

# Statistics for Ecologists

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**Who's that guy?!**

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- 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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- 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

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- 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

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- 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

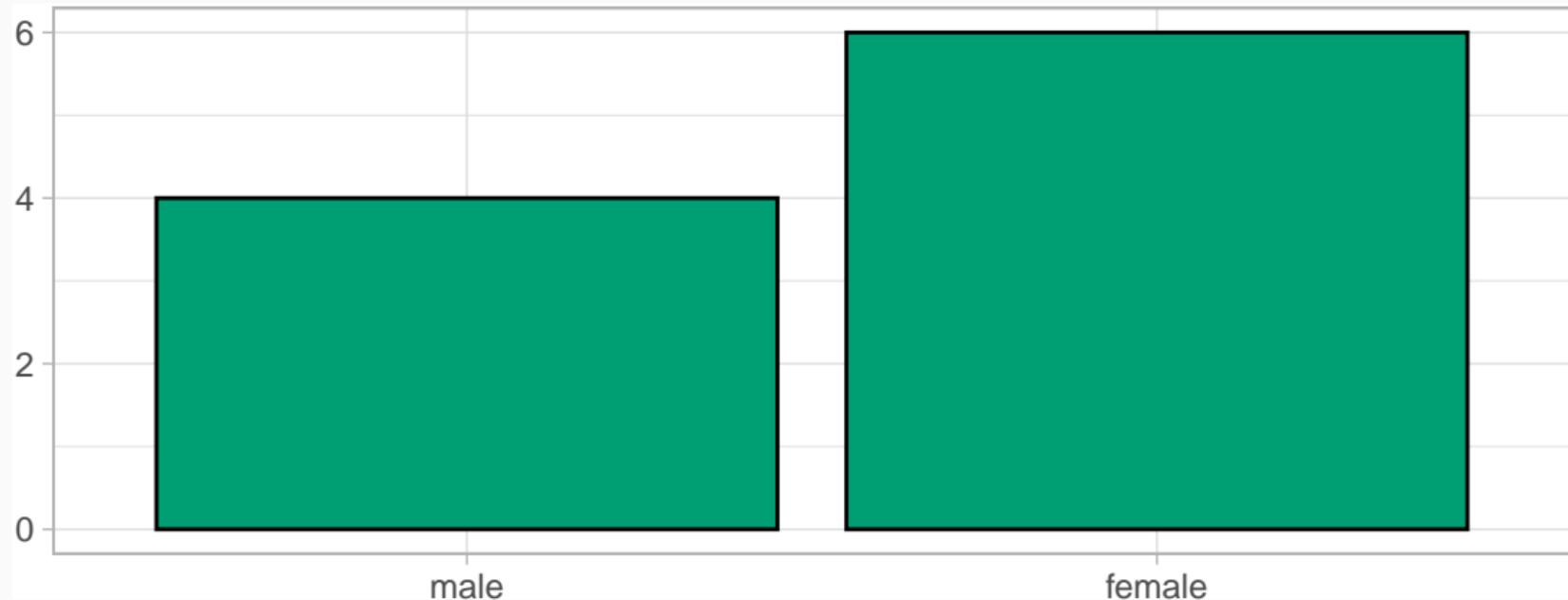
**Context:** A single trial with two outcomes, success/failure

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

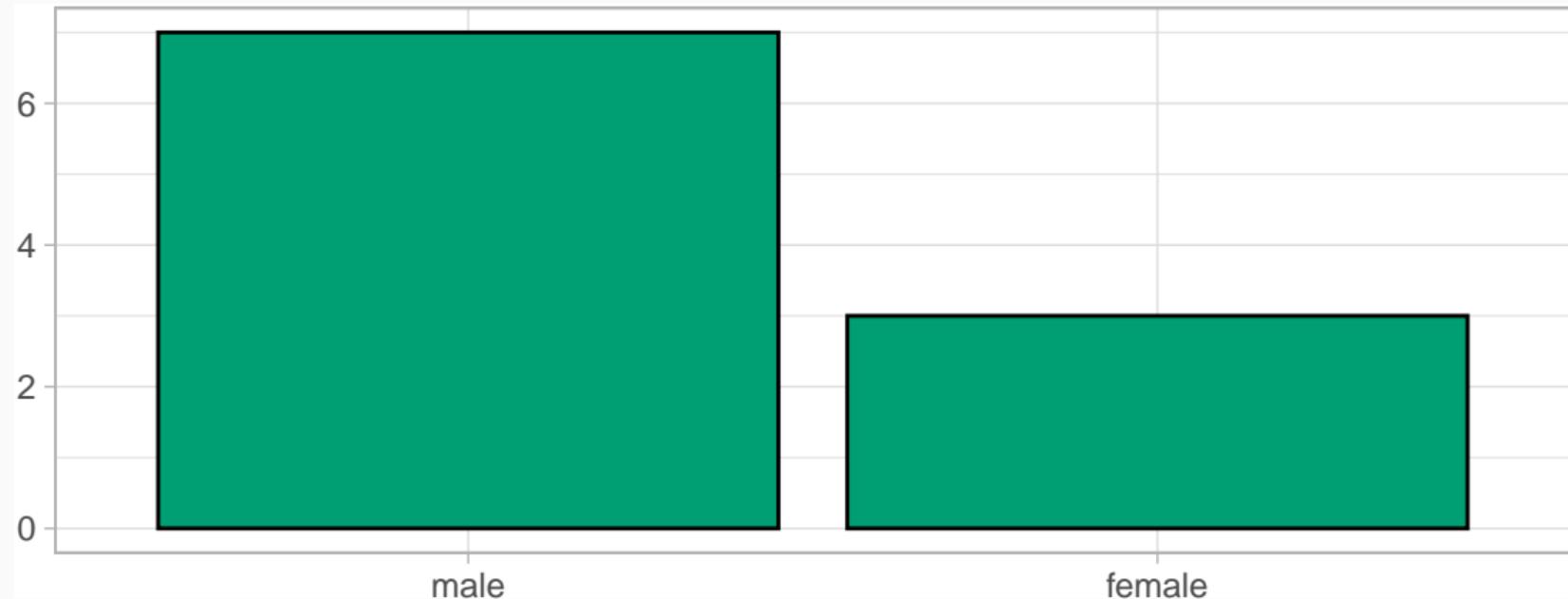
$$\begin{array}{c} \hline x & P(X = x) \\ \hline 1 & p \\ 0 & 1 - p \\ \hline \end{array}$$

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

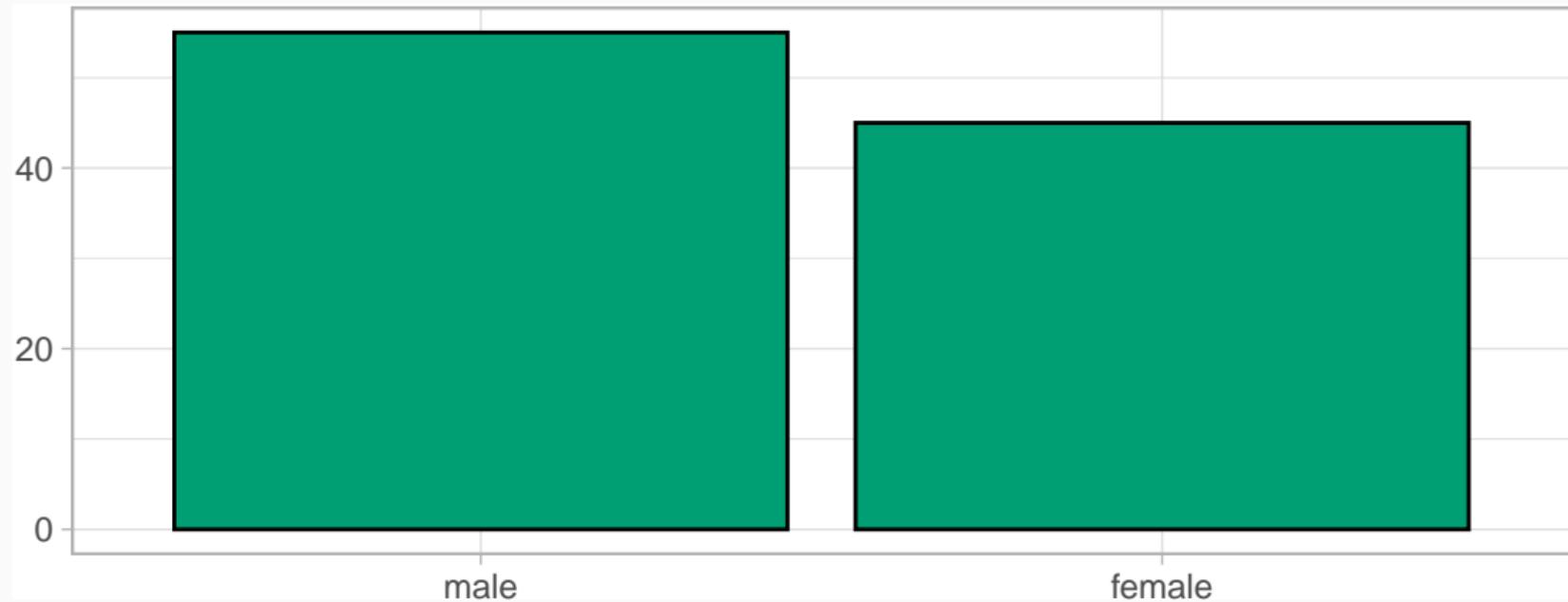
## Ten Bernoulli trials with $p = 0.5$



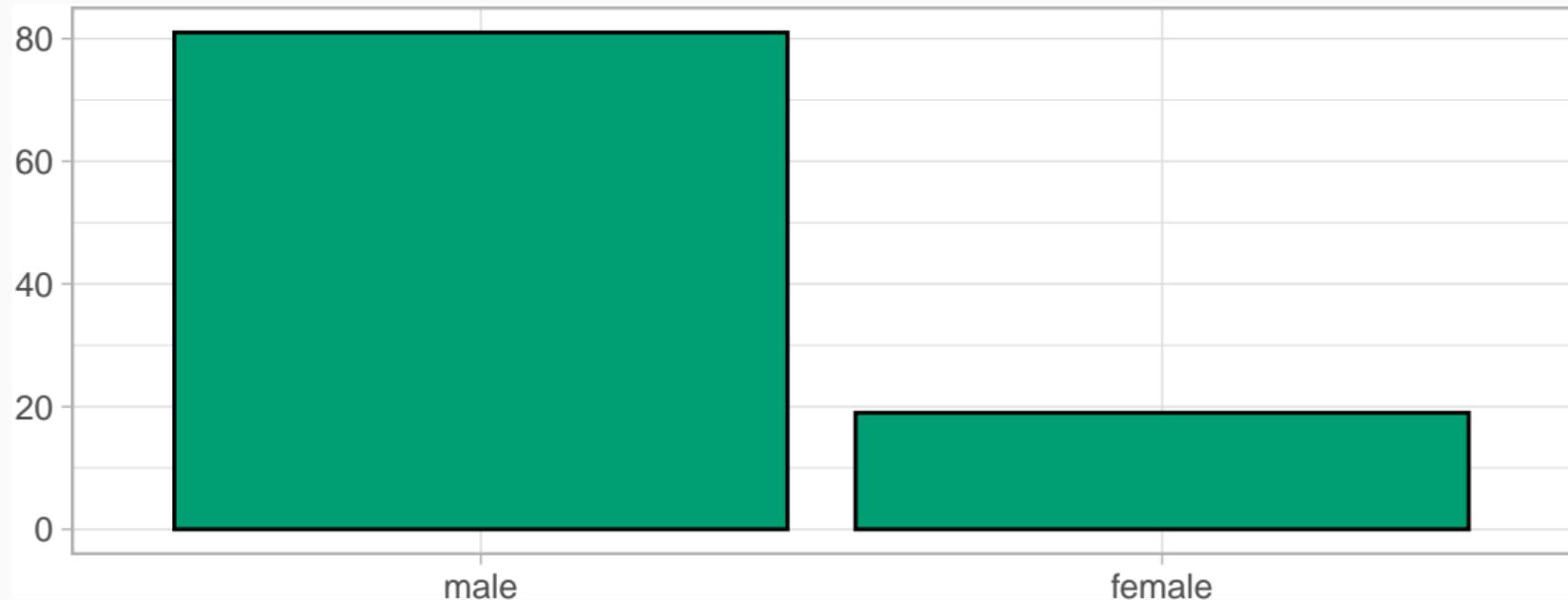
## Ten Bernoulli trials with $p = 0.5$ , again



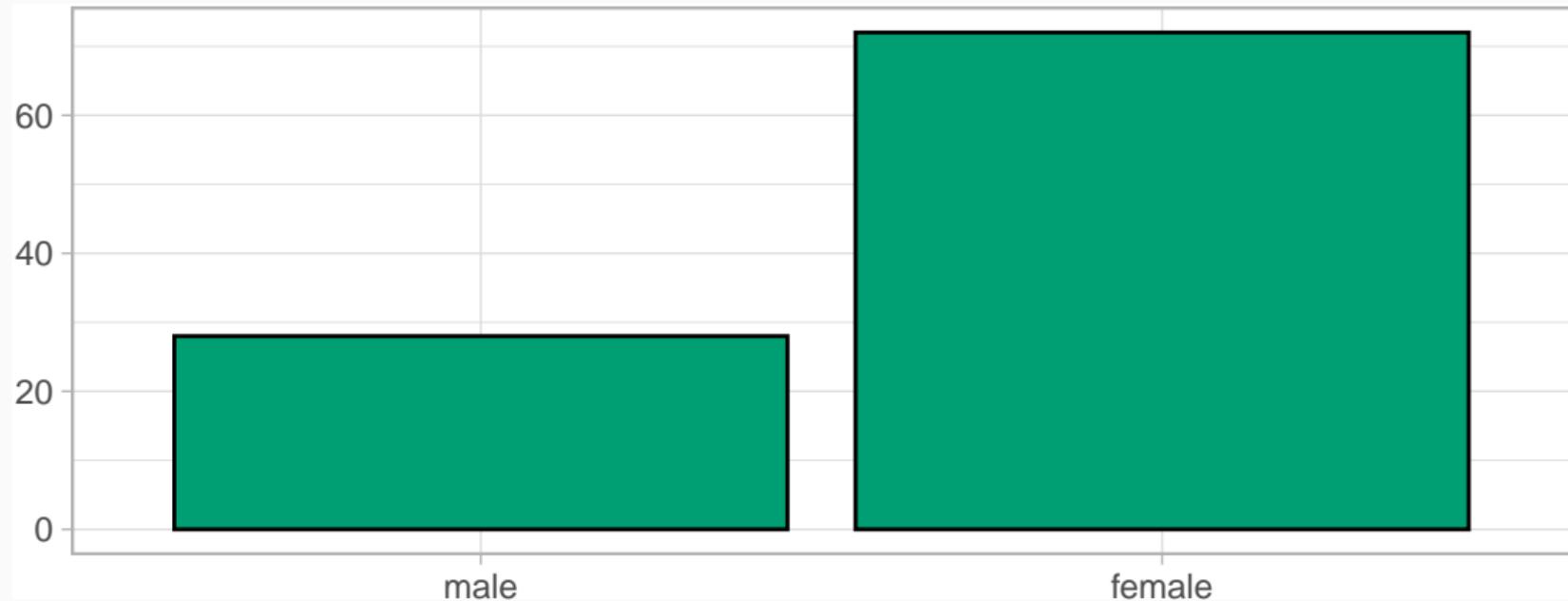
## Hundred Bernoulli trials with $p = 0.5$



## Hundred Bernoulli trials with $p = 0.2$



## Hundred Bernoulli trials with $p = 0.8$



## Summary: Bernoulli distribution

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- **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   | $p^N$           |

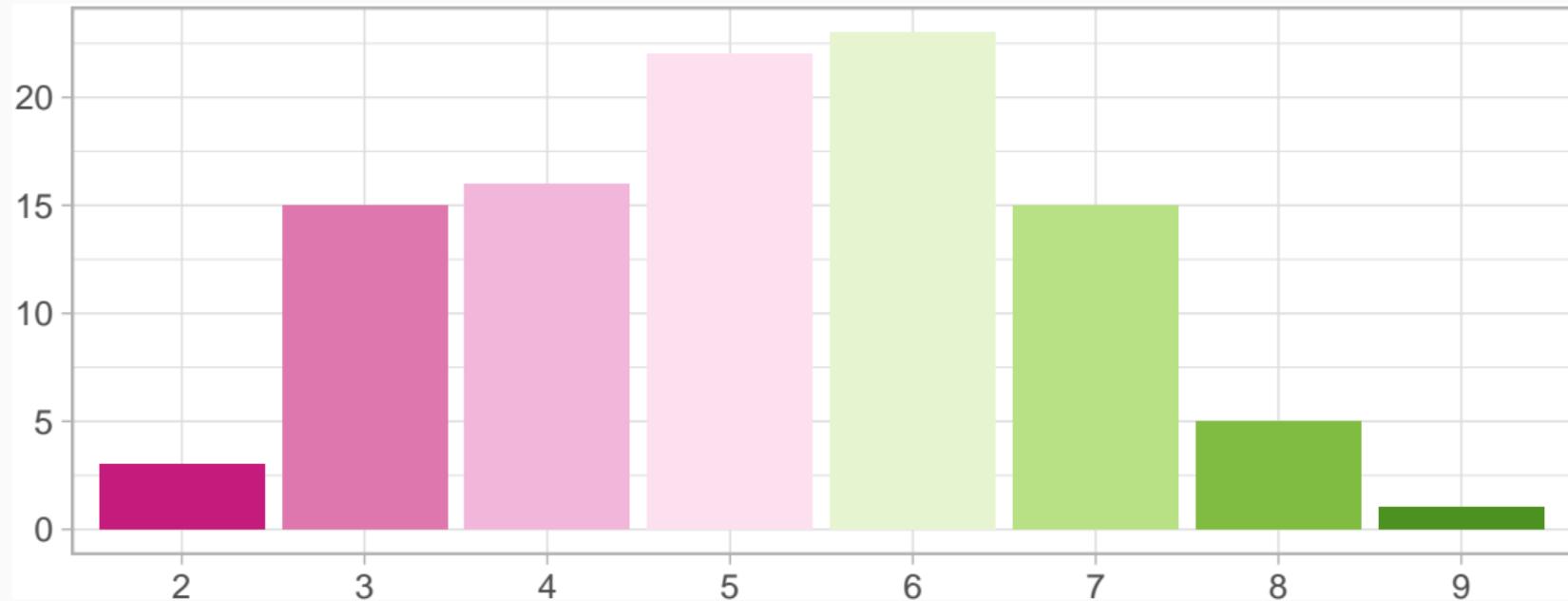
## Binomial distribution

$$\begin{array}{c} \hline x & P(X = x) \\ \hline 0 & (1 - p)^N \\ 1 & Np(1 - p)^{N-1} \\ \dots & \dots \\ N & p^N \\ \hline \end{array}$$

