# Statistics for EES Linear mixed-effects models 

Dirk Metzler

July 8, 2020

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## 1 Indidual differences in exploratory great tits

In slides:<br>mmons.wikimedia.org/wiki/File:Tihane.jpg (creative commons license)

Great Tit
Parus major
(German: Kohlmeise)

## References

[1] Niels J. Dingemanse, M. Moiron, Y.G. Araya-Ajoy, A. Mouchet, R.N. Abbey-Lee (2020) Individual variation in age-dependent reproduction: Fast explorers live fast but senesce young? J Anim Ecol. 89:601-613

- 12 plots of 50 nest boxes observed for 7 years
- 1209 observations with 813 birds, including e.g.:
- clutch size and number of fledglings in a year
- how exploratory is a bird (experiment)
- Main question: do more exploratory birds have their reproductive phase earlier in life?
- Here we focus on age-dependence of exploratory behavior

```
>str(dat)
'data.frame': 1209 obs. of 16 variables:
    $ BirdID : Factor w/ 813 levels "256","271","273",..: 1 1 1 1 2 3 4 4 4 5 ...
    $ Plot : Factor w/ 12 levels "10","11","12",..: 11 11 11 11 1 1 7 7 7 7 ...
    $ BroodID : int 98 533 1702 2902 129 319 207 438 1507 210 ...
    $ Year : Factor w/ 7 levels "2010","2011",..: 1 2 3 4 1 2 1 2 3 1 ...
    $ MassSummer : num 18.1 18.1 17.9 18.4 18.3 17.2 17.5 16.5 16.5 18.1 ...
$ ExpFieldScore: int 43 52 50 58 71 67 62 58 61 57 ...
$ ClutchSize : int 7981191177 811 ...
```

```
$ NumberFledged: int 0 6 5 0 0 10 4 7 7 9 ...
$ AvgDay14Mass : num NA 17.4 17.3 14.1 12.8 ...
$ PredTreat : int 0 0 0 2 0 0 0 0 0 0 %..
$ AgeBreeder : int 0 1 2 3 0 1 0 1 2 0 \ldots..
$ MinAge : int 0 0 0 0 0 1 0 0 0 0 \ldots..
$ MaxAge : int 3 3 3 3 0 1 2 2 2 0 ...
$ Local : int 0 0 0 0 0 0 0 0 0 0 \ldots..
$ Dead : int 1 1 1 1 1 1 1 1 1 1 1 1 %...
$ BSManip : int 0 3 0 0 1 1 0 0 0 1 \ldots..
```

For observation $i$ (line $i$ in data frame) we denote as
$b_{i}$ the bird ID (factor BirdID with 813 levels)
$a_{i}$ age of the bird at that time (numerical AgeBreeder)
$X_{i}$ how explorative was the bird at that time (numerical ExpFieldScore)
$y_{i}$ year of observation (factor Year with 7 levels)
$p_{i}$ plot to which the bird's nest belonged (factor Plot with 12 levels)
First model (only fixed effects):

$$
X_{i}=\delta+\alpha \cdot a_{i}+\beta_{b_{i}}+\gamma_{y_{i}}+\rho_{p_{i}}+\varepsilon_{i}
$$

$\varepsilon_{i} \sim \mathcal{N}\left(0, \sigma^{2}\right)$
needs to estimate $1+1+812+6+11+1=832$ parameters

```
> mod.fix <- lm(ExpFieldScore ~ AgeBreeder + BirdID + Plot + Year,dat)
> drop1(mod.fix,test="F")
Single term deletions
Model:
ExpFieldScore ~ AgeBreeder + BirdID + Plot + Year
            Df Sum of Sq RSS AIC F value Pr (>F)
<none> 101537 6762.7
AgeBreeder 0 0 101537 6762.7
BirdID 779 376408 477945 6992.3 1.6941 1.054e-08 ***
Plot 1 222 101759 6763.2 0.7779 0.378394
Year 5 5428 106965 6812.8 3.8062 0.002264 **
Signif. codes: 0 *** 0.001 ** 0.01 * 0.05 . 0.1 1
> summary(mod.fix)
Cal1:
lm(formula = ExpFieldScore ~ AgeBreeder + BirdID + Plot + Year,
    data = dat)
Residuals: 
Coefficients: (11 not defined because of singularities)
Estimate Std. Error t value Pr(> |t|)
(Intercept) 6.005e+01 8.780e+00 6.840 3.46e-11 ***
AgeBreeder 
BirdID271 1.095e+01 1.903e+01 0.575 0.565622
BirdID273 
BirdID276 rrererere+00 
BirdID277 rren.054e+00 1.903e+01 
```



```
BirdID314 
lllll
BirdID323 -1.018e+00 1.292e+01 
BirdID324 2.315e+01 1.896e+01 1.221 0.222934
```

