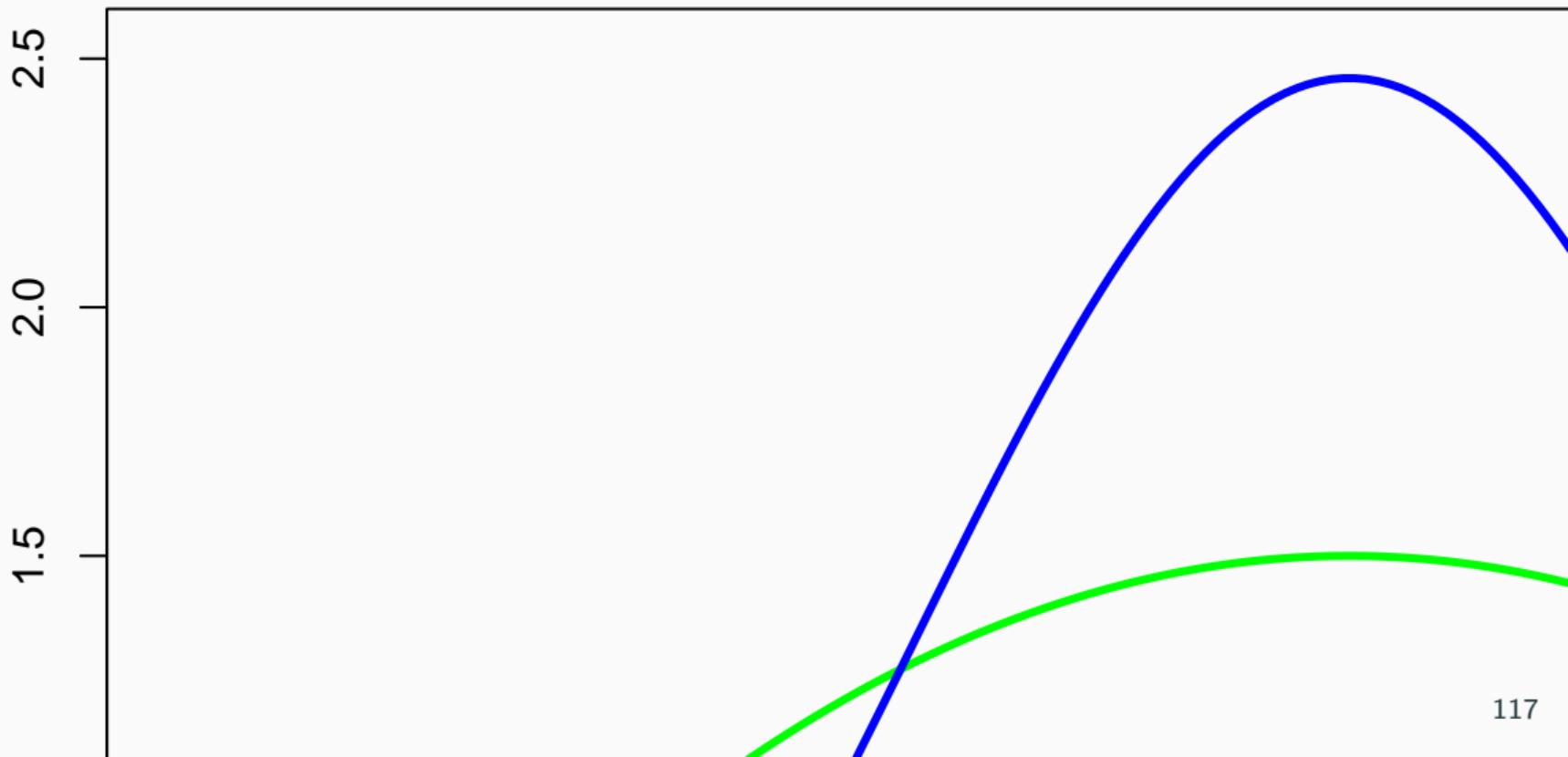
$$\hat{\theta} = k/n = 19/57$$

- Remember lecture on likelihoods

## The Bayesian Approach

- The Bayesian starts off with **a prior**.
- Now, the one thing we know about  $\theta$  is that it is a continuous random variable and that it lies between zero and one.
- Thus, a suitable prior distribution might be the Beta which is defined on this range  $[0, 1]$ .
- What is the Beta distribution?

## What is the Beta distribution?



## The Bayesian Approach

- Suppose we assume a priori that  $\theta \sim Beta(a, b)$  so that  $Pr(\theta) = \theta^{a-1}(1 - \theta)^{b-1}$
- Then we have:

$$\begin{aligned} Pr(\theta | k) &\propto \binom{n}{k} \theta^k (1 - \theta)^{n-k} \theta^{a-1} (1 - \theta)^{b-1} \\ &\propto \theta^{(a+k)-1} (1 - \theta)^{(b+n-k)-1} \end{aligned}$$

- That is:

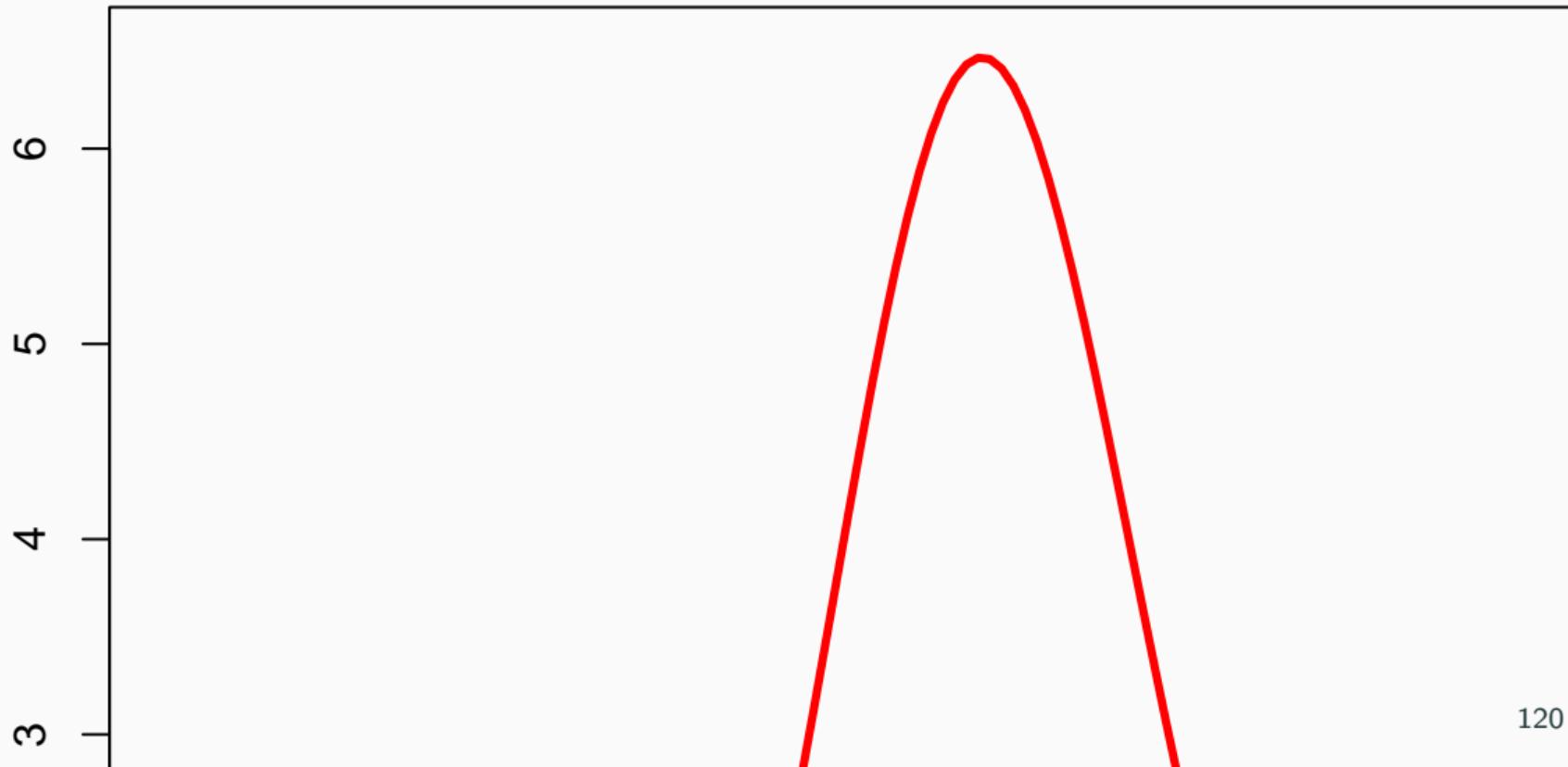
$$\theta | k \sim Beta(a + k, b + n - k)$$

- Take a Beta prior with a Binomial likelihood, you get a Beta posterior (conjugacy)

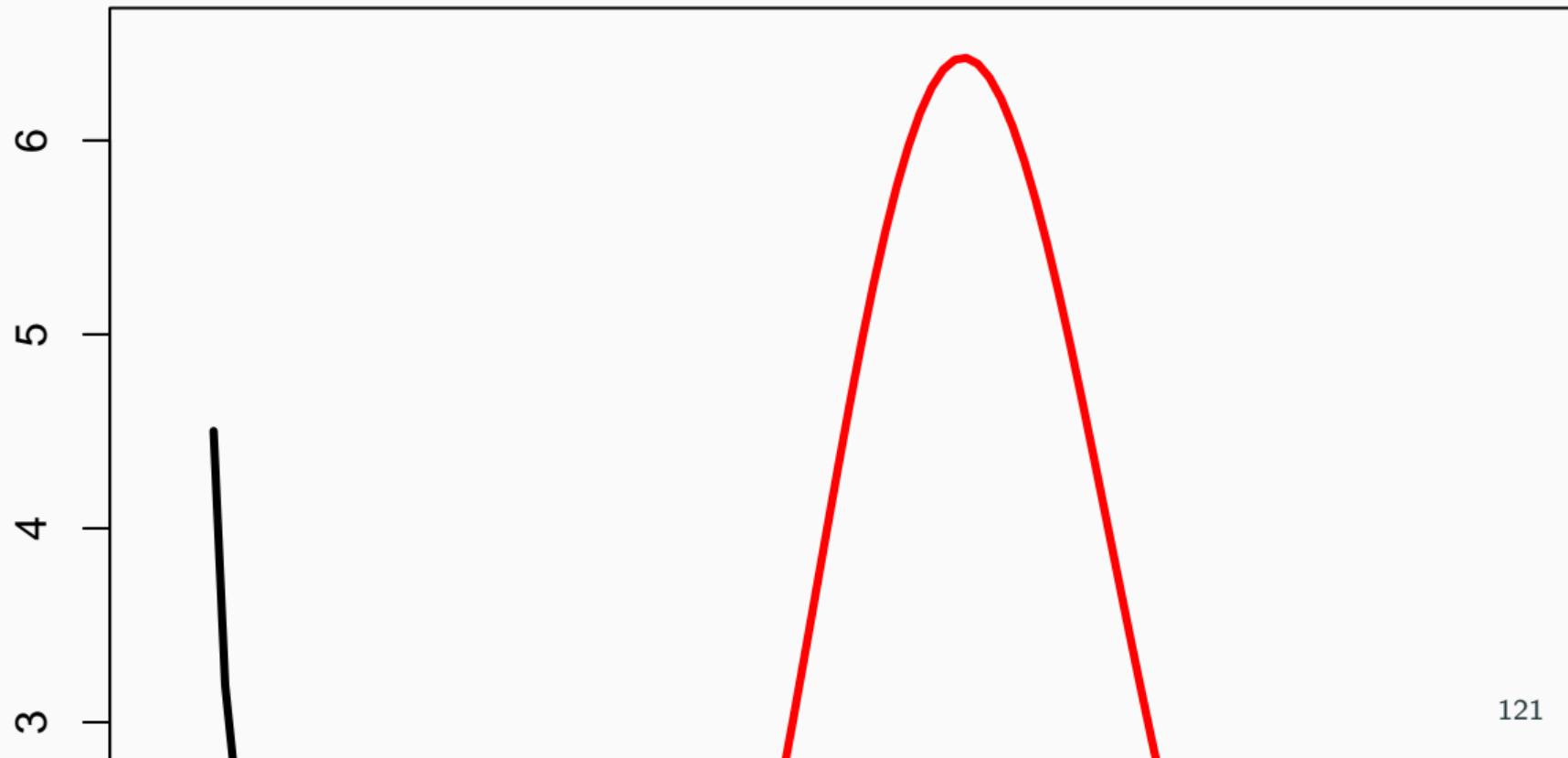
## Application to the deer example

- We have that survival  $\theta | k \sim Beta(a + k, b + n - k)$
- The posterior has an **explicit expression**, easy to manipulate
- $E(\theta | k) = \frac{a + k}{n + a + b}$
- $V(\theta | k) = \frac{(a + k)(b + n - k)}{(n + a + b)^2(n + a + b + 1)}$
- If we take a Uniform prior, i.e.  $Beta(1, 1)$ , then we have
- $\theta_{treatment} \sim Beta(1 + 19, 1 + 57 - 19) = Beta(20, 39)$
- $E(\theta_{treatment}) = 0.339$  and  $V(\theta_{treatment}) = 0.061$

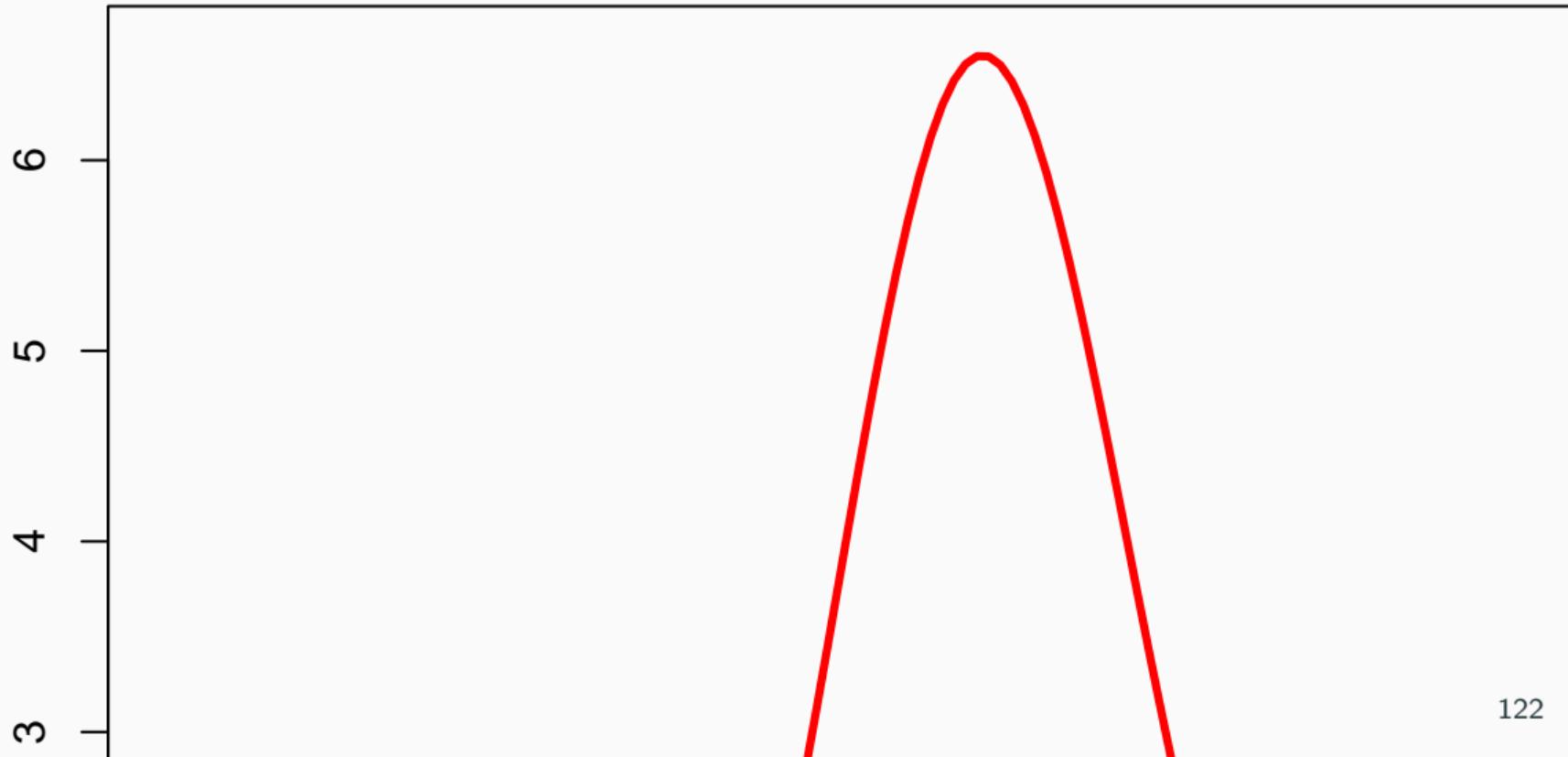
Prior  $\text{Beta}(1, 1)$  and posterior survival  $\text{Beta}(20, 39)$



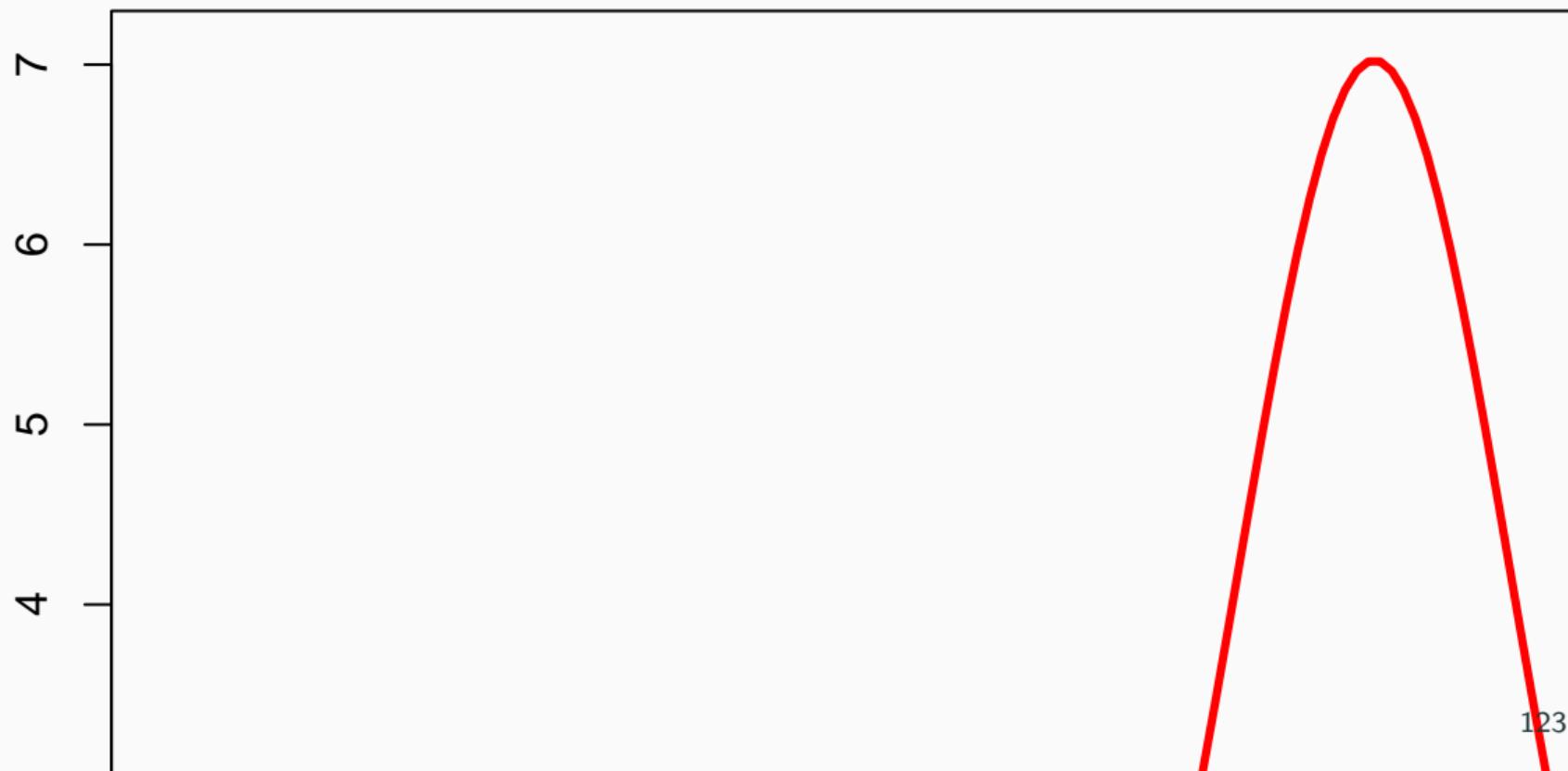
**Prior  $Beta(0.5, 0.5)$  and posterior survival  $Beta(19.5, 38.5)$**



Prior  $\text{Beta}(2, 2)$  and posterior survival  $\text{Beta}(21, 40)$



Prior  $Beta(20, 1)$  and posterior survival  $Beta(39, 49)$



## The Role of the Prior

- In biological applications, the prior is a convenient means of **incorporating expert opinion or information from previous or related studies** that would otherwise need to be ignored.
- With sparse data, the role of the prior can be to enable inference on key parameters that would otherwise be impossible.
- With sufficiently large and informative datasets the prior typically has little effect on the results.
- **Always perform a sensitivity analysis!**

## Informative Priors / No Information

- Informative priors aim to reflect information available to the analyst that is gained independently of the data being studied.
- In the absence of any prior information on one or more model parameters we wish to ensure that this lack of knowledge is properly reflected in the prior.
- **Always perform a sensitivity analysis!**

## Back to the Bayes formula

- Bayes inference is easy! Well, not so easy in real-life applications...
- The issue is in  $\Pr(\theta | \text{data}) = \frac{\Pr(\text{data} | \theta) \Pr(\theta)}{\Pr(\text{data})}$
- $\Pr(\text{data}) = \int L(\text{data} | \theta) \Pr(\theta) d\theta$  is a  $N$ -dimensional integral if  $\theta = \theta_1, \dots, \theta_N$
- Difficult, if not impossible to calculate!
- Until recently, Bayesian analysis of complex models not possible

# Bayesian computation

- In the early 1990s, statisticians rediscovered work from the 1950's in physics

THE JOURNAL OF CHEMICAL PHYSICS VOLUME 21, NUMBER 6 JUNE, 1953

## Equation of State Calculations by Fast Computing Machines

NICHOLAS METROPOLIS, ARIANNA W. ROSENBLUTH, MARSHALL N. ROSENBLUTH, AND AUGUSTA H. TELLER,  
*Los Alamos Scientific Laboratory, Los Alamos, New Mexico*

AND

EDWARD TELLER,\* *Department of Physics, University of Chicago, Chicago, Illinois*

(Received March 6, 1953)

A general method, suitable for fast computing machines, for investigating such properties as equations of state for substances consisting of interacting individual molecules is described. The method consists of a modified Monte Carlo integration over configuration space. Results for the two-dimensional rigid-sphere system have been obtained on the Los Alamos MANIAC and are presented here. These results are compared to the free volume equation of state and to a four-term virial coefficient expansion.