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
```

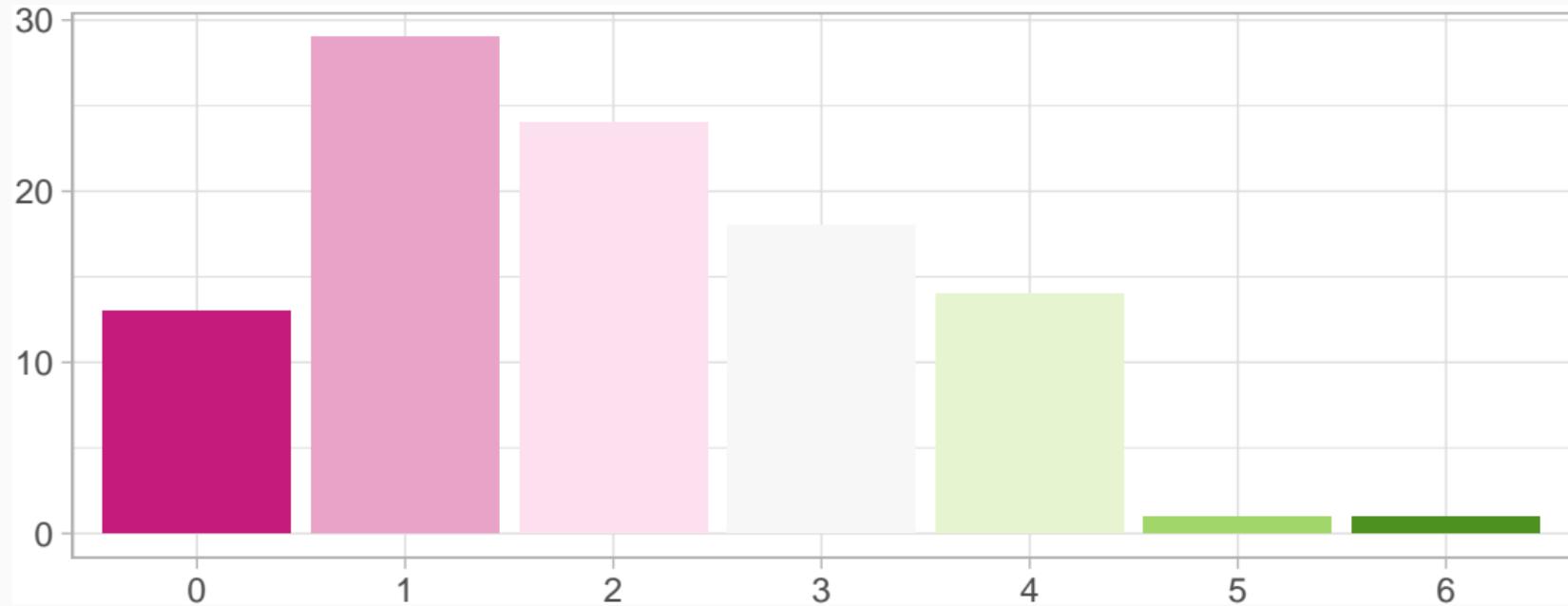
## Hundred Binomial trials with $N = 10$ and $p = 0.5$



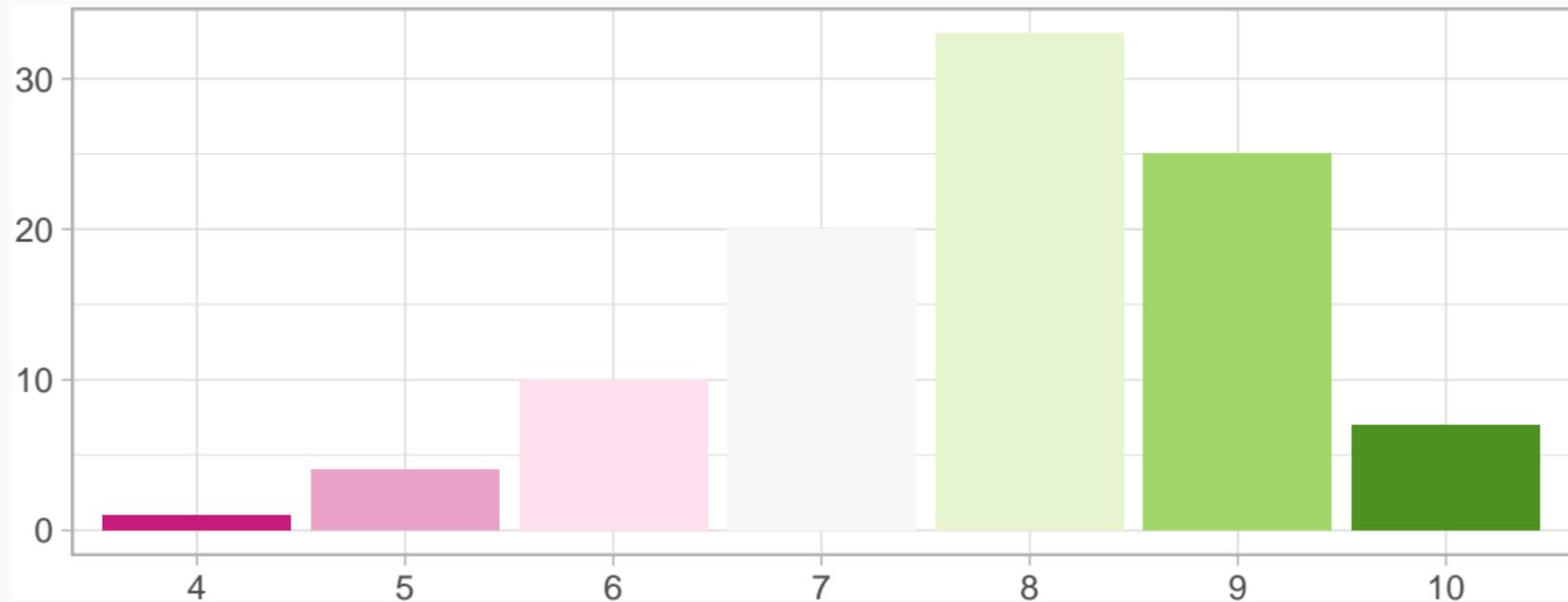
## Hundred Binomial trials with $N = 10$ and $p = 0.5$ , again



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



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



## Playing around with probabilities

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## Playing around with probabilities

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- How to compute this in R?

## Playing around with probabilities

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- 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   | $\lambda e^{-\lambda}$ |
| ... | ...                    |

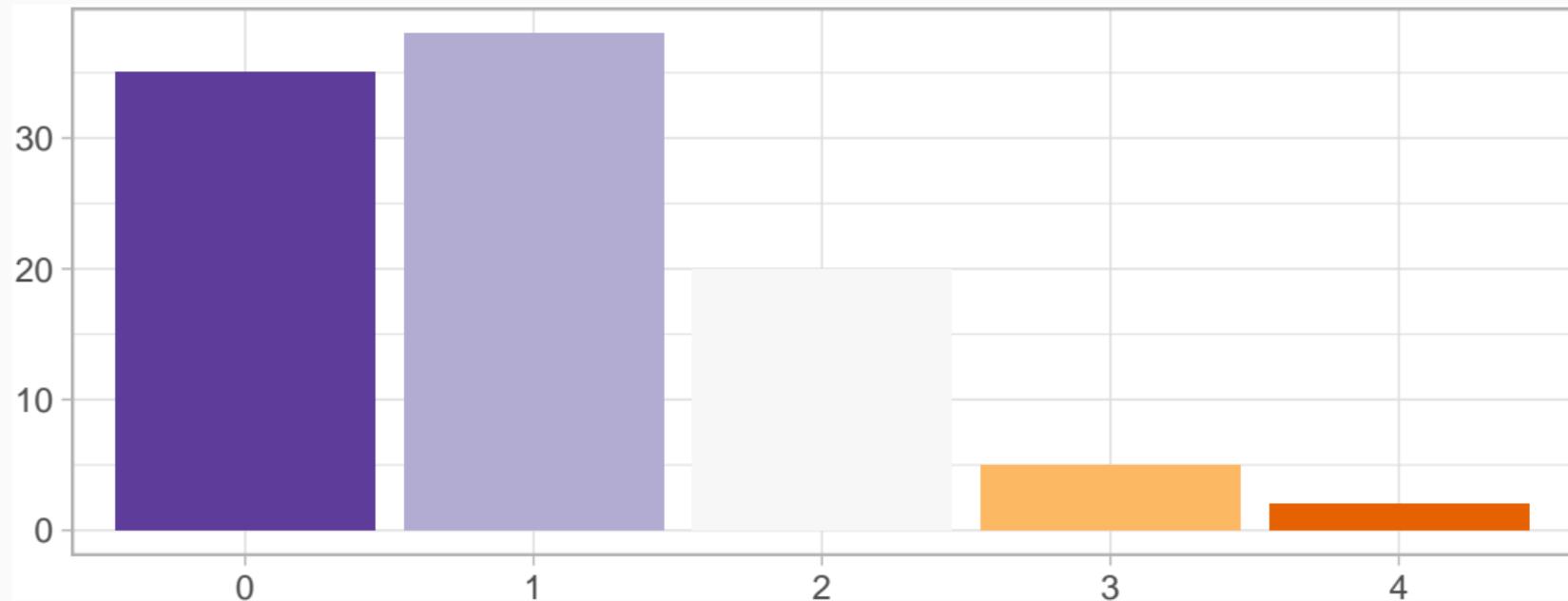
## Poisson distribution

$$\begin{array}{ll} \hline x & P(X = x) \\ \hline 0 & e^{-\lambda} \\ 1 & \lambda e^{-\lambda} \\ \dots & \dots \\ \hline \end{array}$$

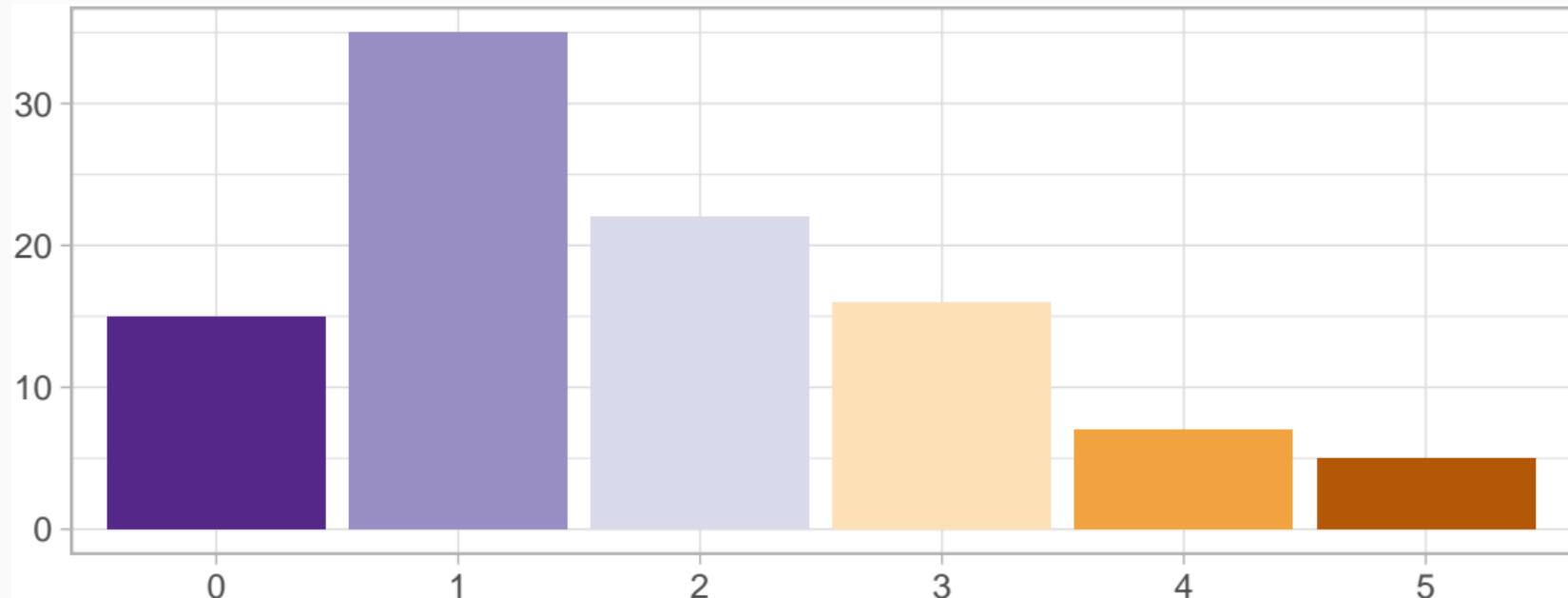
Fortunately, R has this pre-programmed

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

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

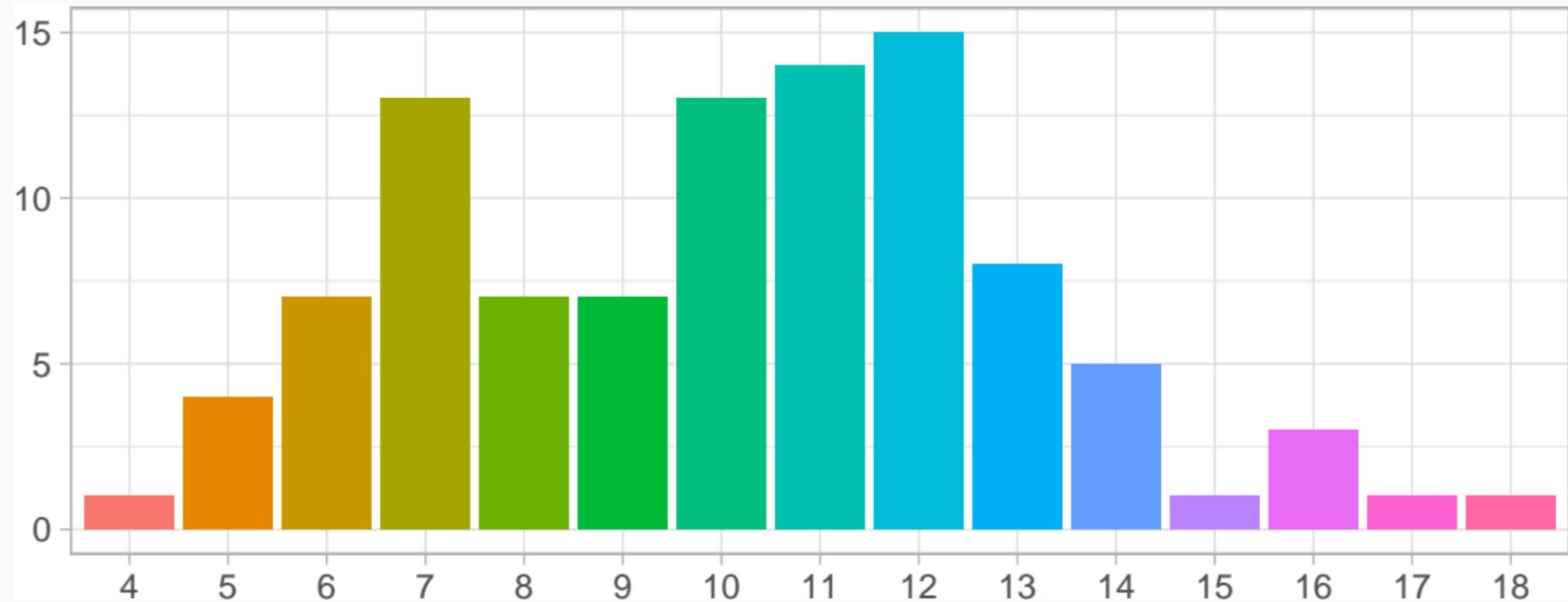


## Hundred Poisson trials with $\lambda = 2$

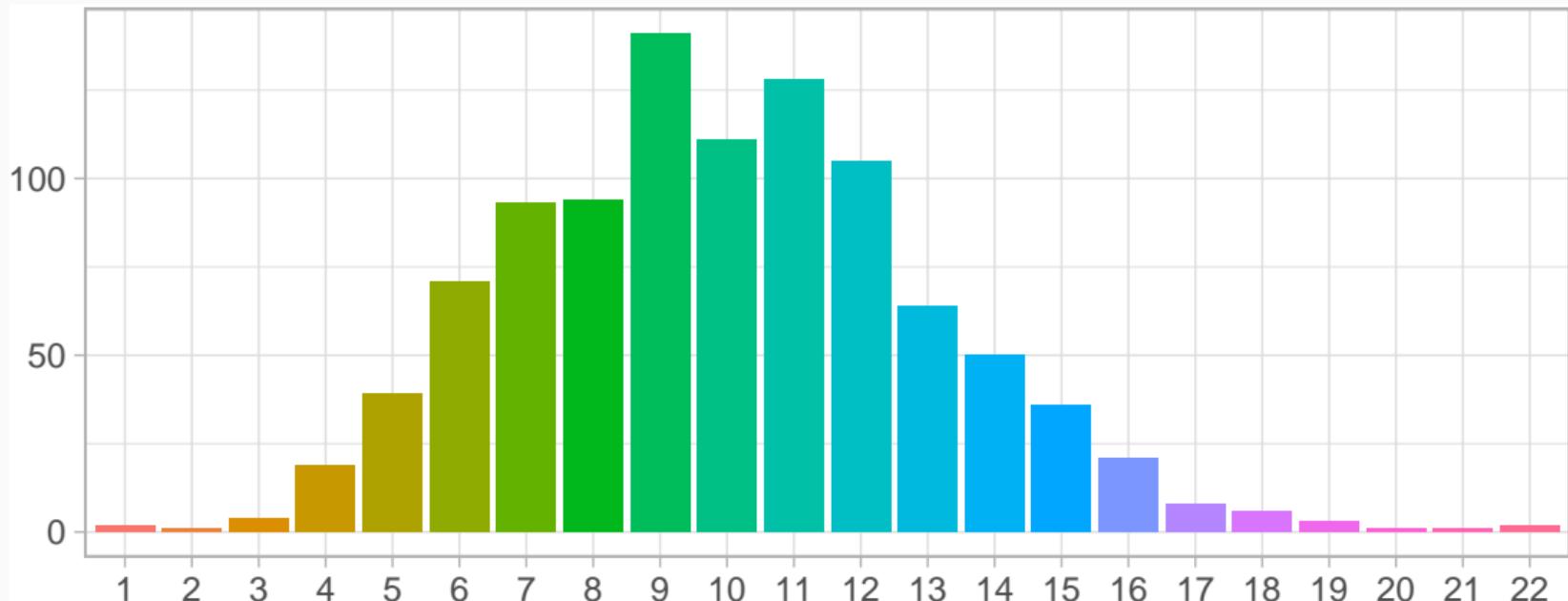


## Hundred Poisson trials with $\lambda = 10$

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



## Summary: Poisson distribution

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- **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

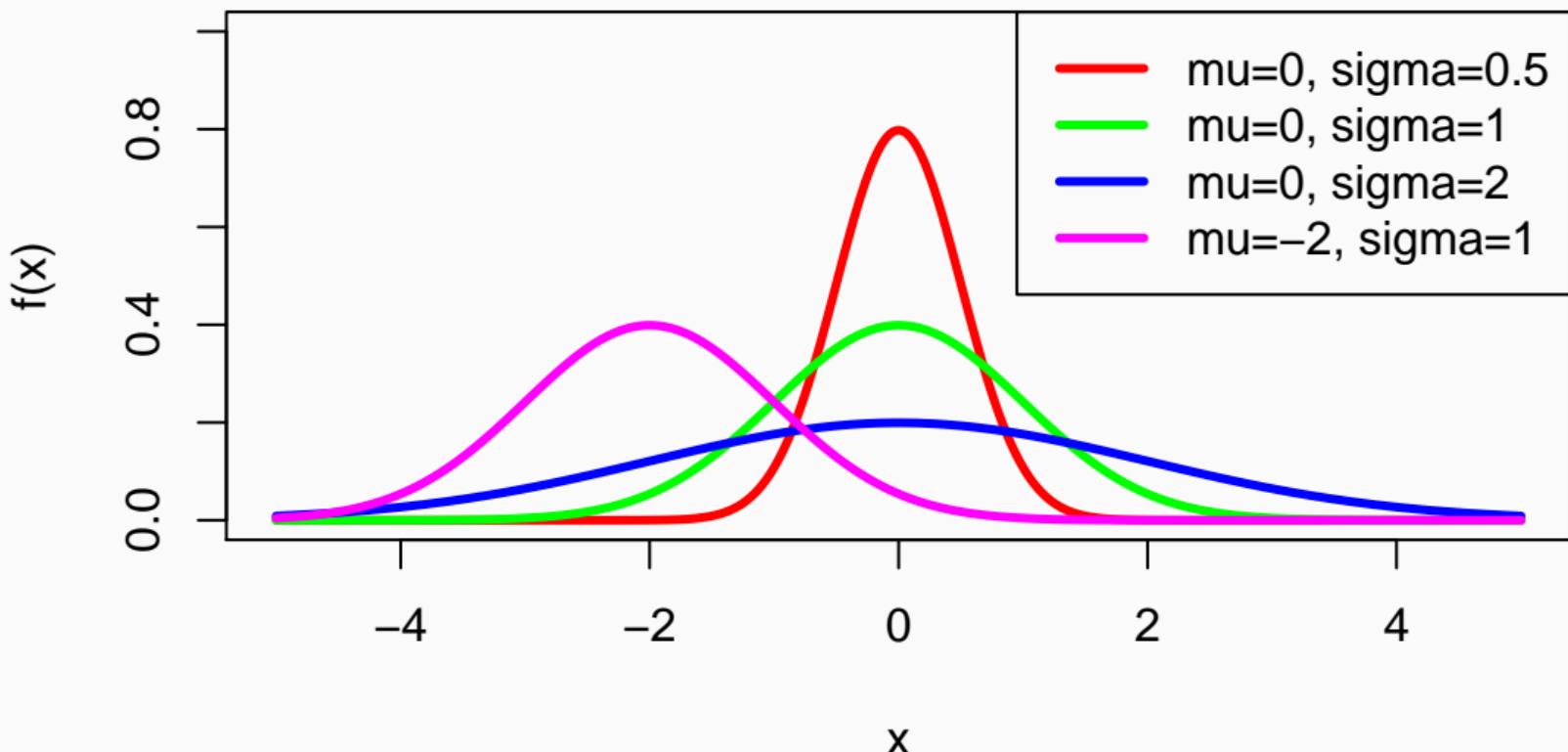
**Context:** Distribution of “adding lots of things together”. Derived from *Central Limit Theorem*, which says that if you add a large number of independent samples from the same distribution the distribution of the sum will be approximately normal.

$X \sim \text{Normal}(\mu, \sigma^2)$  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

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- 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)

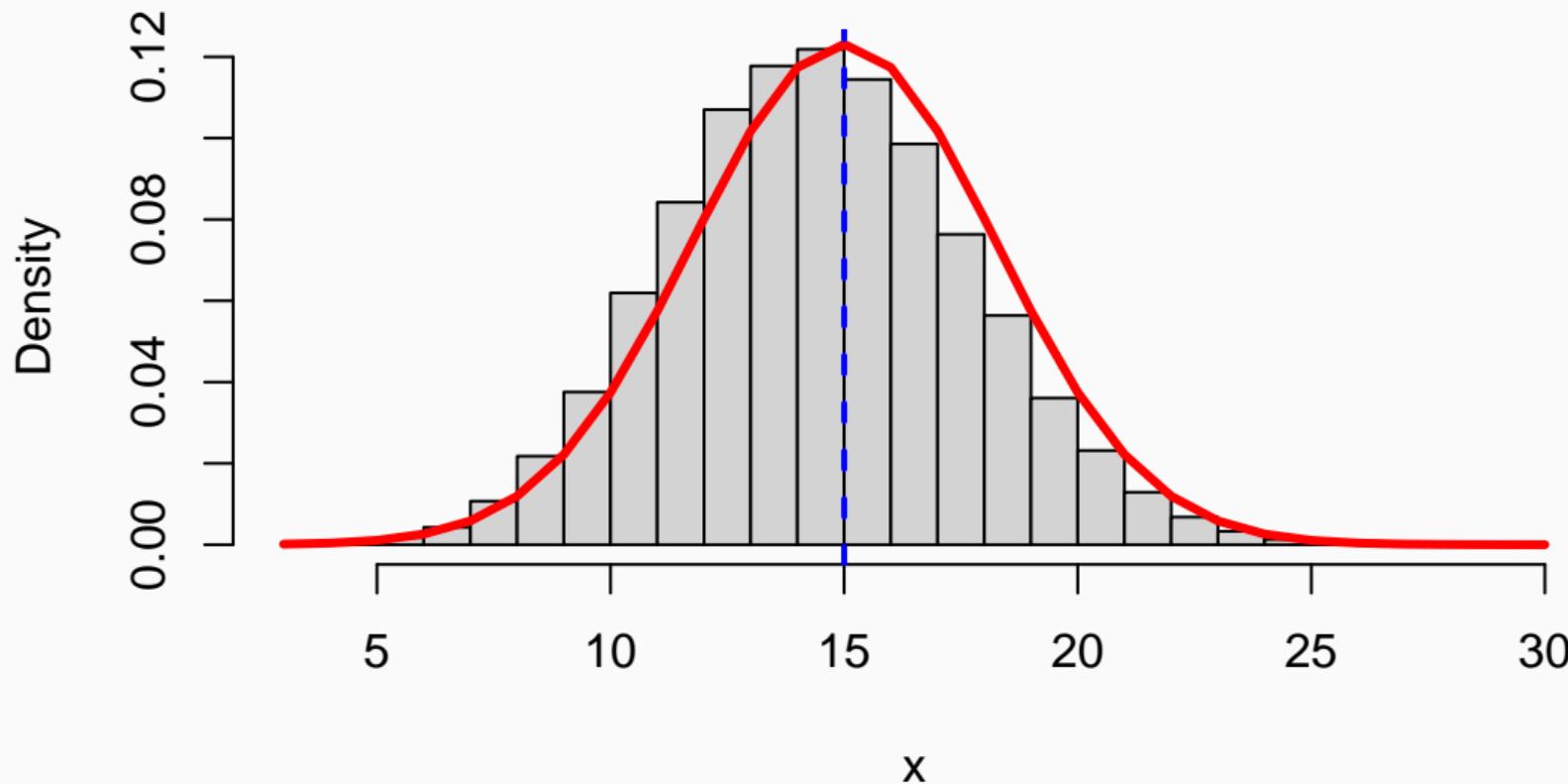
$X \sim \text{Bin}(N = 50, p = 0.3)$

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

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- 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:

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?Distributions

## Likelihoods

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## Fitting distributions to data

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- 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

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- 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  $\theta_1, \theta_2, \dots, \theta_p$

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

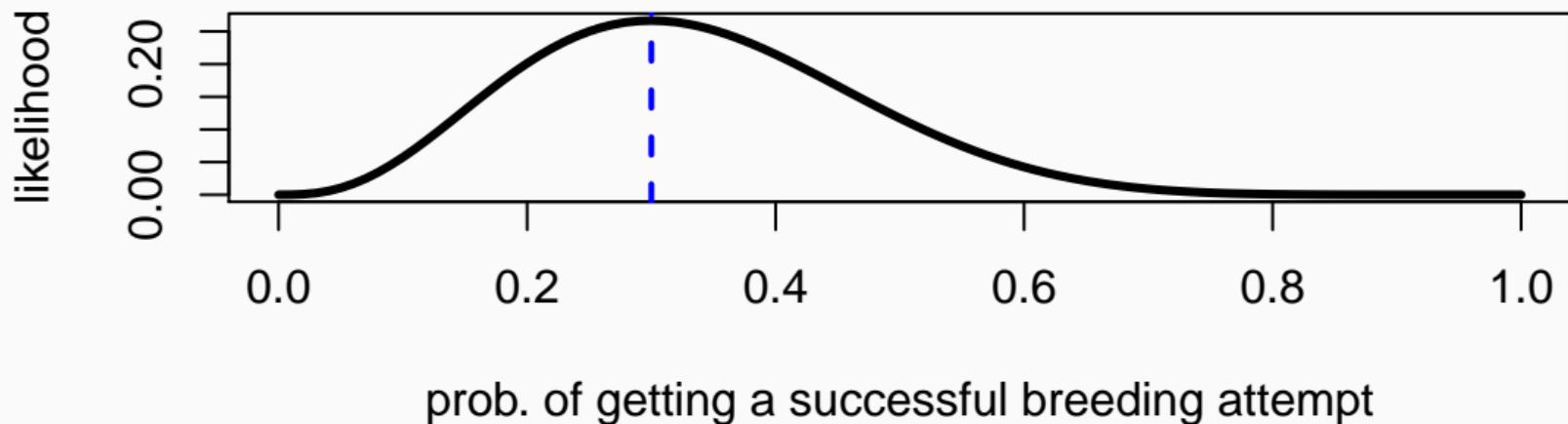
- This is a very important concept

## 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 out of 10 attempts)



The *maximum* of the likelihood is at value 0.3

# The Maximum Likelihood

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- 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

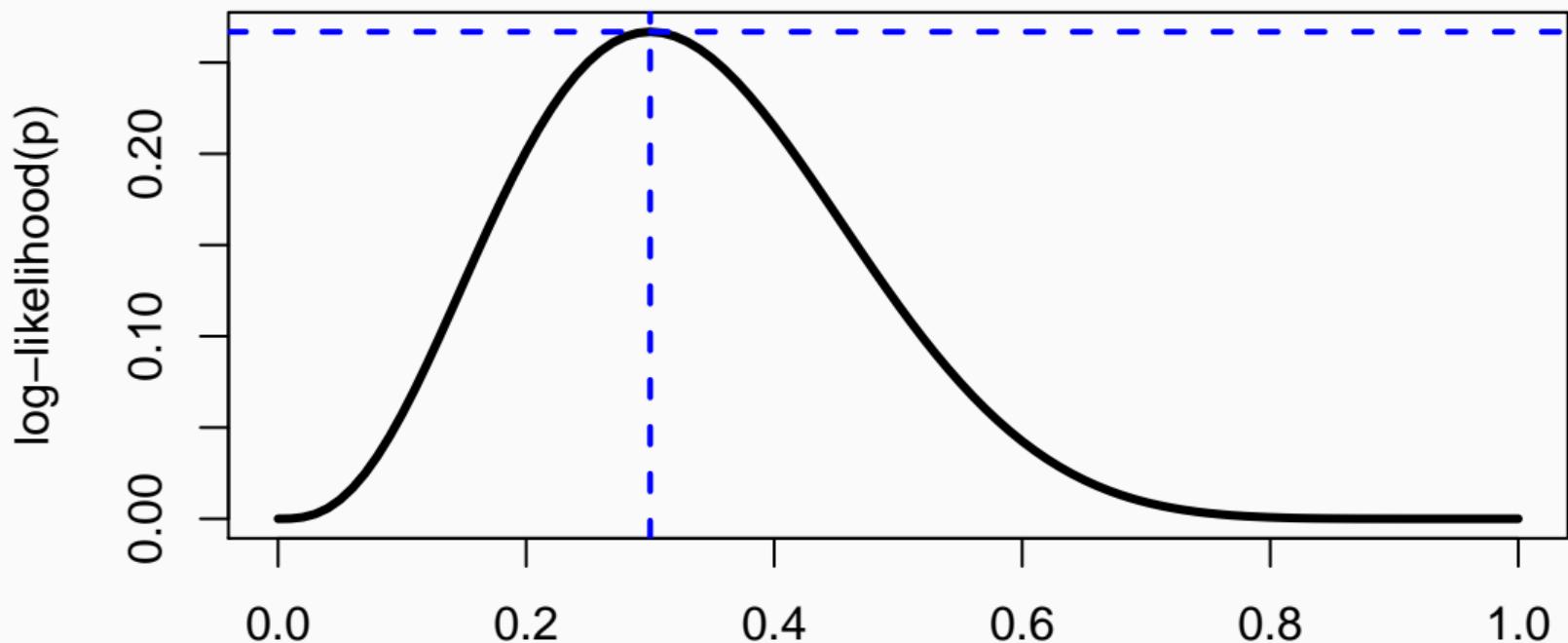
## Using a computer: MLE of $p$ from $Y \sim \text{Bin}(N = 10, p)$ with $k = 3$ successes

```
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 out of 10 attempts



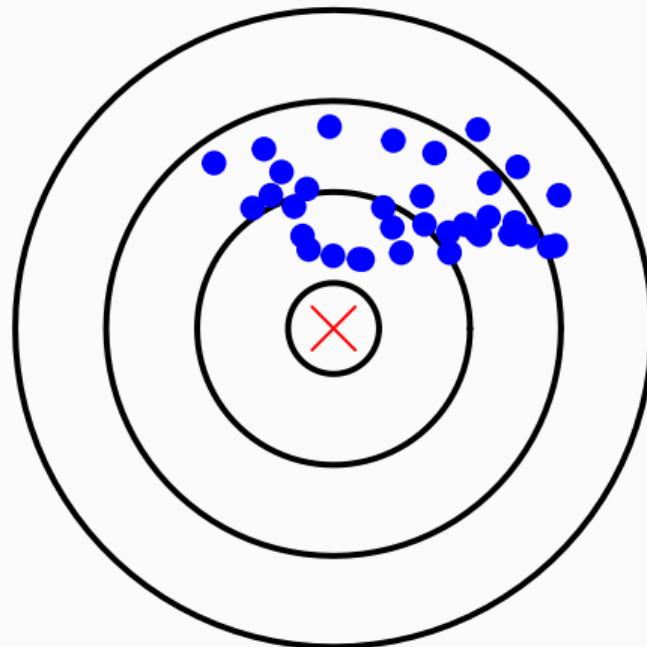
## The Maximum Likelihood Estimate (MLE)

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

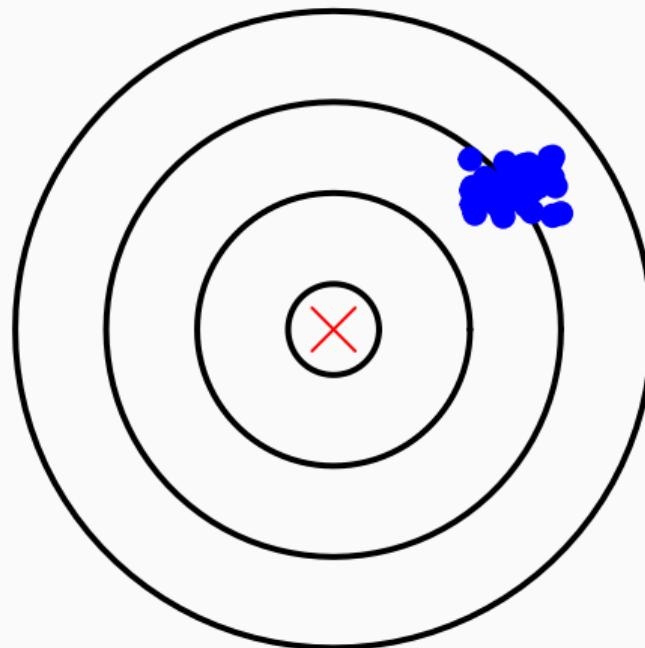
A dart target, with the red cross representing the true parameter value

## Imprecise and biased



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

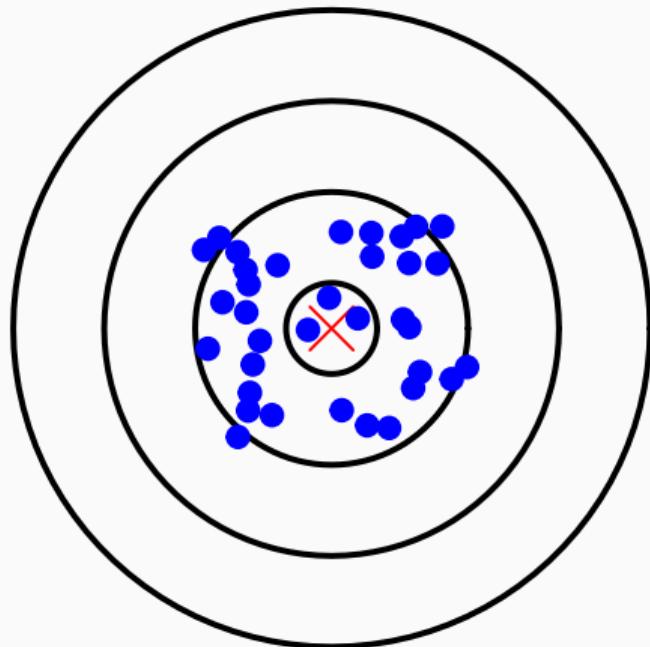
## Precise but biased



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

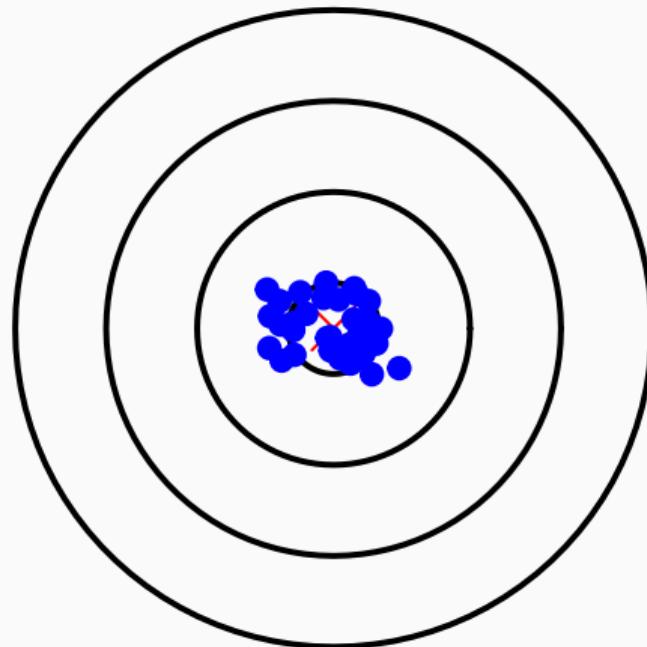
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## Unbiased but imprecise