| BirdID344 | $1.095 \mathrm{e}+01$ | $1.903 \mathrm{e}+01$ | 0.575 | 0.565622 |
| :---: | :---: | :---: | :---: | :---: |
| BirdID345 | -1.805e+01 | $1.903 \mathrm{e}+01$ | -0.949 | 0.343503 |
| BirdID 349 | -2.005e+01 | $1.903 \mathrm{e}+01$ | -1.054 | 0.292779 |
| BirdID363 | -1.405e+01 | $1.903 \mathrm{e}+01$ | -0.738 | 0.460769 |
| BirdID364 | $3.316 \mathrm{e}+00$ | $1.292 \mathrm{e}+01$ | 0.257 | 0.797546 |
| BirdID 367 | $-3.405 \mathrm{e}+01$ | $1.903 \mathrm{e}+01$ | -1.789 | 0.074445 |
| - | . | . | . |  |
| . | . | . |  |  |
| - | . | - | - |  |
| . |  |  | . |  |
| . | . | . |  |  |
| . |  |  |  |  |
| BirdID18269 | $2.556 \mathrm{e}+00$ | $1.899 \mathrm{e}+01$ | 0.135 | 0.892997 |
| BirdID18583 | $8.946 \mathrm{e}+00$ | $1.903 \mathrm{e}+01$ | 0.470 | 0.638661 |
| Plot11 | $-2.120 \mathrm{e}+01$ | $2.404 \mathrm{e}+01$ | -0.882 | 0.378394 |
| Plot12 | NA | NA | NA | NA |
| Plot13 | NA | NA | NA | NA |
| Plot14 | NA | NA | NA | NA |
| Plot15 | NA | NA | NA | NA |
| Plot16 | NA | NA | NA | NA |
| Plot17 | NA | NA | NA | NA |
| Plot18 | NA | NA | NA | NA |
| Plot19 | NA | NA | NA | NA |
| Plot20 | NA | NA | NA | NA |
| Plot21 | NA | NA | NA | NA |
| Year2011 | $-6.593 \mathrm{e}+00$ | $3.012 \mathrm{e}+00$ | -2.189 | 0.029235 |
| Year2012 | $2.313 \mathrm{e}+00$ | $3.002 \mathrm{e}+00$ | 0.770 | 0.441682 |
| Year2013 | -5.277e+00 | $3.043 \mathrm{e}+00$ | -1.734 | 0.083735 |
| Year2014 | $9.874 \mathrm{e}-01$ | $3.040 \mathrm{e}+00$ | 0.325 | 0.745564 |
| Year2015 | -7.741e-01 | $3.095 \mathrm{e}+00$ | -0.250 | 0.802666 |
| Year2016 | NA | NA | NA | NA |
| --- |  |  |  |  |
| Signif. codes: 0 *** $0.001 * * 0.01 * 0.05$. 0.1 |  |  |  |  |
| Residual standard error: 16.89 on 356 degrees of freedom (55 observations deleted due to missingness) |  |  |  |  |
| Multiple R-squared: 0.8028 ,Adjusted R-squared: 0 |  |  |  |  |
| F-statistic: 1.819 on 797 and 356 DF , p-value: $1.133 \mathrm{e}-10$ |  |  |  |  |