- Use **stochastic simulation** to draw samples from posterior distributions
- Avoid explicit calculation of integrals in Bayes formula
- Instead, approximate posterior to arbitrary degree of precision by drawing large sample
- Markov chain Monte Carlo = MCMC**; boost to Bayesian statistics!



## MANIAC: Mathematical Analyzer, Numerical Integrator, and Computer

MANIAC:  
1000 pounds  
5 kilobytes of memory  
70k multiplications/sec

Your laptop:  
4–7 pounds  
2–8 million kilobytes  
Billions of multiplications/sec

## Why are MCMC methods so useful?

- MCMC: stochastic algorithm to produce sequence of dependent random numbers (from Markov chain)
- Converge to equilibrium (aka stationary) distribution
- Equilibrium distribution is the desired posterior distribution
- Several ways of constructing these chains: Metropolis-Hastings, Gibbs sampler, Metropolis-within-Gibbs, . . .
- How to implement them in practice?!

## In practice, when is equilibrium attained?

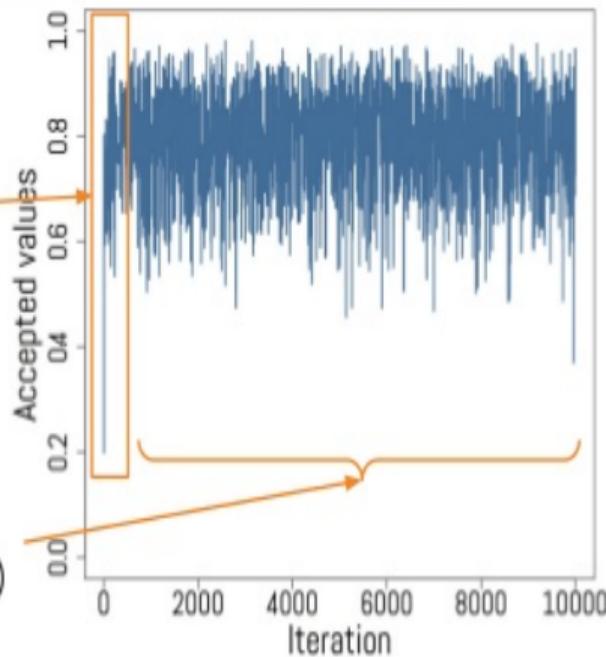
- Run multiple chains from arbitrary starting places (inits)
- Assume convergence when all chains reach same regime
- Discard initial burn-in phase
- Summarize posterior distribution with mean, sd and credible intervals

## In practice, when is equilibrium attained?

Discard initial guesses that are still far from optimum: the

**BURN-IN**

These numbers should be a good sample of the Posterior  $P(\phi | \text{data})$



# Introduction to JAGS (Just Another Gibbs Sampler)

Martyn Plummer



## Let's redo the logistic regression with the White stork data

- We'll need data
- We'll need to build a model - write down the likelihood
- We'll need to specify priors for parameters

## Let us read in the data

```
nbsuccess = c(151,105,73,107,113,87,77,108,118,122,112,120,122,89,69,71,  
      53,41,53,31,35,14,18)  
nbpairs = c(173,164,103,113,122,112,98,121,132,136,133,137,145,117,90,80,  
      67,54,58,39,42,23,23)  
temp = c(15.1,13.3,15.3,13.3,14.6,15.6,13.1,13.1,15.0,11.7,15.3,14.4,14.4,  
      12.7,11.7,11.9,15.9,13.4,14.0,13.9,12.9,15.1,13.0)  
rain = c(67,52,88,61,32,36,72,43,92,32,86,28,57,55,66,26,28,96,48,90,86,  
      78,87)  
datax = list(N=23,nbsuccess = nbsuccess,nbpairs = nbpairs,  
      temp = temp,rain = rain)
```

## What is the model?

$$\text{nbchicks}_i \sim \text{Binomial}(\text{nbpairs}_i, p_i)$$

$$\text{logit}(p_i) = a + b_{\text{temp}} \text{ temp}_i + b_{\text{rain}} \text{ rainfall}_i$$

## Let us build the model

```
{  
# Likelihood  
for( i in 1 : N){  
    nbsuccess[i] ~ dbin(p[i],nbpairs[i])  
    logit(p[i]) <- a + b.temp * temp[i] + b.rain * rain[i]  
}  
# ...
```

## Let us specify priors

```
{  
# Likelihood  
for( i in 1 : N){  
    nbsuccess[i] ~ dbin(p[i],nbpairs[i])  
    logit(p[i]) <- a + b.temp * temp[i] + b.rain * rain[i]  
}  
  
# Priors  
a ~ dnorm(0,0.001)  
b.temp ~ dnorm(0,0.01)  
b.rain ~ dnorm(0,0.01)  
}
```

**Warning:** Jags uses precision for Normal distributions (1 / variance)

## Let us specify a few additional things

```
# list of lists of initial values (one for each MCMC chain)
init1 <- list(a=-.5)
init2 <- list(a=.5)
inits <- list(init1,init2)

# specify parameters that need to be estimated
parameters <- c("a","b.temp","b.rain")

# specify nb iterations for burn-in and final inference
nb.burnin <- 1000
nb.iterations <- 2500
```

## Let us run Jags!

```
# load R2jags to run Jags through R
library(R2jags)
reglogcig.sample <- jags(datax,inits,parameters,n.iter=nb.iterations,
                           model.file="reglogistique.txt",
                           n.chains=2,n.burnin=nb.burnin)

#> Compiling model graph
#> Resolving undeclared variables
#> Allocating nodes
#> Graph information:
#>   Observed stochastic nodes: 23
#>   Unobserved stochastic nodes: 3
#>   Total graph size: 181
#>
#> Initializing model
```

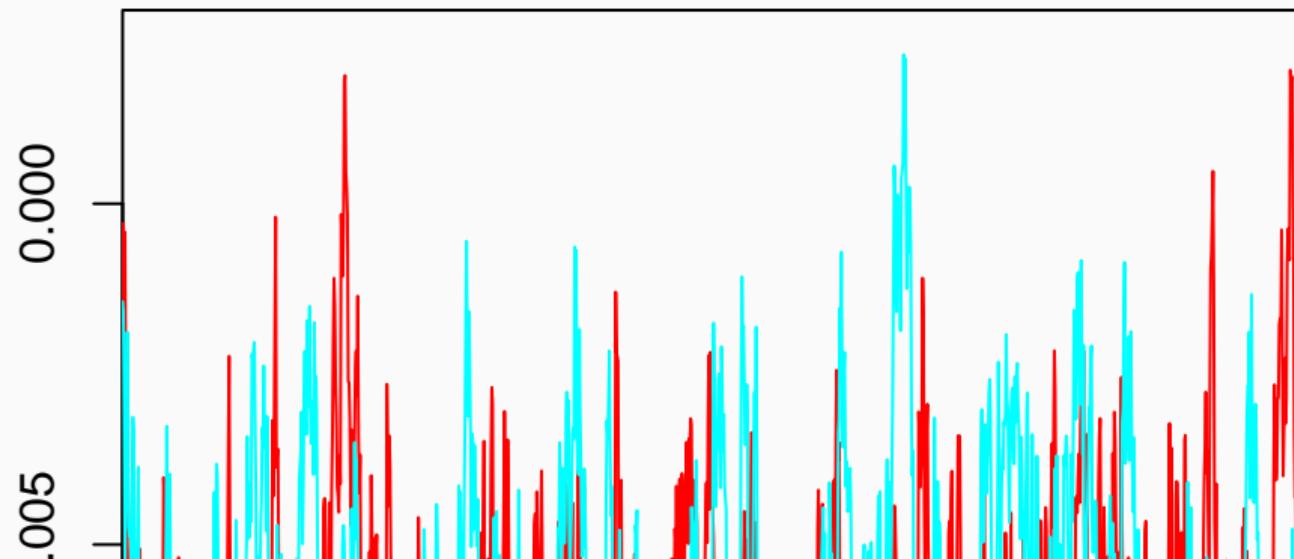
## Display parameter estimates

```
reglogcig.sample
#> Inference for Bugs model at "reglogistique.txt", fit using jags,
#> 2 chains, each with 2500 iterations (first 1000 discarded)
#> n.sims = 3000 iterations saved
#>          mu.vect sd.vect    2.5%     25%     50%     75%   97.5% Rhat n.eff
#> a        1.620   0.614   0.373   1.217   1.653   2.034   2.776 1.014   120
#> b.rain   -0.007   0.003  -0.012  -0.009  -0.007  -0.005  -0.002 1.007   380
#> b.temp    0.026   0.045  -0.060  -0.004   0.025   0.055   0.117 1.010   160
#> deviance 205.730  22.894 201.798 202.833 203.962 205.724 211.479 1.120  3000
#>
#> For each parameter, n.eff is a crude measure of effective sample size,
#> and Rhat is the potential scale reduction factor (at convergence, Rhat=1).
#>
#> DIC info (using the rule, pD = var(deviance)/2)
#> pD = 262.1 and DIC = 467.8
#> DIC is an estimate of expected predictive error (lower deviance is better).
```

## Let us assess convergence

```
R2jags::traceplot(reglogcig.sample,mfrow = c(1, 2),  
varname=c('b.rain','b.temp'), ask = FALSE)
```

**b.rain**



0.05 0.10 0.15  
1400

## Let us explore the results

```
res <- as.mcmc(reglogcig.sample) # convert outputs in a list
res <- rbind(res[[1]],res[[2]]) # put two MCMC lists on top of each other
head(res)

#>           a      b.rain      b.temp deviance
#> [1,] 0.3250383 -0.0017822462 -0.010819894 1168.0554
#> [2,] 1.0819934 -0.0002896054 -0.045386385  733.6820
#> [3,] 1.5275917 -0.0012412205 -0.056259011  522.3072
#> [4,] 1.1585552 -0.0004168704 -0.022488124  420.0934
#> [5,] 1.0370266 -0.0027828682  0.005601119  344.2514
#> [6,] 1.2534198 -0.0032150507 -0.002007754  305.9672
```

## Compute a posteriori $\Pr(\text{rain} < 0)$

```
# probability that the effect of rainfall is negative  
mean(res[, 'b.rain'] < 0)  
#> [1] 0.993
```

## Compute a posteriori $\Pr(\text{temp} < 0)$

```
# probability that the effect of temperature is negative  
mean(res[, 'b.temp'] < 0)  
#> [1] 0.2826667
```

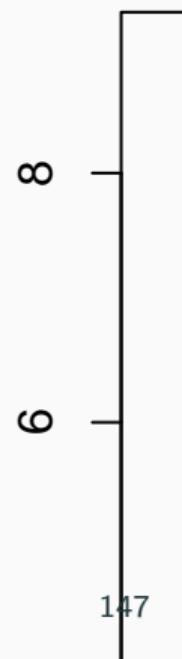
## Get credible interval for the rain effect

```
quantile(res[, 'b.rain'], c(0.025, 0.975))  
#>      2.5%      97.5%  
#> -0.011871062 -0.001714676
```

## Get credible interval for the temperature effect

```
quantile(res[, 'b.temp'], c(0.025, 0.975))  
#>      2.5%     97.5%  
#> -0.05987025  0.11665989
```

### a posteriori density of the rainfall effect



## How to incorporate prior information? A capture-recapture example

- Estimating survival using capture-recapture data
- E.g. 101 i.e. captured, missed and recaptured
- Simplest model: constant survival  $\phi$  and detection  $p$  probabilities

$$\Pr(101) = \phi(1 - p)\phi p$$

- Assuming a vague prior

$$\phi_{prior} \sim \text{Uniform}(0, 1)$$

## Case study

- European dippers in Eastern France (1981-1987)



- Mean posterior is  $\phi_{posterior} = 0.56$  with credible interval [0.51, 0.61]

## How to incorporate prior information?

- Using information on body mass and annual survival of 27 European passersines, we can predict survival of European dippers using only body mass
- For dippers, body mass is 59.8g, therefore  $\phi = 0.57$  with  $sd = 0.073$
- Assuming an **informative prior**  $\phi_{prior} \sim \text{Normal}(0.57, 0.073)$
- Mean posterior  $\phi_{posterior} = 0.56$  with credible interval  $[0.52, 0.60]$
- No increase of precision in posterior inference

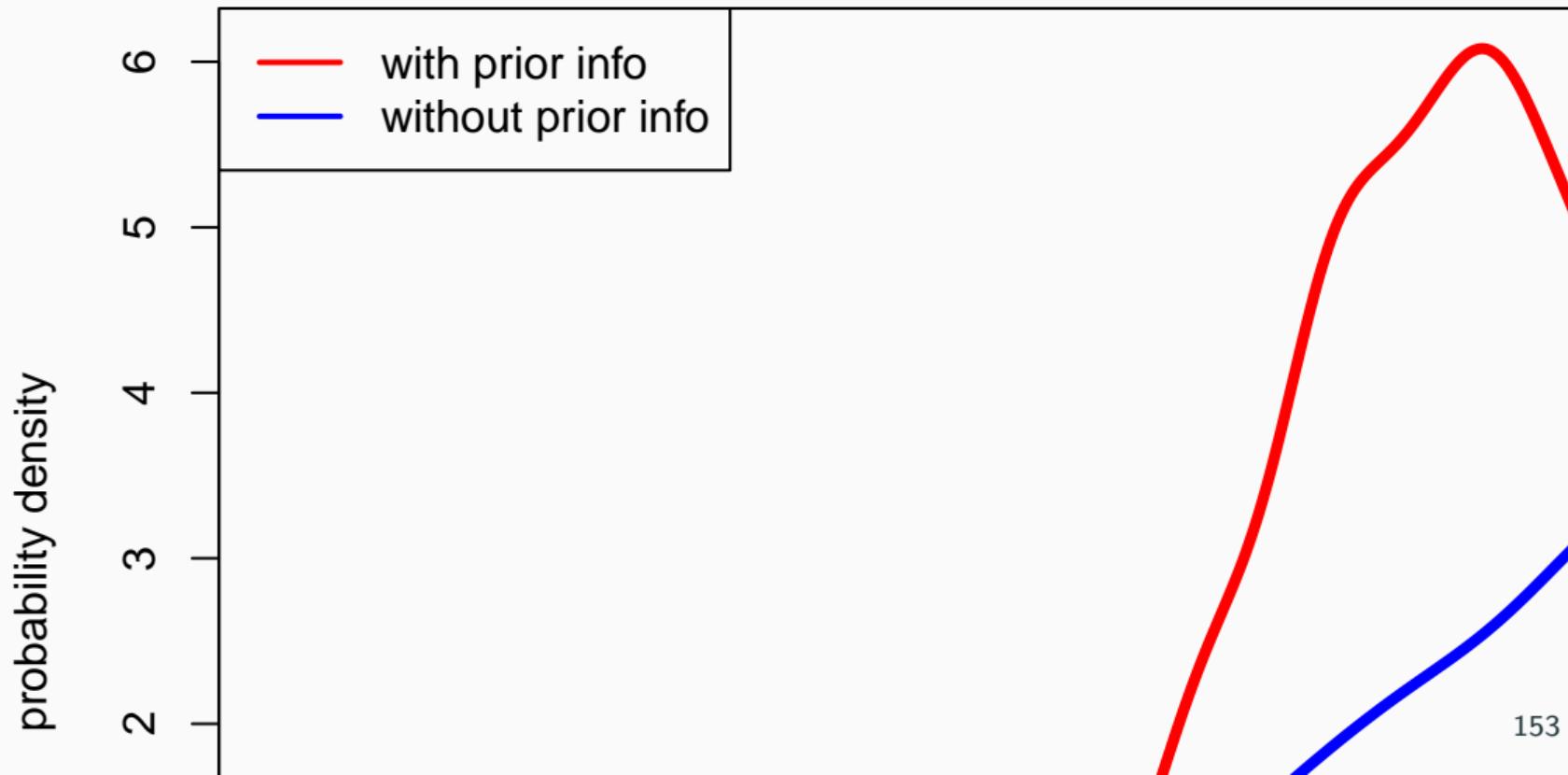
## A general result

This is a general result, the Bayesian and frequentist estimates will always agree if there is sufficient data, so long as the likelihood is not explicitly ruled out by the prior

## How to incorporate prior information?

- Using information on body mass and annual survival of 27 European passernines, we can predict survival of European dippers using only body mass
- For dippers, body mass is 59.8g, therefore  $\phi = 0.57$  with  $sd = 0.073$
- Assuming an informative prior  $\phi_{prior} \sim \text{Normal}(0.57, 0.073)$
- **With 3 first years only**
- Width of credible interval is 0.47 (vague prior) vs. 0.30 (informative prior)
- Huge increase of precision in posterior inference (40% gain)!

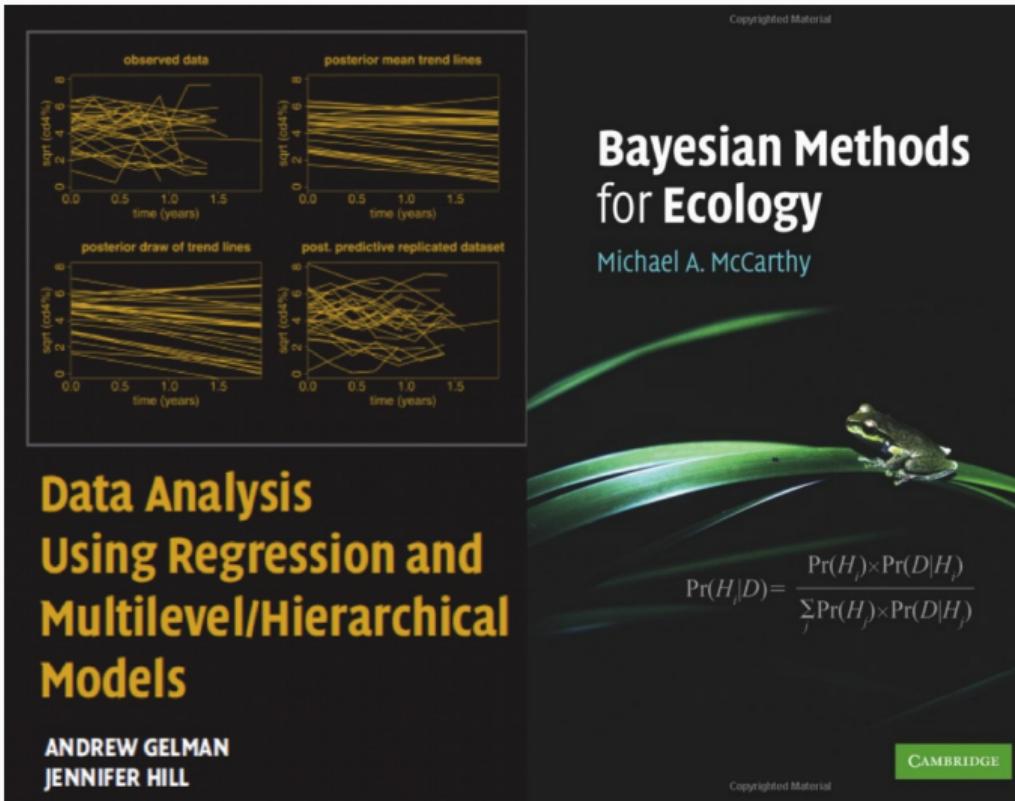
## Compare **vague** vs. **informative** prior



## Take-home message: shall I go for frequentist or Bayes?

- Pros
  - allows formal use of prior information
  - error propagation made easy
  - with same MCMC algorithms, complex (hierarchical) models can be implemented
- Cons
  - computational burden can be high
  - model selection is still difficult to perform
  - checking convergence is painful
  - is Jags too flexible?
- So what?
  - make an informed and pragmatic choice
  - are you after complexity, speed, uncertainties, etc?
  - talk to colleagues

# Textbooks



## On our plate

- Distributions and likelihoods
- Hypothesis testing and multimodel inference
- Introduction to Bayesian inference
- Generalized Linear Models (GLMs)
- Generalized Additive Models (GAMs)
- Mixed Effect Models

## On our plate

- Distributions and likelihoods
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## Generalized Linear Models (GLMs)

---

## Survival of passengers on the Titanic ~ Class

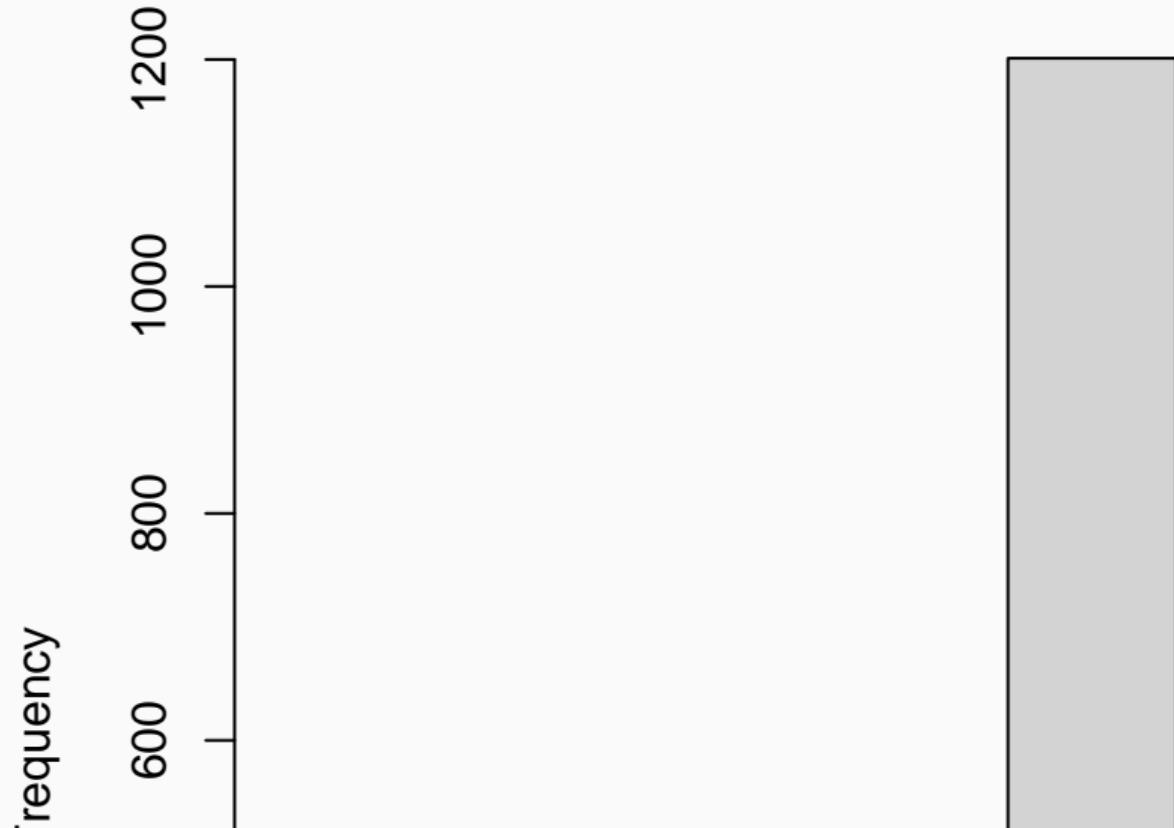
Read titanic\_long.csv dataset.

```
titanic <- read.csv("dat/titanic_long.csv") %>%  
  mutate(across(where(is.character), as_factor))  
head(titanic)  
#>   class    age sex survived  
#> 1 first adult male      1  
#> 2 first adult male      1  
#> 3 first adult male      1  
#> 4 first adult male      1  
#> 5 first adult male      1  
#> 6 first adult male      1
```

## Let's fit a linear model

```
titanic.lm <- lm(survived ~ class, data = titanic)
```

Clearly, the residuals are not normal!