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

**Unbiased and precise!**

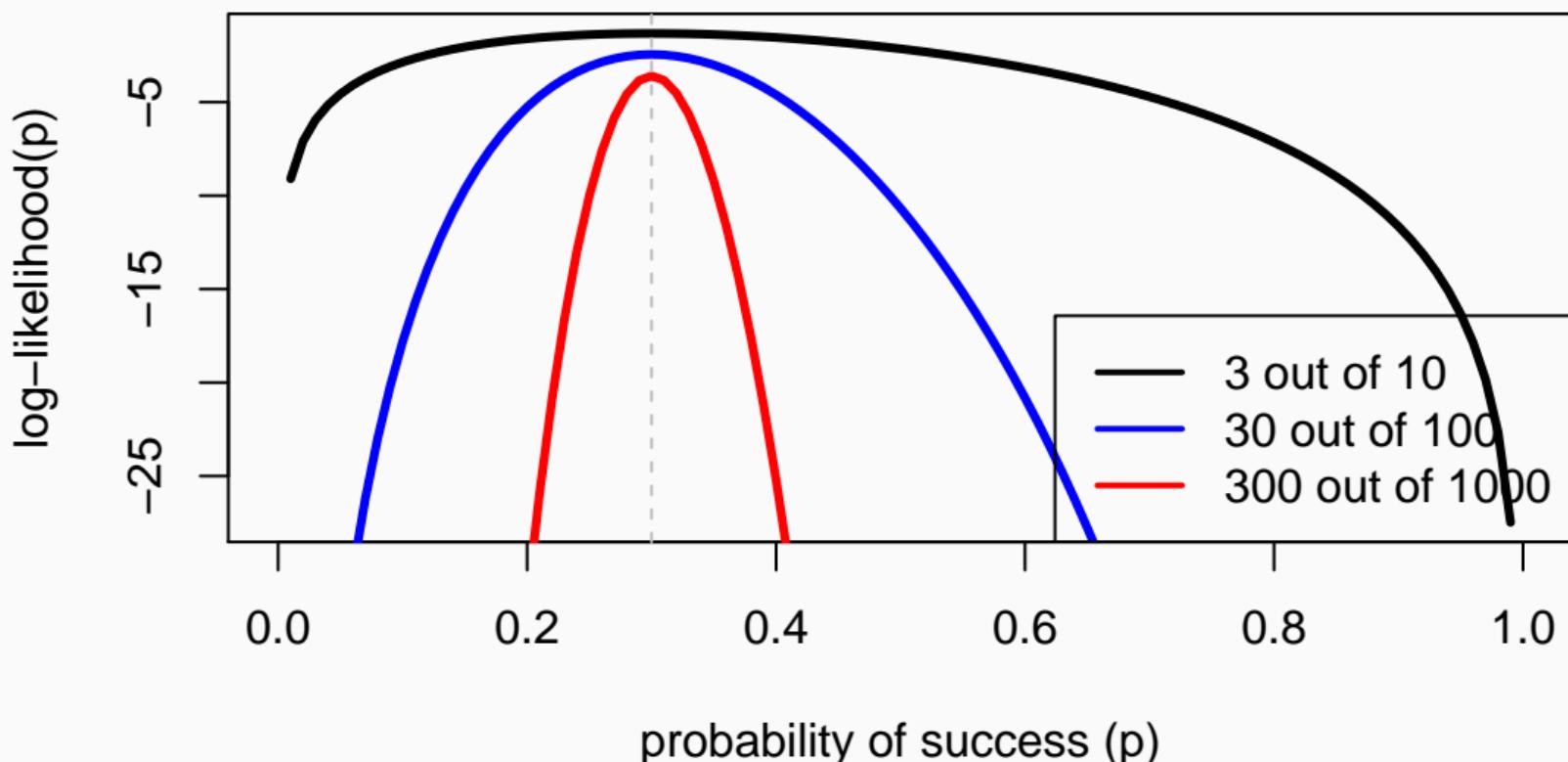


## The Maximum Likelihood Estimate (MLE)

---

- 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

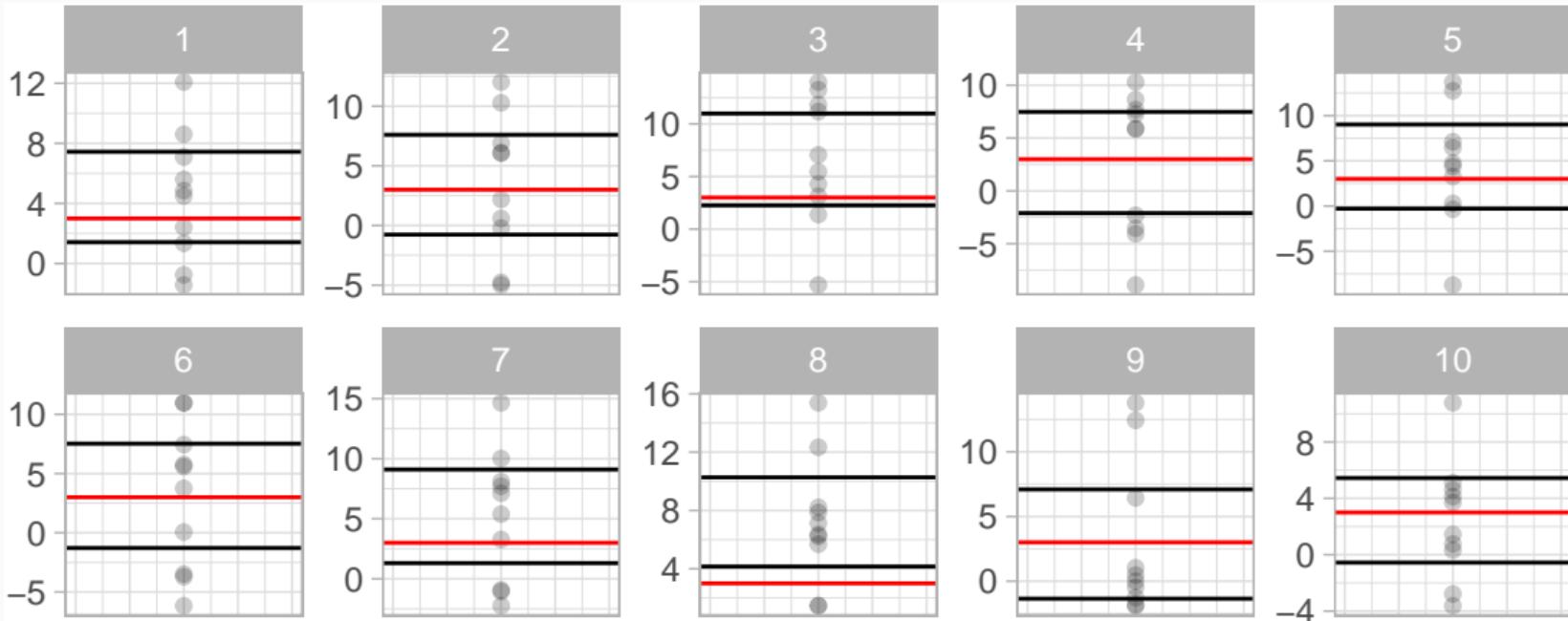
confint(m)
##                   2.5 %  97.5 %
## (Intercept) -0.5749909 5.245549
```

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

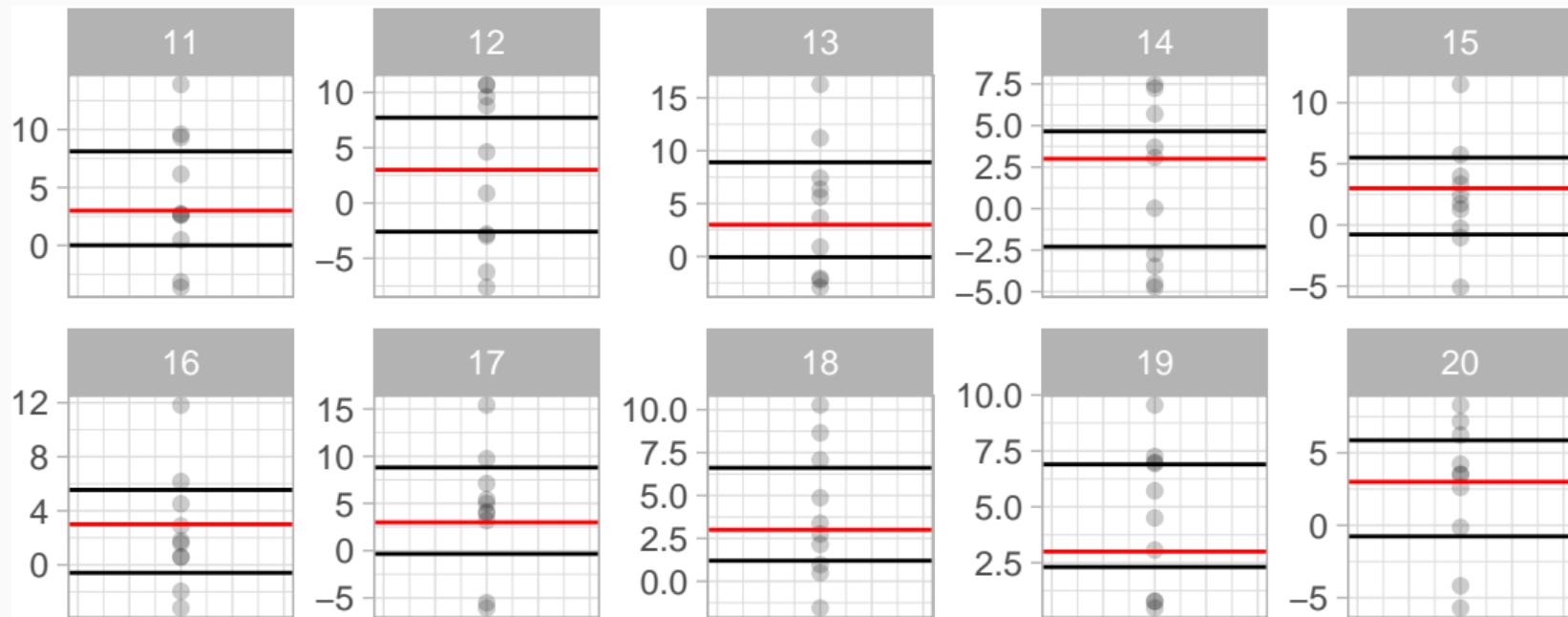
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- Imagine you went outside 20 times and each time you measured the cup of water 10 times. Then you fitted a linear regression model with an intercept only each time and plotted the confidence intervals.
- 19 times out 20 (95%) the 95% confidence intervals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

Does that look approximately correct?



## Does that look approximately correct?



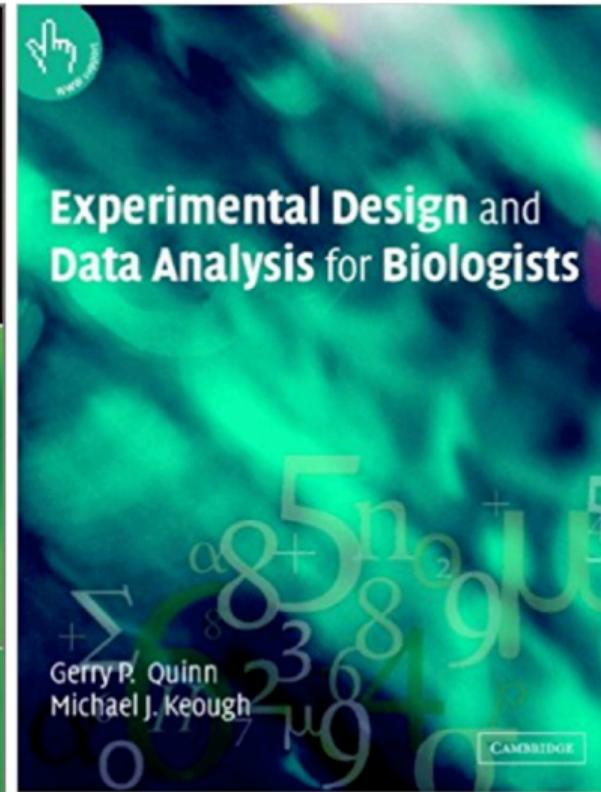
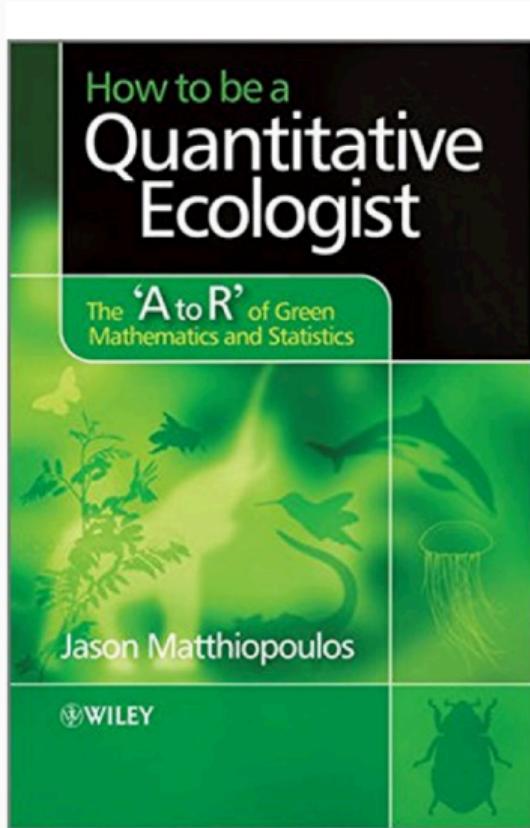
Confidence intervals are just **one realization** of a theoretically repeated experiment.

## Likelihood key facts

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- 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

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- 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

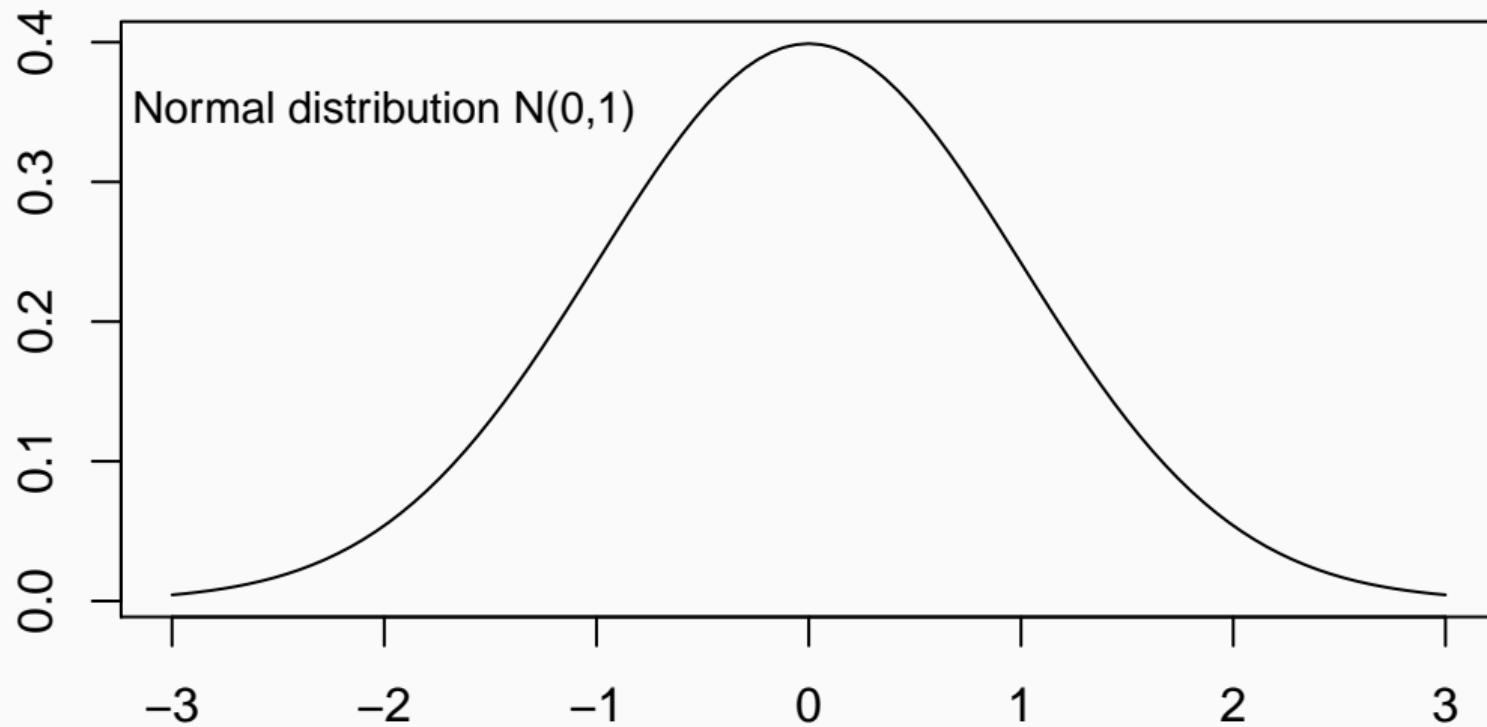
## Hypothesis testing: Rationale

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  $H_0$



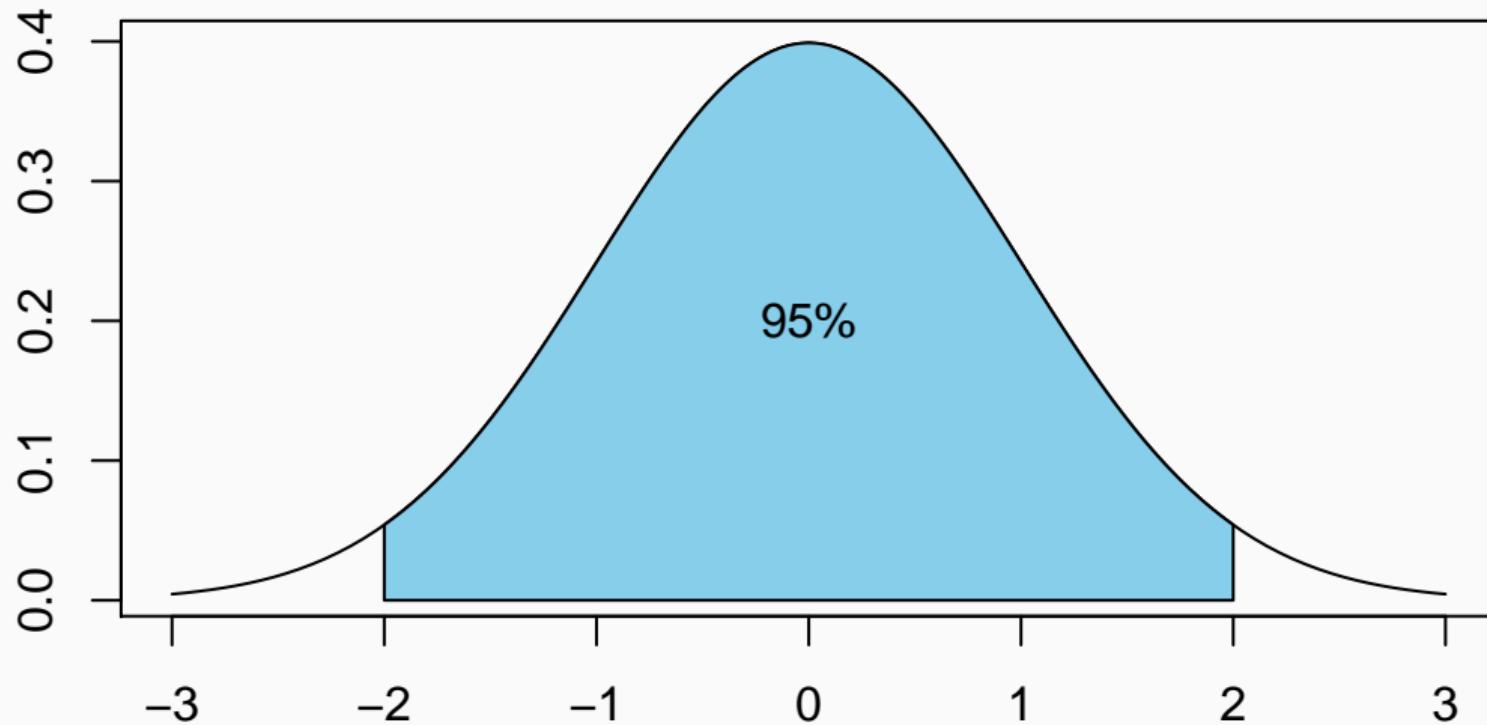
## Hypothesis testing: Rationale

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.

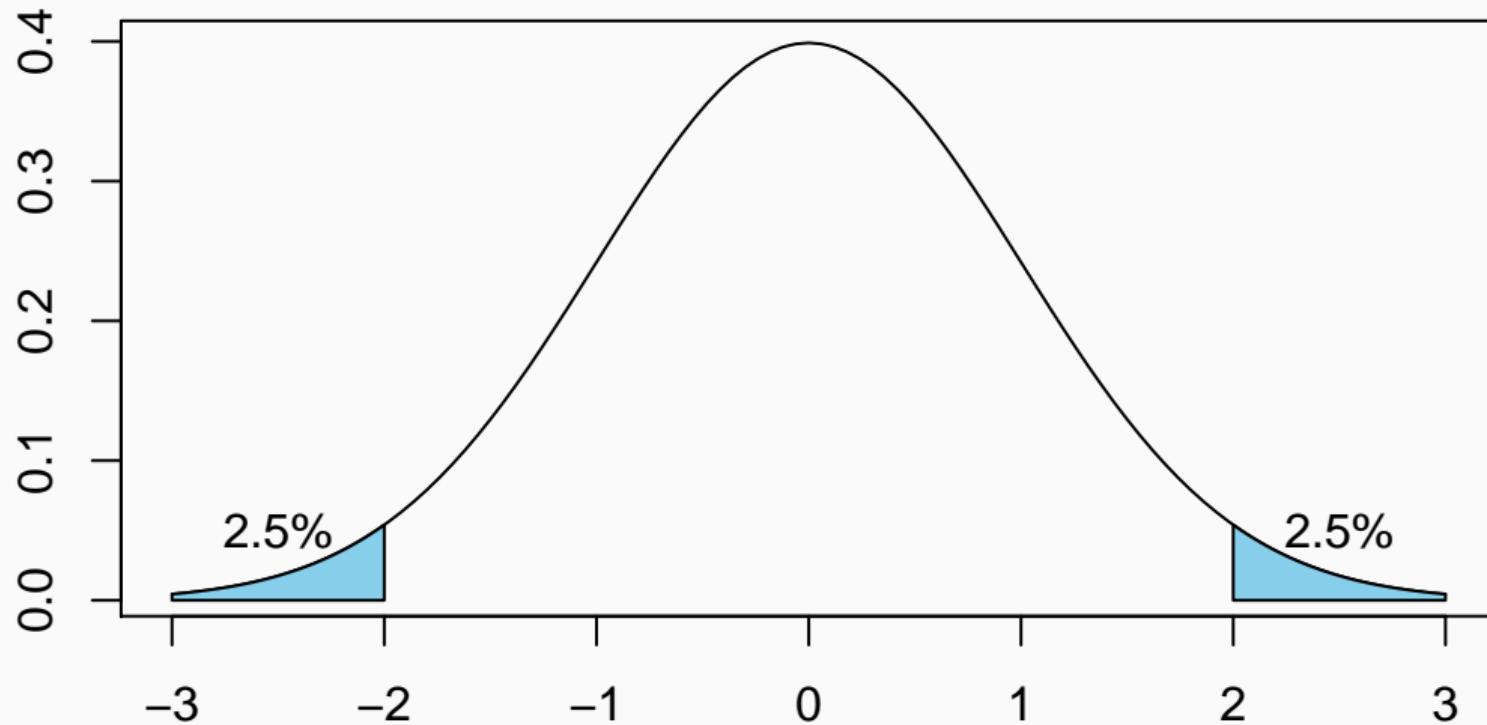
## Hypothesis testing: Rationale

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



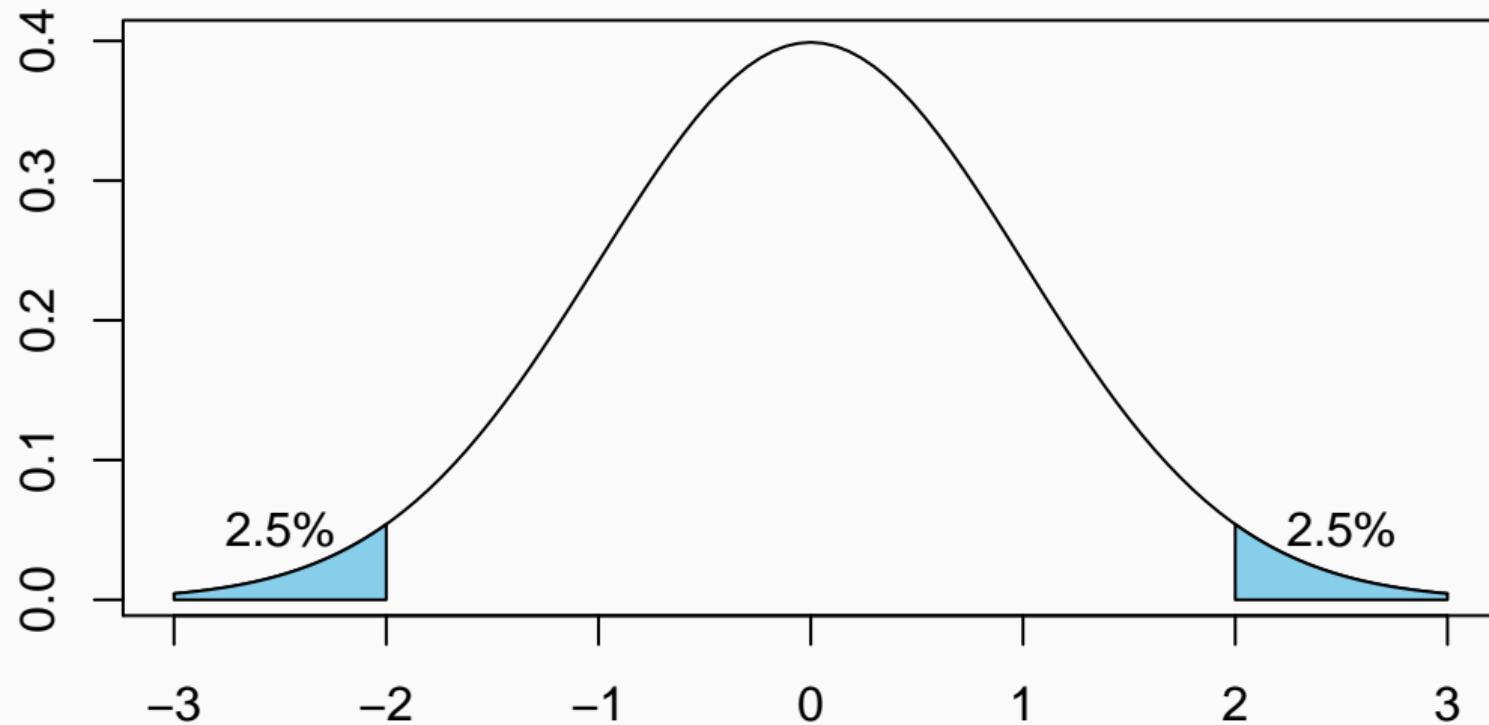
## Hypothesis testing: Rationale

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



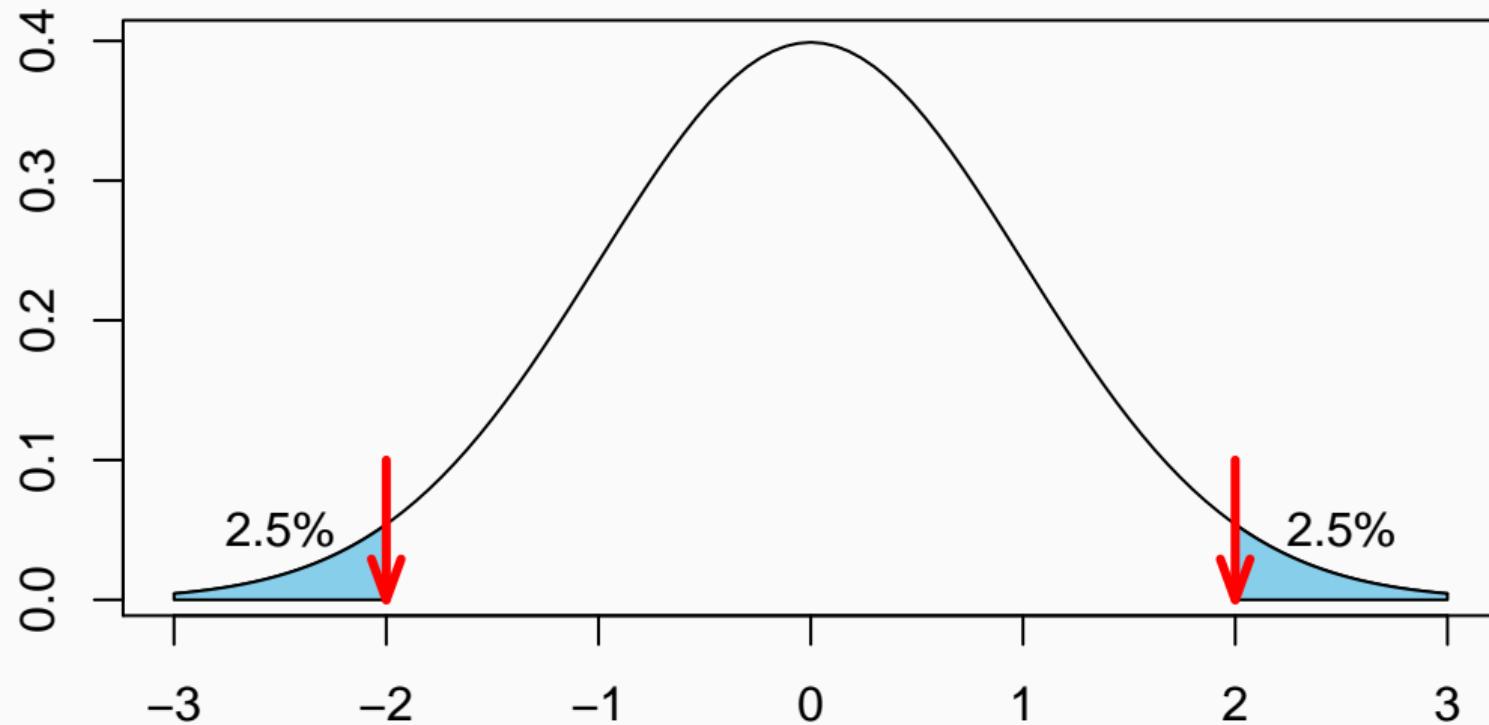
## Hypothesis testing: Rationale

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



## Hypothesis testing: Rationale

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



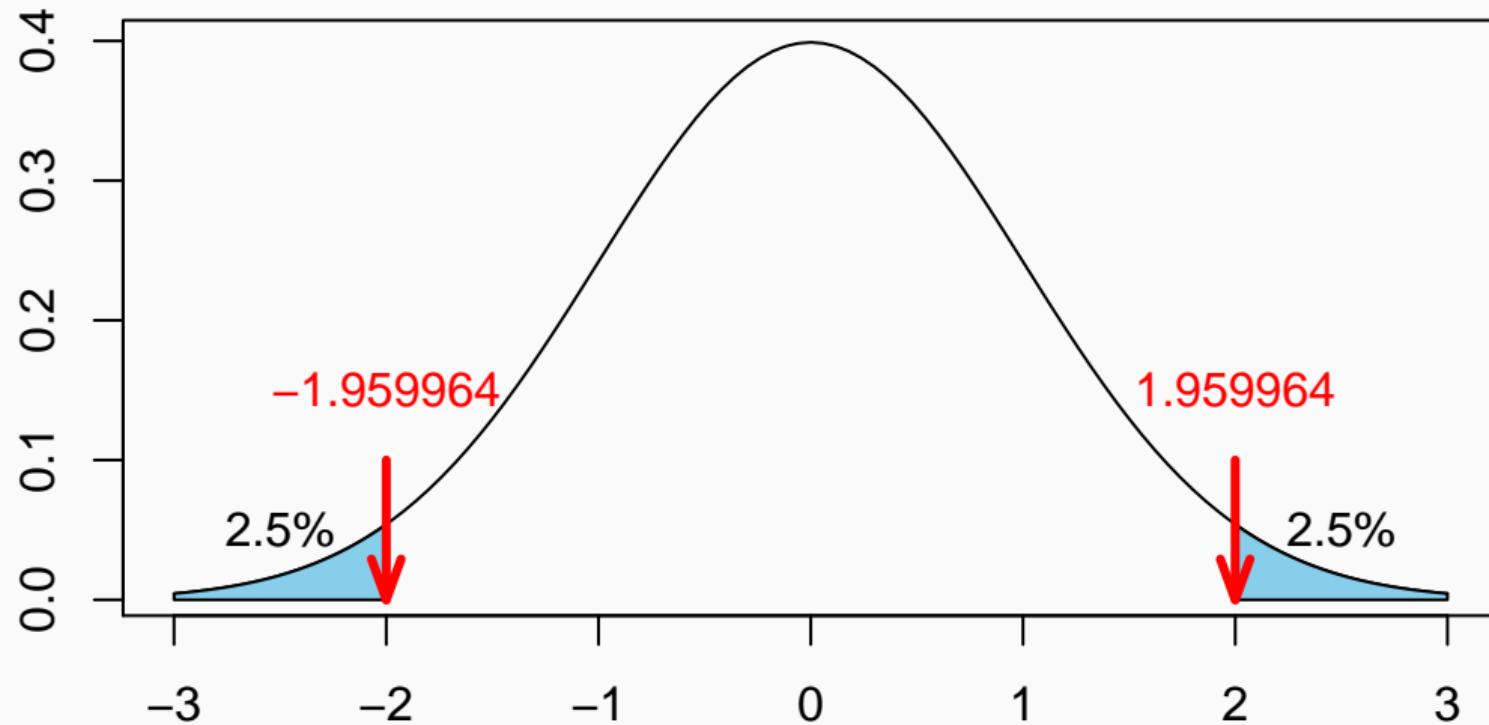
## Hypothesis testing: Rationale

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

- 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)

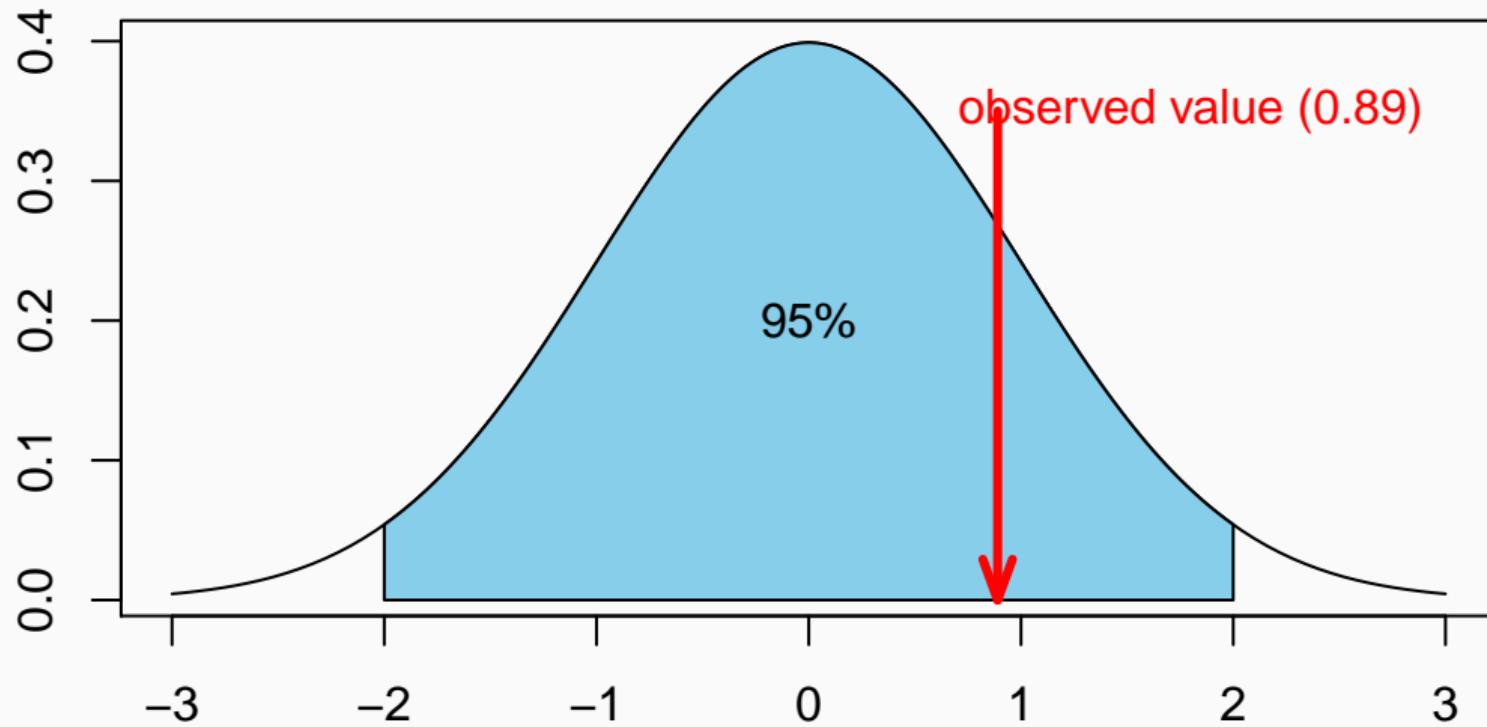
$$\frac{\hat{p} - p_0}{\sqrt{p_0(1 - p_0)/N}} = \frac{12/20 - 0.5}{\sqrt{0.5(1 - 0.5)/20}} = 0.89$$

## 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

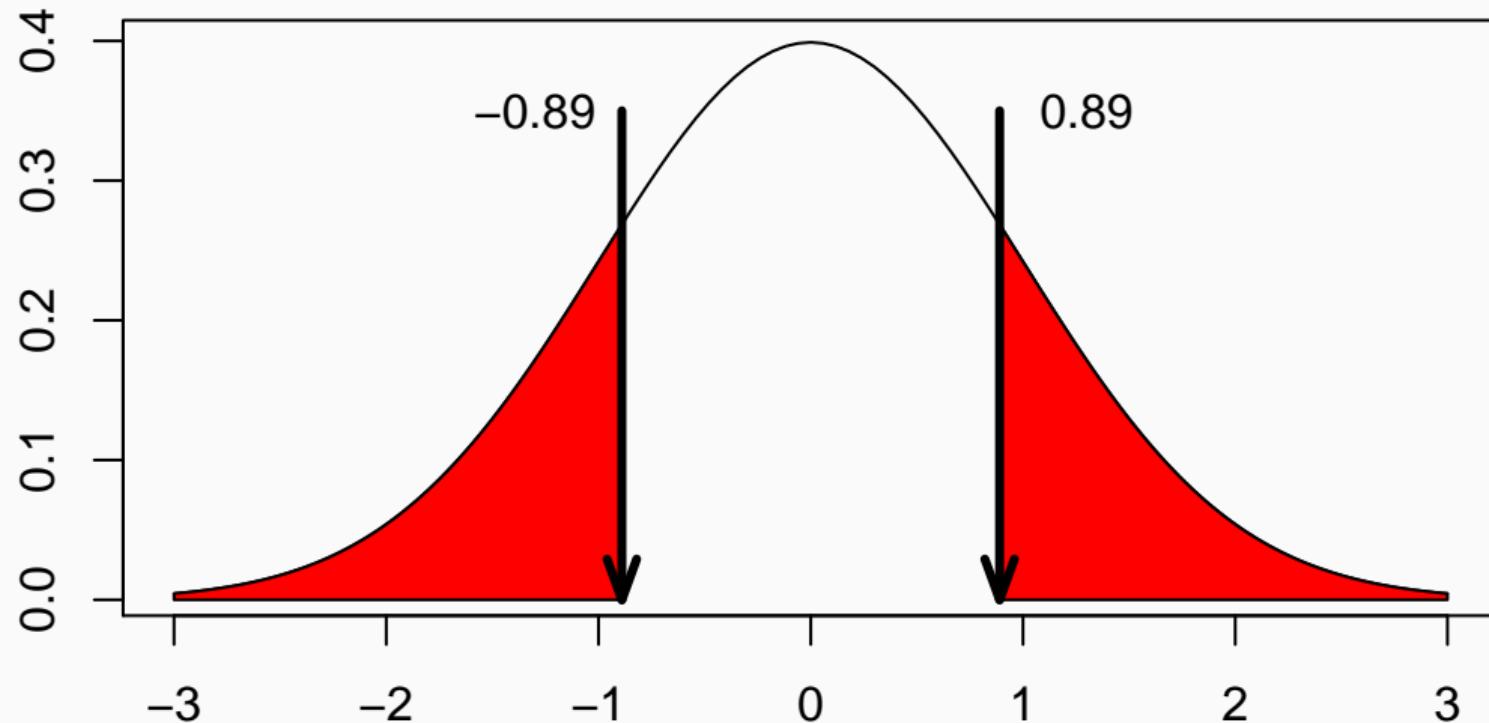


## Hypothesis testing: Rationale

- 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

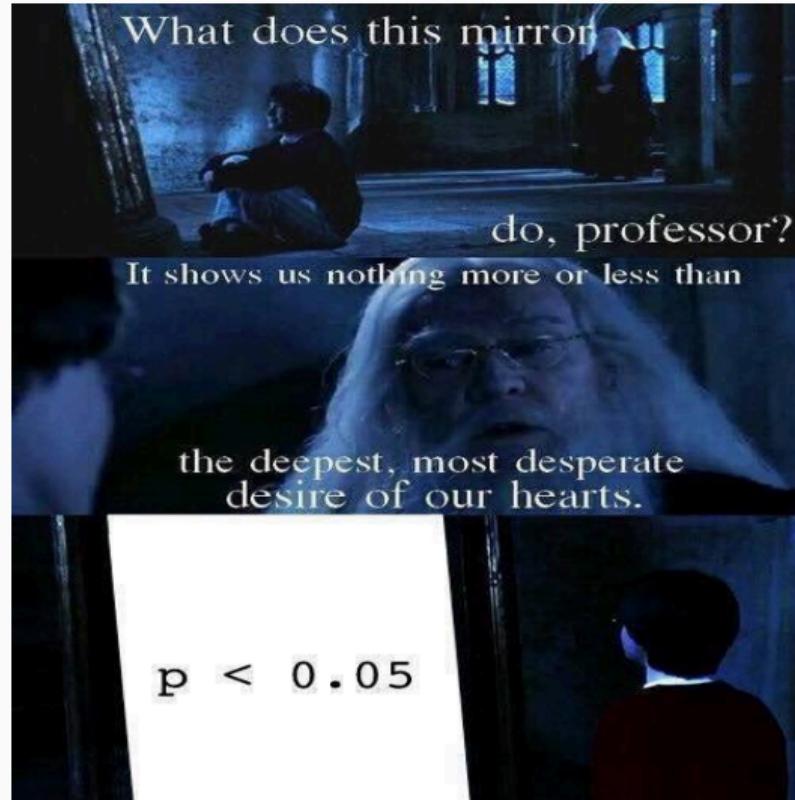


## Hypothesis testing: Rationale

- 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 # two-tailed p-value
## [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.

## Problems with hypothesis testing

---

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- **Results are only qualitative:** We get an idea of whether  $H_0$  is true but not how well supported it is by the data. The use of p-values as measures of evidence has also received criticism.

## Problems with hypothesis testing

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## Problems with hypothesis testing

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- **Null hypotheses are guaranteed to be false:** In the sense that all models are wrong, no population parameter will ever be exactly the same as our expectations.
- **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



## 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  $AIC$  of model  $i$  and the lowest  $AIC$  (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
```