## mixed-effects model

$X_{i}=\delta+\alpha \cdot a_{i}+\beta_{b_{i}}+\gamma_{y_{i}}+\rho_{p_{i}}+\varepsilon_{i}$
$\beta_{1}, \ldots, \beta_{813} \sim \mathcal{N}\left(0, \sigma_{\beta}^{2}\right) \quad \gamma_{2010}, \ldots, \gamma_{2016} \sim \mathcal{N}\left(0, \sigma_{\gamma}^{2}\right) \quad \rho_{1}, \ldots, \rho_{12} \sim \mathcal{N}\left(0, \sigma_{\rho}^{2}\right) \quad \varepsilon_{1}, \ldots, \varepsilon_{1154} \sim \mathcal{N}\left(0, \sigma^{2}\right)$ needs to estimate 6 parameters: $\delta, \alpha, \sigma_{\beta}, \sigma_{\gamma}, \sigma_{\rho}, \sigma$

In R formula notation:

```
ExpFieldScore ~ AgeBreeder + (1|BirdID) + (1|Year) + (1|Plot)
```

```
> library(lme4)
> mod <- lmer(ExpFieldScore ~ AgeBreeder + (1|BirdID) + (1|Year) + (1|Plot), data=dat, subset= !is.na(ExpFieldScore) & !is.na(AgeBreeder))
> summary(mod)
Linear mixed model fit by REML ['lmerMod']
```

Formula: ExpFieldScore ~ AgeBreeder + (1 | BirdID) + (1 | Year) + (1 | Plot)
Data: dat
Subset: !is.na(ExpFieldScore) \& !is.na(AgeBreeder)
REML criterion at convergence: 10204.9
Scaled residuals:

| Min | $1 Q$ | Median | $3 Q$ |
| ---: | ---: | ---: | ---: |
| -3.9693 | -0.5190 | -0.0038 | 0.5368 |
|  | 2.8090 |  |  |

Random effects:
$\begin{array}{lll}\text { Random } & \text { effects: } \\ \text { Groups } & \text { Name } & \text { Variance Std.Dev. }\end{array}$
BirdID (Intercept) $141.151 \quad 11.881$
$\begin{array}{llrr}\text { BirdiD } & \text { (Intercept) } & 141.151 & 11.881 \\ \text { Plot } & \text { (Intercept) } & 10.732 & 3.276\end{array}$
$\begin{array}{lrrr}\text { Year } & \text { (Intercept) } & 8.154 & 2.856 \\ \text { Residual } & & 277.688 & 16.664\end{array}$
Number of obs: 1154, groups: BirdID, 791; Plot, 12; Year, 7
Fixed effects

(Intercept) | Estimate Std. Error t value |  |
| :--- | :--- |
| 71.0436 | 1.6378 |

$\begin{array}{llll}\text { (Intercept) } & 71.0436 & 1.6378 & 43.38 \\ \text { AgeBreeder } & -3.1450 & 0.6265 & -5.02\end{array}$
Correlation of Fixed Effects:
(Intr)
AgeBreeder
-0.245

Is dependence on age significant?

```
> mod0 <- lmer(ExpFieldScore ~ (1|BirdID) + (1|Year) + (1|Plot),
+ data=dat, subset= !is.na(ExpFieldScore) & !is.na(AgeBreeder))
> library(pbkrtest)
```

```
> KRmodcomp(mod,mod0)
F-test with Kenward-Roger approximation; computing time: 2.26 sec.
large : ExpFieldScore ~ AgeBreeder + (1 | BirdID) + (1 | Year) + (1 | Plot)
small : ExpFieldScore ~ (1 | BirdID) + (1 | Year) + (1 | Plot)
            stat ndf ddf F.scaling p.value
Ftest 24.625 1.000 1014.820 1 8.162e-07 ***
Signif. codes: 0 *** 0.001 ** 0.01 * 0.05 . 0.1 1
>
```


## Is bird-ID effect significant?

```
> mod.nb <- lmer(ExpFieldScore ~ AgeBreeder + (1|Year) + (1|Plot),
+ data=dat, subset= !is.na(ExpFieldScore) & !is.na(AgeBreeder))
> anova(mod.nb,mod)
refitting model(s) with ML (instead of REML)
Data: dat
Subset: !is.na(ExpFieldScore) & !is.na(AgeBreeder)
Models:
mod.nb: ExpFieldScore ~ AgeBreeder + (1 | Year) + (1 | Plot)
mod: ExpFieldScore ~ AgeBreeder + (1 | BirdID) + (1 | Year) + (1 | Plot)
    Df AIC BIC logLik deviance Chisq Chi Df Pr(>Chisq)
mod.nb 5 10281 10307-5135.7 10271
mod 6 10221 10251 -5104.3 10209 62.824 1 2.26e-15 ***
Signif. codes: 0 *** 0.001 ** 0.01 * 0.05 . 0.1 1
```