## Generalized linear models (GLMs)

- GLMs extend the linear model to scenarios that involve **non-normal error distributions**, hence the term **generalized**
- The **mean response** is expressed as a **linear function of the predictors** using a **link function**, hence the term **linear**

# Generalized Linear Models

## 1. Response variable

- Bernoulli/Binomial: Binary variables 0/1
- Poisson: Counts 0, 1, 2, ...
- Normal: Real values
- etc

## 2. Predictors (continuous or categorical)

## 3. Link function

- Gaussian: identity
- Binomial: logit
- Poisson: log
- Type in ?family

## Bernoulli/Binomial distribution (logistic regression)

- Response variable: Yes/No (e.g. dead/alive, male/female, presence/absence)
- Link function: logit

$$\text{logit}(p) = \ln \left( \frac{p}{1-p} \right)$$

- Then, if predictor is  $x$

Response  $\sim$  Distribution(Mean Response)

$$Y_i \sim \text{Bernoulli}(p_i)$$

$$\text{logit}(p_i) = a + b x_i$$

$$p_i = \text{logit}^{-1}(a + b x_i) = \frac{e^{a+b x_i}}{1 + e^{a+b x_i}}$$

## Back to survival of Titanic passengers

How many passengers travelled in each class?

```
tapply(titanic$survived, titanic$class, length)
#>   crew  first second  third
#>   885    325    285    706
```

## Back to survival of Titanic passengers

How many survived?

```
tapply(titanic$survived, titanic$class, sum)
#>   crew  first second  third
#>   212    203     118    178
```

## Back to survival of Titanic passengers

What proportion survived in each class?

```
as.numeric(tapply(titanic$survived, titanic$class, mean))  
#> [1] 0.2395480 0.6246154 0.4140351 0.2521246
```

## Back to survival of Titanic passengers (package dplyr)

Arrange passenger survival according to class

```
library(dplyr)  
summarise(group_by(titanic, class, survived), count = n())`
```

## Back to survival of Titanic passengers (package dplyr)

Same manipulation using the pipe operator %>%

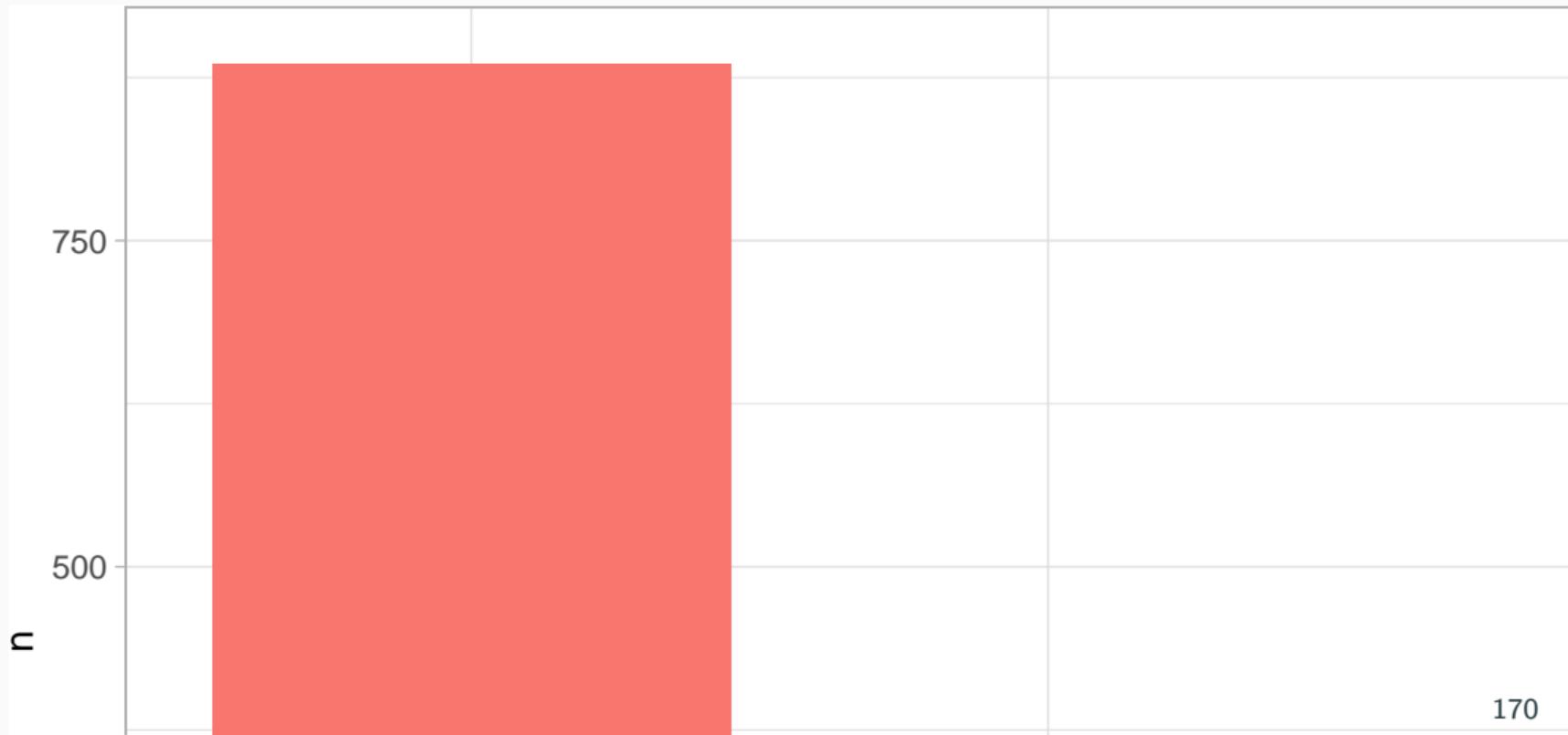
```
titanic %>%  
  group_by(class, survived) %>%  
  summarise(count = n())
```

## Back to survival of Titanic passengers (package dplyr)

Arrange passenger survival according to class

```
#>   class survived   n
#> 1   crew        0 673
#> 2   third       0 528
#> 3   crew        1 212
#> 4   first       1 203
#> 5   third       1 178
#> 6   second      0 167
#> 7   first       0 122
#> 8   second      1 118
```

Or graphically...



## Fitting GLMs in R: `glm` function

```
titanic.glm <- glm(survived ~ class, data=titanic, family=binomial)
#> # A tibble: 4 x 5
#>   term      estimate std.error statistic p.value
#>   <chr>     <dbl>     <dbl>     <dbl>     <dbl>
#> 1 (Intercept) -1.16      0.0788    -14.7    1.05e-48
#> 2 classfirst    1.66      0.139      12.0    4.97e-33
#> 3 classsecond   0.808     0.144      5.62    1.91e- 8
#> 4 classthird    0.0678    0.117      0.579   5.62e- 1
```

These estimates are on the logit scale!

# Interpreting logistic regression outputs

Parameter estimates on the logit scale:

```
#> (Intercept) classfirst classsecond classthird  
#> -1.15515905 1.66434399 0.80784987 0.06784632
```

We need to back-transform using the inverse logit function:

```
plogis(coef(titanic.glm)[1]) # crew survival probability  
#> (Intercept)  
#> 0.239548
```

Looking at the data, the proportion of crew who survived is:

```
sum(titanic$survived[titanic$class == "crew"]) /  
nrow(titanic[titanic$class == "crew", ])  
#> [1] 0.239548
```

## Probability of survival for 1st class passengers?

Needs to add intercept (baseline) to the parameter estimate:

```
plogis(coef(titanic.glm)[1] + coef(titanic.glm)[2])  
#> (Intercept)  
#> 0.6246154
```

Again this value matches the data:

```
sum(titanic$survived[titanic$class == "first"]) /  
nrow(titanic[titanic$class == "first", ])  
#> [1] 0.6246154
```

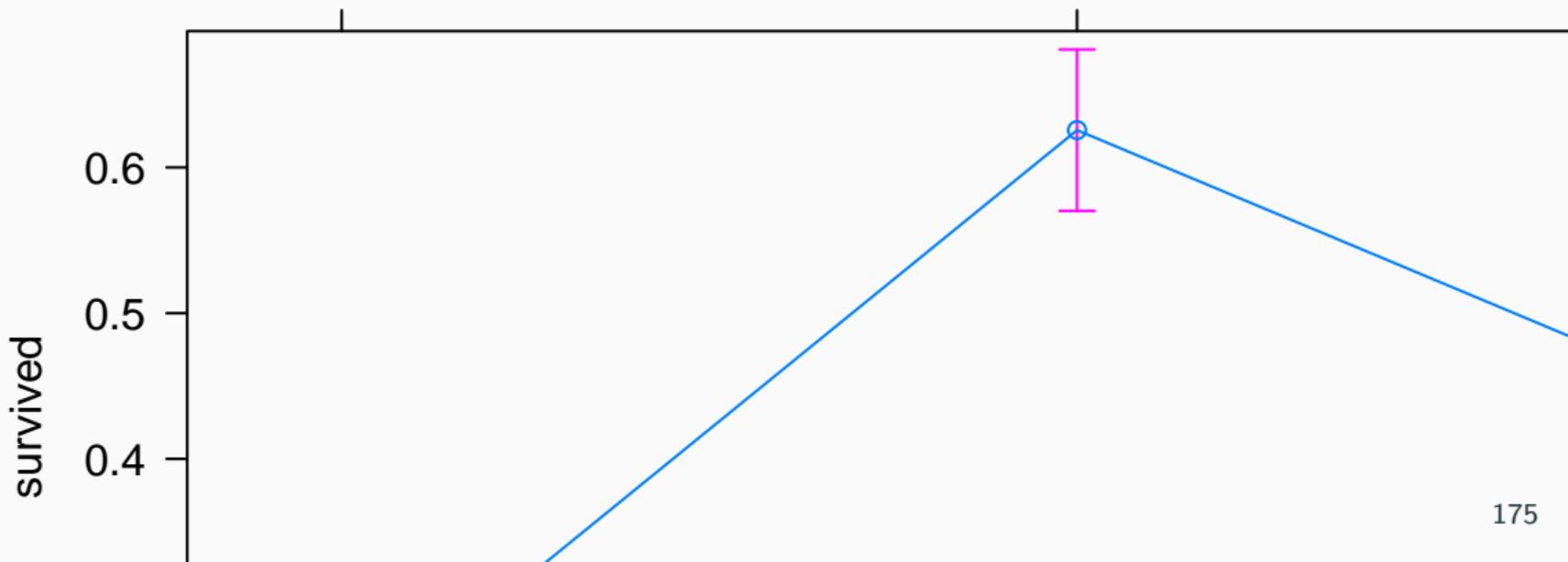
## Model interpretation using effects package

```
library(effects)
allEffects(titanic.glm)
#> model: survived ~ class
#>
#>   class effect
#>   class
#>       crew      first     second      third
#> 0.2395480 0.6246154 0.4140351 0.2521246
```

## Effects plot

```
plot(allEffects(titanic.glm))
```

class effect plot



## Recapitulating

1. Import data: `read.table` or `read.csv`.
2. Check data: `summary`.
3. Plot data: `plot`.
4. Fit model: `glm`. Don't forget to specify `family`.
5. Examine models: `summary` or `tidy`.
6. Use `plogis` to apply back-transformation (*invlogit*) to parameter estimates (`coef`).  
Alternatively, use `allEffects` from `effects` package.
7. Plot model: `plot(allEffects(model))`. Alternatively, use package `visreg` (examples below).
8. Examine residuals: check out our favorite textbook and the vignette of the DHARMA package.

**Did men have higher survival than  
women?**

---

## Plot first

```
titanic %>%
  mutate(survived = as_factor(survived)) %>%
  dplyr::count(sex, survived) %>%
  ggplot(aes(x = sex, y = n, fill = survived)) +
  geom_col()
```

1500

## Fit model

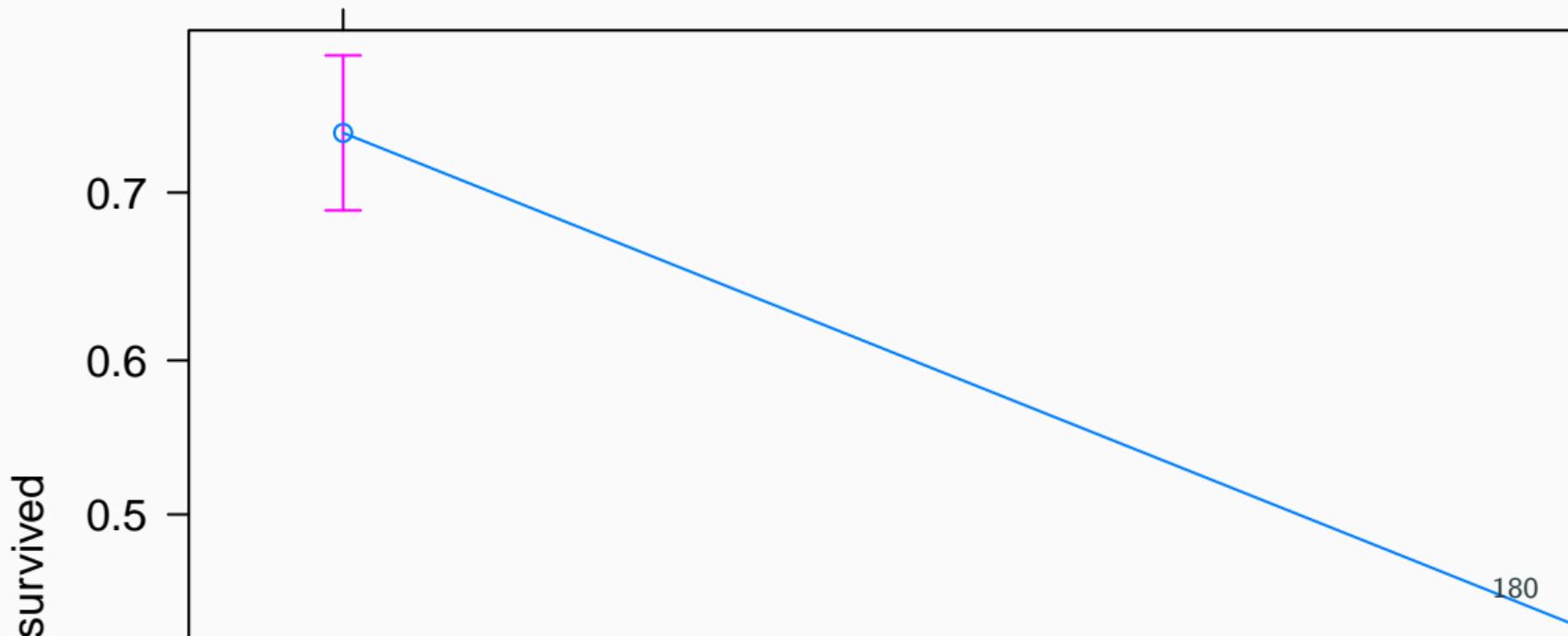
```
titanic.sex <- glm(survived ~ sex, data = titanic, family = binomial)
#> # A tibble: 2 x 5
#>   term      estimate std.error statistic p.value
#>   <chr>      <dbl>     <dbl>      <dbl>    <dbl>
#> 1 (Intercept)  1.00     0.104     9.65 5.16e-22
#> 2 sexmale     -2.32     0.120    -19.4  1.22e-83
```

## Effects

```
allEffects(titanic.sex)
#> model: survived ~ sex
#>
#> sex effect
#> sex
#>   female      male
#> 0.7319149 0.2120162
```

## Effects

**sex effect plot**



**Did women have higher survival and travelled more in first class?**

---

## Let's look at the data

```
tapply(titanic$survived, list(titanic$class, titanic$sex), sum)
#>      female male
#> crew      20   192
#> first     141   62
#> second    93   25
#> third     90   88
```

Mmmm...

## Fit model with both factors (interactions)

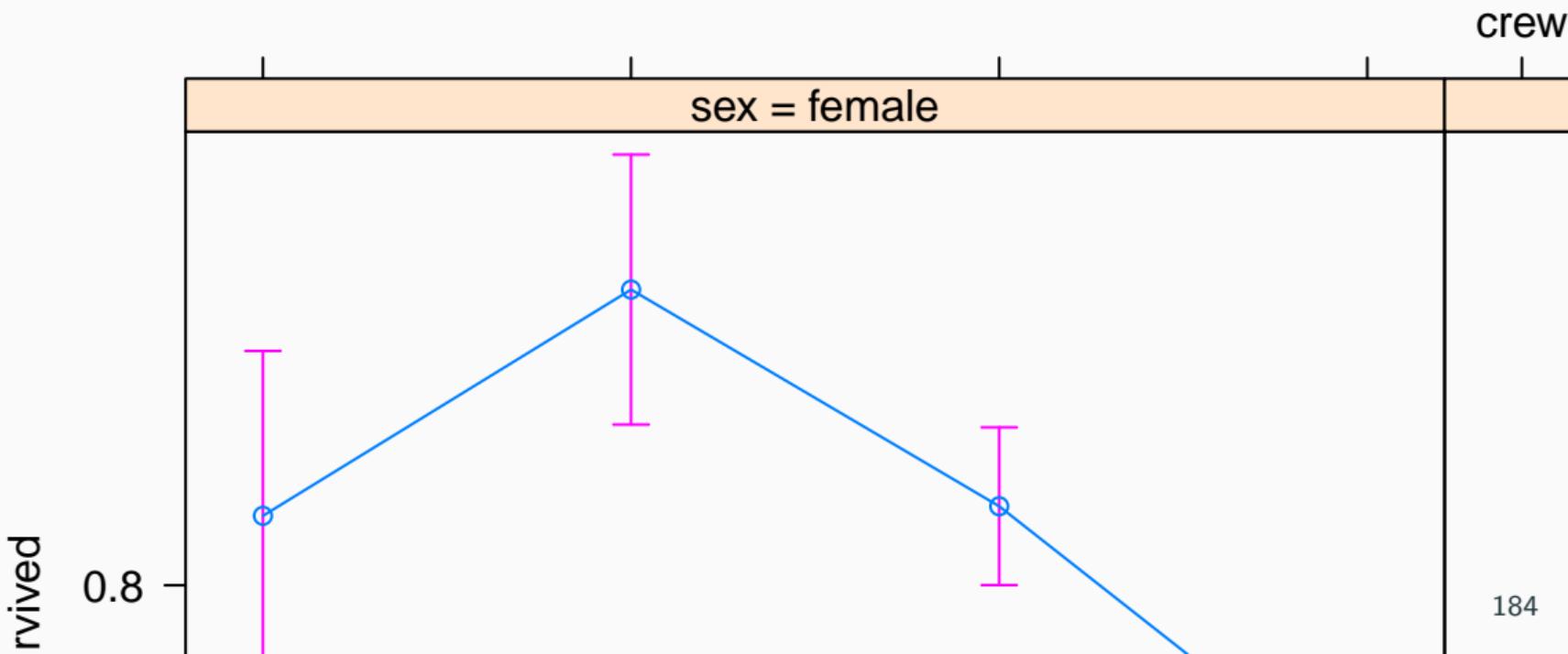
```
titanic.s.cl <- glm(survived ~ class * sex, data=titanic, family=binomial)
#> # A tibble: 8 x 5
#>   term            estimate std.error statistic    p.value
#>   <chr>          <dbl>     <dbl>      <dbl>      <dbl>
#> 1 (Intercept)    1.90      0.619      3.06     0.00218
#> 2 classfirst     1.67      0.800      2.08     0.0374
#> 3 classsecond    0.0705    0.686      0.103    0.918
#> 4 classthird    -2.06     0.636     -3.24     0.00118
#> 5 sexmale        -3.15     0.625     -5.04    0.000000468
#> 6 classfirst:sexmale -1.06    0.820     -1.29     0.196
#> 7 classsecond:sexmale -0.639   0.724     -0.882    0.378
#> 8 classthird:sexmale  1.74     0.651      2.68     0.00746
```

## Effects

```
allEffects(titanic.s.cl)
#> model: survived ~ class * sex
#>
#> class*sex effect
#>          sex
#> class      female      male
#> crew     0.8695652 0.2227378
#> first    0.9724138 0.3444444
#> second   0.8773585 0.1396648
#> third    0.4591837 0.1725490
```

## Effects

class\*sex effect p



## Conclusions

Use AIC to test the effect formally:

```
AIC(glm(survived ~ 1, data = titanic, family = binomial)) # null model  
#> [1] 2771.457  
AIC(titanic.glm) # class effect  
#> [1] 2596.555  
AIC(titanic.sex) # sex effect  
#> [1] 2338.988  
AIC(titanic.s.cl) # interaction of sex and class  
#> [1] 2179.733
```

So, women had higher probability of survival than men, irrespective of the class.