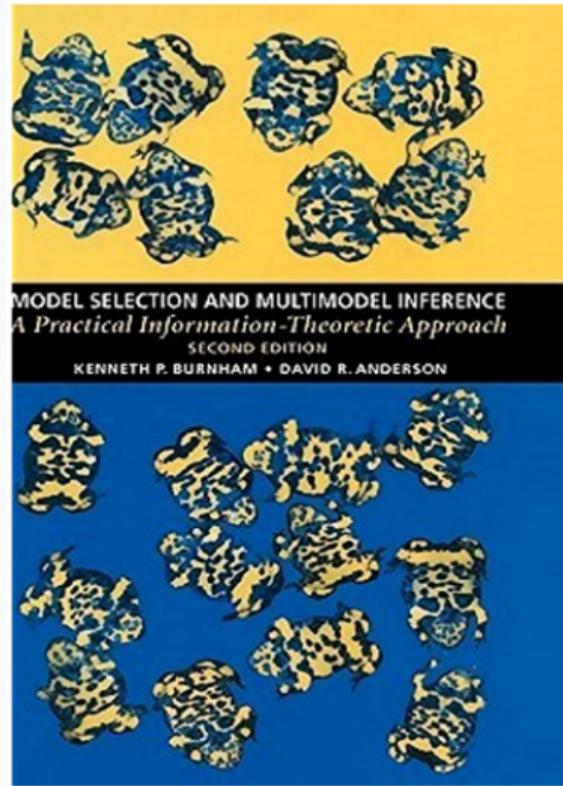
- The **full** average assumes that a variable is included in every model, but in some models the corresponding coefficient is set to zero.
- The **subset** (or **conditional**) average only averages over the models where the parameter appears.

## 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

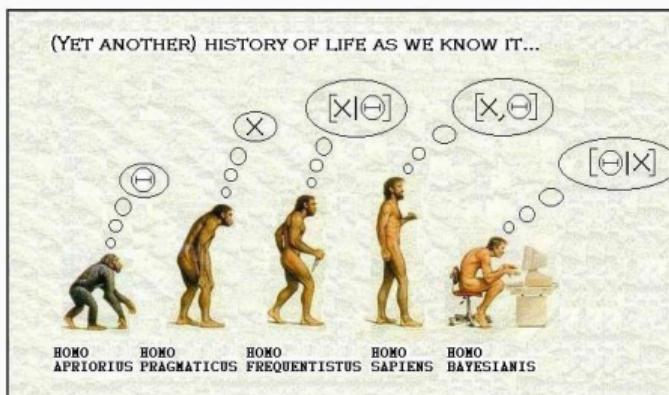
- The Bayesian approach dates back to 18th century to Reverend Thomas Bayes.



- 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:

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

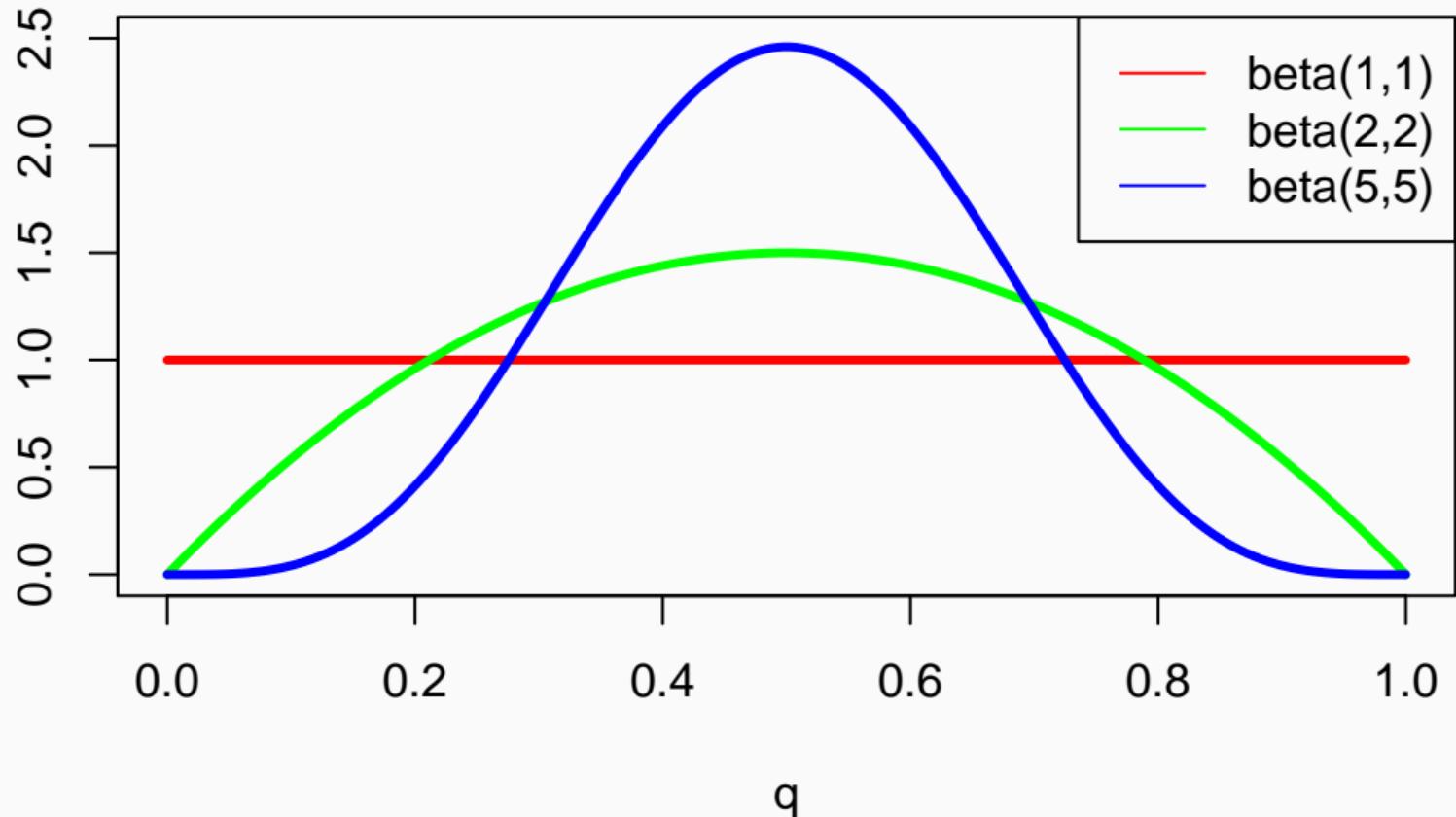
- Remember lecture on likelihoods

## 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:

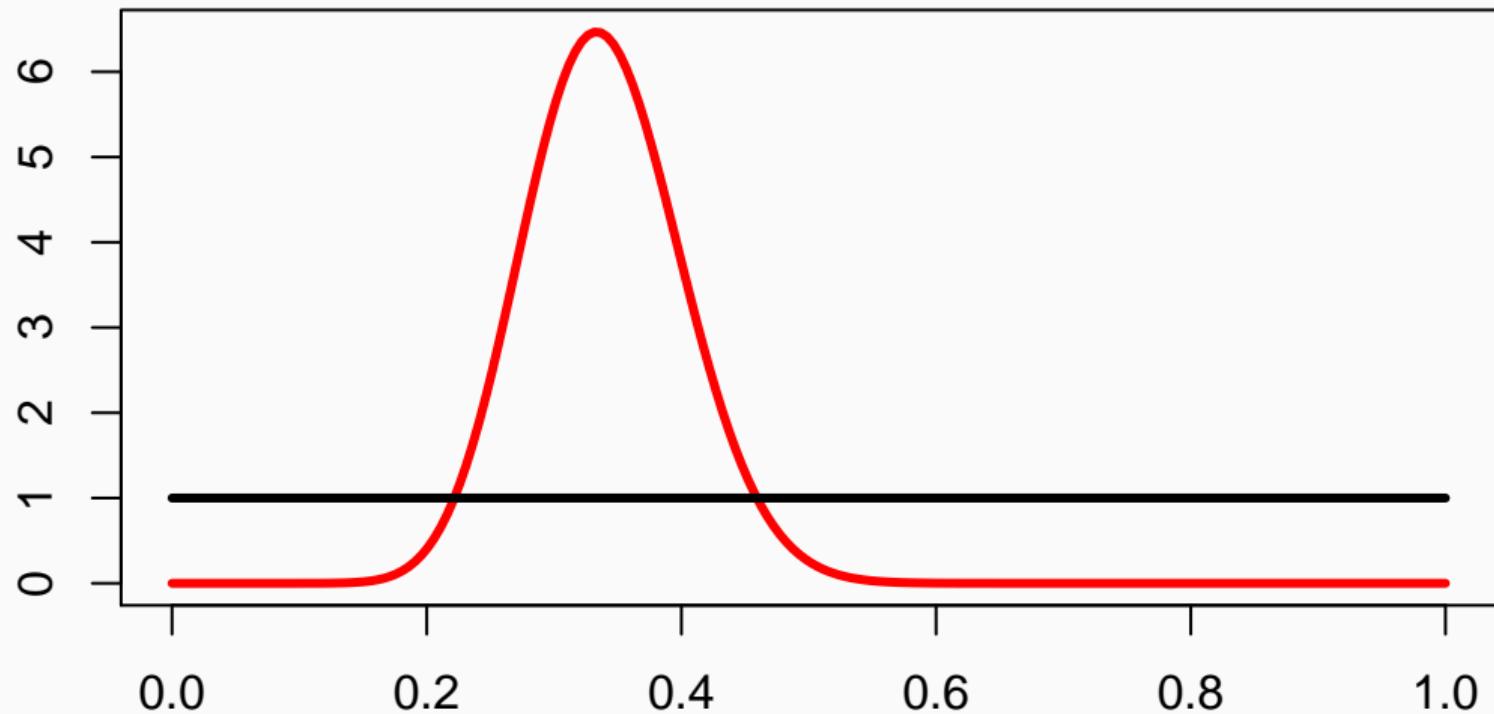
$$\theta | k \sim Beta(a + k, b + n - k)$$

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

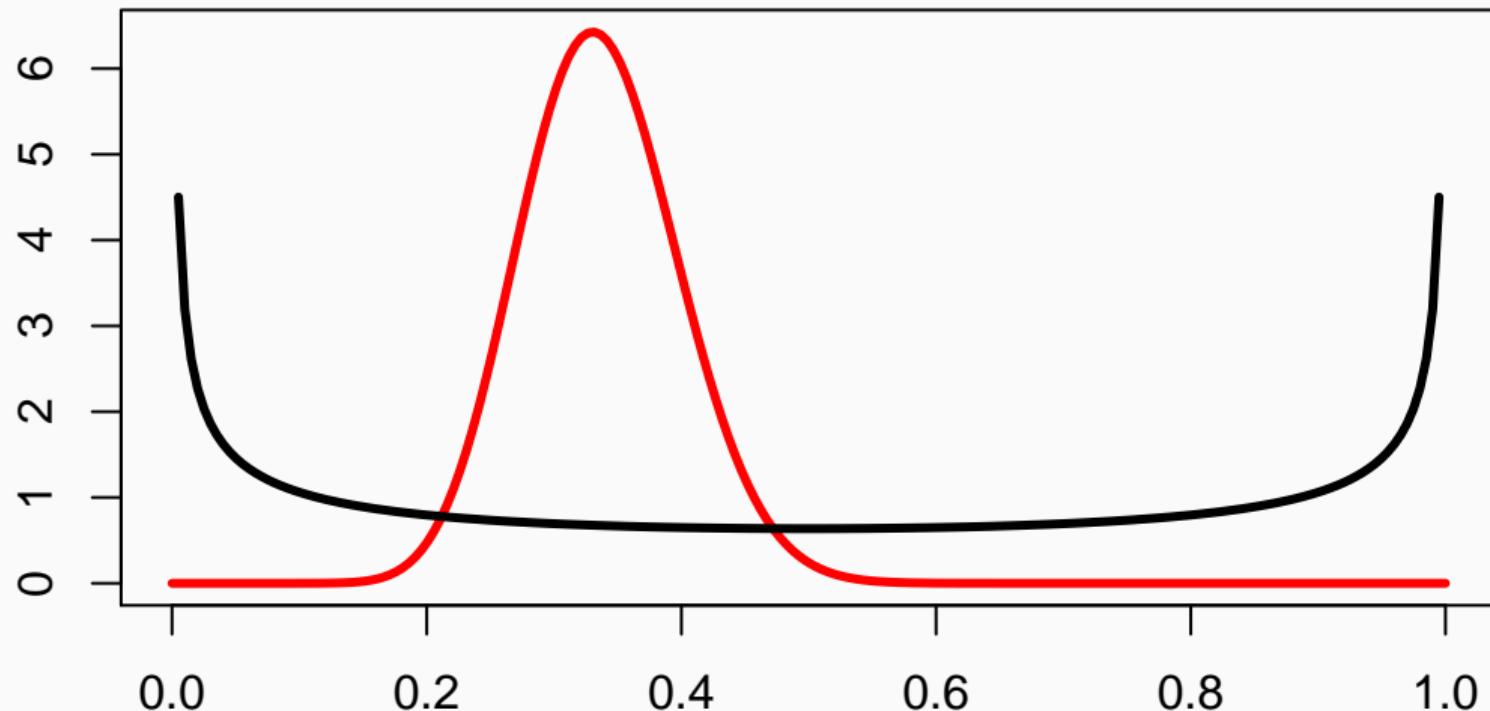
## Application to the deer example

- We have that survival  $\theta \mid k \sim Beta(a + k, b + n - k)$
- The posterior has an **explicit expression**, easy to manipulate
- $E(\theta \mid k) = \frac{a + k}{n + a + b}$
- $V(\theta \mid k) = \frac{(a + k)(b + n - k)}{(n + a + b)^2(n + a + b + 1)}$
- 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  $V(\theta_{treatment}) = 0.061$

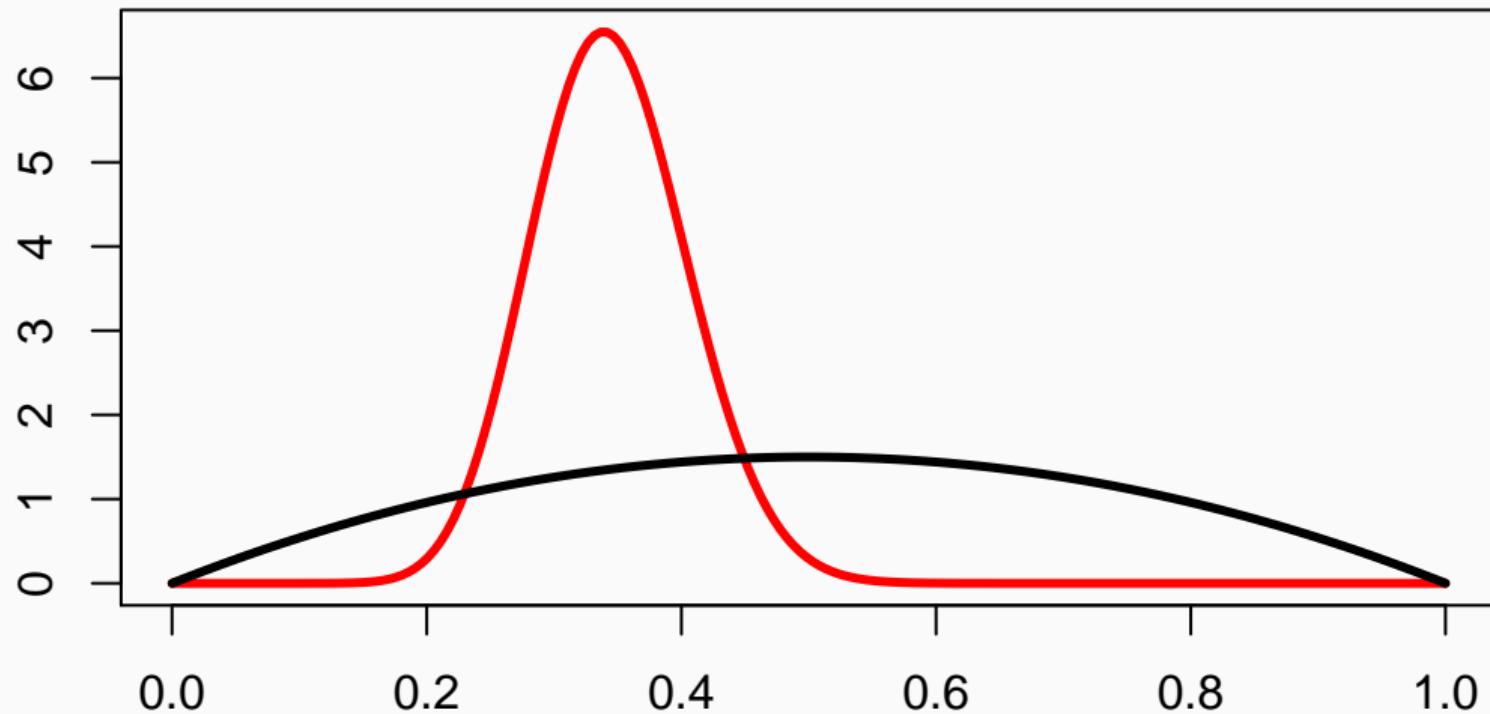
Prior  $Beta(1, 1)$  and posterior survival  $Beta(20, 39)$