## Is bird-ID effect significant?

```
> PBmodcomp(mod,mod.nb) ## more robust but takes a while
Parametric bootstrap test; time: 109.31 sec; samples: 1000 extremes: 0;
Requested samples: 1000 Used samples: 570 Extremes: 0
large : ExpFieldScore ~ AgeBreeder + (1 | BirdID) + (1 | Year) + (1 | Plot)
small : ExpFieldScore ~ AgeBreeder + (1 | Year) + (1 | Plot)
    stat df p.value
LRT 62.824 1 2.22e-15 ***
PBtest 62.824 0.001751 **
---
Signif. codes: 0 *** 0.001 ** 0.01 * 0.05 . 0.1 1
```


## Parametric Bootstrapping

Is model mod significantly better than a null model mod0?

- Fit mod and mod0 to the data; let $L$ be the likelihood ratio of mod vs. mod0.
- repeat $N$ times (e.g. $N=1000$ ):
- simulate data from mod0 (with parameters as fitted to original data).
- fit both models mod and mod0 to the simulated data and calculate the likelihood ratio $L_{i}$ for each iteration $i$.
- p-value: fraction of $\left(L, L_{1}, L_{2}, \ldots, L_{N}\right)$ that are at least as large as $L$.
library(lattice)
qm <- qqmath (ranef (mod, condVar=TRUE))
$\mathrm{qm}[[1]]$; qm[[2]]; qm[[3]]



plot(mod)
qqnorm(residuals(mod))



Does age-dependence of exploring vary among birds?

$$
X_{i}=\delta+\alpha \cdot a_{i}+\beta_{b_{i}}+\phi_{b_{i}} \cdot a_{i}+\gamma_{y_{i}}+\rho_{p_{i}}+\varepsilon_{i}
$$

$\phi_{1}, \ldots, \phi_{813} \sim \mathcal{N}\left(0, \sigma_{\phi}^{2}\right)$
$>\bmod 2<-\operatorname{lmer}(E x p F i e l d S c o r e ~ \sim ~ A g e B r e e d e r ~+~(1 ~+~ A g e B r e e d e r ~| | ~ B i r d I D) ~+~(1 \mid Y e a r) ~+~(1 \mid P l o t), ~$
$+$ data=dat, subset= !is.na(ExpFieldScore) \& !is.na(AgeBreeder))
> PBmodcomp (mod2, mod) \#\# takes a while
Parametric bootstrap test; time: 139.38 sec ; samples: 1000 extremes: 2 ;
Requested samples: 1000 Used samples: 658 Extremes: 2
large : ExpFieldScore ~AgeBreeder + ( (1 | BirdID) + (0 + AgeBreeder | BirdID) ) + (1 | Year) + (1 | Plot)
small : ExpFieldScore ~ AgeBreeder + (1 | BirdID) + (1 | Year) + (1 | Plot)
stat df p.value
LRT 7.991710 .004699 **
PBtest 7.9917 0.004552 **
Signif. codes: $0 * * * 0.001 * * 0.01 * 0.05$. $0.1 \quad 1$
Warnings:
1: In checkConv(attr (opt, "derivs"), opt\$par, ctrl = control\$checkConv, : unable to evaluate scaled gradient
2: In checkConv(attr(opt, "derivs"), opt\$par, ctrl = control\$checkConv, : Model failed to converge: degenerate Hessian with 1 negative eigenvalues

## 2 The random effect of the beach

Image in slides:<br>https://commons.wikimedia.org/wiki/File:Wadden_sea_and_a_silhouette_of_the_Maria_church_in_Wierum.jpg