## Logistic regression for proportions

---

## Read Titanic data in different format

```
titanic.prop <- read.csv("dat/Titanic_prop.csv") %>%  
  mutate(across(where(is.character), as_factor))  
  
head(titanic.prop)  
#>   X Class     Sex   Age  No Yes  
#> 1 1  1st Female Adult    4 140  
#> 2 2  1st Female Child    0   1  
#> 3 3  1st   Male Adult 118  57  
#> 4 4  1st   Male Child    0   5  
#> 5 5  2nd Female Adult  13  80  
#> 6 6  2nd Female Child    0  13
```

These are the same data, but compacted.

## Bernoulli becomes a Binomial

Response  $\sim$  Distribution(Mean Response)

$$Y_i \sim \text{Binomial}(N_i, p_i)$$

$$\text{logit}(p_i) = a + b x_i$$

$$p_i = \text{logit}^{-1}(a + b x_i) = \frac{e^{a+b x_i}}{1 + e^{a+b x_i}}$$

## Use `cbind(n.success, n.failures)` as response

```
prop.glm <- glm(cbind(Yes, No) ~ Class, data = titanic.prop,
                  family = binomial)

#> # A tibble: 4 x 5
#>   term      estimate std.error statistic p.value
#>   <chr>     <dbl>     <dbl>     <dbl>    <dbl>
#> 1 (Intercept)  0.509     0.115     4.44 8.79e- 6
#> 2 Class2nd    -0.856     0.166    -5.16 2.51e- 7
#> 3 Class3rd    -1.60      0.144    -11.1 1.07e-28
#> 4 ClassCrew   -1.66      0.139    -12.0 4.97e-33
```

## Effects

```
allEffects(prop.glm)
#> model: cbind(Yes, No) ~ Class
#>
#> Class effect
#> Class
#>      1st       2nd       3rd      Crew
#> 0.6246154 0.4140351 0.2521246 0.2395480
```

Compare with former model based on raw data. Same results!

## **Logistic regression with continuous predictors**

---

## Read in GDP and infant mortality data (1998)

```
un <- read.csv("dat/UN_GDP_infantmortality.csv")
un$X <- as.factor(un$X)
names(un) <- c("country", "mortality", "gdp")
```

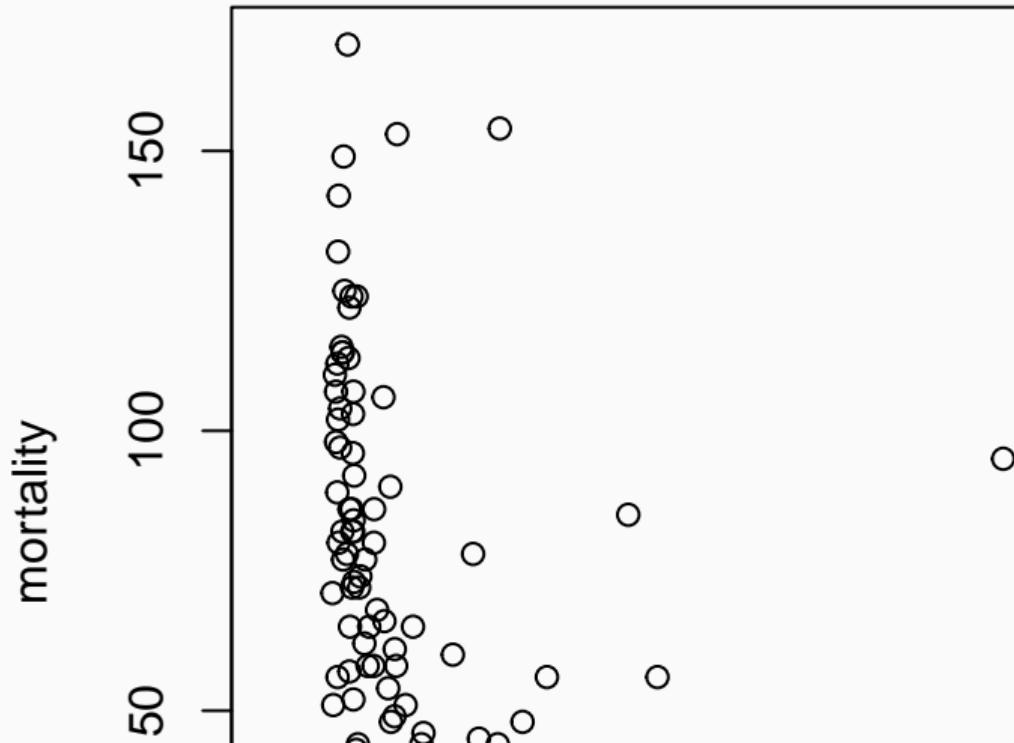
- mortality: Infant mortality rate, infant deaths per 1000 live births.
- gdp: GDP per capita, in US dollars.

## Explore the data

```
head(un)
#>      country mortality gdp
#> 1  Afghanistan     154 2848
#> 2    Albania        32  863
#> 3   Algeria        44 1531
#> 4 American.Samoa    11    NA
#> 5   Andorra        NA    NA
#> 6    Angola       124  355
```

## Explore the data “Infant mortality (per 1000 births)”

```
plot(mortality~gdp,data=un,main="")
```



## Fit model

```
gdp.glm <- glm(cbind(mortality, 1000 - mortality) ~ gdp,
                 data = un, family = binomial)

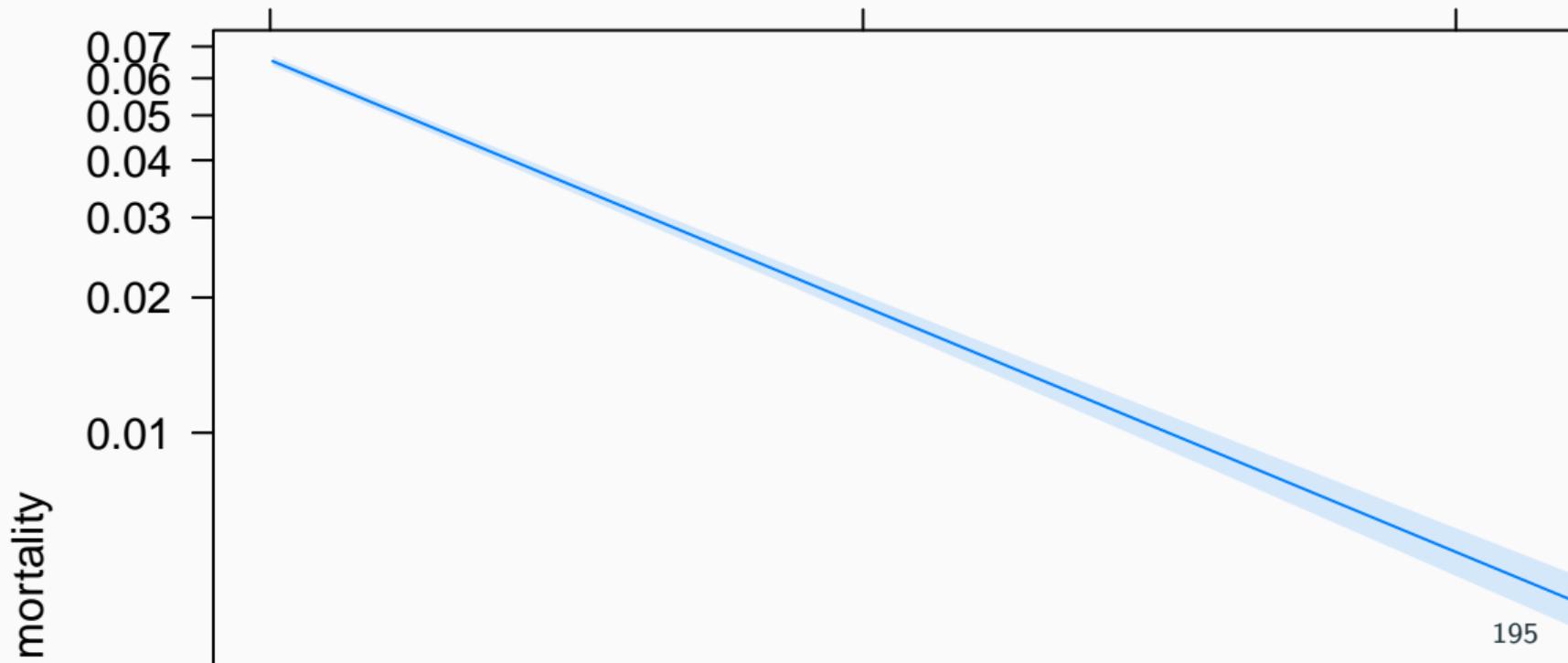
#> # A tibble: 2 x 5
#>   term      estimate std.error statistic p.value
#>   <chr>      <dbl>     <dbl>     <dbl>    <dbl>
#> 1 (Intercept) -2.66     0.0131    -203.    0.
#> 2 gdp        -0.000128  0.00000346    -37.0  1.96e-299
```

## Effects

```
allEffects(gdp.glm)
#> model: cbind(mortality, 1000 - mortality) ~ gdp
#>
#> gdp effect
#> gdp
#>      40          10000         20000         30000         40000
#> 0.0652177296 0.0191438829 0.0054028095 0.0015096074 0.0004206154
```

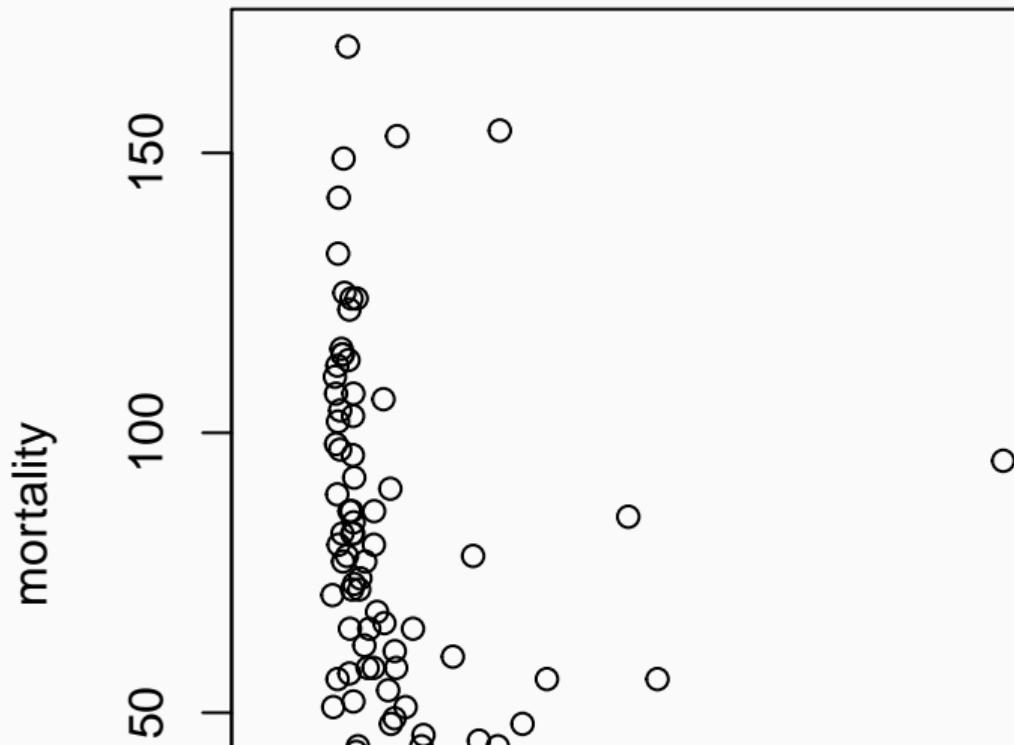
## Effects plot

```
plot(allEffects(gdp.glm), ylab = "mortality", main = "")
```



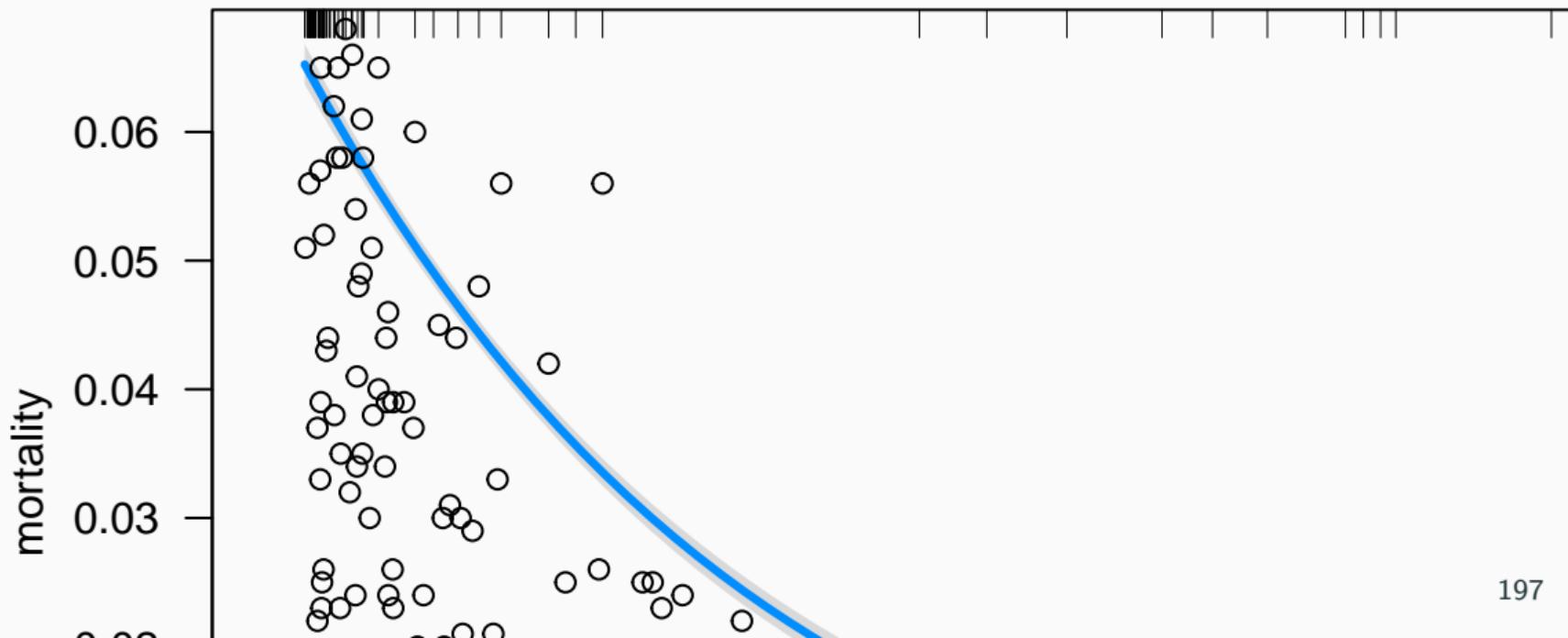
## Plot model and data (Infant mortality per 1000 births)

```
plot(mortality~gdp,data=un,main="")
```



## Plot model using visreg package

```
visreg(gdp.glm, scale = "response", ylab = "mortality")
points(mortality/1000 ~ gdp, data = un)
```



## Overdispersion

---

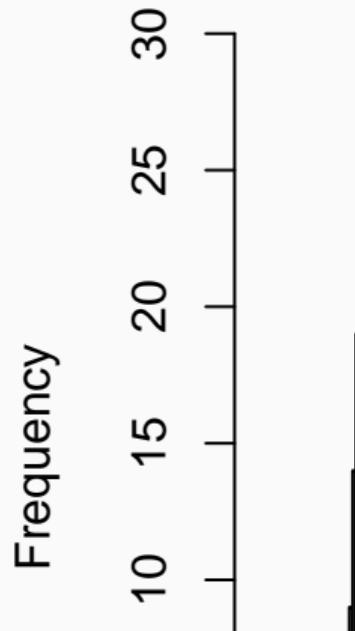
## What is overdispersion?

- The variance is higher than expected from a Poisson or Binomial process
- Often due to pseudoreplication, dependence among statistical units
- To account for these cases, the trick is to consider ‘quasi’ functions that use the parameter  $\phi$  to increase the expected variance (check out practical #1)

## Testing for overdispersion (with DHARMa package)

```
testOverdispersion(simulateResiduals(gdp.glm, refit = TRUE))
```

Dispersion test sig



## Overdispersion in logistic regression with proportions

```
gdp.overdisp <- glm(cbind(mortality, 1000 - mortality) ~ gdp,
                     data = un, family = quasibinomial)

#> # A tibble: 2 x 5
#>   term      estimate std.error statistic p.value
#>   <chr>      <dbl>     <dbl>      <dbl>    <dbl>
#> 1 (Intercept) -2.66      0.0598     -44.5  1.06e-102
#> 2 gdp        -0.000128  0.0000158     -8.11  5.96e- 14
```

## Mean estimates do not change after accounting for overdispersion

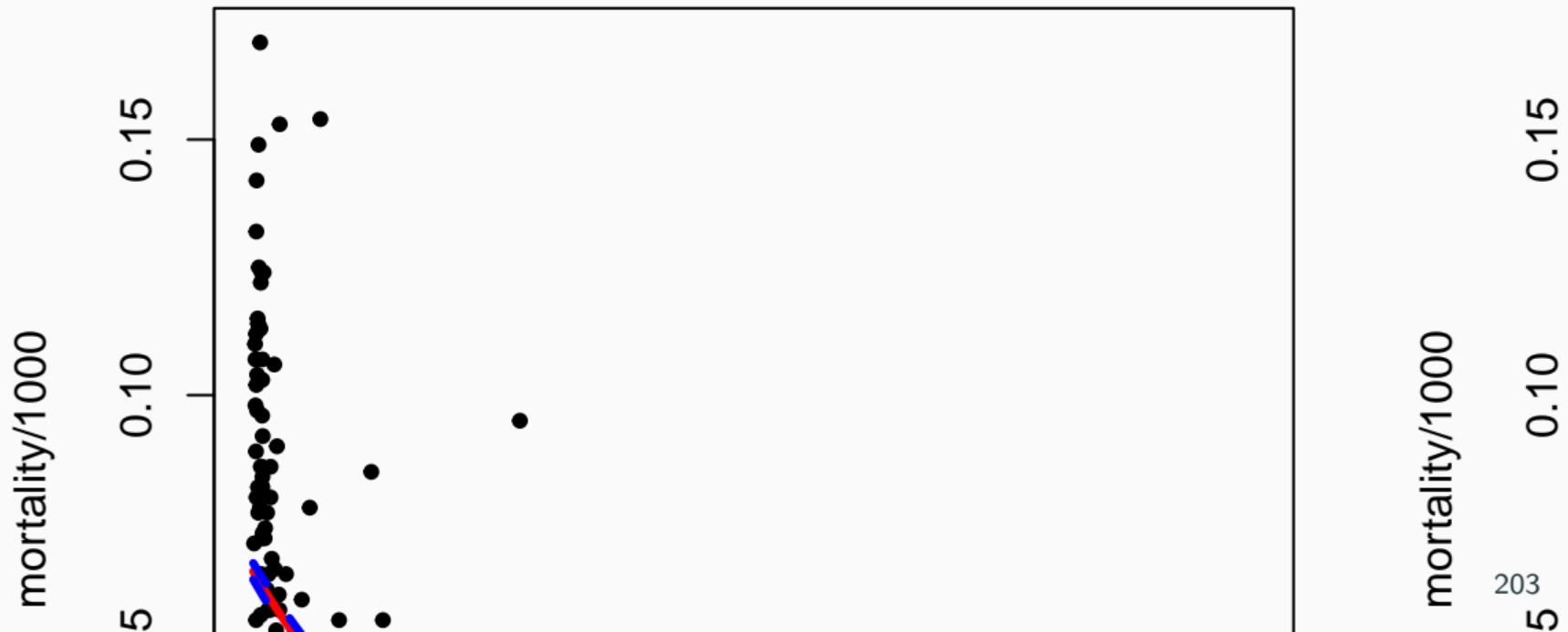
```
allEffects(gdp.overdisp)
#> model: cbind(mortality, 1000 - mortality) ~ gdp
#>
#> gdp effect
#> gdp
#>        40          10000         20000         30000         40000
#> 0.0652177296 0.0191438829 0.0054028095 0.0015096074 0.0004206154
```

## Mean estimates do not change after accounting for overdispersion

```
allEffects(gdp.glm)
#> model: cbind(mortality, 1000 - mortality) ~ gdp
#>
#> gdp effect
#> gdp
#>      40          10000         20000         30000         40000
#> 0.0652177296 0.0191438829 0.0054028095 0.0015096074 0.0004206154
```

**But standard errors do!**

# Binomial



## GLMs for counts: Poisson regression

---

## Types of response variable

- Gaussian: `lm`
- Bernoulli/Binomial: `glm` (family `binomial/quasibinomial`)
- Counts: `glm` (family `poisson/quasipoisson`)

## Poisson regression

- Discrete response variable: Counts (0, 1, 2, 3...)
- Link function:  $\log$

Response  $\sim$  Distribution(Mean Response)

$$Y_i \sim \text{Poisson}(\lambda_i)$$

$$\log(\lambda_i) = a + b x_i$$

$$\lambda_i = e^{a+b x_i}$$

## Example dataset: Seedling counts in $0.5m^2$ quadrats

```
seedl <- read.csv("dat/seedlings.csv")
names(seedl)
#> [1] "X"      "count"   "row"     "col"     "light"
```