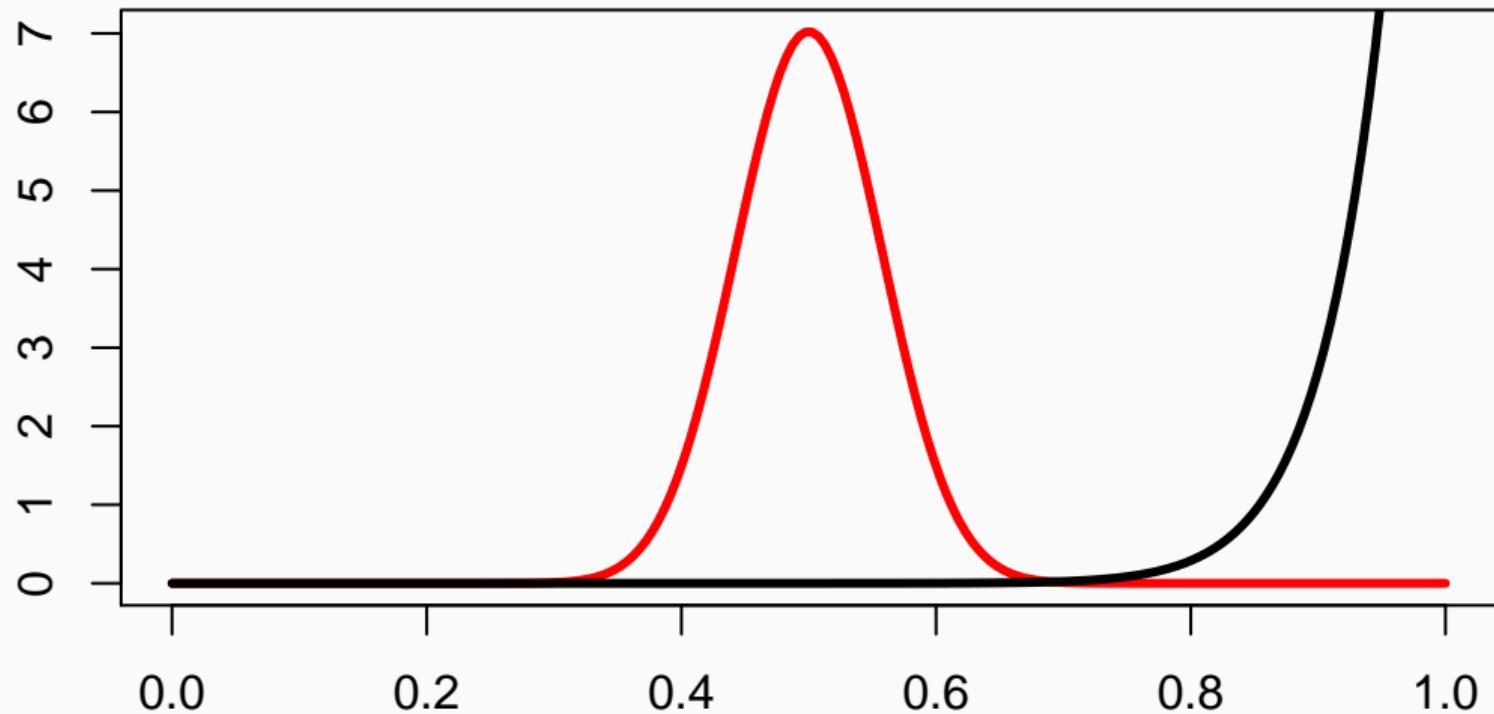
Prior  $Beta(0.5, 0.5)$  and posterior survival  $Beta(19.5, 38.5)$



Prior  $Beta(2, 2)$  and posterior survival  $Beta(21, 40)$



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!**

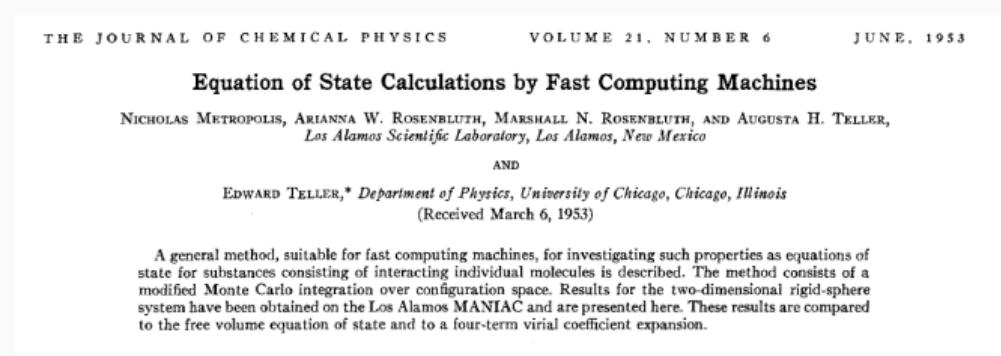
## Back to the Bayes formula

---

- 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



- 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

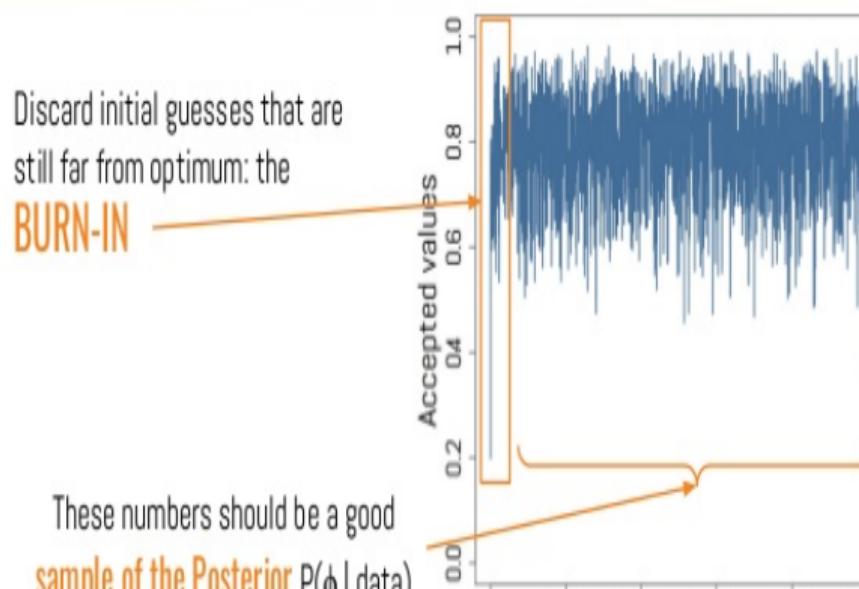
## Why are MCMC methods so useful?

---

- 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



# 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?

---

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

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

## 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
##
```

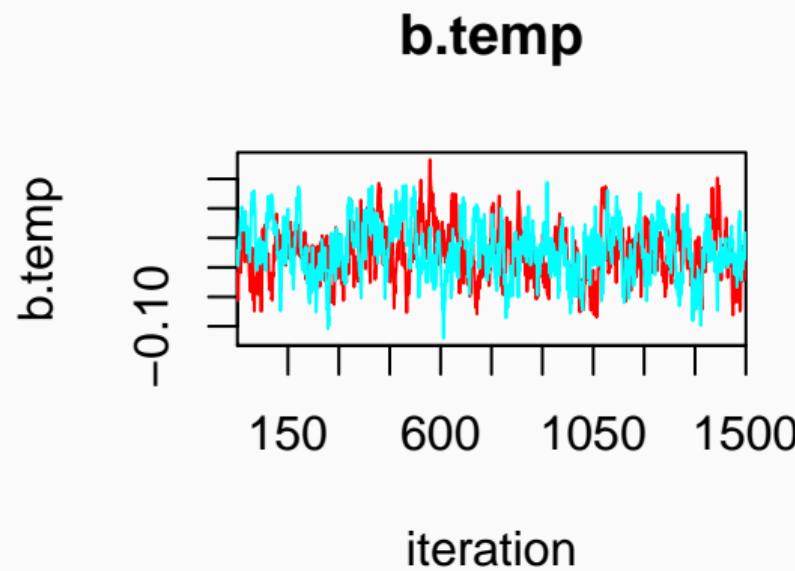
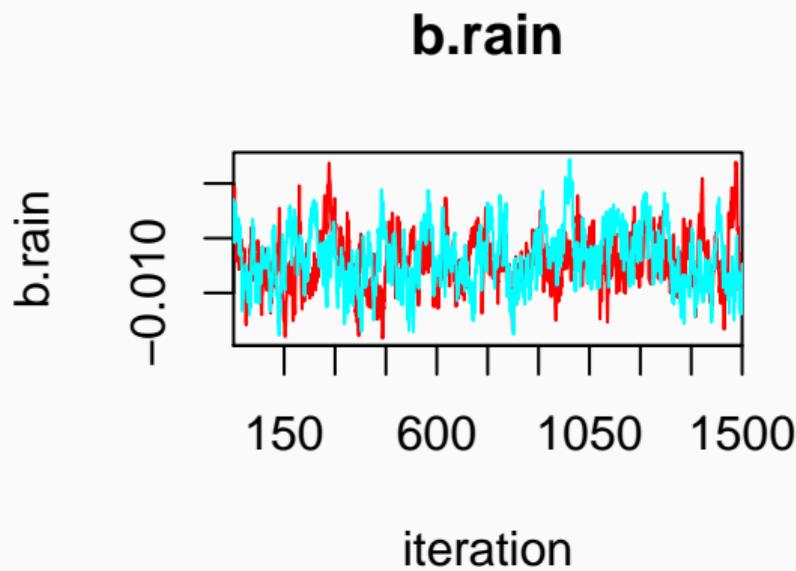
## Display parameter estimates

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
## a          1.620   0.614   0.373   1.217   1.653   2.034   2.776 1.014
## b.rain     -0.007   0.003  -0.012  -0.009  -0.007  -0.005  -0.002 1.007
## b.temp      0.026   0.045  -0.060  -0.004   0.025   0.055   0.117 1.010
## deviance 205.730  22.894 201.798 202.833 203.962 205.724 211.479 1.120
##
## 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)
##
```

## Let us assess convergence

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



## 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

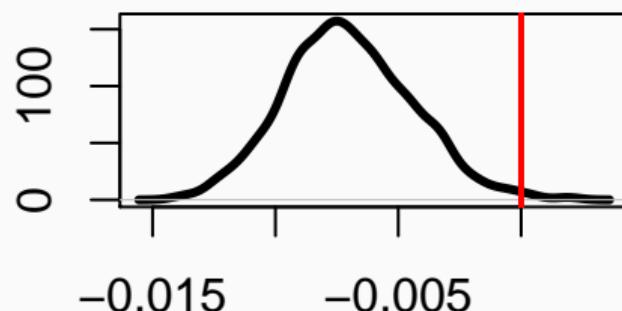
```
quantile(res[, 'b.rain'], c(0.025, 0.975))  
##           2.5%         97.5%  
## -0.011871062 -0.001714676
```

## Get credible interval for the temperature effect

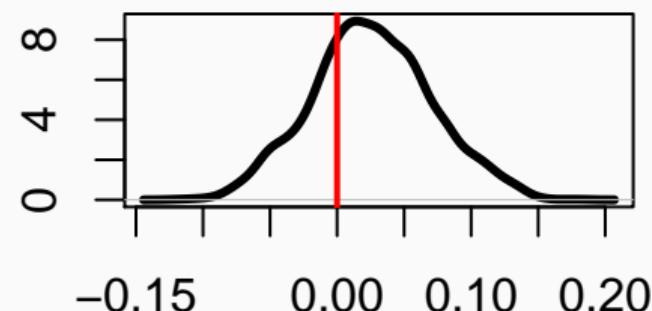
```
quantile(res[, 'b.temp'], c(0.025, 0.975))
```

```
##           2.5%         97.5%
## -0.05987025  0.11665989
```

### a posteriori density of the rainfall effect



### a posteriori density of the temperature effect



There is an influence of rainfall, but not temperature (credible interval does not contain 0)

## 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 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**  $\phi_{prior} \sim \text{Normal}(0.57, 0.073)$
- Mean posterior  $\phi_{posterior} = 0.56$  with credible interval  $[0.52, 0.60]$
- No increase of precision in posterior inference

## A general result

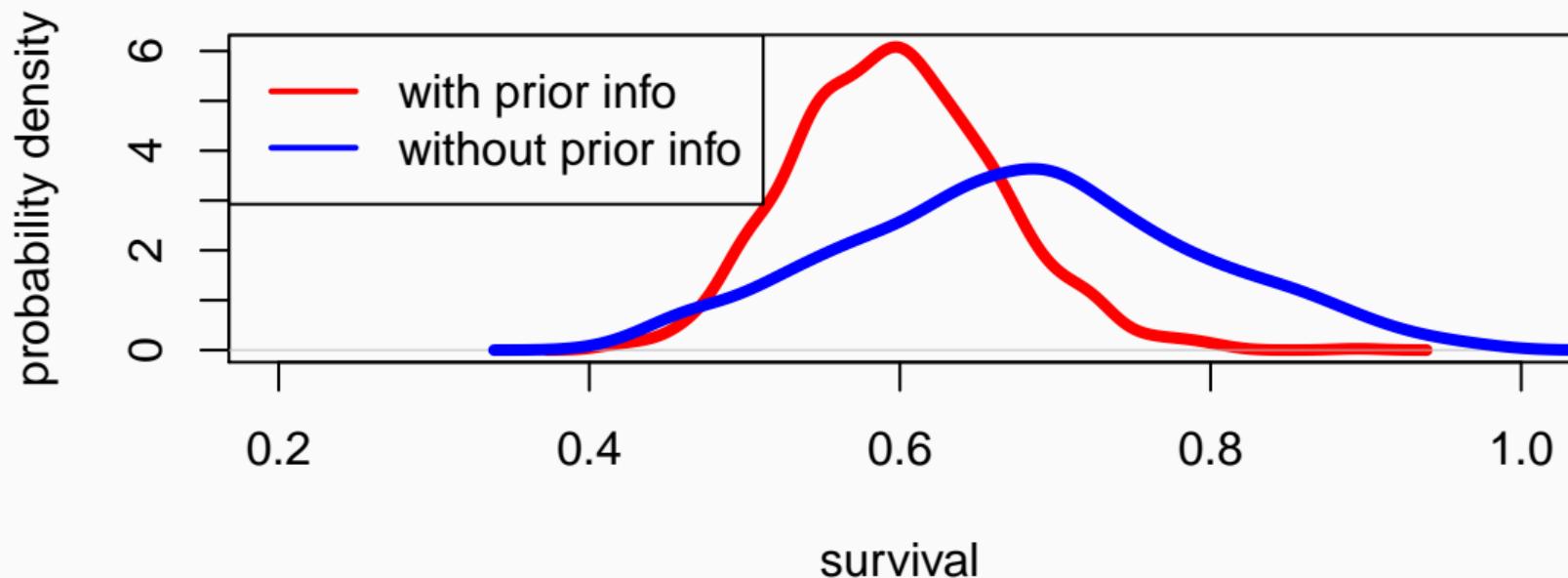
---

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 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  $\phi_{prior} \sim \text{Normal}(0.57, 0.073)$
- **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
- Hypothesis testing and multimodel inference
- Introduction to Bayesian inference
- Generalized Linear Models (GLMs)
- Generalized Additive Models (GAMs)
- Mixed Effect Models

## Generalized Linear Models (GLMs)

---

## Survival of passengers on the Titanic ~ Class

Read titanic\_long.csv dataset.

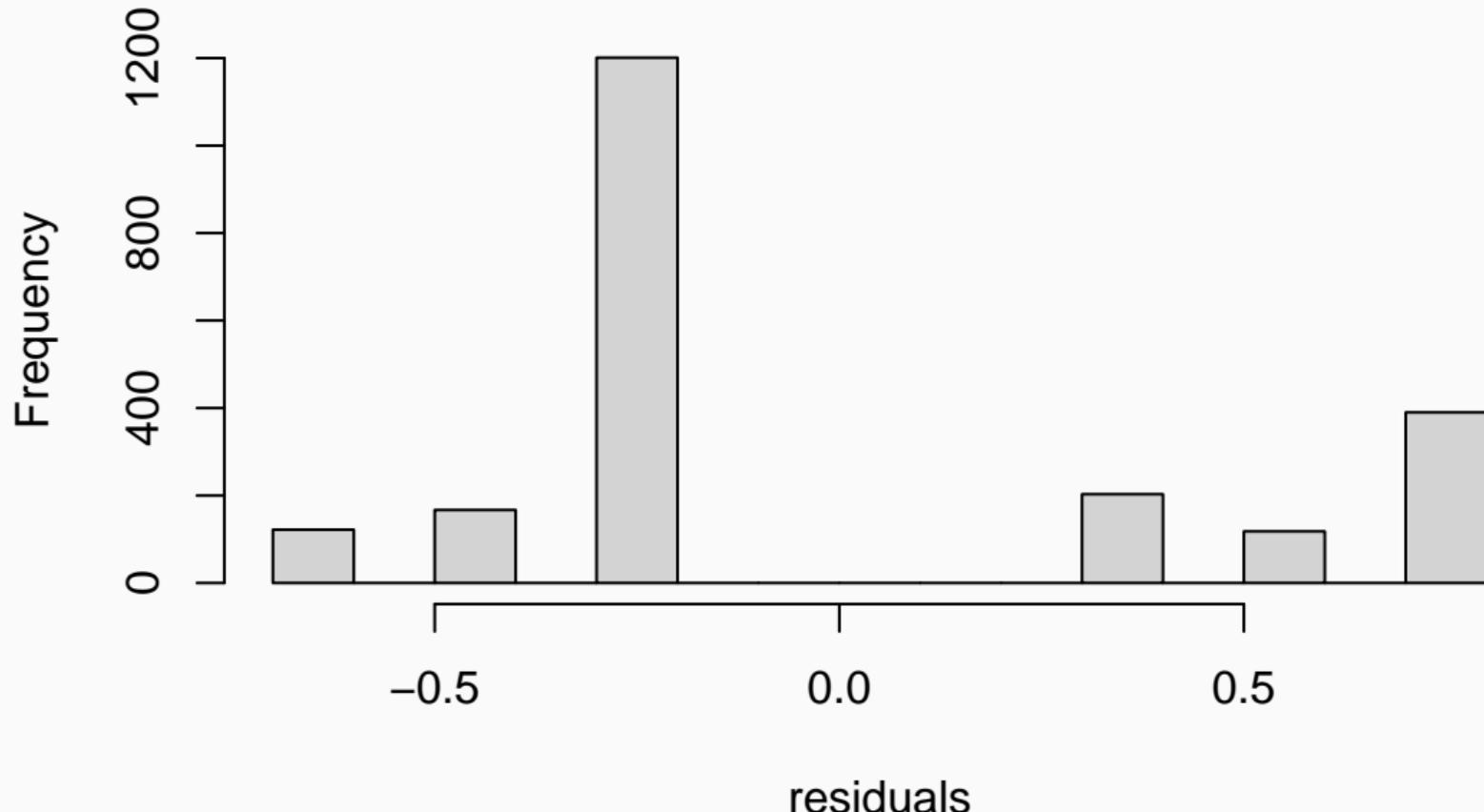
```
titanic <- read.csv("dat/titanic_long.csv") %>%  
  mutate(across(where(is.character), as_factor))  
head(titanic)  
##   class    age   sex survived  
## 1 first adult male      1  
## 2 first adult male      1  
## 3 first adult male      1  
## 4 first adult male      1  
## 5 first adult male      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)
##   first  second   third    crew
##     325     285     706    885
```

## Back to survival of Titanic passengers

---

How many survived?

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

## Back to survival of Titanic passengers

---

What proportion survived in each class?

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

## 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)

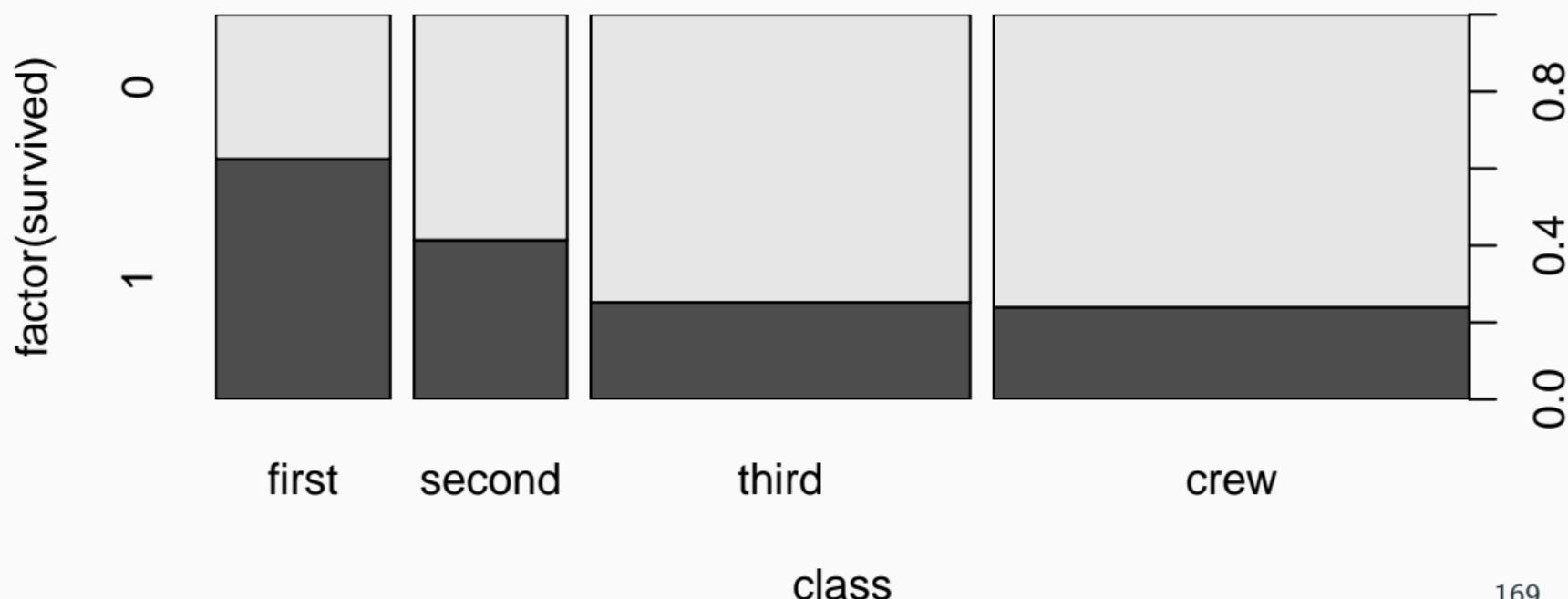
---

Arrange passenger survival according to class

```
## # A tibble: 8 x 3
## # Groups:   class [4]
##   class  survived count
##   <chr>    <int> <int>
## 1 crew        0    673
## 2 crew        1    212
## 3 first       0    122
## 4 first       1    203
## 5 second      0    167
## 6 second      1    118
## 7 third       0    528
## 8 third       1    178
```

Or graphically...

```
plot(factor(survived) ~ class, data = titanic)
```



## 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)  0.509    0.115     4.44 8.79e- 6
## 2 classsecond -0.856    0.166    -5.16 2.51e- 7
## 3 classthird  -1.60     0.144    -11.1 1.07e-28
## 4 classcrew   -1.66     0.139    -12.0 4.97e-33
```

These estimates are on the logit scale!

## Interpreting logistic regression outputs

Parameter estimates on the logit scale:

```
## (Intercept) classsecond classthird classcrew  
## 0.5091849 -0.8564941 -1.5964977 -1.6643440
```

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

```
plogis(coef(titanic.glm)[1]) # crew survival probability  
## (Intercept)  
## 0.6246154
```

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)  
## 0.4140351
```

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
##      first     second      third      crew
## 0.6246154 0.4140351 0.2521246 0.2395480
```

## Effects plot

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



## 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

```
plot(factor(survived) ~ sex, data = titanic)
```



## 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) -1.31     0.0588    -22.3 2.10e-110
## 2 sexfemale    2.32     0.120      19.4 1.22e- 83
```

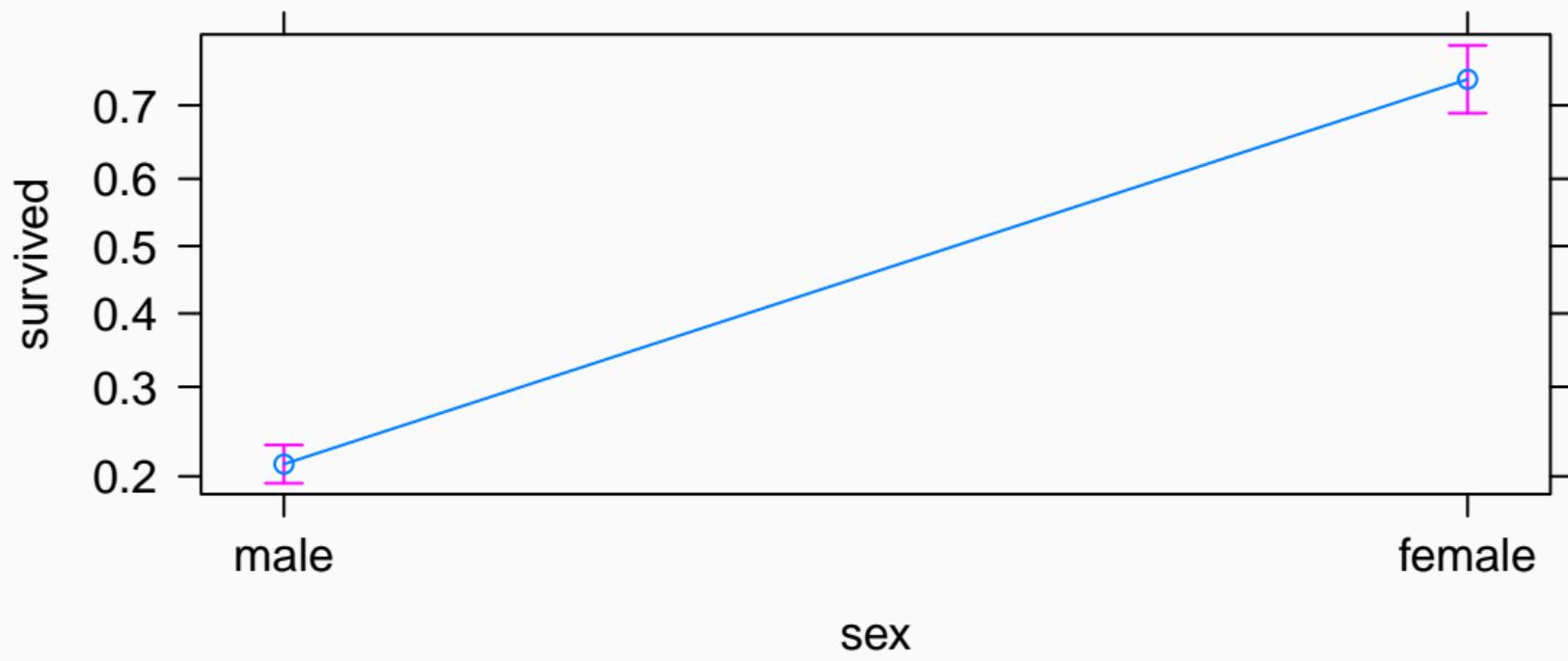
## Effects

---

```
allEffects(titanic.sex)

##  model: survived ~ sex
##
##  sex effect
##  sex
##      male    female
##  0.2120162 0.7319149
```

## 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)

##           male female
## first      62    141
## second     25     93
## third      88     90
## crew      192     20
```

Mmmm...

## Fit model with both factors (interactions)

```
titanic.s.cl <- glm(survived ~ class * sex, data=titanic, family=binomial)

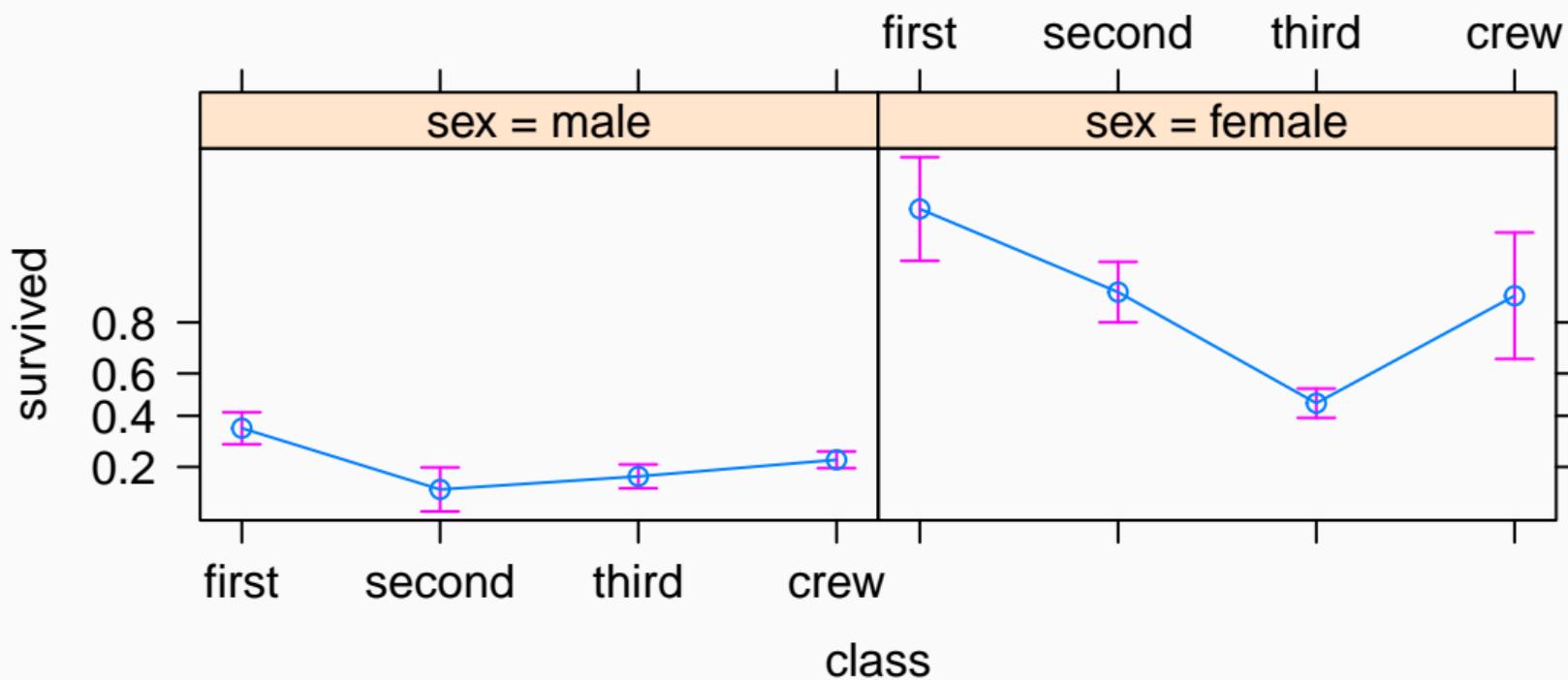
## # A tibble: 8 x 5
##   term            estimate std.error statistic p.value
##   <chr>          <dbl>     <dbl>      <dbl>    <dbl>
## 1 (Intercept) -0.644      0.157     -4.10  4.08e- 5
## 2 classecond   -1.17       0.267     -4.40  1.06e- 5
## 3 classthird   -0.924      0.196     -4.72  2.36e- 6
## 4 classcrew    -0.606      0.177     -3.43  6.12e- 4
## 5 sexfemale     4.21        0.531      7.92  2.29e-15
## 6 classecond:sexfemale -0.420     0.645     -0.652 5.15e- 1
## 7 classthird:sexfemale -2.80       0.562     -4.98  6.21e- 7
## 8 classcrew:sexfemale -1.06       0.820     -1.29  1.96e- 1
```

## Effects

---