(creative commons license)
We revisit the RIKZ dataset.
Species abundance and many other variables were measured at 9 beaches.
On every beach, 5 plots were sampled in the intertidal range.
Each plot was sampled only once. Thus, each line in the data table corresponds to one plot.

```
> rikz <- read.csv("RIKZ_Tab4.csv")
> rikz$Beach <- factor(rikz$Beach)
> rikz$Week <- factor(rikz$Week)
> str(rikz)
'data.frame': 45 obs. of 15 variables:
$ ShannonW : num 0.76 0.72 0.85 0.53 0.74 0.13 0.4 0.29 1.02 1 ...
$ Richness : int 11 10 13 11 10 8 9 8 19 17 ...
$ angle1 : int 32 62 65 55 23 129 126 52 26 143 ...
$ angle2 : int 96 96 96 96 96 89 89 89 89 89 ...
$ exposure : int 10 10 10 10 10 8 8 8 8 8 ...
$ salinity : num 29.4 29.4 29.4 29.4 29.4 29.6 29.6 29.6 29.6 29.6 ...
$ temperature: num 17.5 17.5 17.5 17.5 17.5 20.8 20.8 20.8 20.8 20.8 ...
$ NAP : num 0.045 -1.036 -1.336 0.616 -0.684 ...
$ penetrability: num 254 227 237 249 252 ...
$ grainsize : num 222 200 194 221 202 ...
$ humus : num 0.05 0.3 0.1 0.15 0.05 0.1 0.1 0.1 0.15 0 ...
$ chalk : num 2.05 2.5 3.45 1.6 2.45 2.5 1.85 1.7 2.3 2.6 ...
$ sorting1 : num 69.8 59 59.2 67.8 57.8 ...
$ Beach : Factor w/ 9 levels "1","2","3","4",..: 1 1 1 1 1 2 2 2 2 2 ...
$ Week : Factor w/ 4 levels "1","2","3","4": 1 1 1 1 1 1 1 1 1 1 ...
```

Today we use the following columns:
ShannonW A biodiversity index based on the Shannon entropy.
Richness The number of species.
Beach Which beach.
NAP The altitude of the plot compared to the average sea level.
exposure An index composed of wave action, length of the surf zone, slope, grain size, depth of the anaerobic layer.
salinity Salt contents.
humus Fraction of organic material.
In an earlier analysis, NAP turned out to have an impact on species richness. Does ShannonW also depend on NAP?

```
> mod1 <- lm(ShannonW~NAP,data=rikz)
> summary(mod1)
[..]
Coefficients:
    Estimate Std. Error t value Pr (>|t|)
(Intercept) 0.47141 0.03627 12.996 < 2e-16 ***
NAP -0.22583 0.03478 -6.493 7.01e-08 ***
```

Signif. codes: 0 *** $0.001 * * 0.01 * 0.05$. $0.1 \quad 1$
Residual standard error: 0.2294 on 43 degrees of freedom
Multiple R-squared: 0.4951,Adjusted R-squared: 0.4833
F-statistic: 42.16 on 1 and $43 \mathrm{DF}, \mathrm{p}$-value: $7.01 \mathrm{e}-08$

Can we really pool the data from the different beaches?
> library(lattice)
> dotplot(residuals(mod1) ${ }^{\sim}$ rikz\$Beach,jitter. $x=T R U E, p c h=1$ )

> xyplot(ShannonW~NAP|Beach, data=rikz)


```
> mod2 <- lm(ShannonW~NAP+Beach,data=rikz)
> summary(mod2)
[..]
    Estimate Std. Error t value Pr(>|t|)
(Intercept) 0.620395 0.086771 7.150 2.45e-08 ***
```

| NAP | -0.207945 | 0.031366 | -6.630 | $1.15 \mathrm{e}-07$ | $* * *$ |
| :--- | ---: | ---: | ---: | ---: | :--- |
| Beach2 | 0.004665 | 0.123148 | 0.038 | 0.96999 |  |
| Beach3 | -0.328311 | 0.121791 | -2.696 | 0.01072 | $*$ |
| Beach4 | -0.345859 | 0.125102 | -2.765 | 0.00903 | $* *$ |
| Beach5 | 0.025370 | 0.125550 | 0.202 | 0.84103 |  |
| Beach6 | -0.185777 | 0.122910 | -1.511 | 0.13964 |  |
| Beach7 | -0.363441 | 0.128055 | -2.838 | 0.00750 | $* *$ |
| Beach8 | -0.125882 | 0.124720 | -1.009 | 0.31975 |  |
| Beach9 | -0.077617 | 0.125268 | -0.620 | 0.53953 |  |
| --- |  |  |  |  |  |
| Signif. codes: | $0 * * *$ | $0.001 * *$ | $0.01 *$ | 0.05 | 0.1 |