- Light is the proportion of global solar radiation (GSF Global Site Factor)

## Explore data

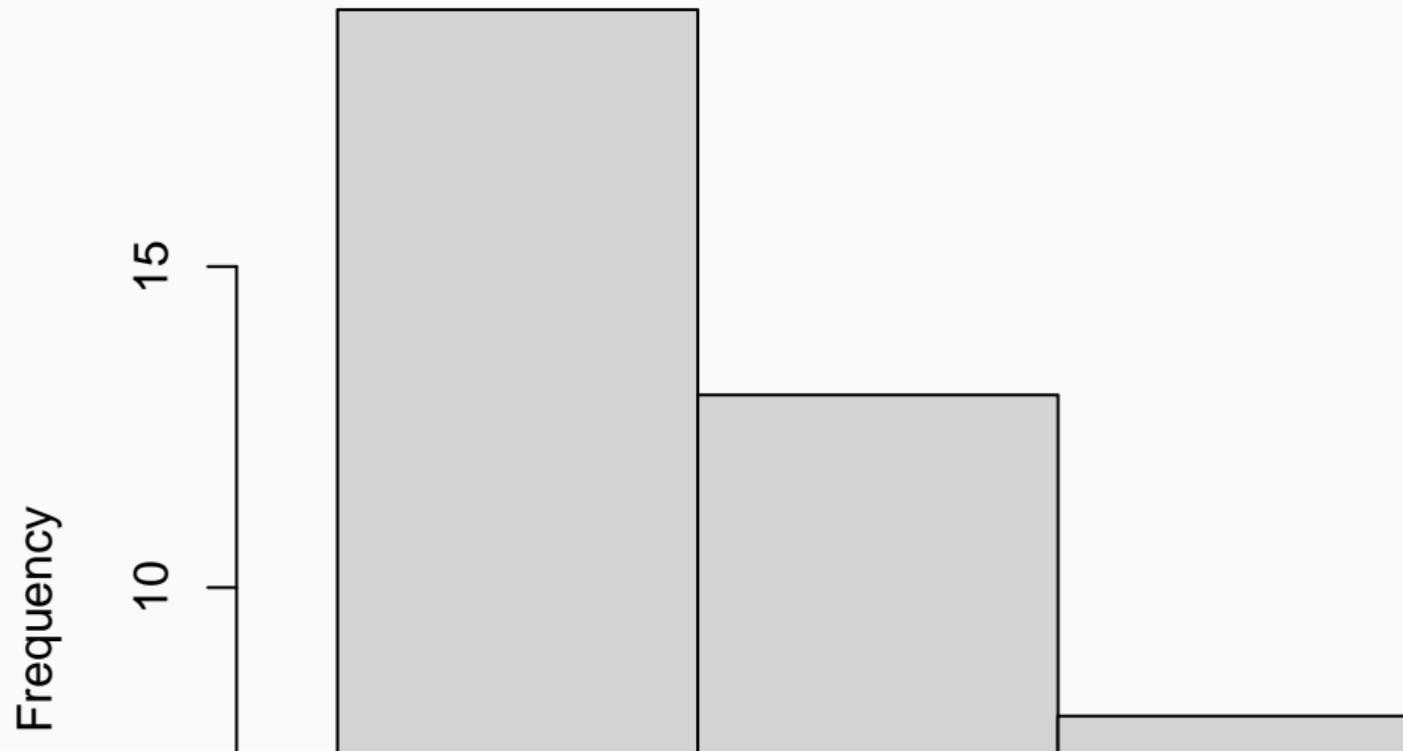
```
head(seed1)
#>   X count row col    light
#> 1 1     0   1   1 70.71854
#> 2 2     1   1   2 88.26021
#> 3 3     2   1   3 67.35133
#> 4 4     3   1   4 67.57850
#> 5 5     4   1   5 26.63098
#> 6 6     3   1   6 15.79433
```

## Explore data

```
table(seed1$count)
#>
#> 0 1 2 3 4 5 7
#> 7 12 13 8 7 2 1
```

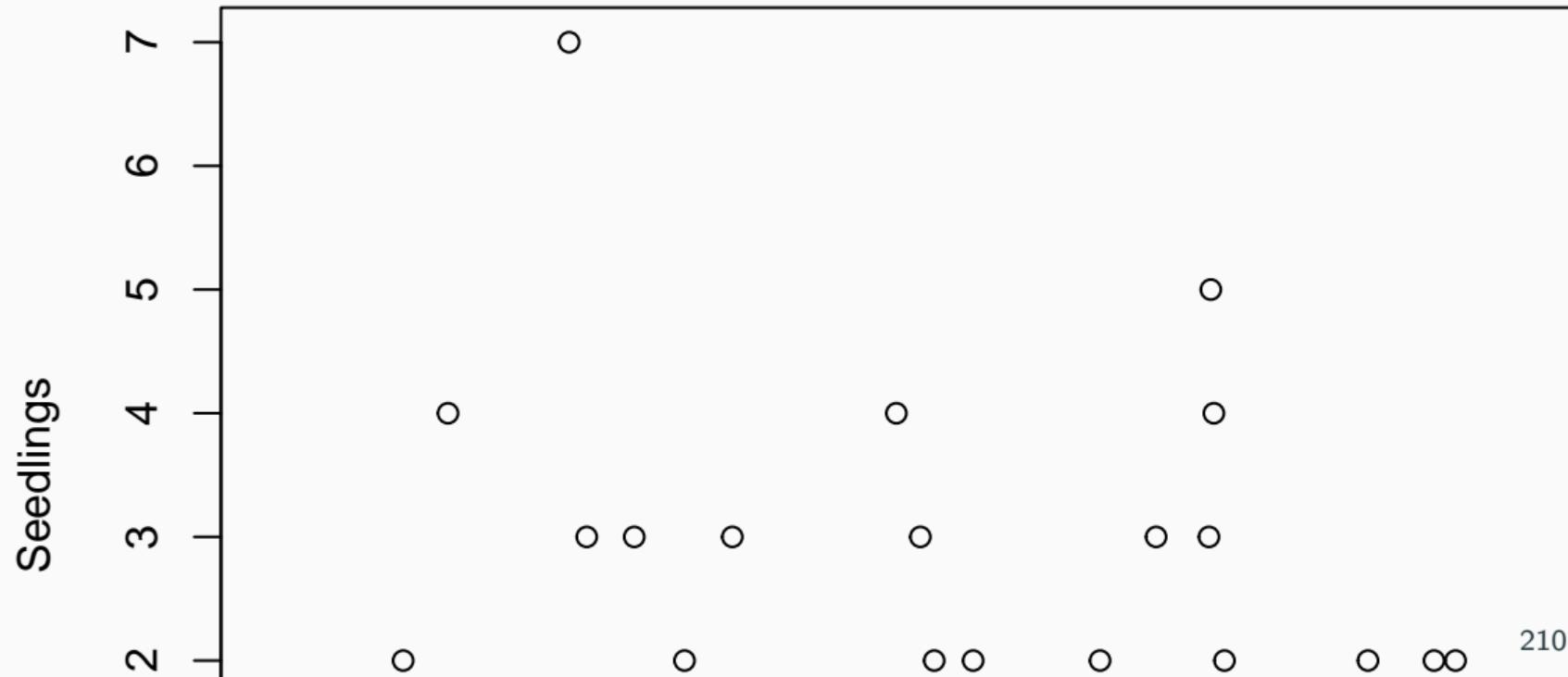
## Explore data

```
hist(seed1$count, main = "")
```



## Relationship between Nseedlings and light?

```
plot(seedl$light, seedl$count, xlab = "Light (GSF)", ylab = "Seedlings")
```



## Let's fit a GLM (Poisson regression)

```
seedl.glm <- glm(count ~ light, data = seedl, family = poisson)
tidy(seedl.glm)

#> # A tibble: 2 x 5
#>   term      estimate std.error statistic    p.value
#>   <chr>      <dbl>     <dbl>      <dbl>      <dbl>
#> 1 (Intercept)  0.882     0.189      4.67  0.00000304
#> 2 light       -0.00258   0.00353     -0.730  0.465
```

## Does light explain variation in counts

```
AIC(seed1.glm) # model with light  
#> [1] 182.0335  
AIC(glm(count ~ 1, data = seed1, family = poisson)) # null model  
#> [1] 180.5706
```

Should consider multimodel inference...

## Interpreting Poisson regression output

Parameter estimates (log scale):

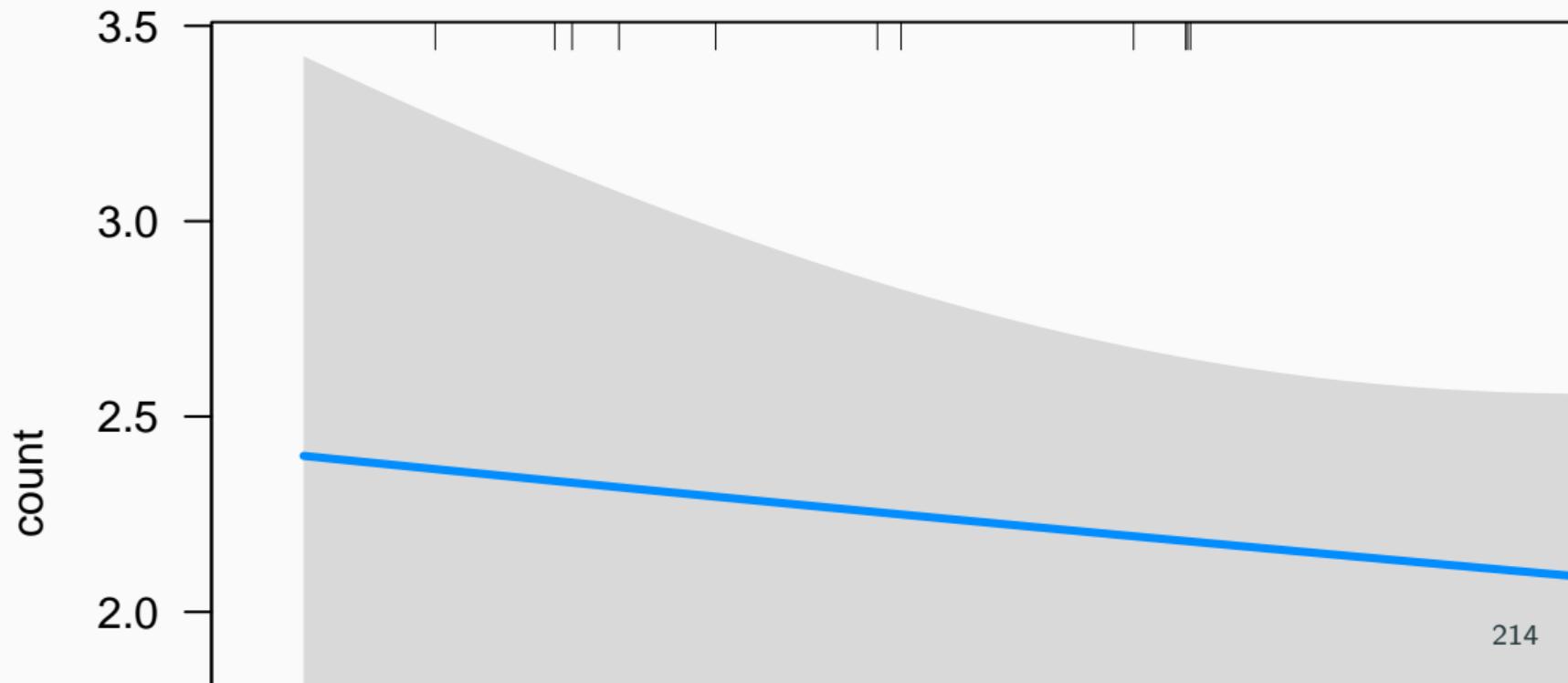
```
coef(seed1.glm)
#> (Intercept)      light
#> 0.881805022 -0.002575656
```

Let's back-transform the intercept for  $light = 0$  to get corresponding number of seedlings

```
exp(coef(seed1.glm)[1])
#> (Intercept)
#> 2.415255
```

## What is the relationship between Nseedlings and light? Use visreg package

```
visreg(seedl.glm, scale = "response")
```

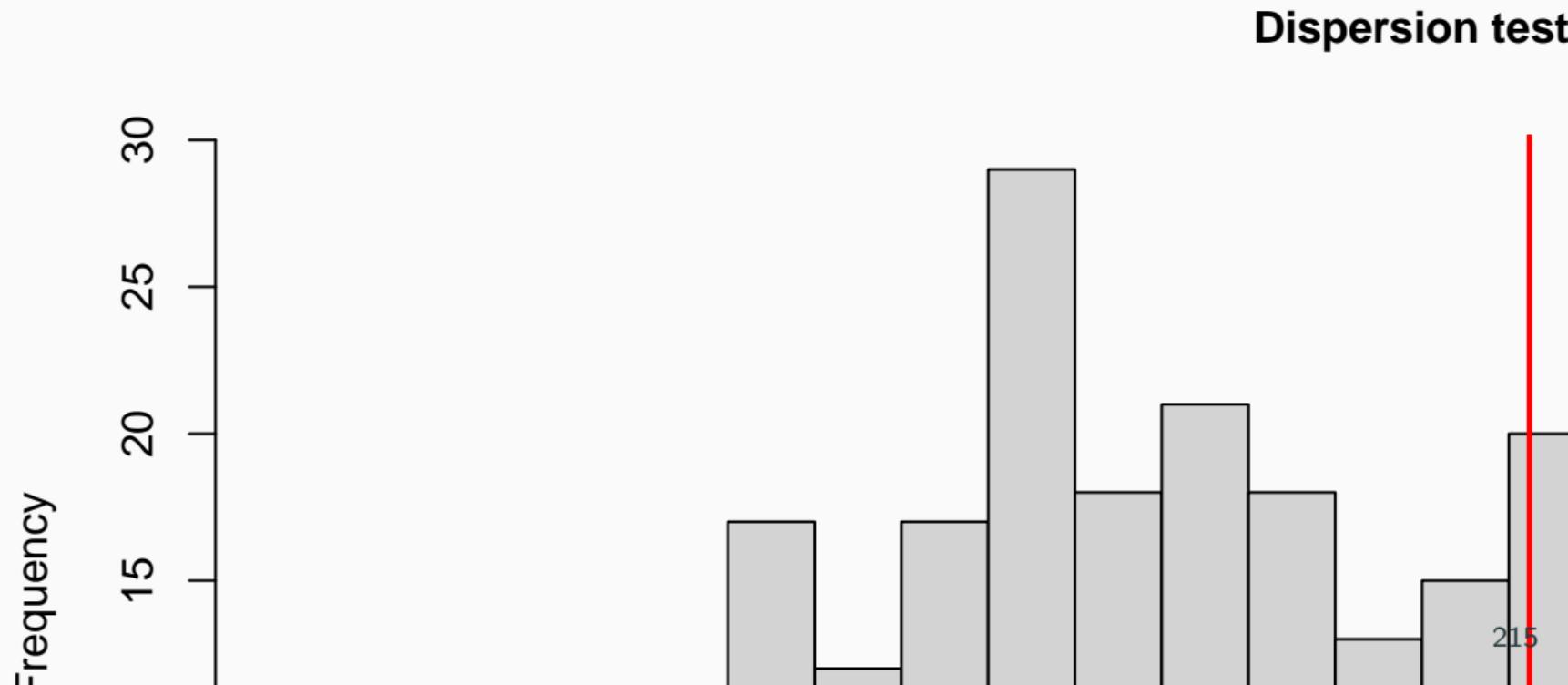


## Poisson regression: Overdispersion

---

## Always check overdispersion with count data

```
testOverdispersion(simulateResiduals(seedl.glm, refit = TRUE))
```



## Accounting for overdispersion in count data

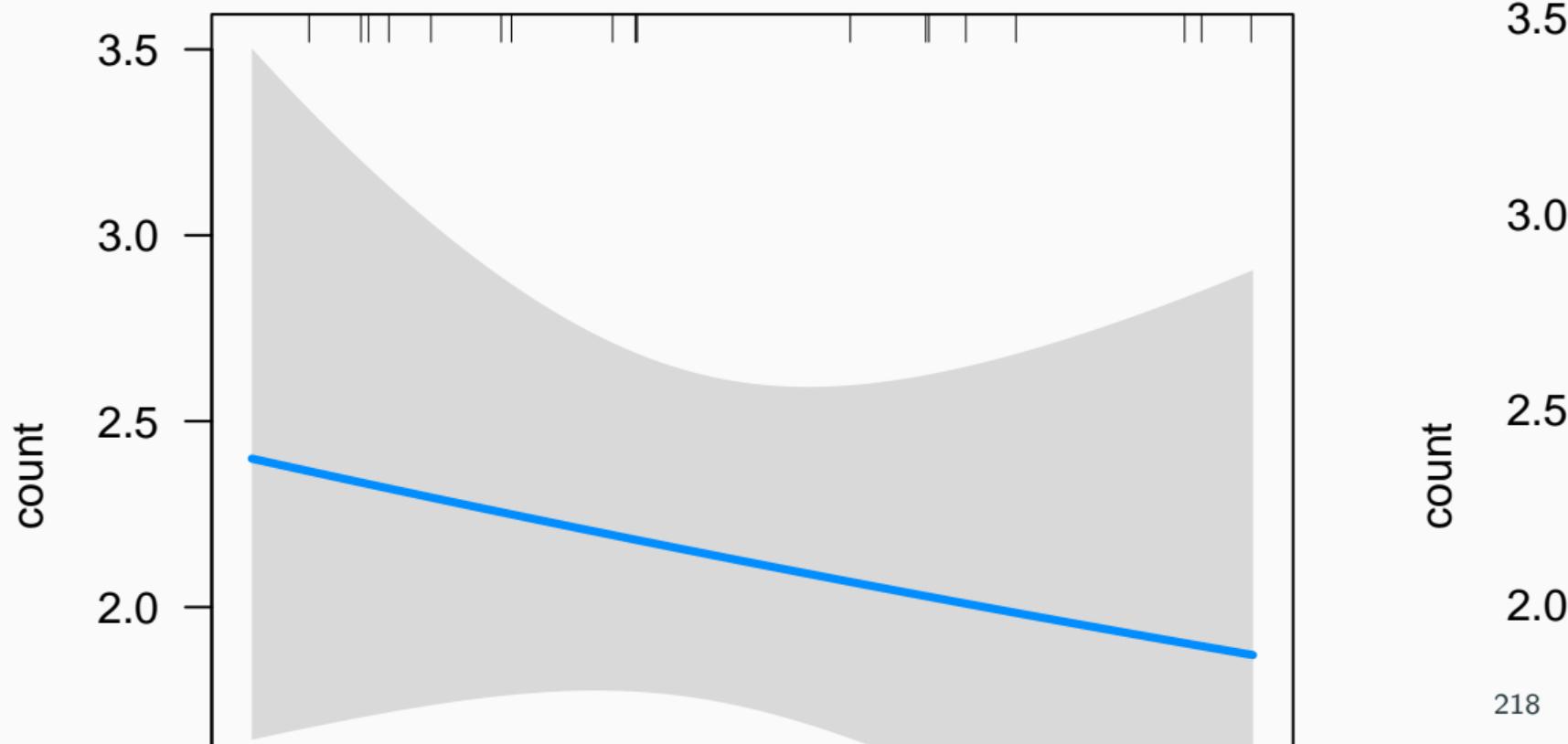
Use family quasipoisson

```
seedl.overdisp <- glm(count ~ light, data = seedl, family = quasipoisson)
tidy(seedl.overdisp)
#> # A tibble: 2 x 5
#>   term      estimate std.error statistic p.value
#>   <chr>      <dbl>     <dbl>      <dbl>    <dbl>
#> 1 (Intercept)  0.882     0.201      4.38  0.0000637
#> 2 light       -0.00258   0.00376     -0.685 0.496
```

## Mean estimates do not change after accounting for overdispersion

```
allEffects(seed1.overdisp)
#> model: count ~ light
#>
#> light effect
#> light
#>      3       30       50       70       100
#> 2.396665 2.235657 2.123408 2.016794 1.866826
allEffects(seed1.glm)
#> model: count ~ light
#>
#> light effect
#> light
#>      3       30       50       70       100
#> 2.396665 2.235657 2.123408 2.016794 1.866826
```

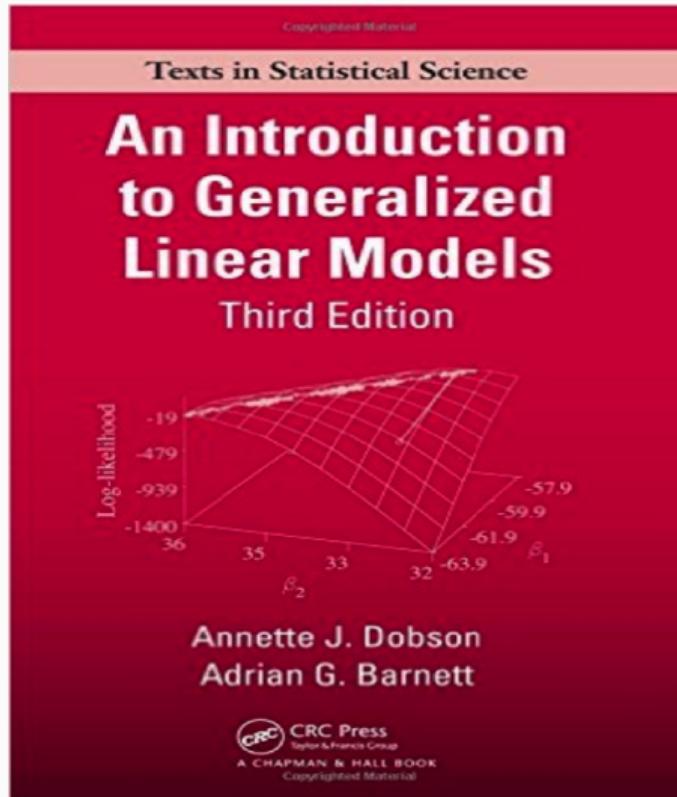
Standard errors do not change here



## GLMs in a nutshell

	Distribution	Link	$\text{Link}^{-1}$	Use for	R syntax
normal	identity	1		real values	<code>lm()</code>
poisson	log	exp		counts	<code>glm(,family=poisson)</code>
binomial	logit	$1/(1 + \exp(-x))$		binary, proportions	<code>glm(,family=binomial)</code>

## Textbooks



# Practical #1

---

## This Class

---

## On our plate

- Distributions and likelihoods
- Hypothesis testing and multimodel inference
- Introduction to Bayesian inference
- Generalized Linear Models (GLMs)
- Generalized Additive Models (GAMs)
- Mixed Effect Models

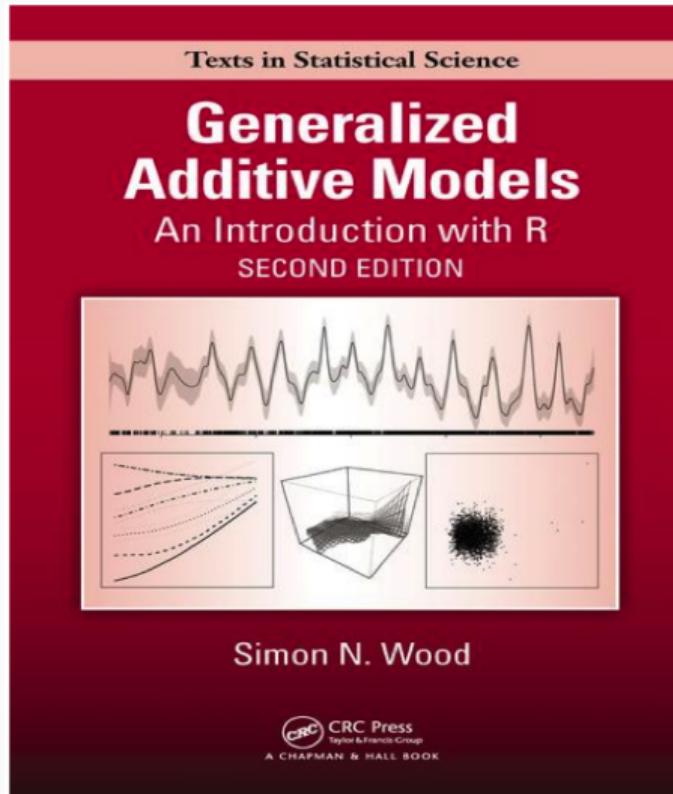
# **Generalized Additive Models (GAMs)**

---

## Courses

- Generalized Additive Models in R: A Free Interactive Course by Noam Ross. A friendly introduction requiring only basic knowledge of R and linear regression. 4-5 hours of slides and interactive exercises.
- Materials from a workshop on GAMs given by Noam Ross and colleagues.