```
allEffects(titanic.s.cl)

##  model: survived ~ class * sex
##
##  class*sex effect
##          sex
##  class      male    female
##  first   0.3444444 0.9724138
##  second  0.1396648 0.8773585
##  third   0.1725490 0.4591837
##  crew    0.2227378 0.8695652
```

**class\*sex effect plot**

## 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

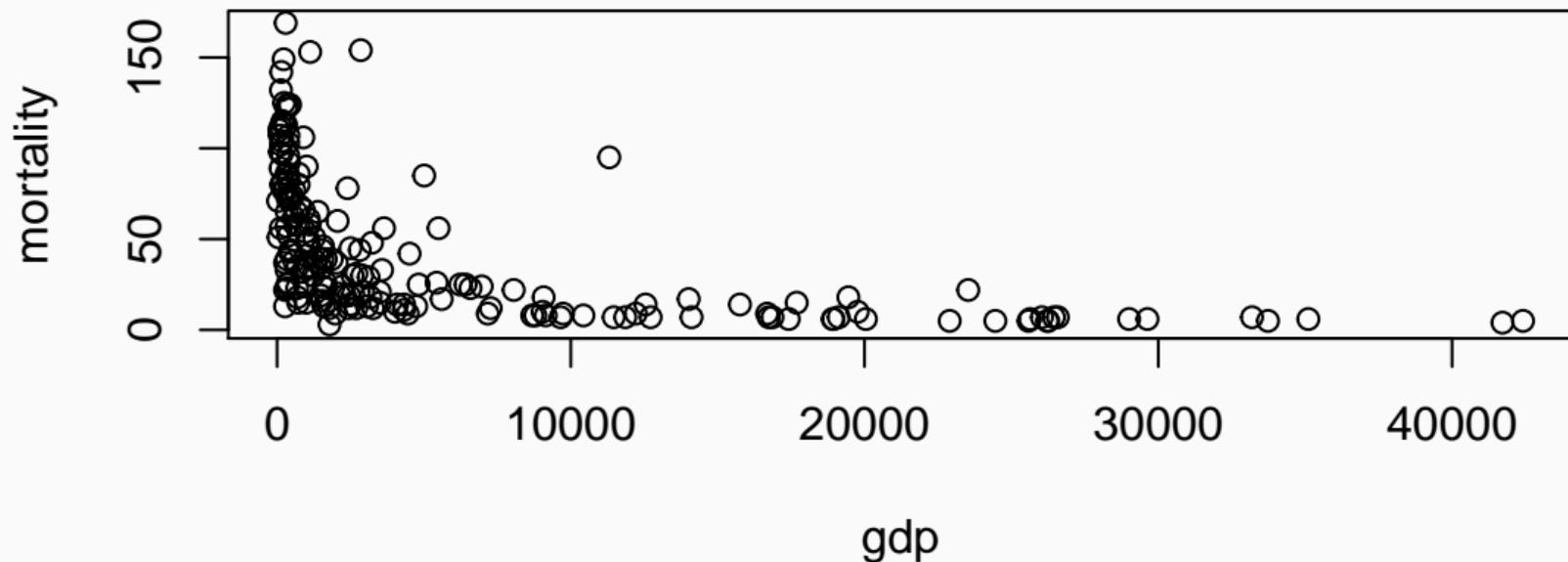
---

```
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
```

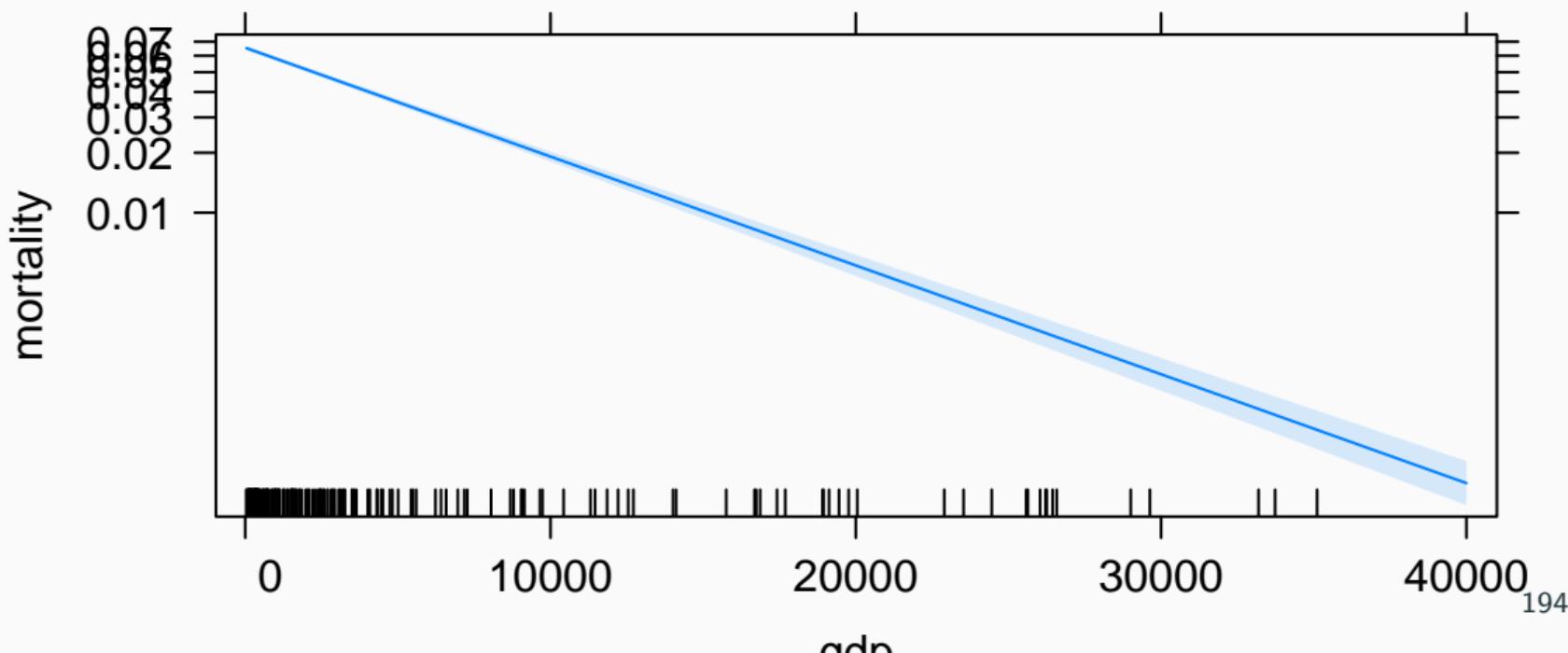
## Effects

```
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
```

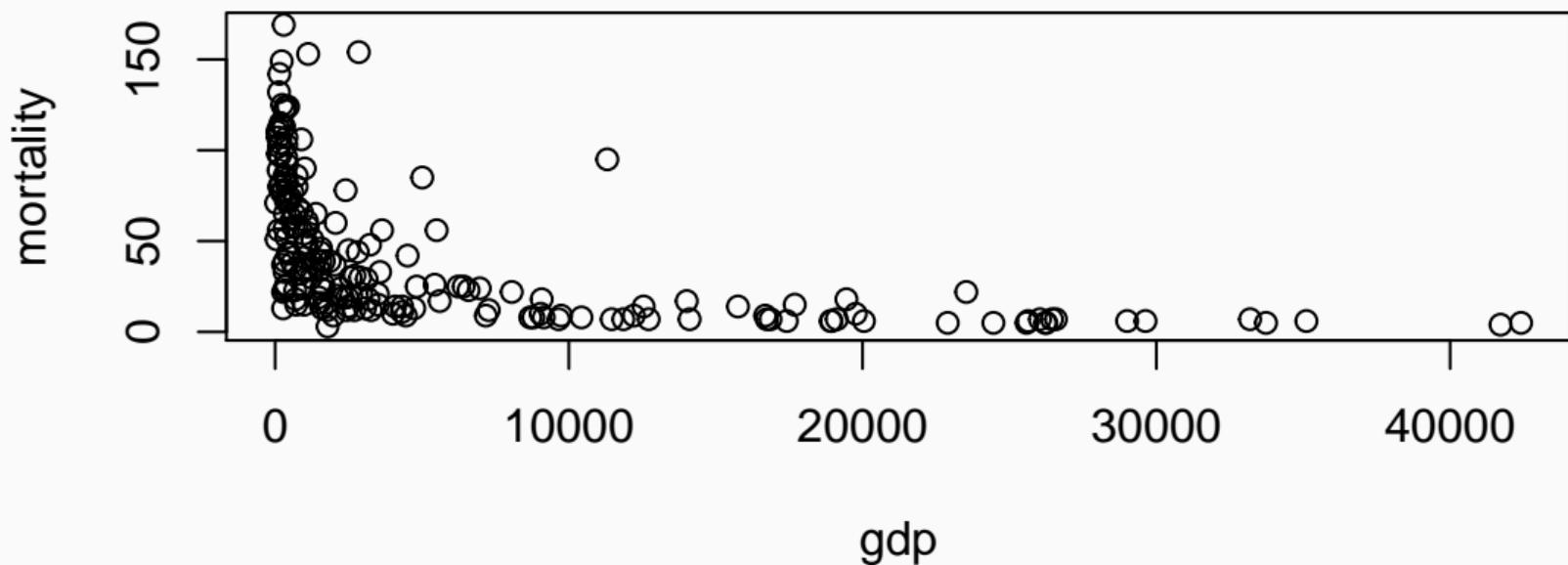
## Effects plot

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



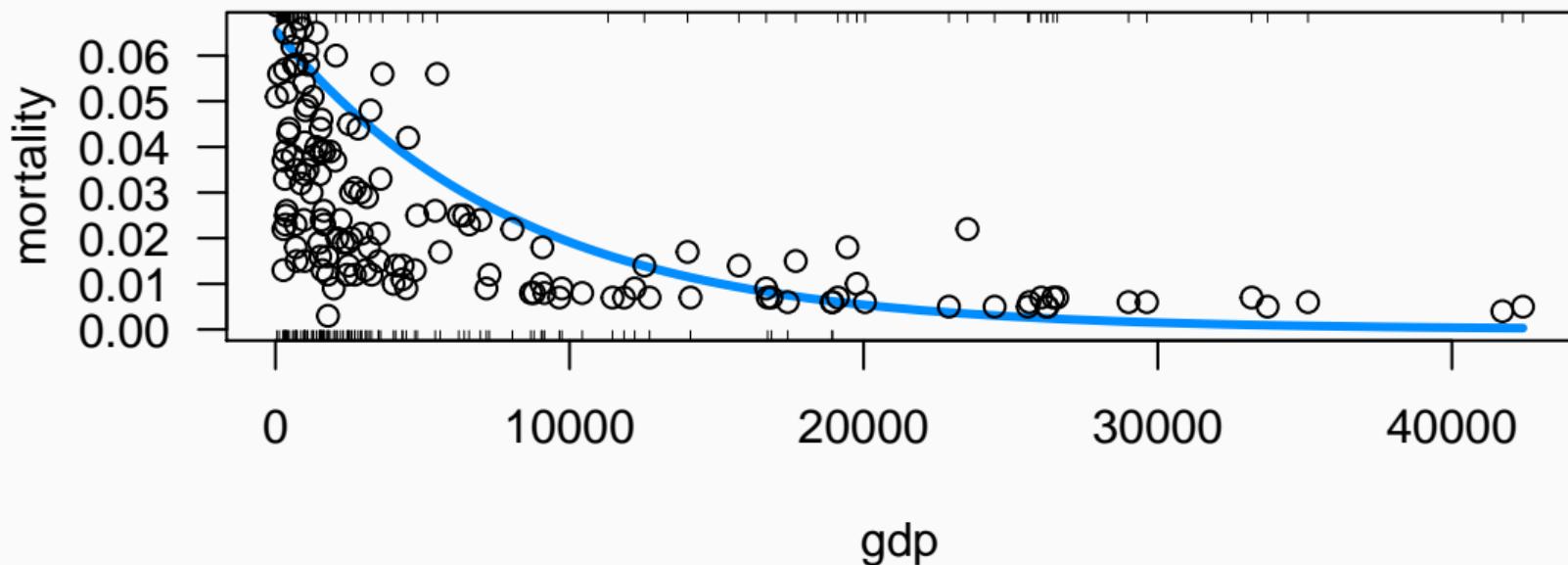
## Plot model and data (Infant mortality per 1000 births)

```
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?

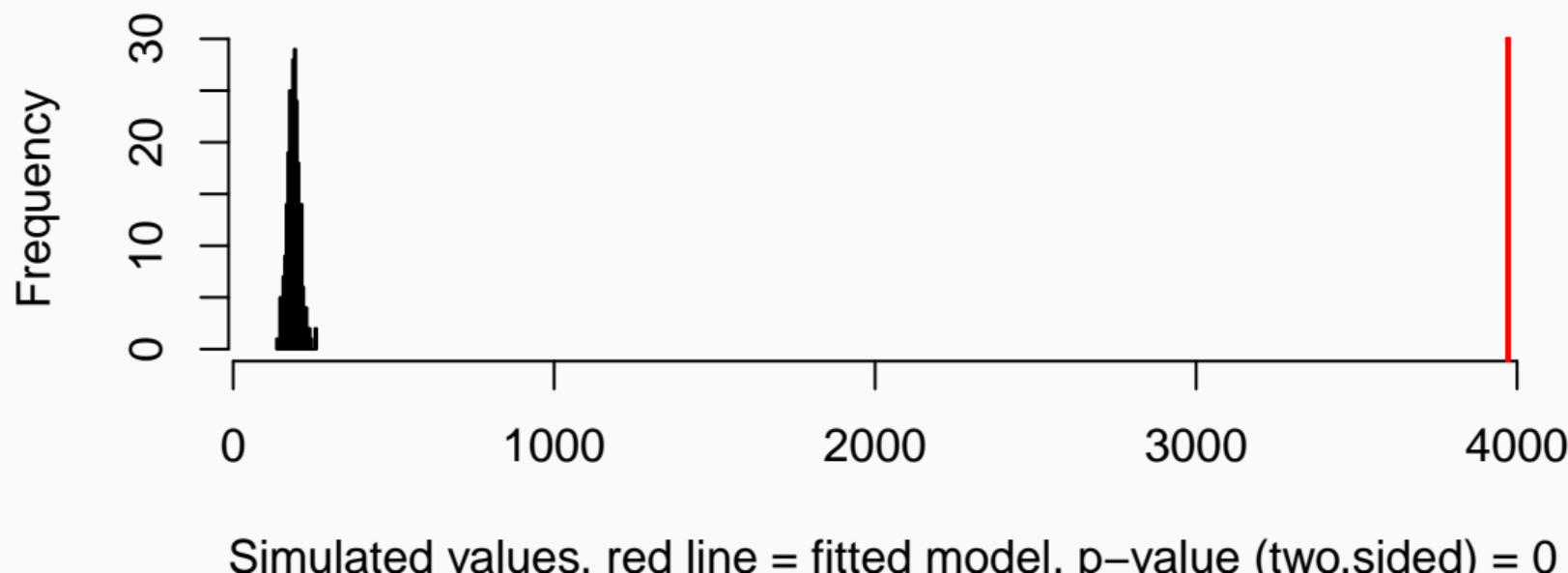
---

- 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 significant



## 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)

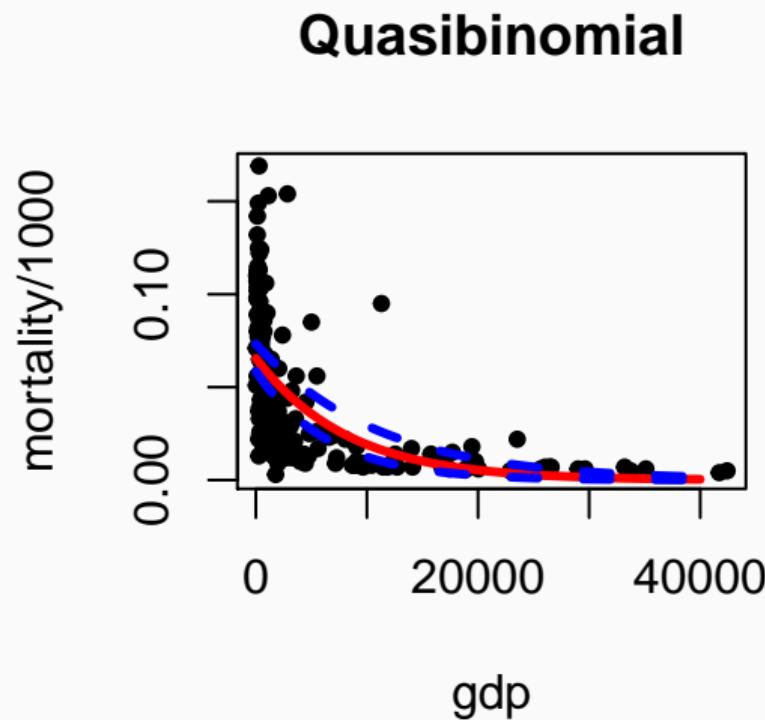
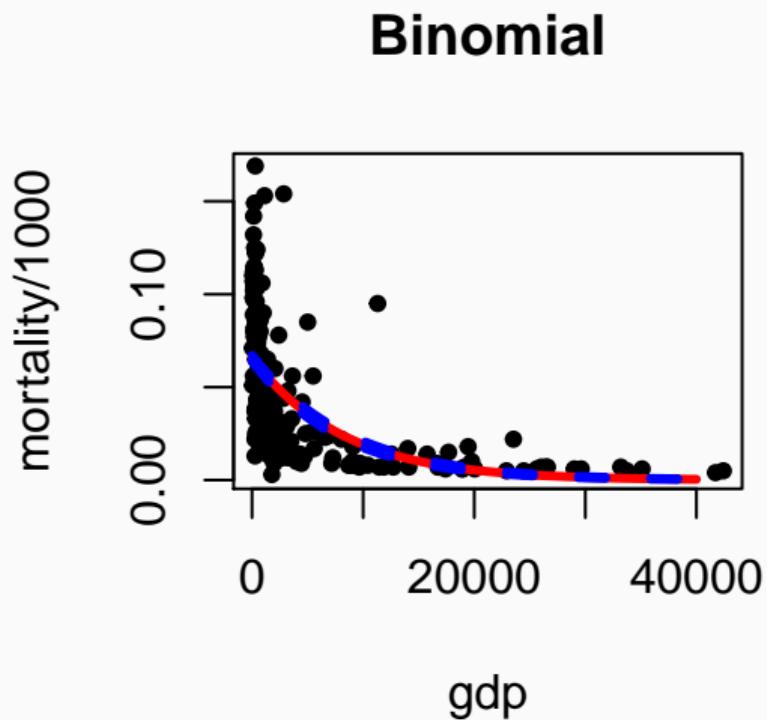
##  model: cbind(mortality, 1000 - mortality) ~ gdp
##
##  gdp effect
##  gdp
##        40          10000         20000         30000         40000
## 0.0652177296 0.0191438829 0.0054028095 0.0015096074 0.0004206154
```

## 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!



## 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
```

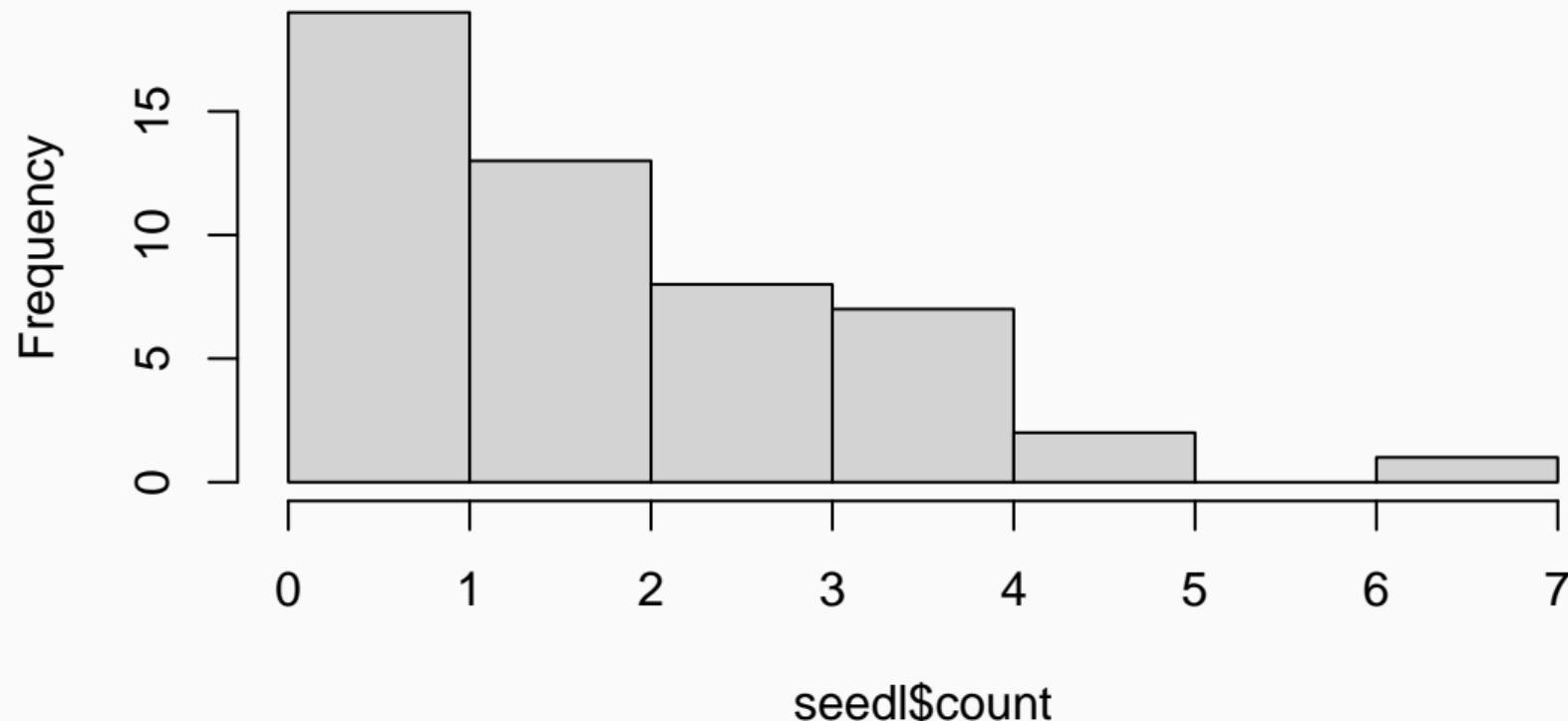
## Explore data

---

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

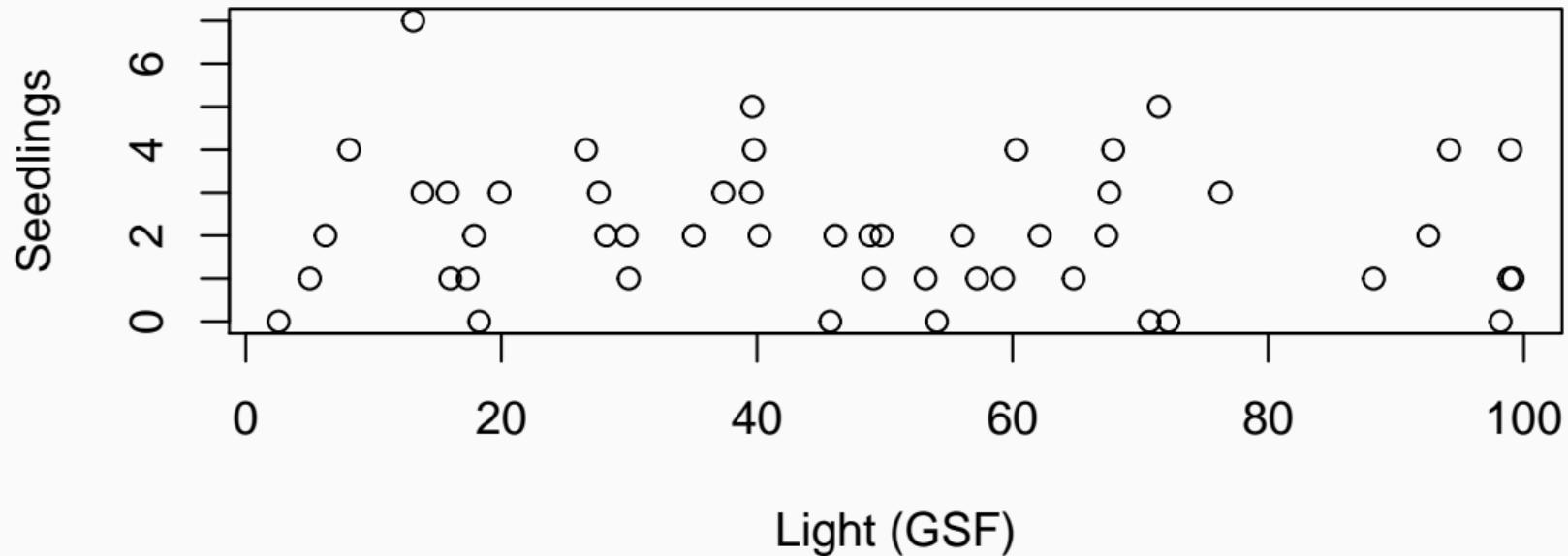
## Explore data

```
hist(seed$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(seedl.glm) # model with light  
## [1] 182.0335  
AIC(glm(count ~ 1, data = seedl, family = poisson)) # null model  
## [1] 180.5706
```

Should consider multimodel inference...