## Textbooks



Simon N. Wood

 CRC Press  
Taylor & Francis Group  
A CHAPMAN & HALL BOOK

## This Class

---

## On our plate

- Distributions and likelihoods
- Hypothesis testing and multimodel inference
- Introduction to Bayesian inference
- Generalized Linear Models (GLMs)
- Generalized Additive Models (GAMs)
- Mixed Effect Models

## Mixed effect models

---

## What are random effects?

- Mixed models include both fixed and random effects
- Random effects are statistical parameters that attempt to explain noise caused by sub-populations of the population you are trying to model
- A random-effect model assumes that the dataset being analysed consists of a hierarchy of different populations whose differences relate to that hierarchy
- Measurement that come in groups

## Why do we need random effects?

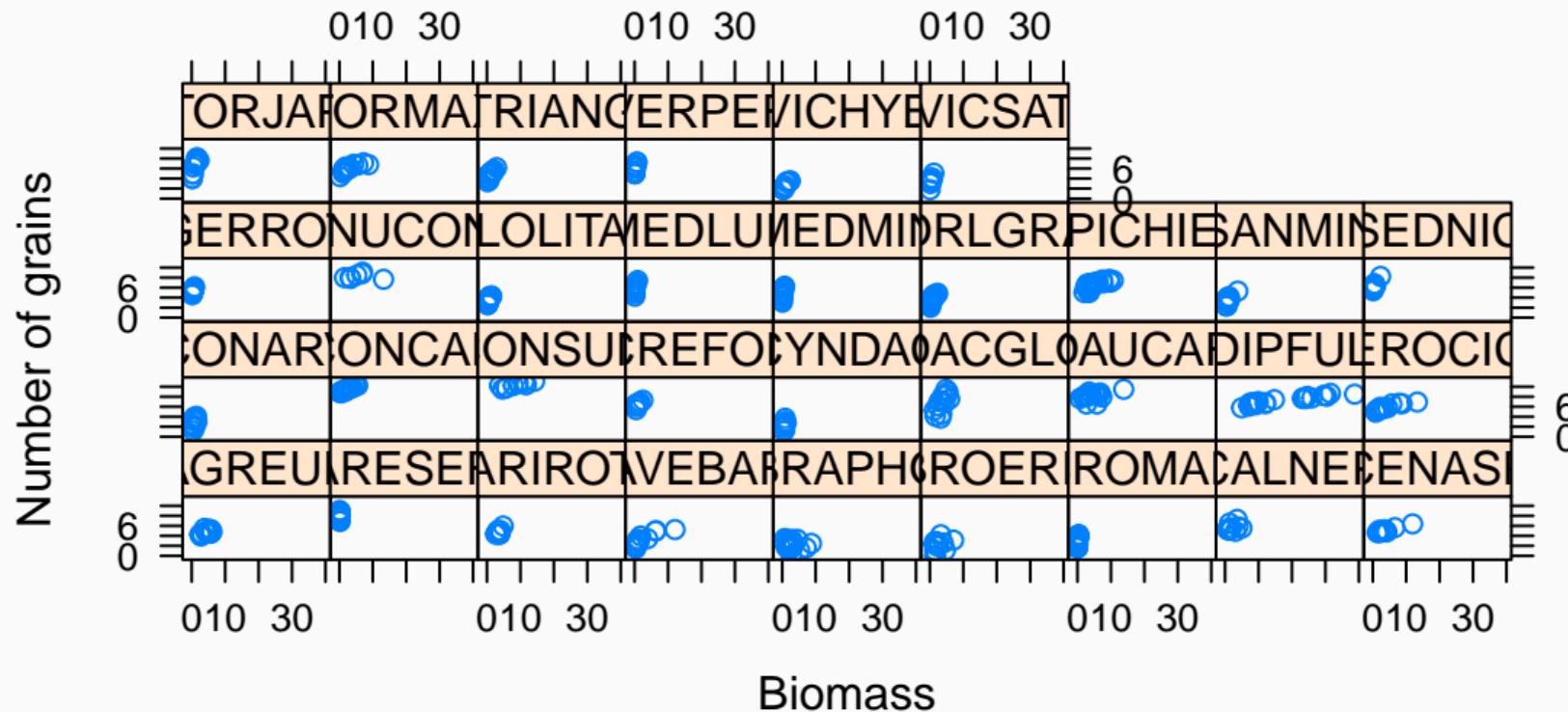
- Interested in variance components (environmental vs. genetic variance)
- Control for bias due to pseudoreplication (time, space, individual)

## Plant example, universality of the allometric relationship?



Courtesy of Eleni Kazakou.

## Plant example, universality of the allometric relationship?



## Fixed or random?

- Factors can either be fixed or random
- A factor is **fixed** when the levels under study are the only levels of interest
  - If we were to sample again, we would take the same factor levels (sex, age)
- A factor is **random** when the levels under study are a random sample from a larger population and the goal of the study is to make a statement regarding the larger population
  - If we were to sample again, we would not necessarily take the same factor levels (individuals, species, . . . )

## GLM formulation

$$Y_i \sim \text{Distribution}(\text{Mean Response}_i)$$

$$\text{Mean Response}_i = \beta_0 + \beta_1 x_{i1} + \dots + \beta_P x_{iP}$$

## GLMM formulation

$$Y_{ij} \sim \text{Distribution}(\text{Mean Response}_{ij})$$

$$\text{Mean Response}_{ij} = \beta_{0j} + \beta_1 x_{i1} + \dots + \beta_P x_{iP}$$

$$\beta_{0j} \sim \text{Normal}(\mu_{group}, \sigma^2_{group})$$

## Model fitting in R

- Linear Mixed Models (LMMs) and Generalized Linear Mixed Models (GLMMs)

```
library(lme4)
my_LMM <- lmer(y ~ x + (1 | group)) # LMM
my_GLMM <- glmer(y ~ x + (1 | group), family = Distribution) # GLMM
```

- $x$  is the **fixed** factor(s)
- $1$  is the **random** factor(s), here the intercept
- $group$  is for the **grouping** variable

## Model fitting in practice?



## Back to the plant example

$$Y_{i,\text{species}} \sim \text{Normal}(\text{Mean Response}_{i,\text{species}}, \sigma_{\text{residual}}^2)$$

$$\text{Mean Response}_{i,\text{species}} = \beta_0 \text{species} + \beta_1 x_i$$

$$\beta_0 \text{species} \sim \text{Normal}(\mu_{sp}, \sigma_{sp}^2)$$

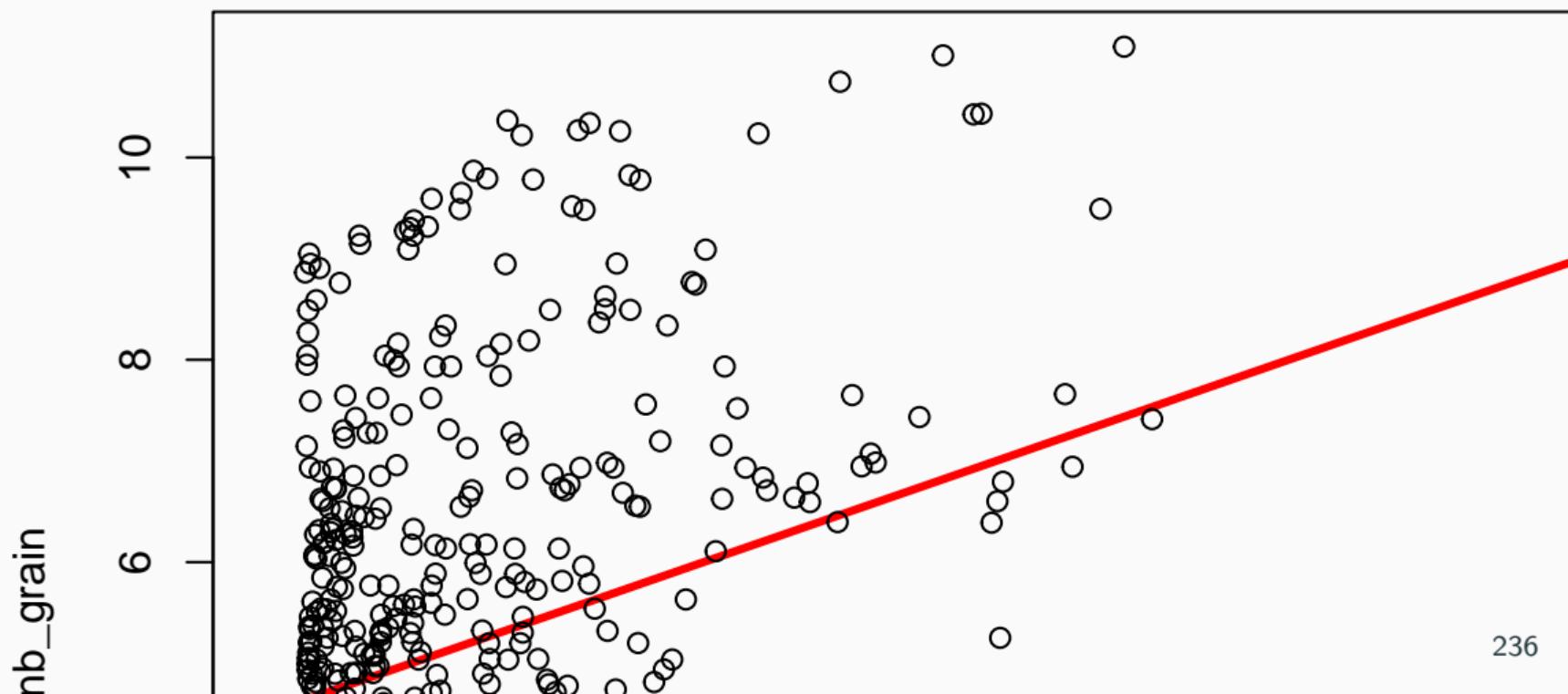
## Back to the plant example

Fit **one** linear model, with no distinction of species: **complete pooling**

```
allom.lm <- lm (nb_grain ~ Biomass,dat)
tidy(allom.lm)
#> # A tibble: 2 x 5
#>   term      estimate std.error statistic p.value
#>   <chr>      <dbl>     <dbl>      <dbl>    <dbl>
#> 1 (Intercept)  4.64     0.109     42.4  3.11e-165
#> 2 Biomass      0.197    0.0204     9.65 2.92e- 20
```

## Back to the plant example

Fit **one** linear model, with no distinction of species: **complete pooling**



## Back to the plant example

Fit **as many** linear models as we have species: **no pooling**

## Back to the plant example

Fit linear **mixed** model, with species as a random effect on the **intercept**

```
library(lme4)
allom.lmm <- lmer(nb_grain ~ Biomass + (1 | Species),dat)
allom.lmm
#> Linear mixed model fit by REML ['lmerMod']
#> Formula: nb_grain ~ Biomass + (1 | Species)
#> Data: dat
#> REML criterion at convergence: 1258.391
#> Random effects:
#> Groups   Name        Std.Dev.
#> Species  (Intercept) 1.9825
#> Residual           0.7478
#> Number of obs: 488, groups: Species, 33
#> Fixed Effects:
#> (Intercept)      Biomass
#>             4.956       0.132
```

## Back to the plant example

Fit linear **mixed** model, with species as random effect on both **intercept** and **slope**

```
allom.lmm2 <- lmer (nb_grain ~ Biomass + (1 + Biomass | Species), dat)
allom.lmm2
#> Linear mixed model fit by REML ['lmerMod']
#> Formula: nb_grain ~ Biomass + (1 + Biomass | Species)
#> Data: dat
#> REML criterion at convergence: 1126.882
#> Random effects:
#> Groups   Name        Std.Dev. Corr
#> Species  (Intercept) 2.1179
#>          Biomass     0.8719  -0.27
#> Residual           0.5751
#> Number of obs: 488, groups: Species, 33
#> Fixed Effects:
#> (Intercept)      Biomass
#>        4.5019      0.8426
```

## Back to the plant example

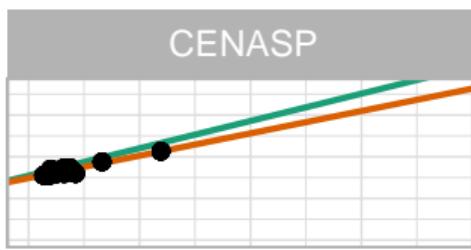
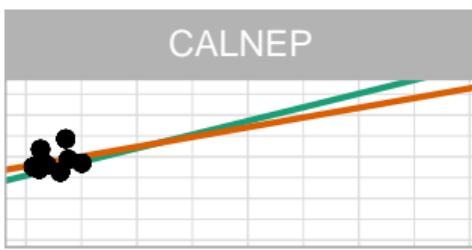
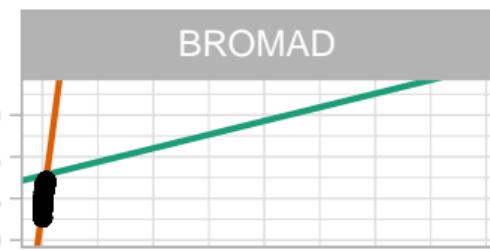
..., with species as random effect on both intercept and slope, without correlation

```
allom.lmm3 <- lmer (nb_grain ~ Biomass + (1 | Species) +
                      (0 + Biomass | Species), dat)

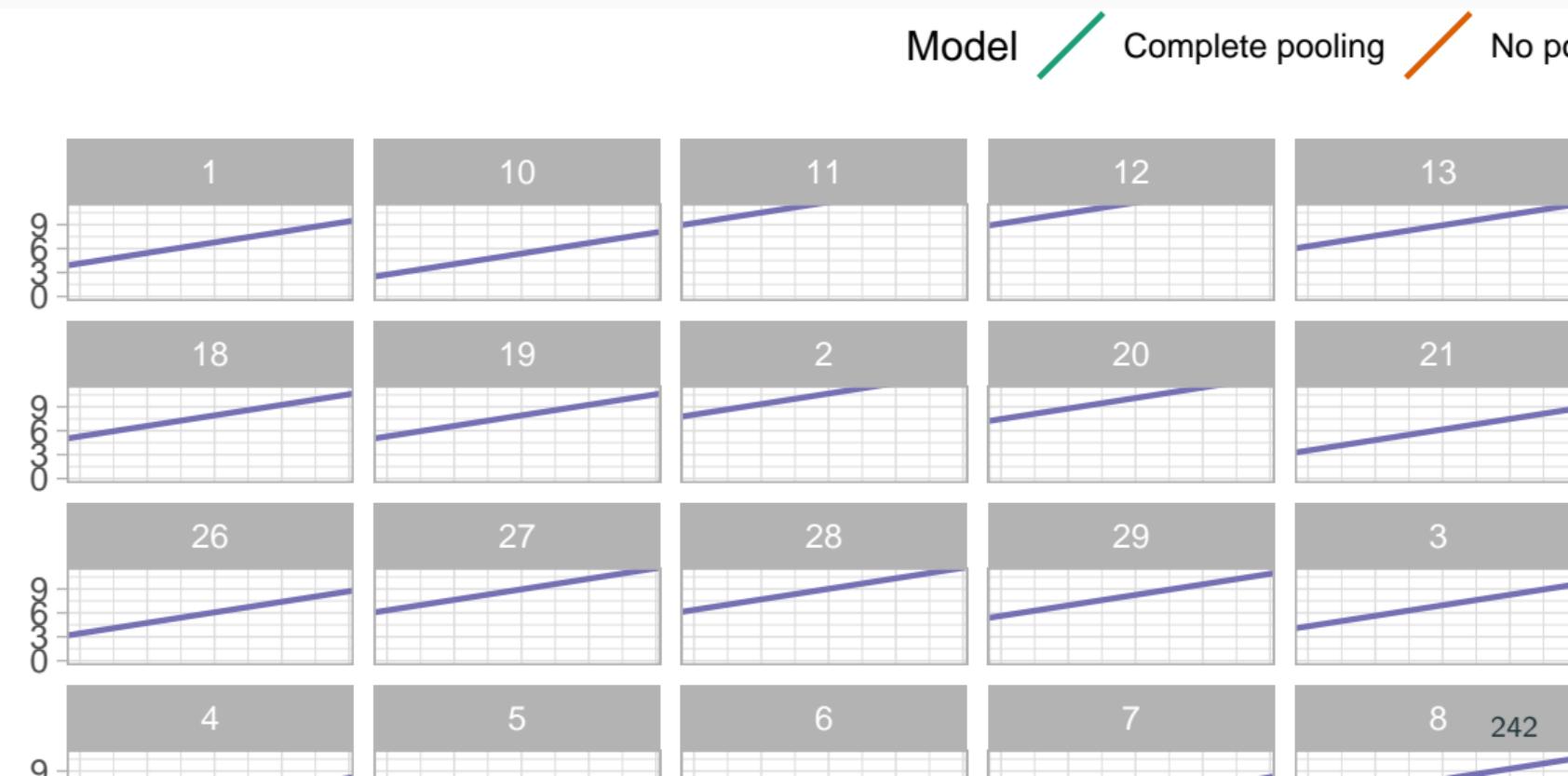
allom.lmm3
#> Linear mixed model fit by REML ['lmerMod']
#> Formula: nb_grain ~ Biomass + (1 / Species) + (0 + Biomass / Species)
#> Data: dat
#> REML criterion at convergence: 1128.986
#> Random effects:
#> Groups      Name      Std.Dev.
#> Species     (Intercept) 2.1032
#> Species.1   Biomass    0.8720
#> Residual           0.5751
#> Number of obs: 488, groups: Species, 33
#> Fixed Effects:
#> (Intercept)      Biomass
#>        4.5011      0.8499
```

## 'Old school' linear models, complete pooling vs. no pooling

Model      Complete pooling



## Linear mixed model, with species as a random effect on the intercept

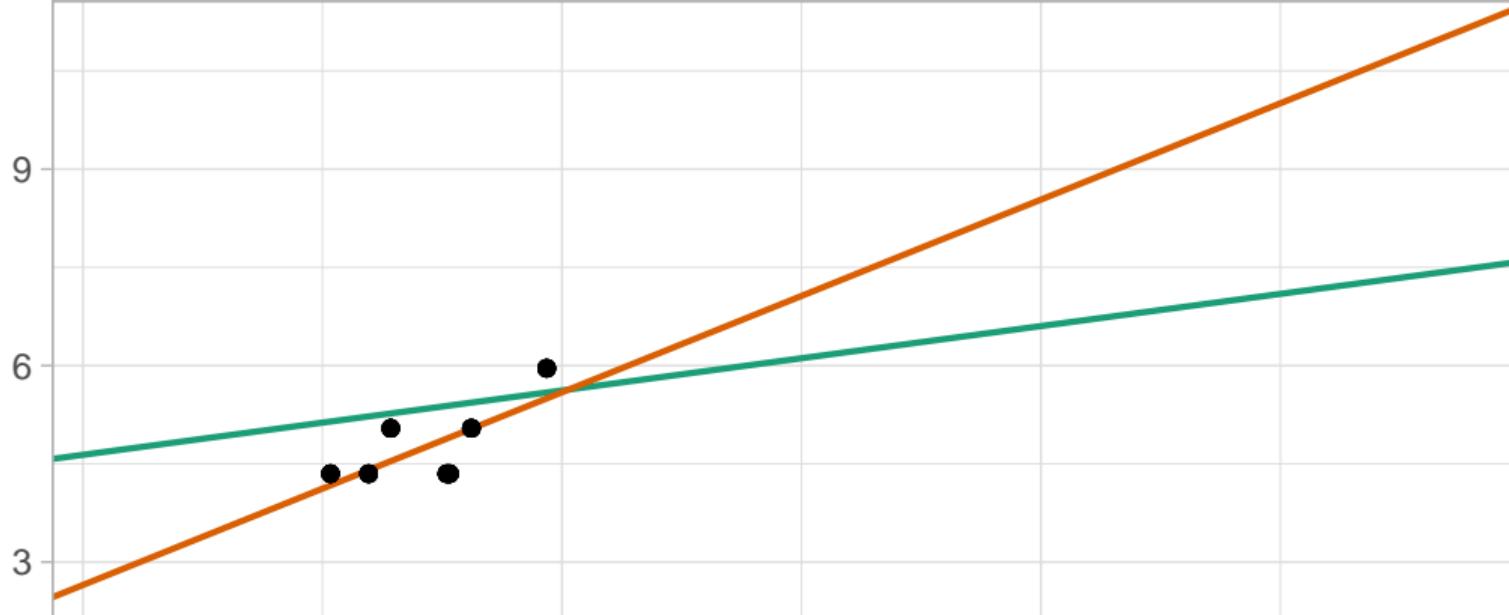


Let's zoom in

Model

Complete pooling

ARIROT



243

## **What about a Bayesian approach?**

---

## Model with complete data pooling

Likelihood for measurement  $i$  in species  $j$ :

$$\text{number.seeds}_{ij} = a + b \text{ biomass}_{ij} + \epsilon_{ij}$$

with  $\epsilon_{ij} \sim \text{Normal}(0, \sigma^2)$

Alternatively:

$$\text{number.seeds}_{ij} \sim \text{Normal}(a + b \text{ biomass}_{ij}, \sigma^2)$$

Priors:

$$a, b \sim \text{Normal}(0, 1000)$$

$$\sigma \sim \text{Uniform}(0, 100)$$

## **Bayesian linear regression - in Jags**

---

## Read in and manipulate data

```
# read in data
VMG <- read.table("dat/VMG.csv", header=TRUE, dec= ".", sep =";")
VMG$Sp <- as.factor(VMG$Sp)
# nb of seeds (log)
y <- log(VMG$NGrTotest)
# biomass
x <- VMG$Vm
# species name
Sp <- VMG$Sp
# species label
species <- as.numeric(Sp)
# species name
nbspecies <- length(levels(Sp))
# total nb of measurements
n <- length(y)
```

## Implement the model in Jags

```
model <-
paste("
model{
for(i in 1:n){
  y[i] ~ dnorm(mu[i],tau.y)
  mu[i] <- a+b*x[i]
}
tau.y<-1/(sigma.y*sigma.y)
sigma.y~dunif(0,100)
a~dnorm(0,0.001)
b~dnorm(0,0.001)
}
")
writeLines(model,"pooling.bug")
```

## Prepare ingredients for running Jags

```
# data
allom.data <- list(y=y,n=n,x=x)

# initial values
init1<-list(a=rnorm(1), b=rnorm(1),sigma.y=runif(1))
init2<-list(a=rnorm(1), b=rnorm(1),sigma.y=runif(1))
inits<-list(init1,init2)

# parameters to be estimated
allom.parameters <- c("a", "b", "sigma.y")
```

# Run Jags!

```
allom.1 <- jags(allom.data,inits,allom.parameters,
                  n.iter = 2500,model.file="pooling.bug",
                  n.chains = 2, n.burn = 1000)

#> Compiling model graph
#> Resolving undeclared variables
#> Allocating nodes
#> Graph information:
#>   Observed stochastic nodes: 488
#>   Unobserved stochastic nodes: 3
#>   Total graph size: 1956
#>
#> Initializing model
```

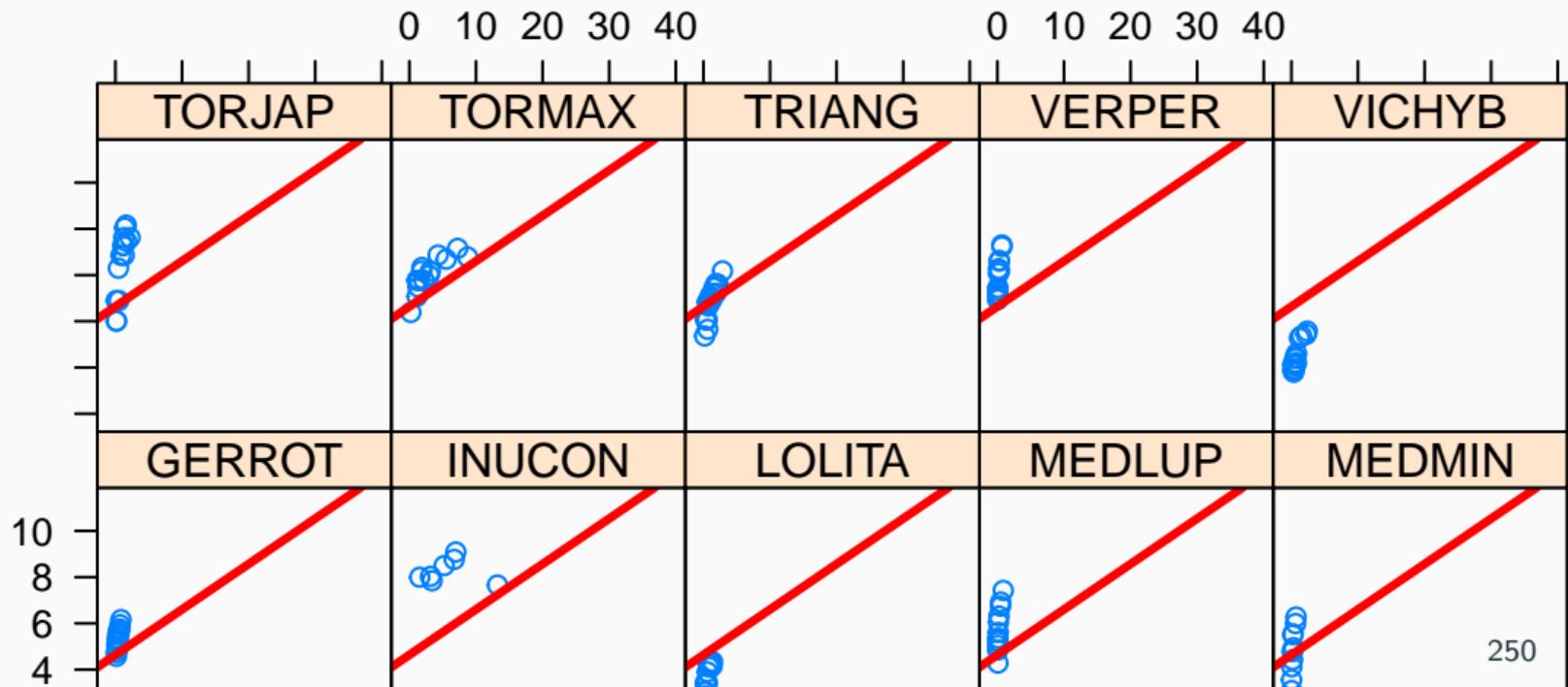
## Display results

allom.1

```
#> Inference for Bugs model at "pooling.bug", fit using jags,
#> 2 chains, each with 2500 iterations (first 1000 discarded)
#> n.sims = 3000 iterations saved
#>          mu.vect sd.vect    2.5%     25%     50%     75%   97.5%   Rhat
#> a        4.638   0.110   4.421   4.566   4.637   4.708   4.857 1.001
#> b        0.197   0.021   0.157   0.183   0.197   0.211   0.238 1.001
#> sigma.y  2.080   0.066   1.956   2.032   2.079   2.125   2.212 1.001
#> deviance 2098.782  2.510 2095.998 2096.954 2098.105 2099.923 2105.226 1.001
#>          n.eff
#> a        1800
#> b        3000
#> sigma.y 3000
#> deviance 3000
#>
#> For each parameter, n.eff is a crude measure of effective sample size,
#> and Rhat is the potential scale reduction factor (at convergence, Rhat=1).
```

# Output

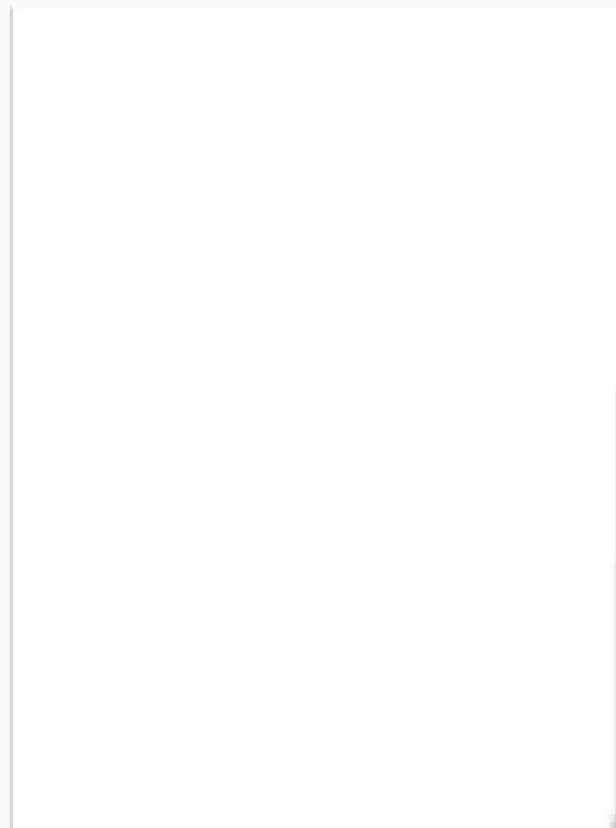
complete pooling (no sp)



## Models with mixed effects

---

## Varying-intercept model



## Varying-intercept model

Likelihood for measurement  $i$  in species  $j$ :

$$\text{number.seeds}_{ij} = a_j + b \text{ biomass}_{ij} + \epsilon_{ij}$$

with  $a_j \sim \text{Normal}(\mu_a, \sigma_a^2)$  species random effect that captures inter-species variability  
and  $\epsilon_{ij} \sim \text{Normal}(0, \sigma^2)$  residual variance

Priors:

$$\mu_a, b \sim \text{Normal}(0, 1000)$$

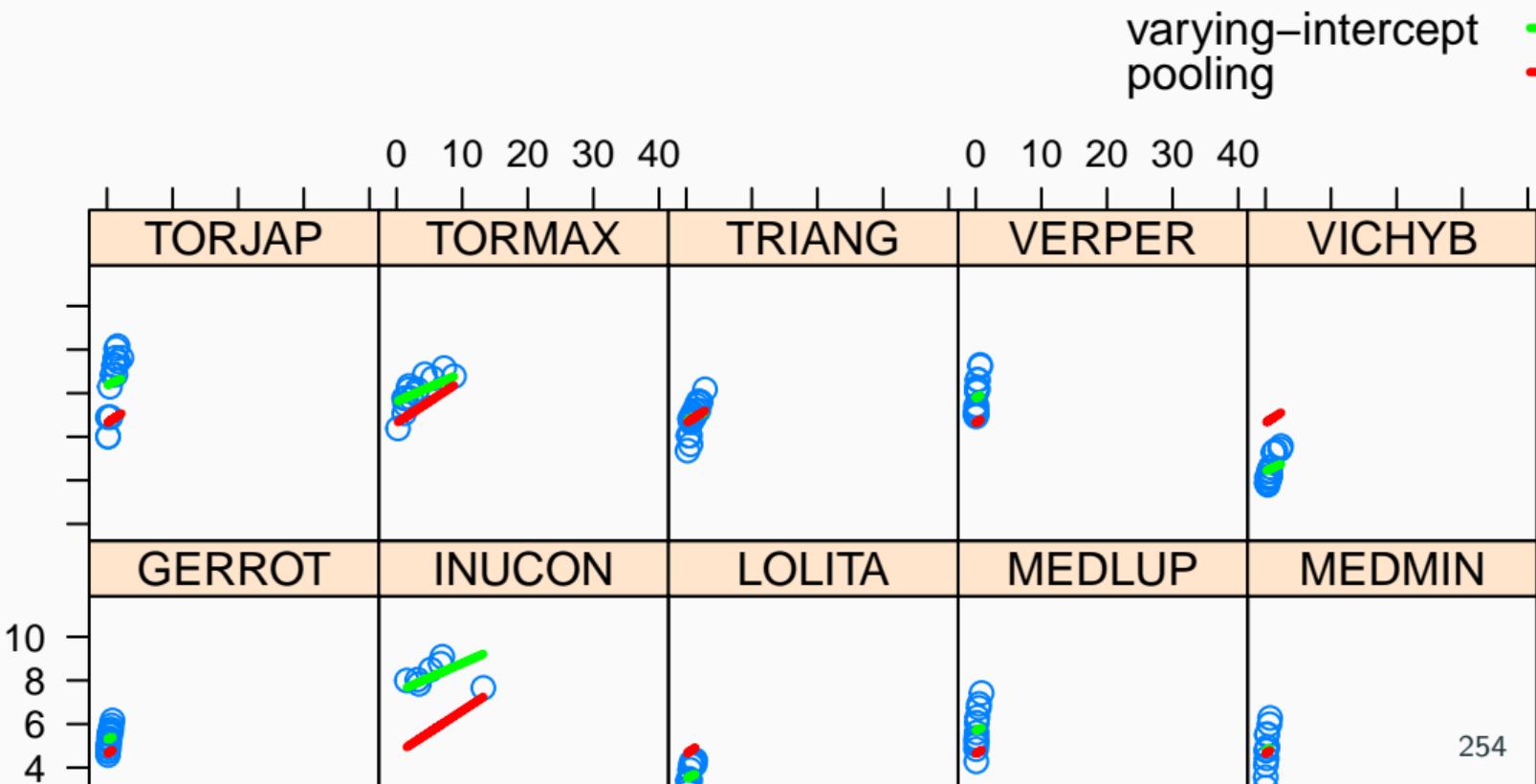
$$\sigma, \sigma_a \sim \text{Uniform}(0, 100)$$

## Varying-intercept model in Jags

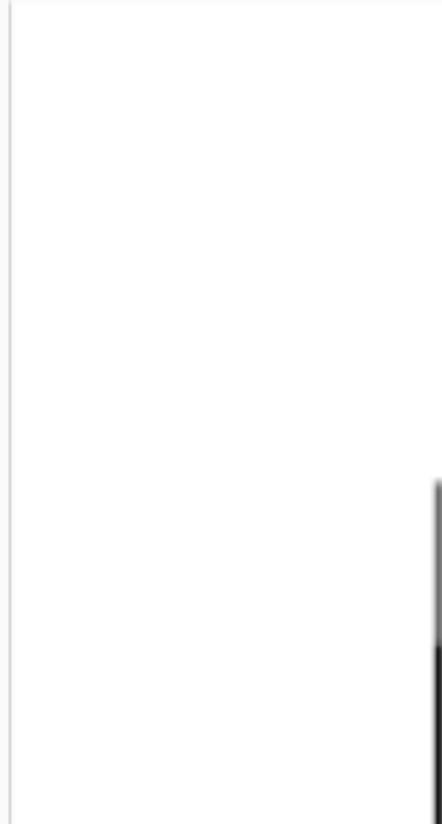
```
model <- paste("
model{
  for (k in 1:n){
    y[k] ~ dnorm (y.hat[k], tau.y)
    y.hat[k] <- a[species[k]] + b *x[k]
  tau.y <- pow(sigma.y, -2)
  sigma.y ~ dunif (0, 100)
  for (j in 1:nbspecies){
    a[j] ~ dnorm(mu.a, tau.a)}
  mu.a ~ dnorm (0, .001)
  tau.a <- pow(sigma.a, -2)
  sigma.a ~ dunif (0, 100)
  b ~ dnorm (0, .001)
}
")
writeLines(model, "varint.bug")
```

```
allom.data <- list(n = n
```

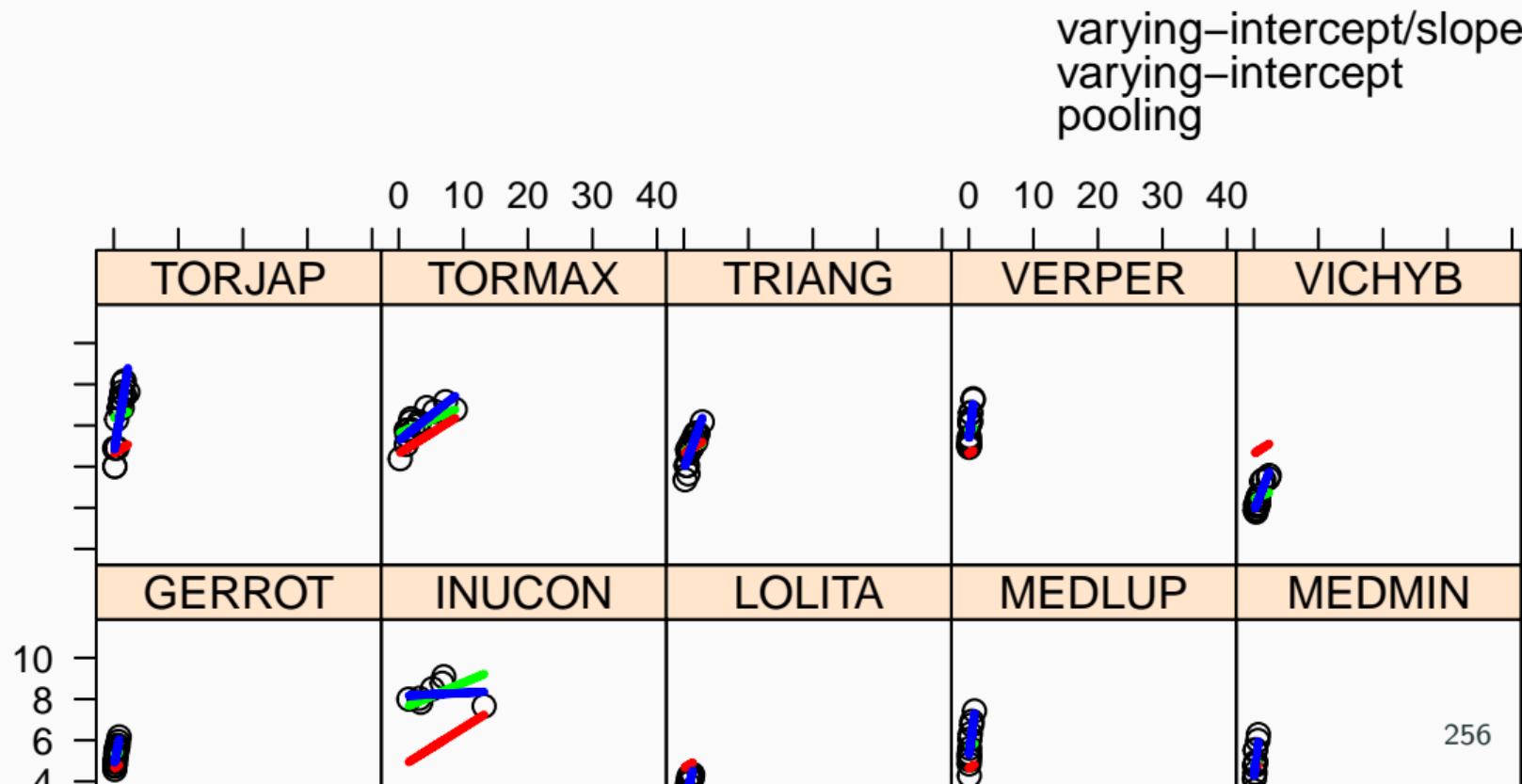
## Compare **complete pooling** vs **varying-intercept**



## Varying intercept, varying slope model



## Compare **complete pooling** vs **varying intercept** vs **varying intercept and slope**



## Generalized Linear Mixed Models

---

Plant example was a LMM, now let's explore a GLMM



This is not a GLMM

mangl.at

## White stork: Is breeding success affected by weather conditions?

```
nbchicks = c(151,105,73,107,113,87,77,108,118,122,112,120,122,89,69,71,  
           53,41,53,31,35,14,18)  
nbpairs = c(173,164,103,113,122,112,98,121,132,136,133,137,145,117,90,  
           80,67,54,58,39,42,23,23)  
temp = c(15.1,13.3,15.3,13.3,14.6,15.6,13.1,13.1,15.0,11.7,15.3,14.4,  
        14.4,12.7,11.7,11.9,15.9,13.4,14.0,13.9,12.9,15.1,13.0)  
rainfall = c(67,52,88,61,32,36,72,43,92,32,86,28,57,55,66,26,28,96,48,  
            90,86,78,87)  
year = seq(1,length(nbchicks))
```

## Standard GLM on proportions

$$\text{nbchicks}_i \sim \text{Binomial}(\text{nbpairs}_i, p_i)$$

$$\text{logit}(p_i) = \beta_0 + \beta_1 \text{ temp}_i + \beta_2 \text{ rainfall}_i$$

## Standard GLM on proportions in R

```
stork_glm <- glm(cbind(nbchicks,nbpairs-nbchicks) ~ temp + rainfall,  
                  family = binomial)  
  
tidy(stork_glm)  
#> # A tibble: 3 x 5  
#>   term      estimate std.error statistic p.value  
#>   <chr>      <dbl>     <dbl>      <dbl>    <dbl>  
#> 1 (Intercept)  1.62      0.629      2.58  0.00999  
#> 2 temp        0.0239    0.0465      0.515  0.607  
#> 3 rainfall    -0.00656  0.00260     -2.52  0.0116
```