## Interpreting Poisson regression output

Parameter estimates (log scale):

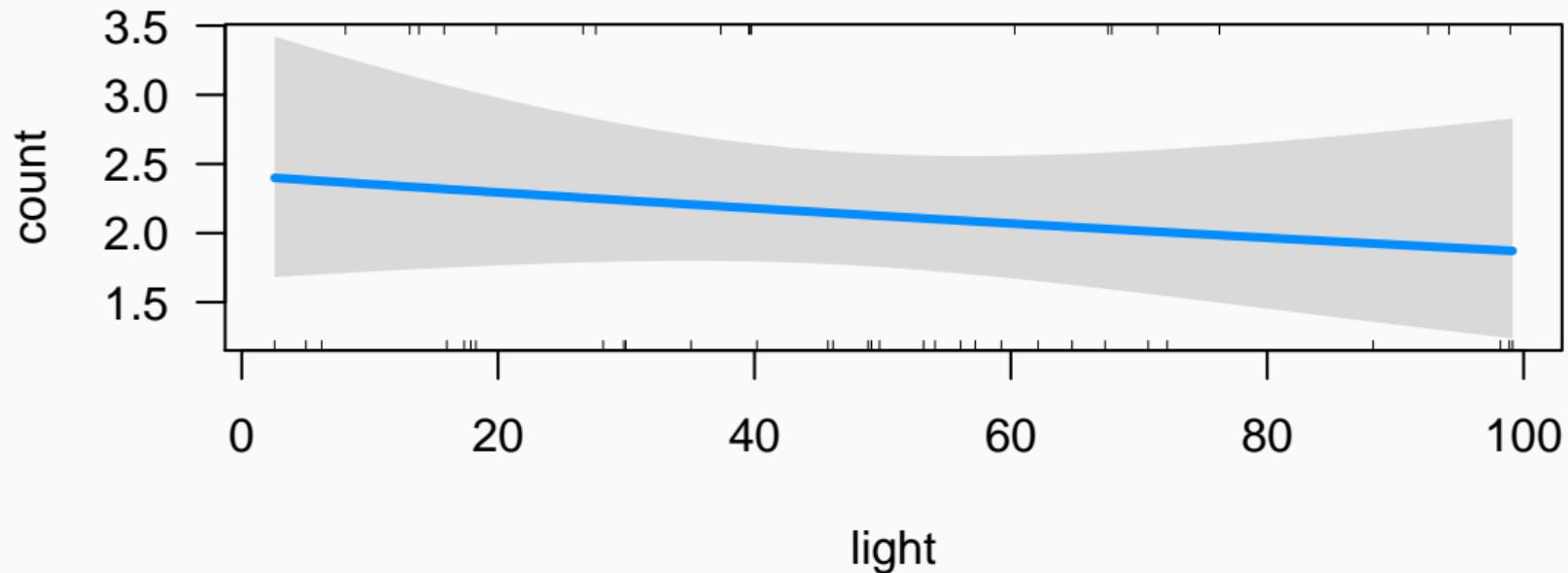
```
coef(seed1.glm)
## (Intercept)      light
## 0.881805022 -0.002575656
```

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(seed1.glm, scale = "response")
```

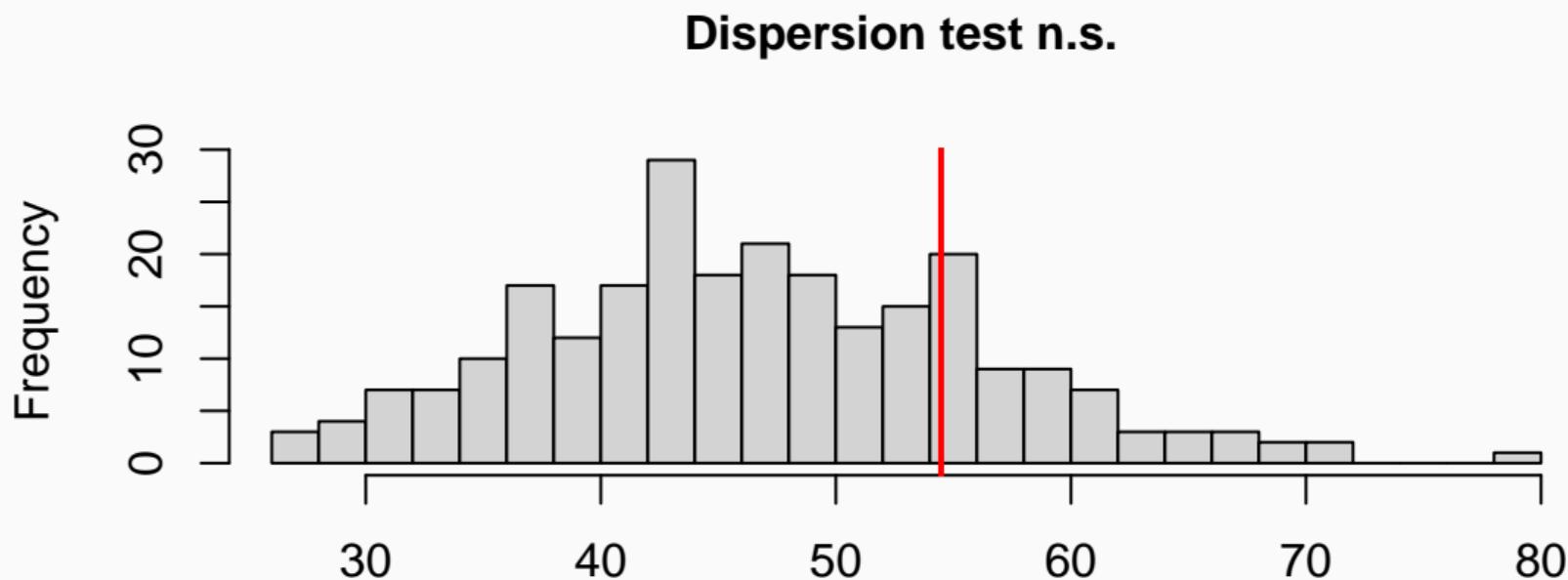


## Poisson regression: Overdispersion

---

## Always check overdispersion with count data

```
testOverdispersion(simulateResiduals(seed1.glm, refit = TRUE))
```



Simulated values, red line = fitted model, p-value (two.sided) = 0.432<sup>214</sup>

## Accounting for overdispersion in count data

Use family quasipoisson

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

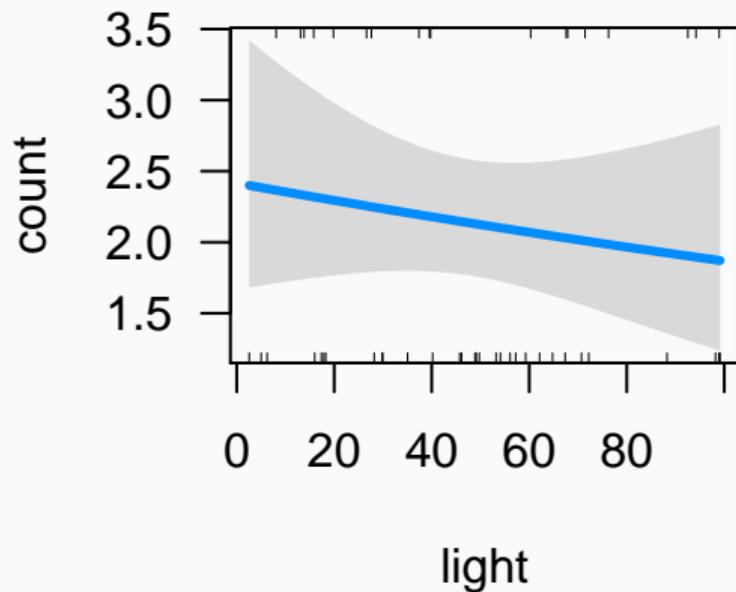
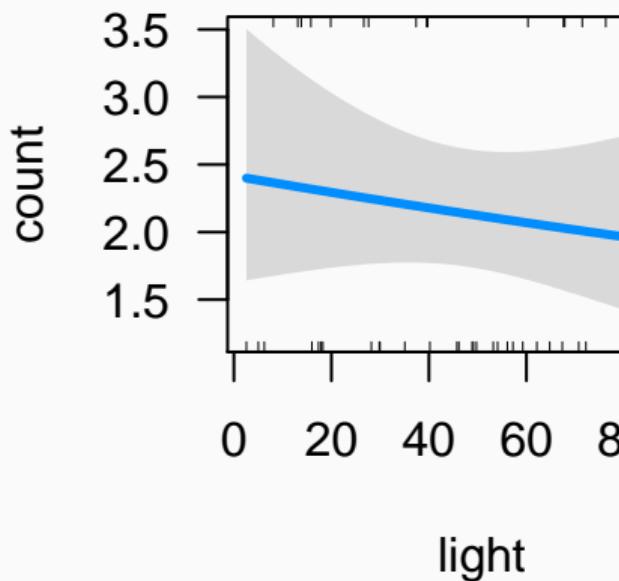
```
## # A tibble: 2 x 5
##   term      estimate std.error statistic p.value
##   <chr>      <dbl>     <dbl>     <dbl>    <dbl>
## 1 (Intercept)  0.882     0.201     4.38  0.0000637
## 2 light       -0.00258    0.00376   -0.685  0.496
```

## 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
```

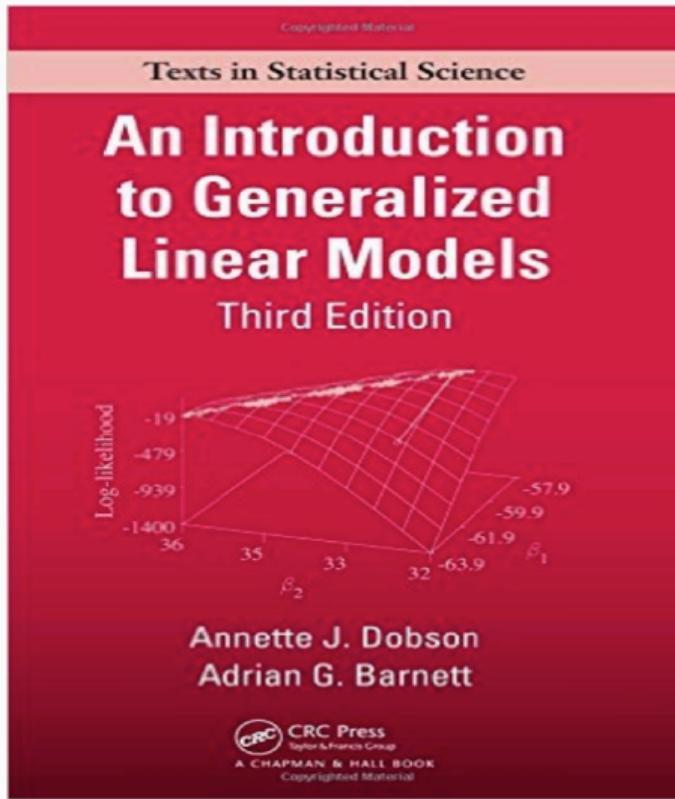
Standard errors do not change here



## GLMs in a nutshell

| Distribution | Link     | Link <sup>-1</sup> | 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

---

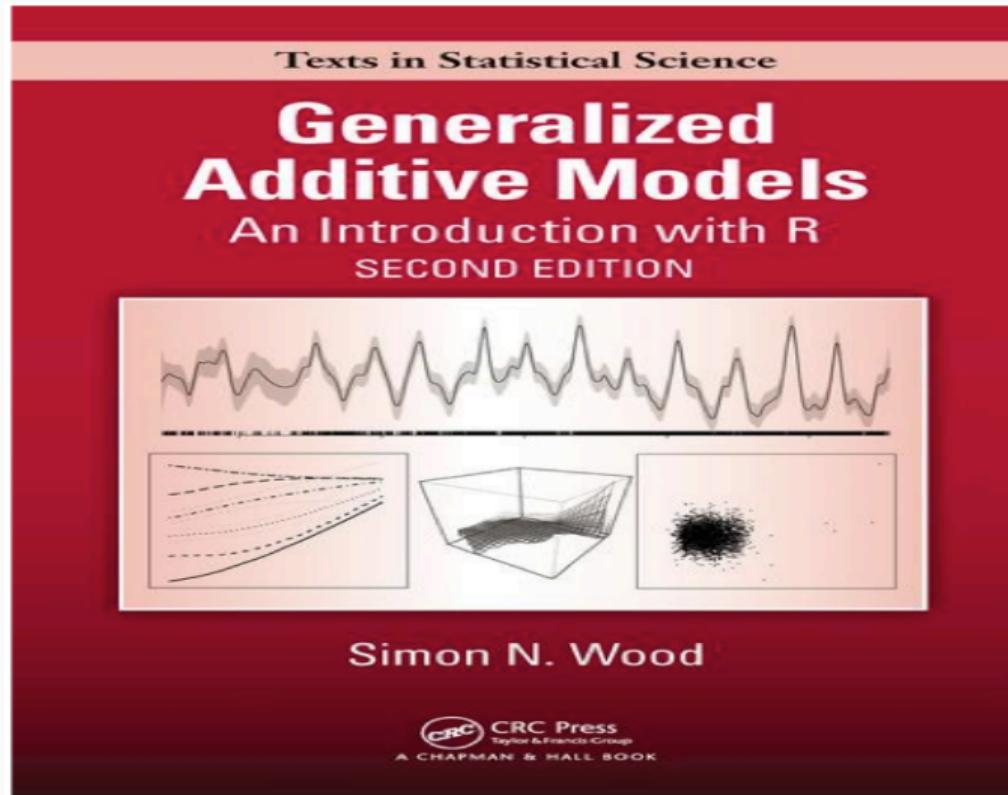
- Distributions and likelihoods
- Hypothesis testing and multimodel inference
- Introduction to Bayesian inference
- Generalized Linear Models (GLMs)
- Generalized Additive Models (GAMs)
- Mixed Effect Models

# **Generalized Additive Models (GAMs)**

---

- 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



## 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?

---

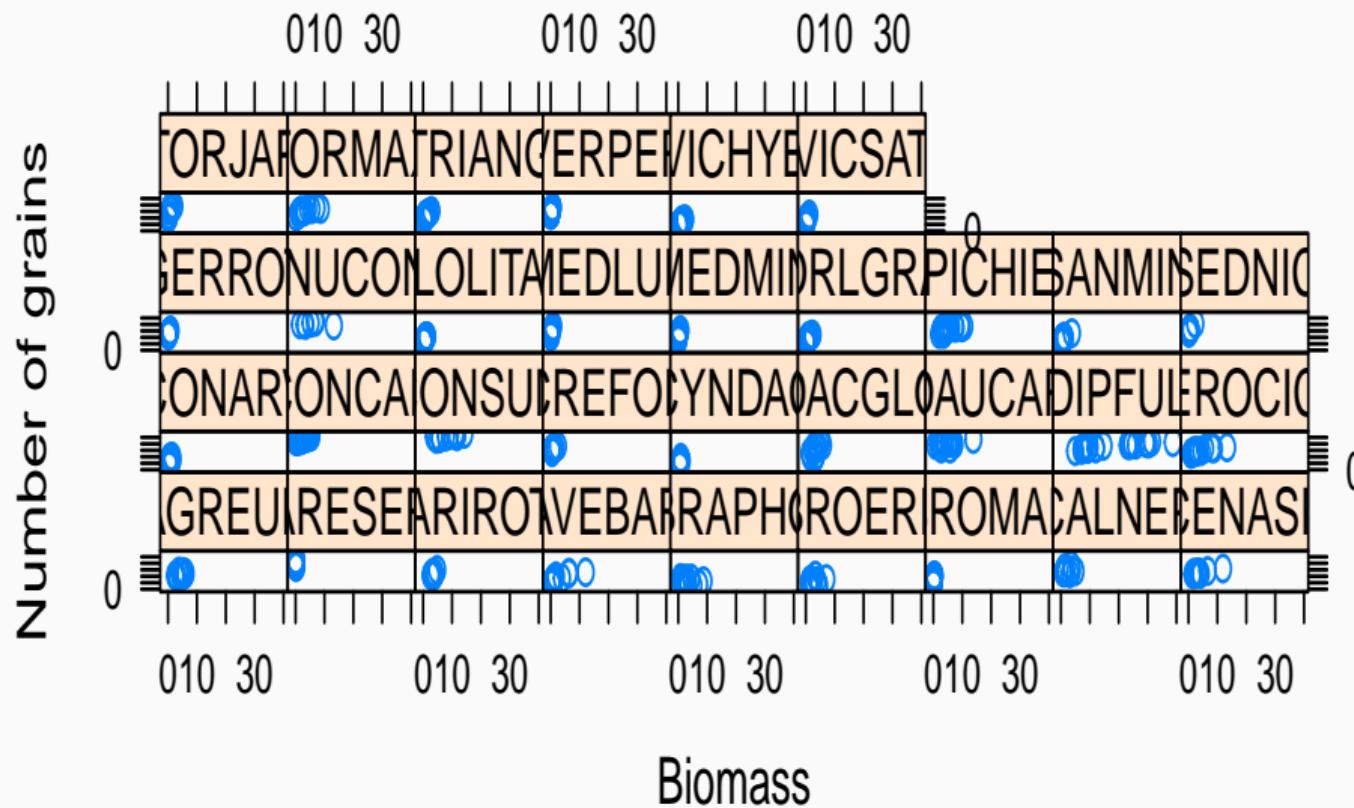
- Interested in variance components (environmental vs. genetic variance)
- Control for bias due to pseudoreplication (time, space, individual)

## Plant example, universality of the allometric relationship?



By Eleni Kazakou, former Master student / Post-doc of the University of the Aegean

## 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

---

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

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

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

## 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?



BENECREATOR.EU

## Back to the plant example

---

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

$$\text{Mean Response}_{i,species} = \beta_{0species} + \beta_1 x_i$$

$$\beta_{0species} \sim \text{Normal}(\mu_{sp}, \sigma_{sp}^2)$$

## Back to the plant example

---

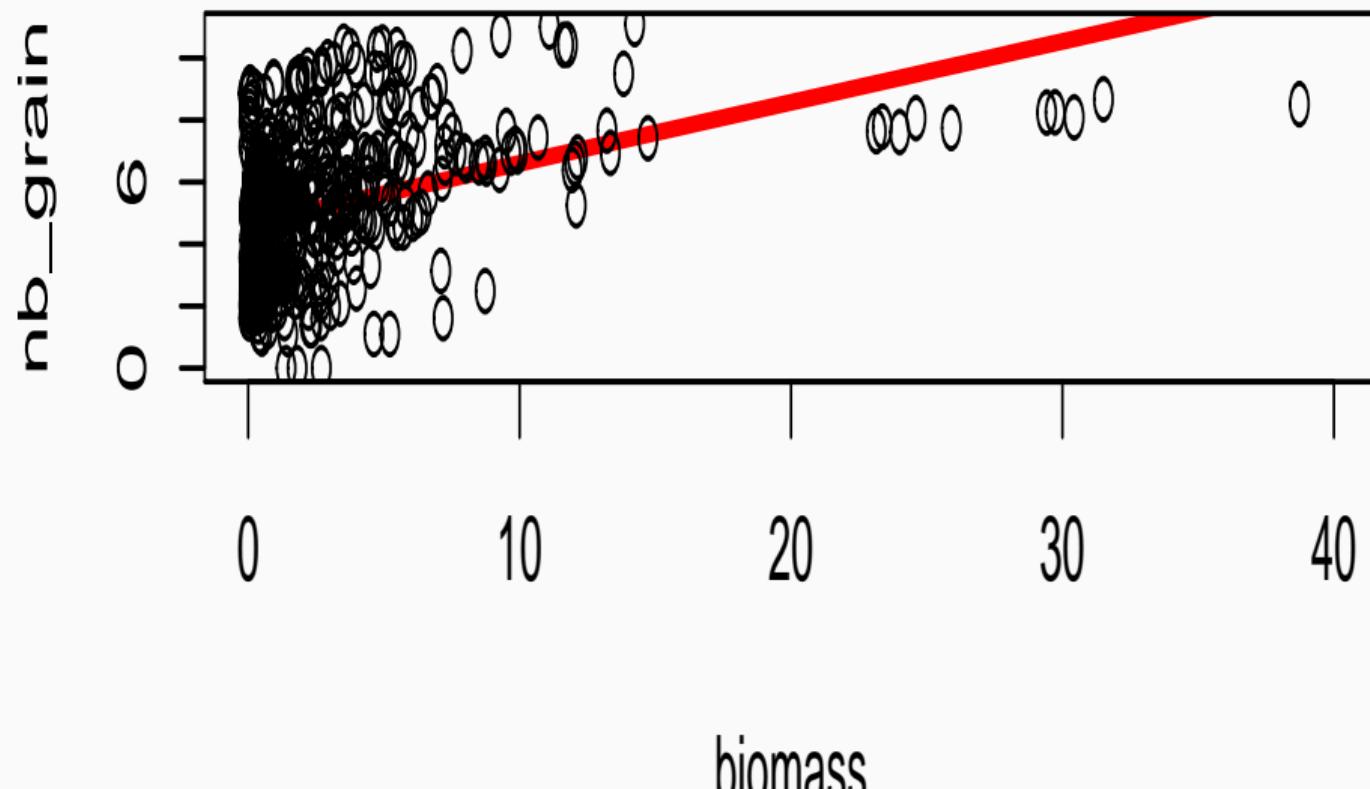
Fit **one** linear model, with no distinction of species: **complete pooling**

```
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
```

## 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
```

## Back to the plant example

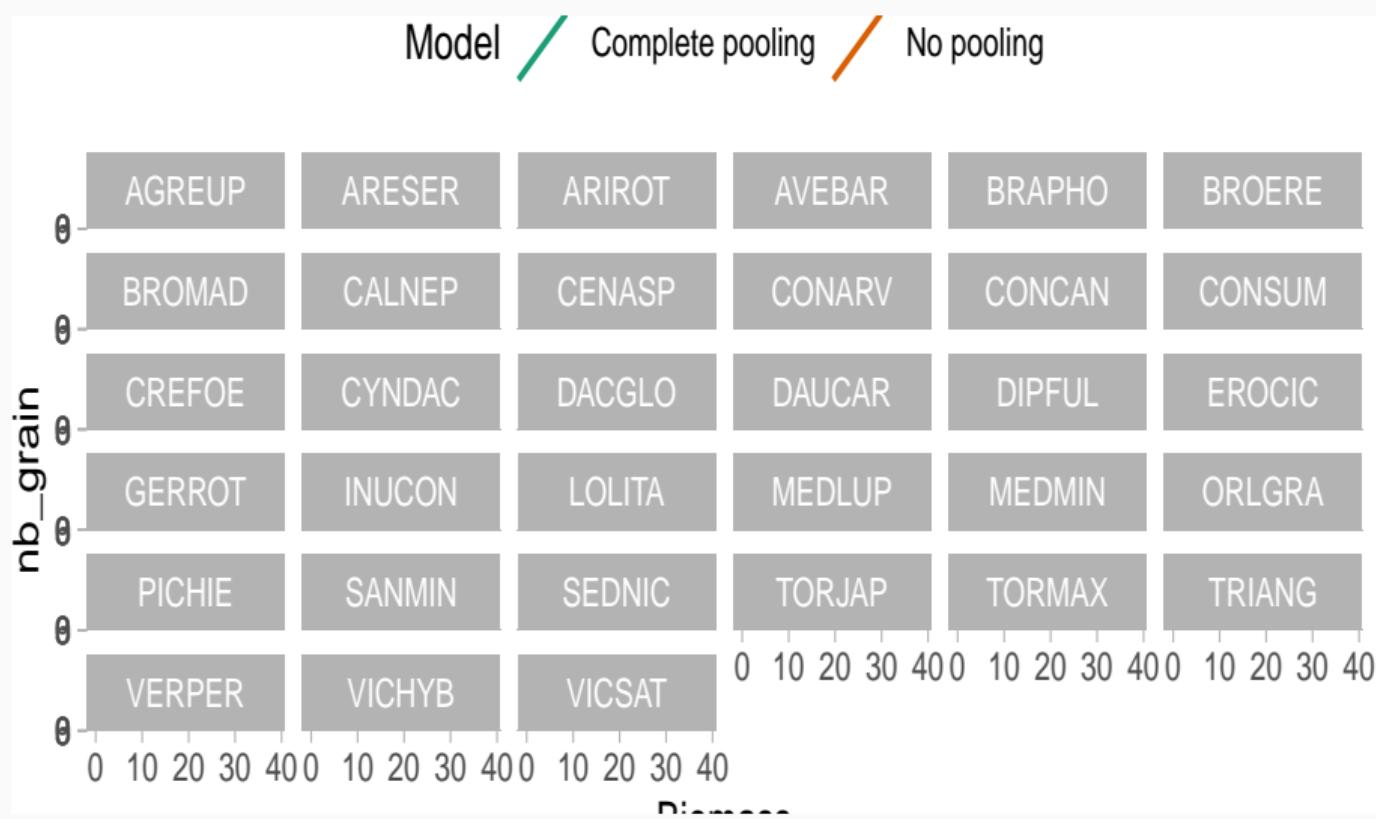
..., with species as random effect on both intercept and slope, **without correlation**

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

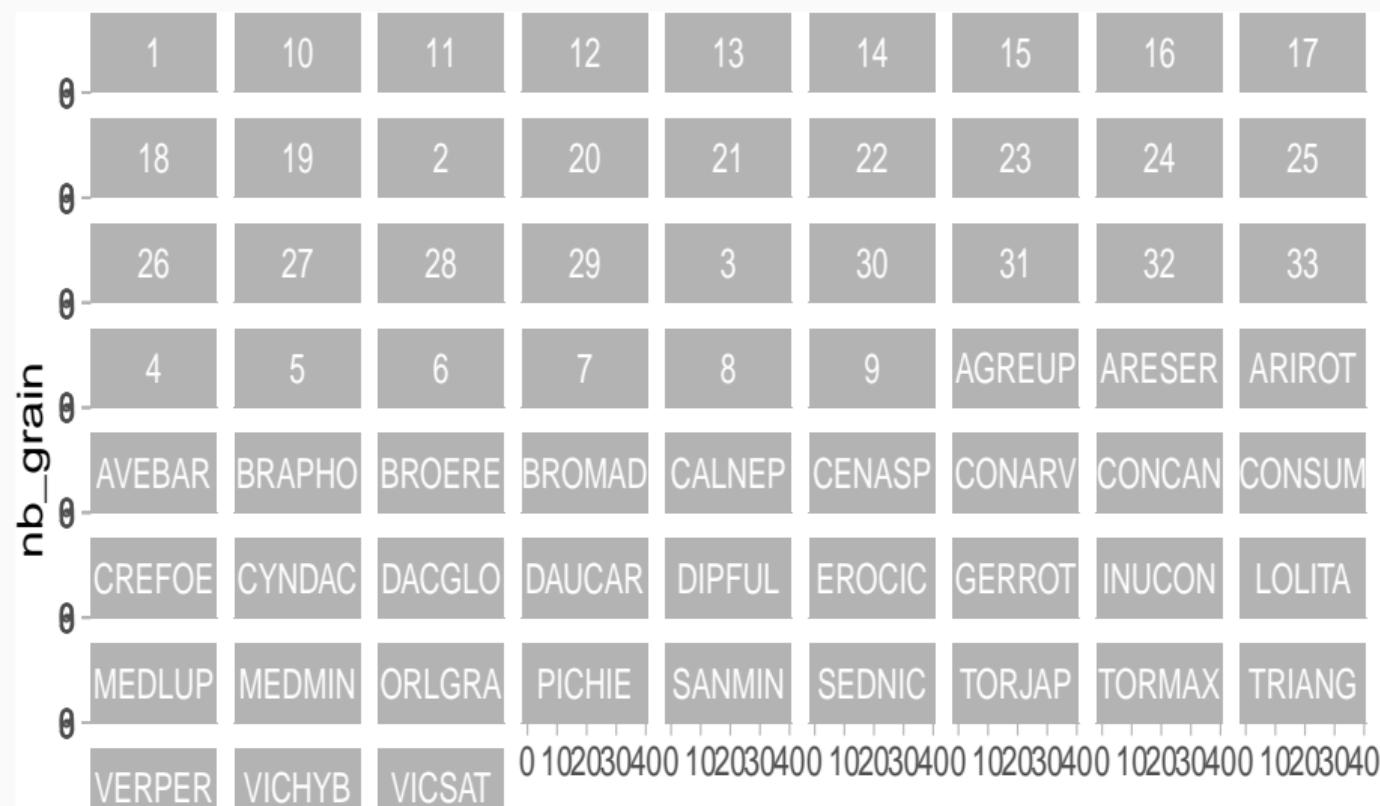
allom.lmm3

## 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
```

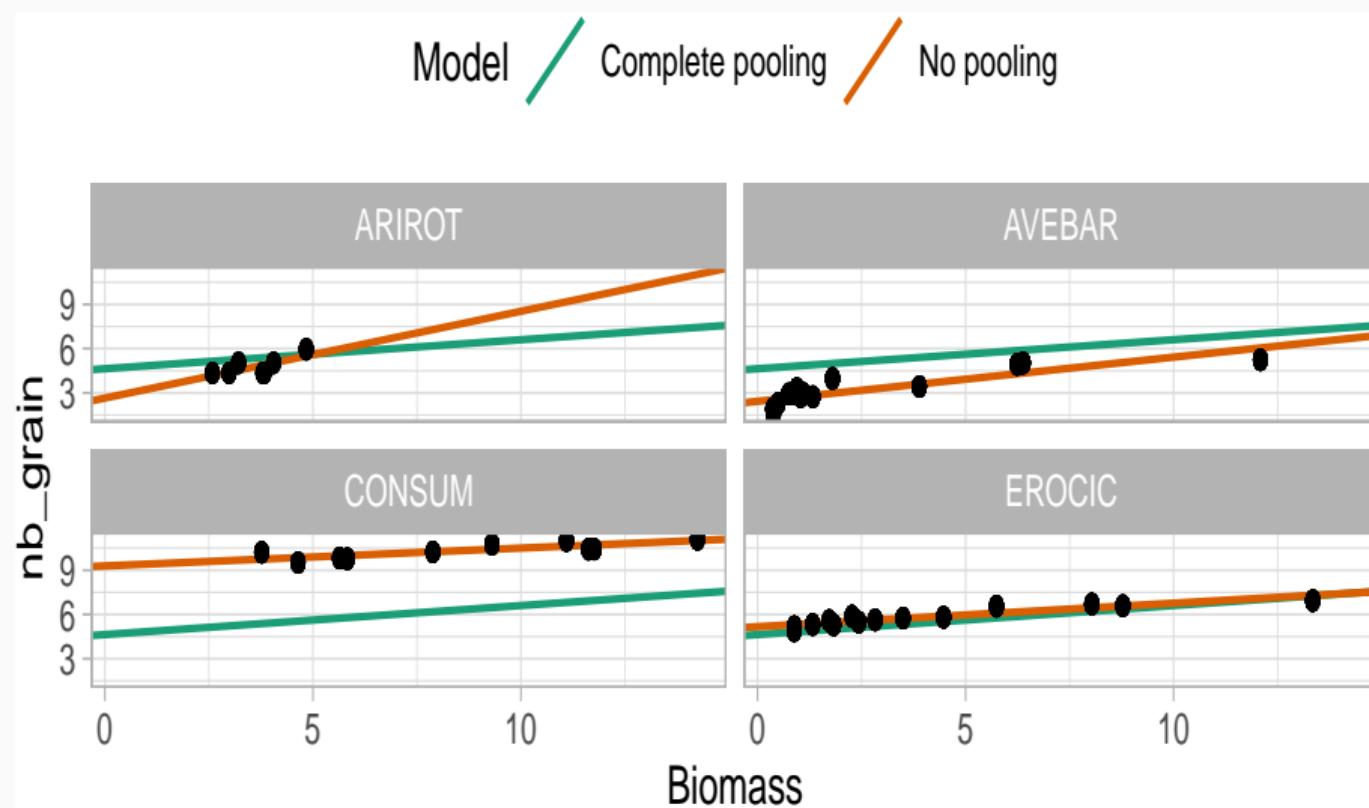
## 'Old school' linear models, complete pooling vs. no pooling