## GLMM on proportions with year as a random effect

$$\text{nbchicks}_i \sim \text{Binomial}(\text{nbpairs}_i, p_i)$$

$$\text{logit}(p_i) = \beta_{0i} + \beta_1 \text{ temp}_i + \beta_2 \text{ rainfall}_i$$

$$\beta_{0i} \sim \text{Normal}(\mu_y, \sigma_y^2)$$

## GLMM on proportions with year as a random effect in R

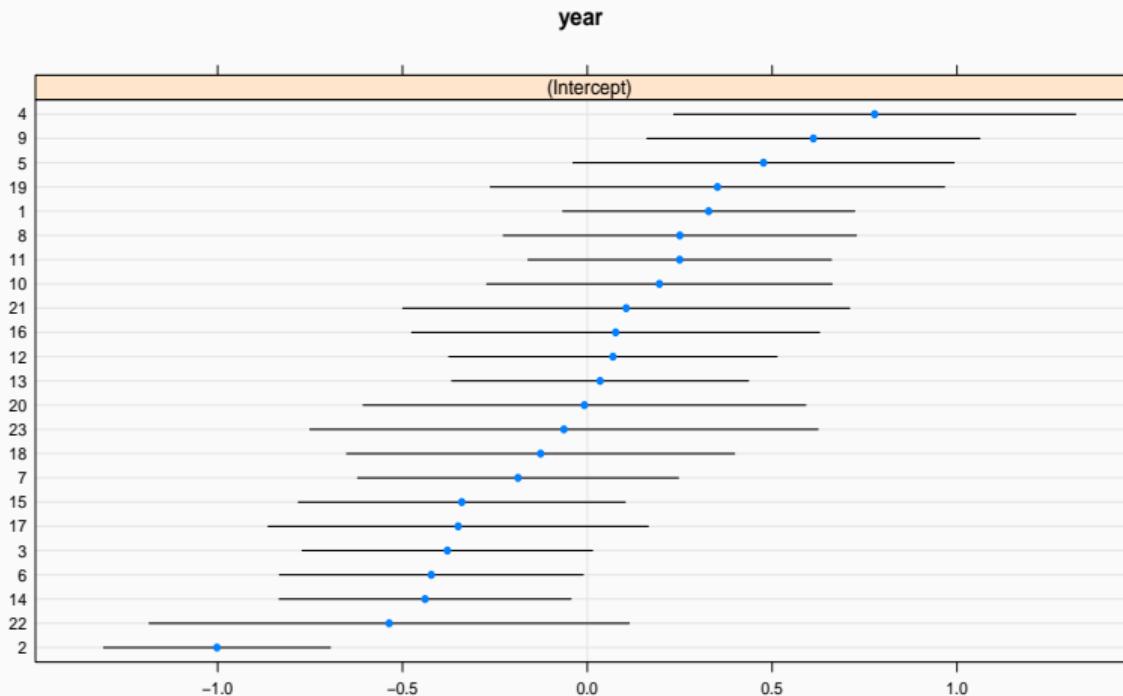
```
m <- glmer(cbind(nbchicks,nbpairs-nbchicks) ~ temp + rainfall  
           + (1 | year), family = binomial)
```

## GLMM on proportions with year as a random effect in R

```
#> Generalized linear mixed model fit by maximum likelihood (Laplace  
#> Approximation) [glmerMod]  
#> Family: binomial ( logit )  
#> Formula: cbind(nbchicks, nbpairs - nbchicks) ~ temp + rainfall + (1 |  
#>     year)  
#>     AIC      BIC      logLik deviance df.resid  
#> 159.7418 164.2838 -75.8709 151.7418      19  
#> Random effects:  
#> Groups Name      Std.Dev.  
#> year   (Intercept) 0.478  
#> Number of obs: 23, groups: year, 23  
#> Fixed Effects:  
#> (Intercept)      temp      rainfall  
#>     2.478277    -0.026616    -0.008226
```

# Yearly random intercepts

```
#> $year
```



# Methods in Ecology and Evolution



*Methods in Ecology and Evolution* 2013, 4, 133–142

doi: 10.1111/j.2041-210x.2012.00261.x

## A general and simple method for obtaining $R^2$ from generalized linear mixed-effects models

Shinichi Nakagawa<sup>1,2\*</sup> and Holger Schielzeth<sup>3</sup>

<sup>1</sup>National Centre for Growth and Development, Department of Zoology, University of Otago, 340 Great King Street, Dunedin 9054, New Zealand; <sup>2</sup>Department of Behavioral Ecology and Evolutionary Genetics, Max Planck Institute for Ornithology,

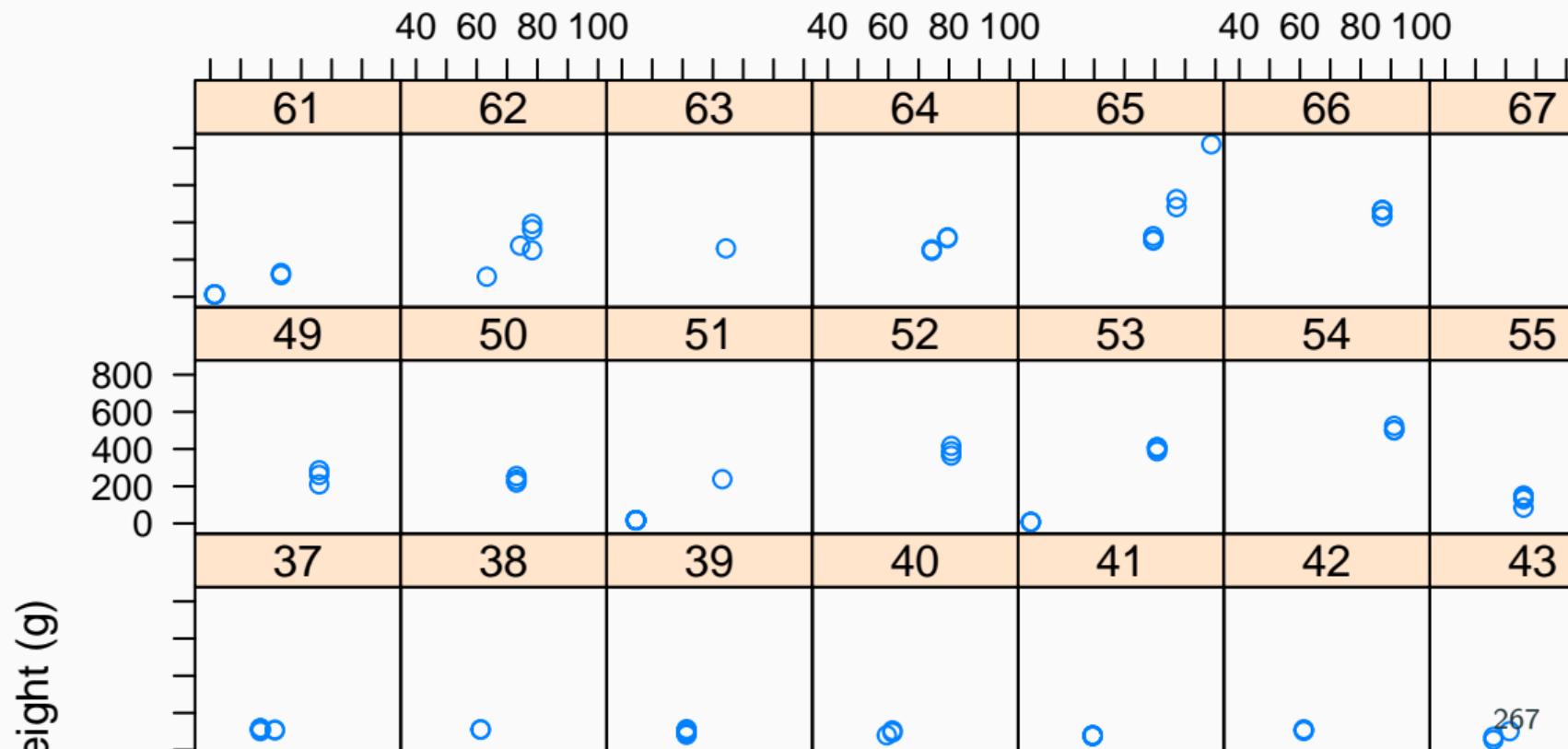
## **Bonus: Generalized Additive Mixed Models!**

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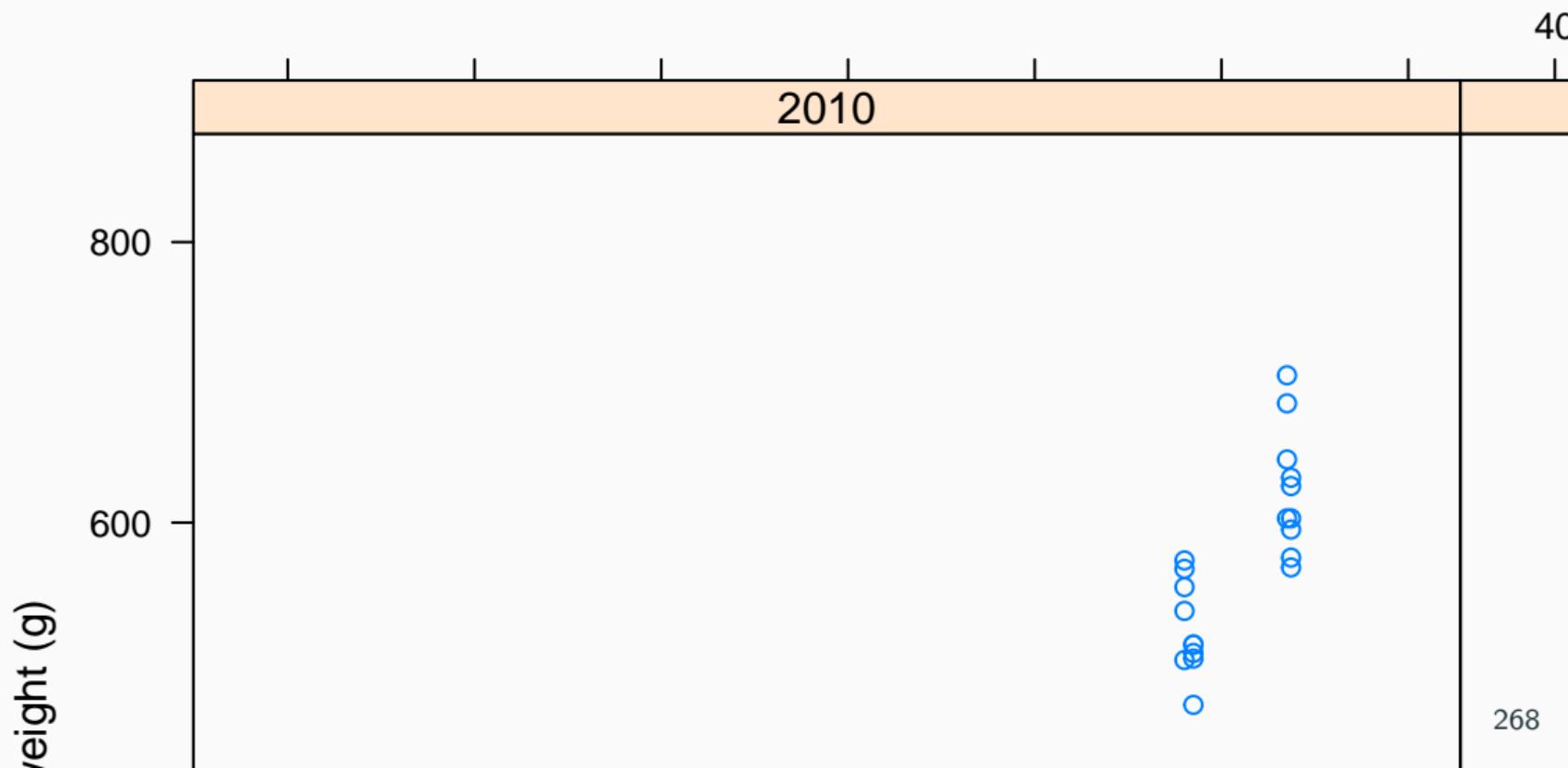
## Wild boar example



# Weight of offspring per female as a function of gestation duration



## Weight of offspring per year as a function of gestation duration



## Is duration of gestation affecting offspring weight?

```
m1 <- lmer(offspring_weight~gestation+as.factor(year)+(1|female_id),data=dat)
m2 <- lmer(offspring_weight~gestation+(1|female_id),data=dat)
m3 <- lmer(offspring_weight~1+(1|female_id),data=dat)
m4 <- lmer(offspring_weight~as.factor(year)+(1|female_id),data=dat)
AIC(m1,m2,m3,m4)

#>      df      AIC
#> m1  5 3891.633
#> m2  4 3908.311
#> m3  3 4597.567
#> m4  4 4590.088
```

One single best model (by far), no need for multimodel inference

## Best model parameter estimates

```
m1
#> Linear mixed model fit by REML ['lmerMod']
#> Formula: offspring_weight ~ gestation + as.factor(year) + (1 | female_id)
#>   Data: dat
#> REML criterion at convergence: 3881.633
#> Random effects:
#> Groups      Name      Std.Dev.
#> female_id (Intercept) 43.35
#> Residual            45.36
#> Number of obs: 361, groups:  female_id, 68
#> Fixed Effects:
#>             (Intercept)      gestation  as.factor(year)2011
#>             -539.41          11.61        -42.70
```

The intercept is negative, which is unusual for a weight...

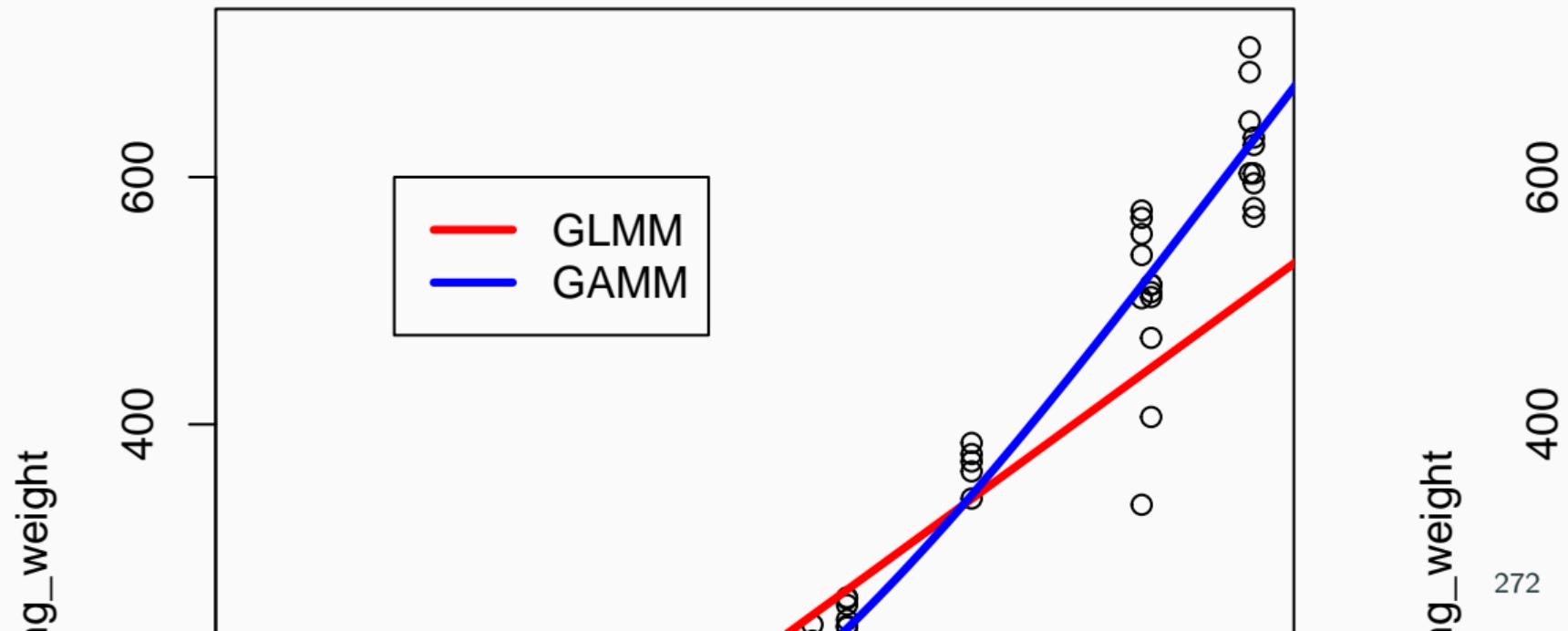
## GAMM to the rescue!

```
library(mgcv)
m1_gamm<-gam(offspring_weight~s(gestation,by=year)+  

                s(female_id,bs='re',by=dum),data=dat)
AIC(m1,m1_gamm)
#>              df      AIC
#> m1      5.00000 3891.633
#> m1_gamm 70.68489 3382.765
```

# Plotting

2010



## Summary

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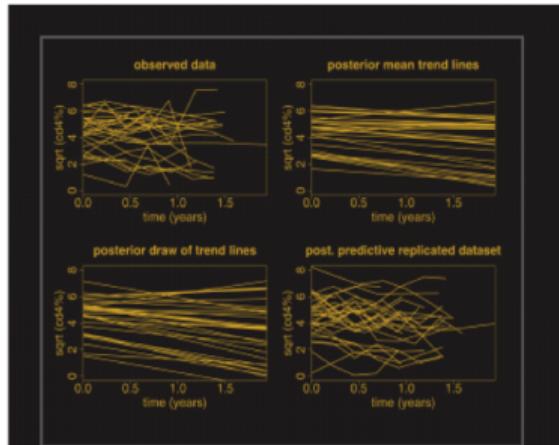
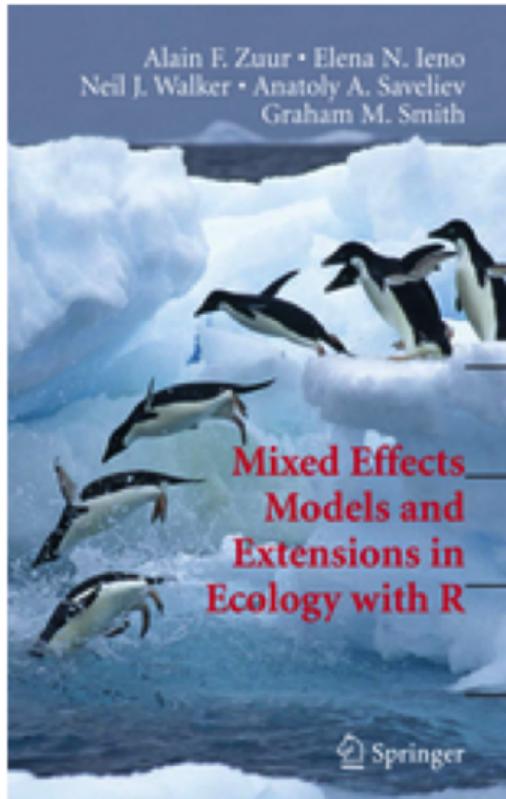
## Mixed models in a nutshell

- We can **generalize to a wider population** - e.g. can say something about the allometry relationship that we might expect in the population of species from which our sample was selected (plant example)
- **Fewer parameters** are needed than separate linear regressions per species - we only needed few additional parameters – e.g. the variance to allow the intercepts to vary from species to species. By contrast, the standard species by species approach would require 33 additional parameters (plant example)

## Mixed models in a nutshell

- Information can be **shared between groups** - By assuming that the random effects come from a common distribution, a multilevel model can share information between groups. This can improve the precision of predictions for species / individual that have little data
- Possible extension to the **inclusion of predictors at the group level** - e.g. if our data included say functional traits for species (herbaceous), we could include a term in the species level model to describe the difference in number of seeds according to functional characteristics (plant example)

# Textbooks



## Data Analysis Using Regression and Multilevel/Hierarchical Models

ANDREW GELMAN  
JENNIFER HILL

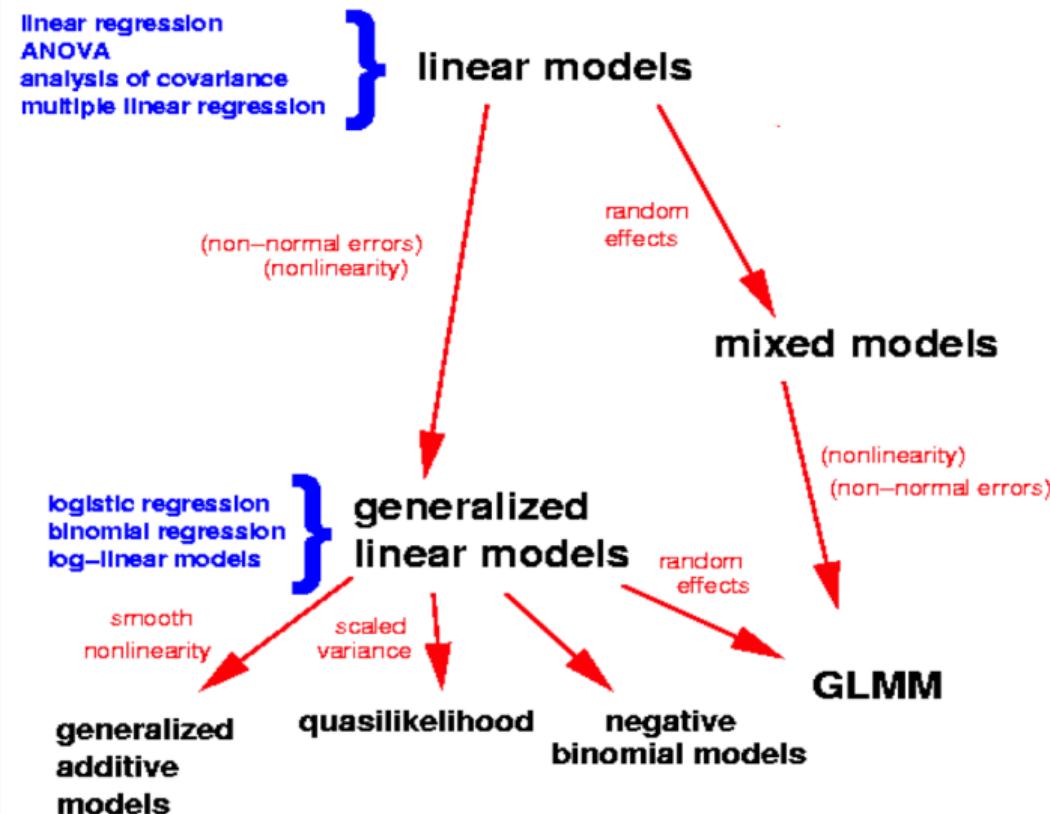
## This Class

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## What we studied

- Distributions and likelihoods
- Hypothesis testing and multimodel inference
- Introduction to Bayesian inference
- Generalized Linear Models (GLMs)
- Generalized Additive Models (GAMs)
- Mixed Effect Models

# This class in a nutshell (from Zuur et al. book)



## Practical #3

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