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



Let's zoom in



## **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
```

## 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
```

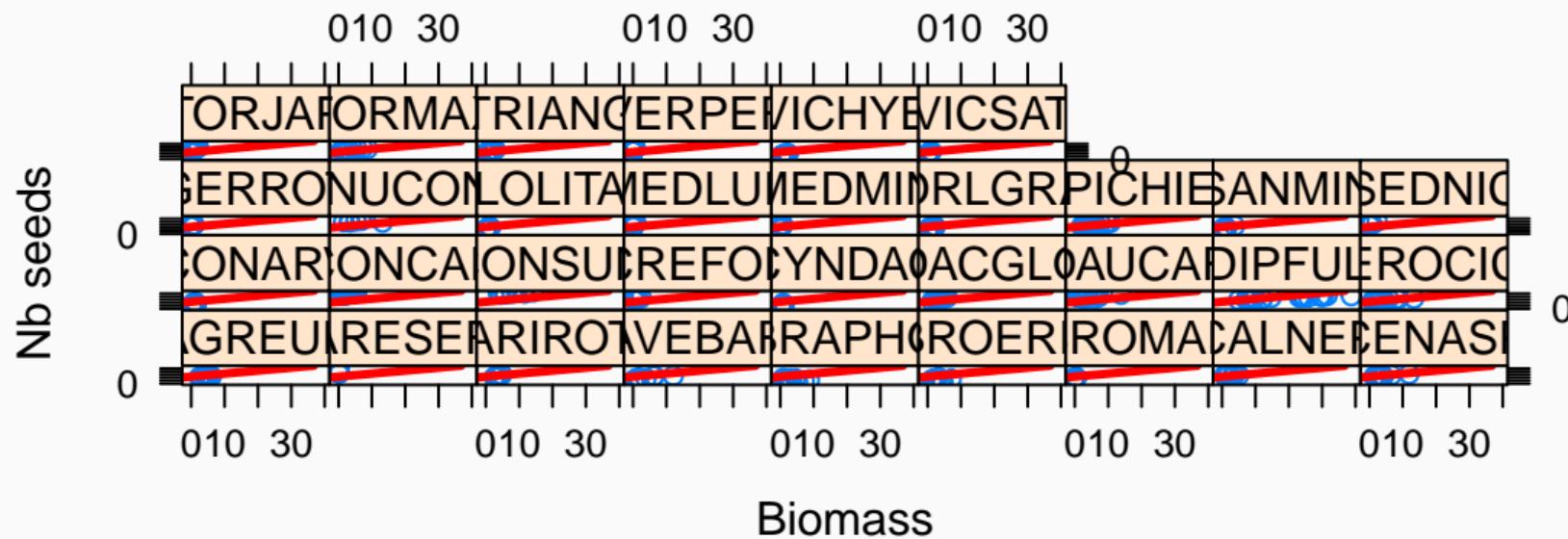
## Display results

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%
## a         4.638   0.110   4.421   4.566   4.637   4.708   4.857
## b         0.197   0.021   0.157   0.183   0.197   0.211   0.238
## sigma.y   2.080   0.066   1.956   2.032   2.079   2.125   2.212
## deviance 2098.782   2.510 2095.998 2096.954 2098.105 2099.923 2105.226
##          n.eff
## a         1800
## b         3000
## sigma.y  3000
```

## Output

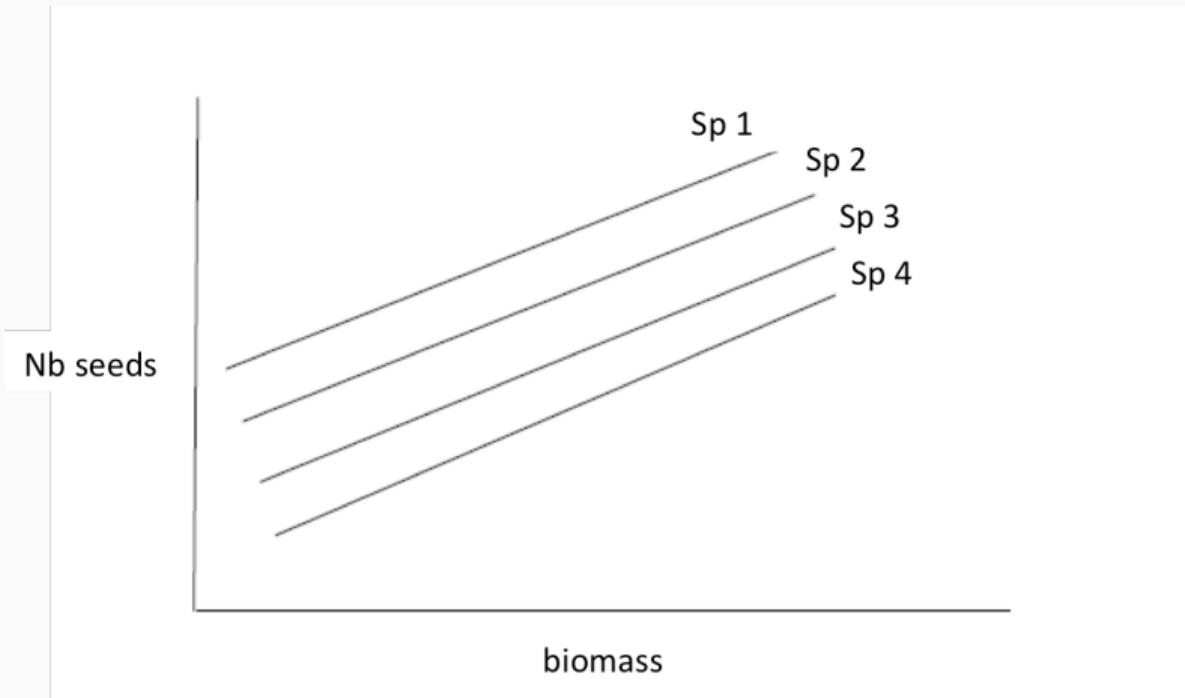
## complete pooling (no species effect)



## 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:

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

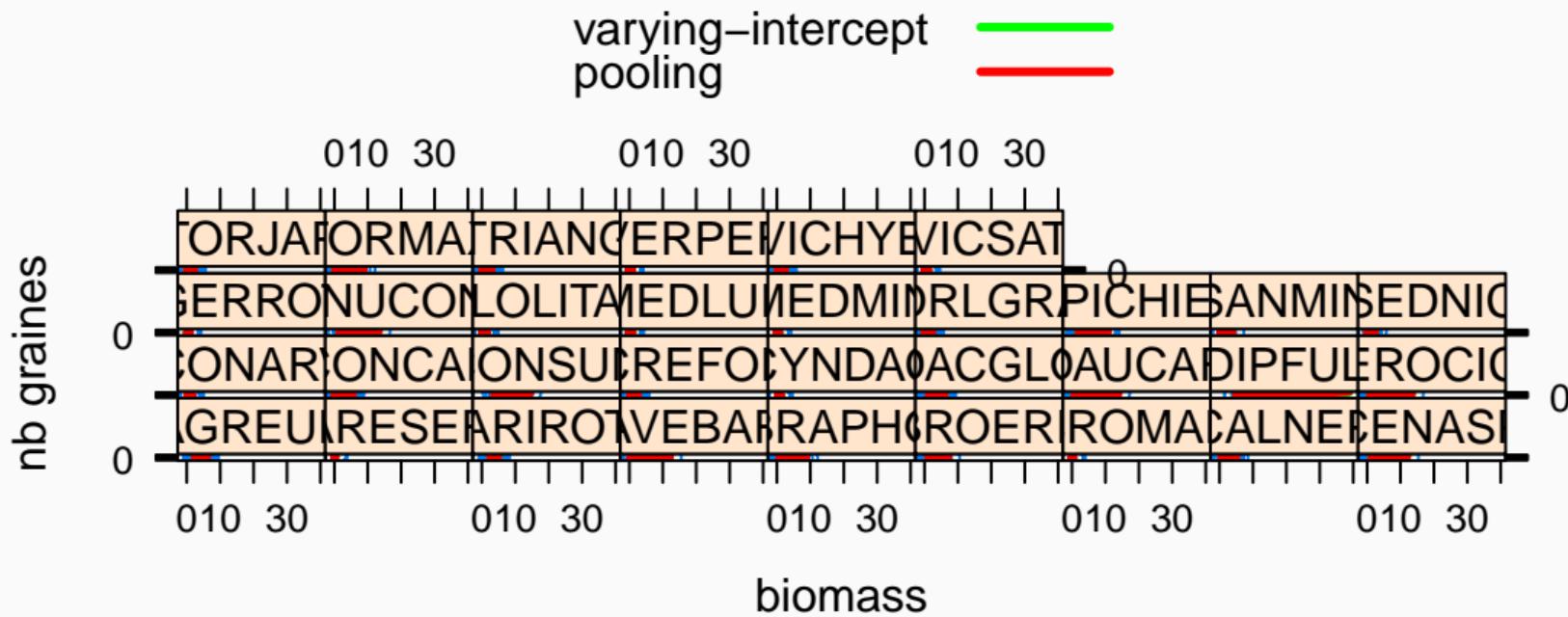
$$\sigma, \sigma_a \sim \text{Uniform}(0, 100)$$

## Varying-intercept model in Jags

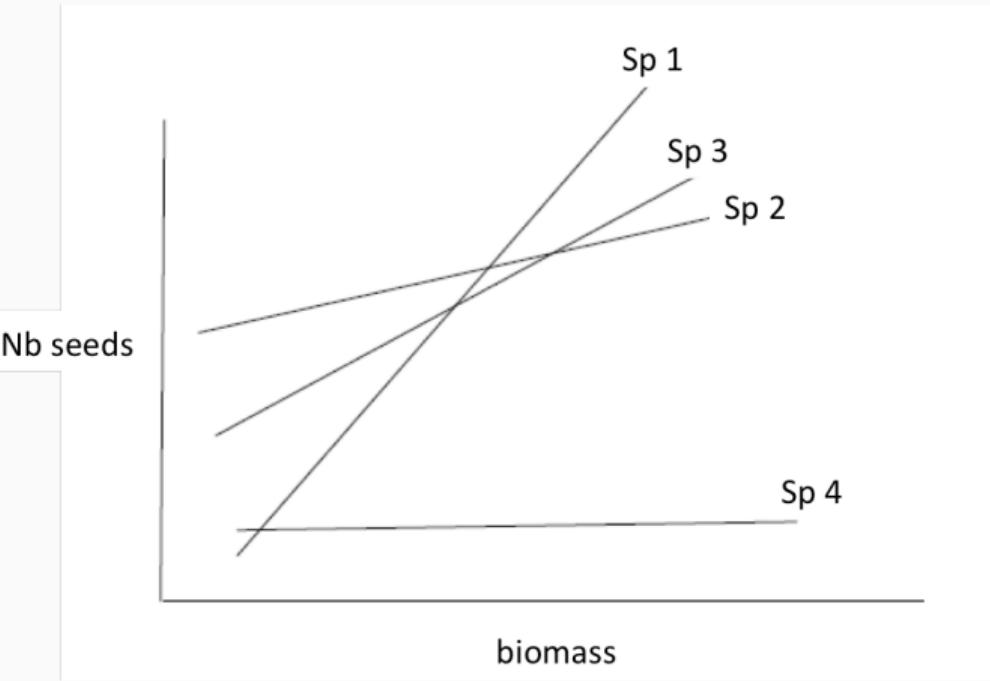
---

```
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)
}
```

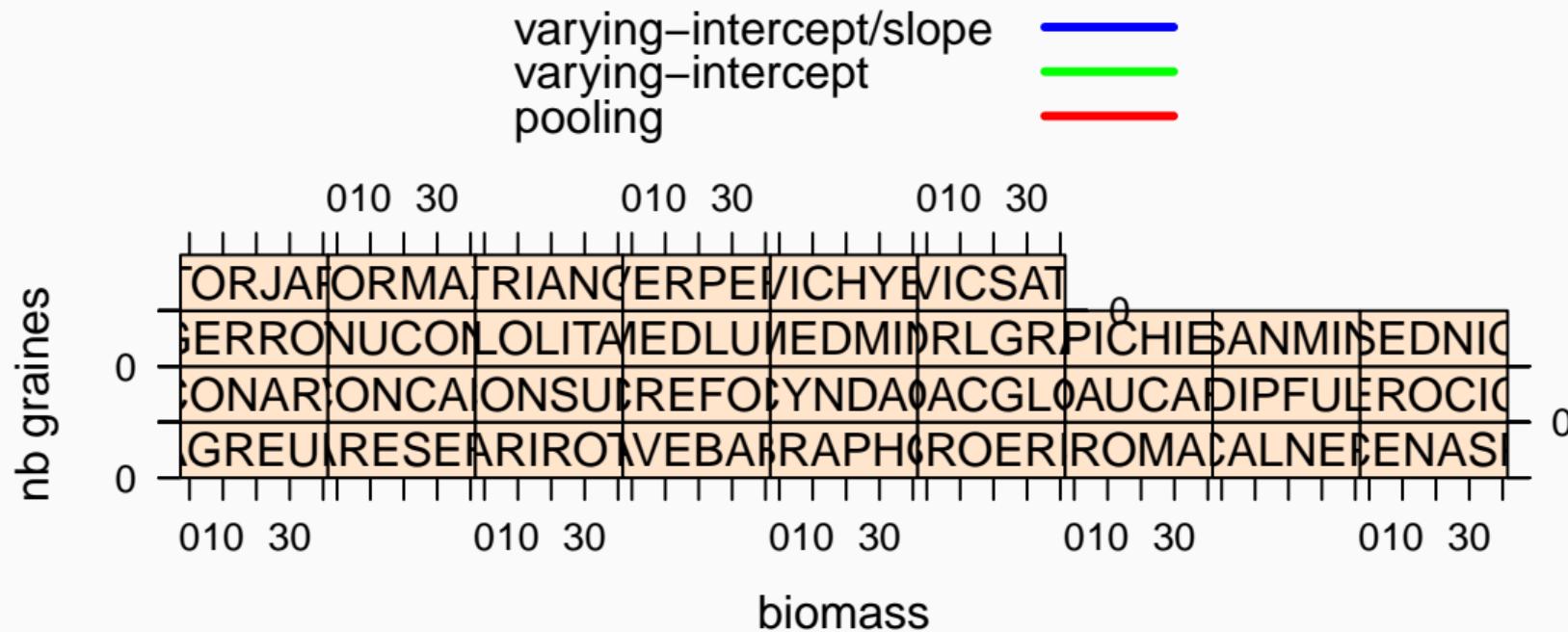
## Compare **complete pooling** vs **varying-intercept**



## 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



## 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)  
  
m  
  
## 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
```

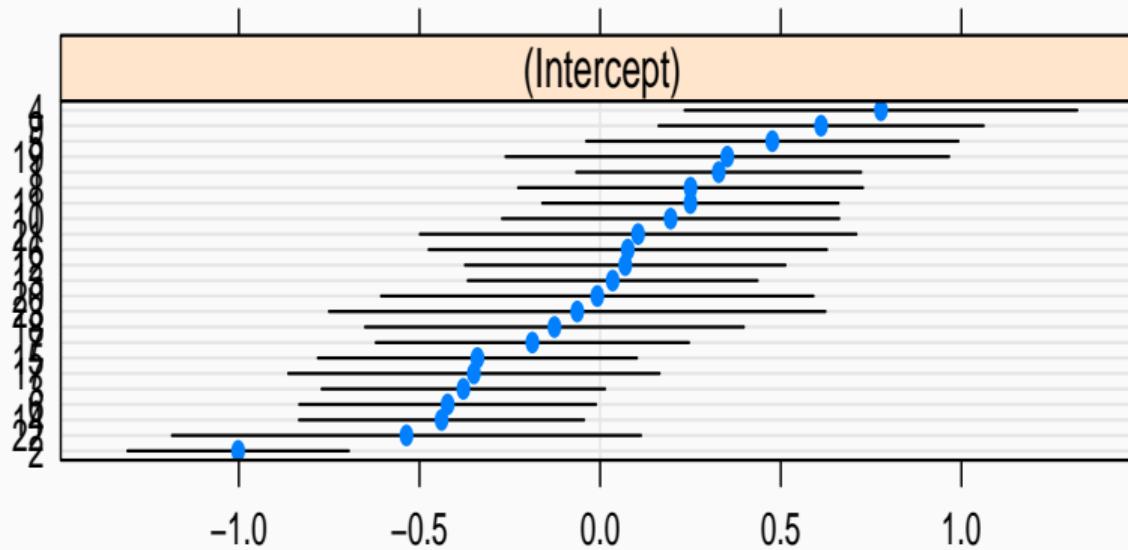
## Plotting effects of model predictors

---

## Yearly random intercepts

```
## $year
```

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>

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

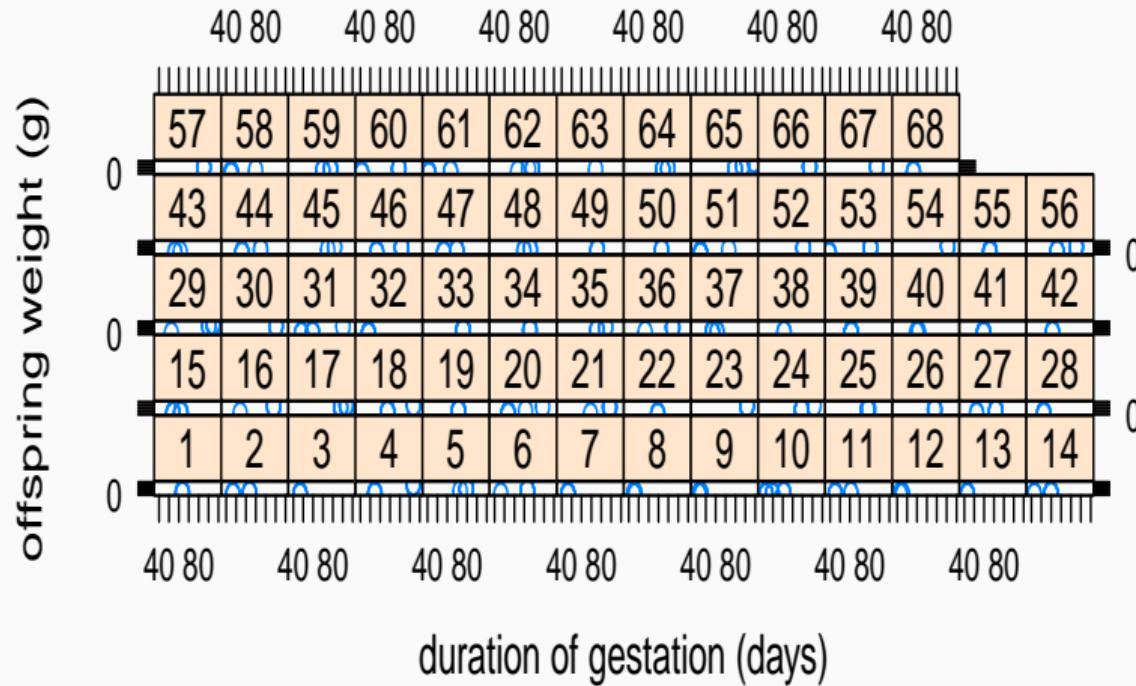
---

## Wild boar example

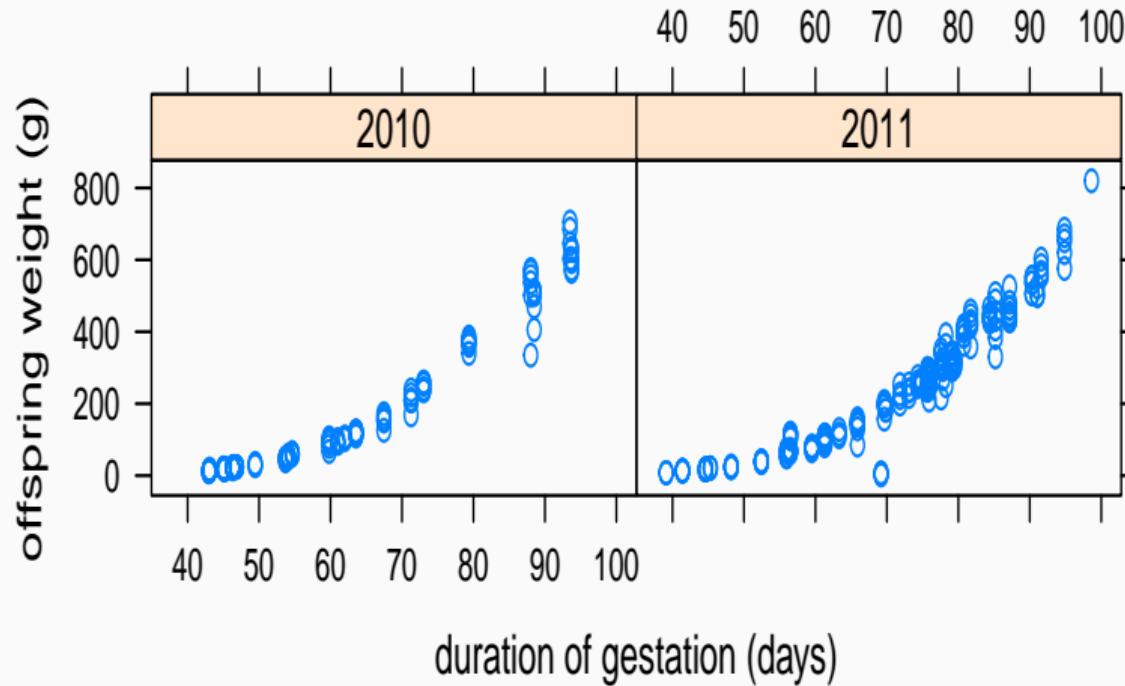
---



## 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

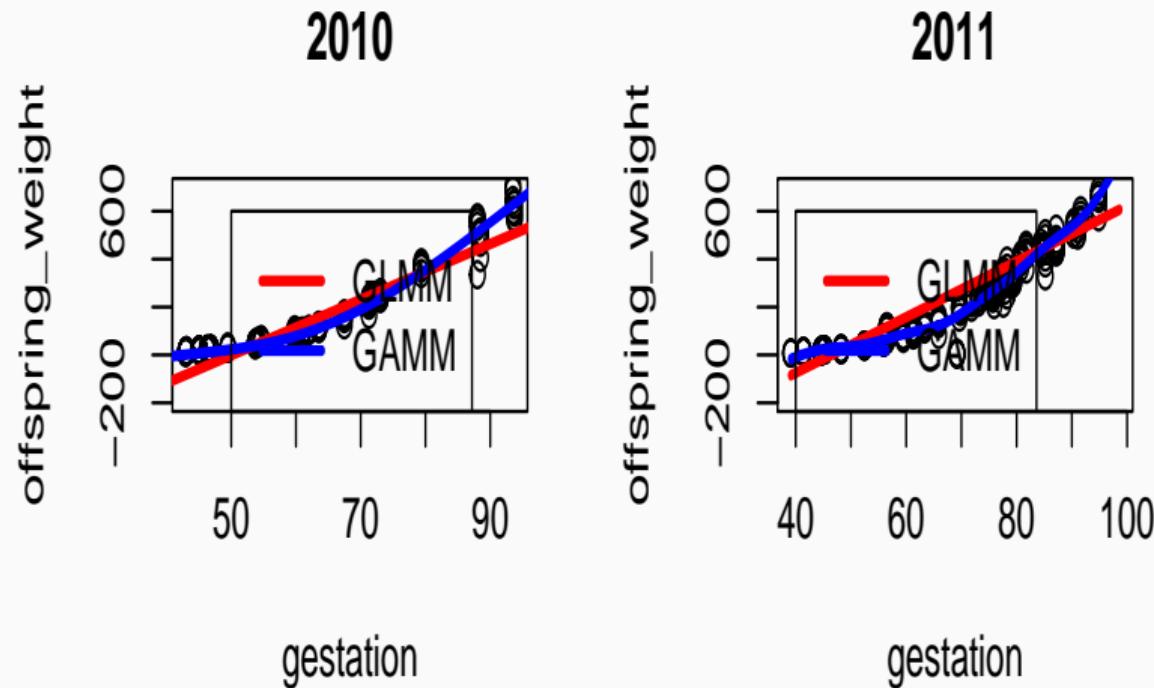
```
## Linear mixed model fit by REML ['lmerMod']
## Formula: offspring_weight ~ gestation + as.factor(year) + (1 | female_id)
##   Data: dat
## REML criterion at convergence: 3881.633
## Random effects:
##   Groups      Name        Std.Dev.
##   female_id (Intercept) 43.35
##   Residual            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

## 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



## **Summary**

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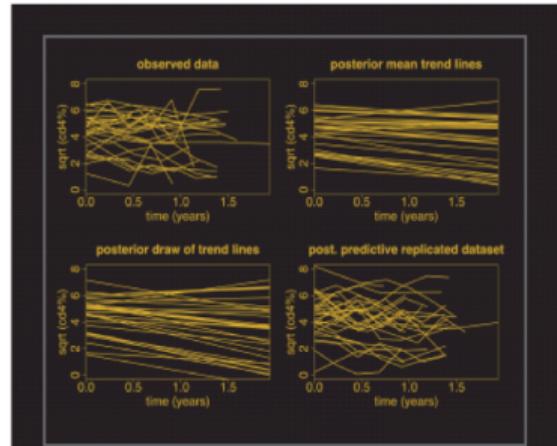
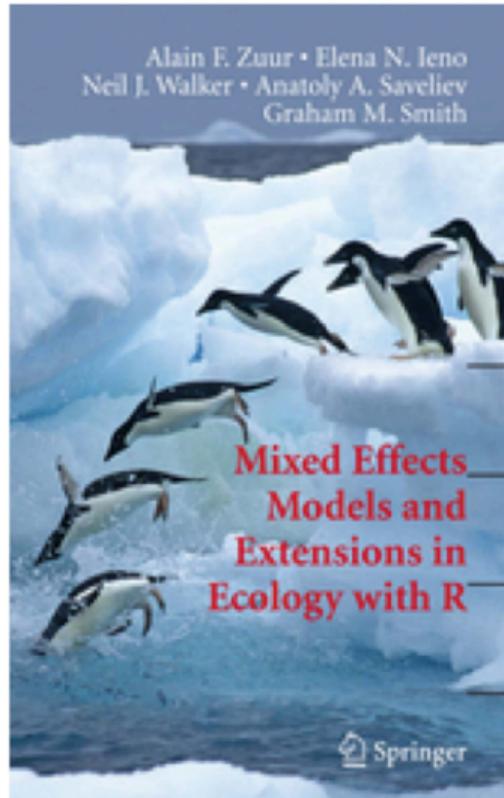
## Mixed models in a nutshell

- 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

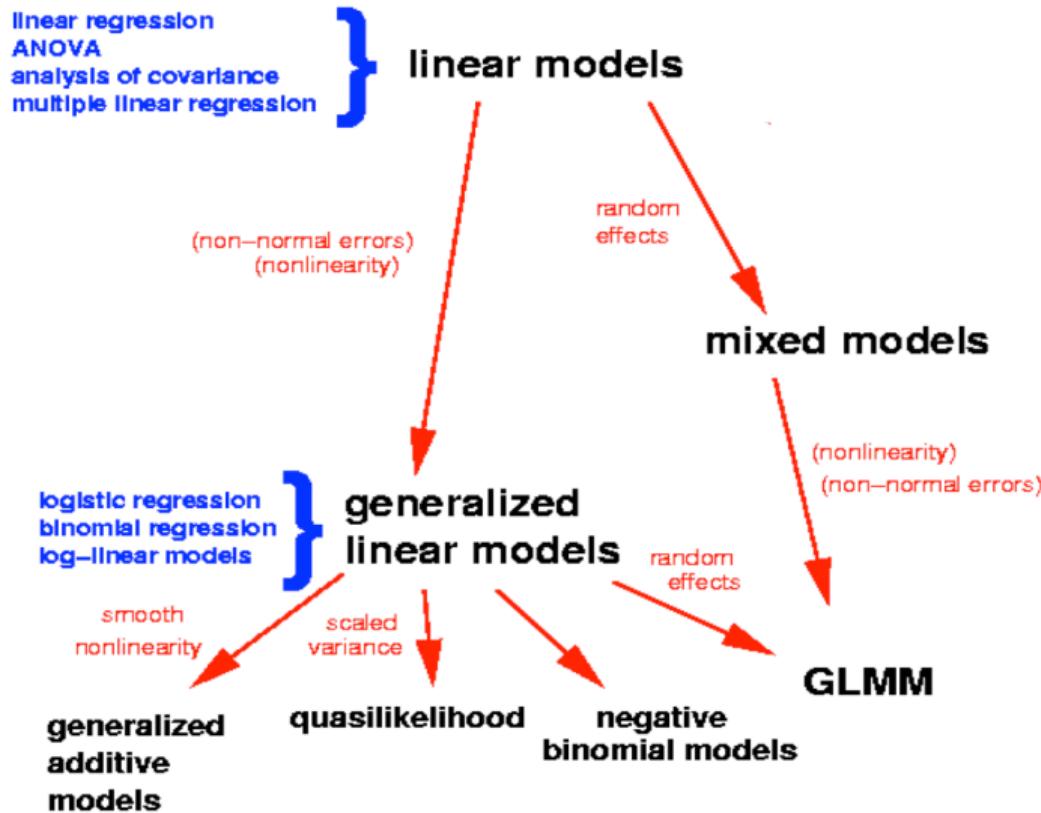
## This Class

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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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