Residual standard error: 0.1911 on 35 degrees of freedom Multiple R-squared: 0.7148,Adjusted R-squared: 0.6415 F-statistic: 9.747 on 9 and 35 DF, p-value: $2.850 \mathrm{e}-07$

$>\bmod 3<-\operatorname{lm}($ ShannonW~NAP*Beach, data=rikz)
> summary(mod3)
[..]
Estimate Std. Error t value $\operatorname{Pr}(>|t|)$

| (Intercept) | 0.663388 | 0.097592 | 6.798 | $2.67 \mathrm{e}-07$ | *** |
| :---: | :---: | :---: | :---: | :---: | :---: |
| NAP | -0.118188 | 0.113333 | -1.043 | 0.30627 |  |
| Beach2 | 0.002042 | 0.129370 | 0.016 | 0.98752 |  |
| Beach3 | -0.371311 | 0.126891 | -2.926 | 0.00688 | ** |
| Beach4 | -0.413504 | 0.135632 | -3.049 | 0.00510 |  |
| Beach5 | 0.130807 | 0.142539 | 0.918 | 0.36691 |  |
| Beach6 | -0.245660 | 0.127976 | -1.920 | 0.06554 |  |
| Beach7 | -0.528549 | 0.165405 | -3.195 | 0.00354 |  |
| Beach8 | -0.188925 | 0.131537 | -1.436 | 0.16241 |  |
| Beach9 | -0.086618 | 0.136291 | -0.636 | 0.53043 |  |
| NAP: Beach2 | -0.236876 | 0.145877 | -1.624 | 0.11604 |  |
| NAP: Beach3 | -0.075049 | 0.149266 | -0.503 | 0.61919 |  |
| NAP: Beach4 | -0.044999 | 0.142857 | -0.315 | 0.75519 |  |
| NAP: Beach5 | -0.335176 | 0.156110 | -2.147 | 0.04093 | * |
| NAP: Beach6 | -0.017519 | 0.133795 | -0.131 | 0.89679 |  |
| NAP: Beach7 | 0.050573 | 0.166465 | 0.304 | 0.76361 |  |

```
NAP:Beach8 -0.049864 0.132654 -0.376 0.70993
NAP:Beach9 -0.149265 0.142921 -1.044 0.30556
[..]
```



```
> anova(mod1,mod2,mod3)
[..]
Model 1: ShannonW ~ NAP
Model 2: ShannonW ~ NAP + Beach
Model 3: ShannonW ~ NAP * Beach
    Res.Df RSS Df Sum of Sq F Pr(>F)
143 2.26293
2 35 1.27812 8 0.98481 3.7433 0.00458 **
3 27 0.88792 8 0.39020 1.4831 0.20951
[..]
> AIC(mod1,mod2,mod3)
    df AIC
mod1 3 -0.8457103
mod2 11 -10.5528837
mod3 19 -10.9445763
```

- Model 2 (where beaches have an additive effect) is significantly better than model 1 , and model 3 is not significantly better than model 2 .
- AIC favours (takes the lowest value for) model 3.
- How can AIC be negative? It is still defined as $-2 \cdot \log (L)+2 \cdot d$, whereas $d$ is the number of parameters and $L$ is the likelihood of the ML parameter estimate in the model. Since the response variable ShannonW has a continuos distribution (assumed to be normal), the likelihood is the probability density of the data given the parameter values. Densities can be larger than 1 . If $L>1$, then $\log (L)>0$ and AIC can be negative.
- We are not interested in the precise effect of each beach
- We do not want to estimate 8 extra paramters for the beaches
- Is there another way to take the difference between the beaches into account?
- Assume that the effect $\alpha_{k}$ of beach $k$ is random. Do not estimate all $\alpha_{k}$ but only their standard deviation $\sigma_{\alpha}$.


## Mixed-effects model

Let $S_{i}$ and $N_{i}$ be the ShannonW and the NAP observed at plot $i$, which is on beach $k_{i}$.

$$
S_{i}=a+b \cdot N_{i}+\alpha_{k_{i}}+\varepsilon_{i}
$$

$\varepsilon_{1}, \varepsilon_{2}, \ldots, \varepsilon_{45}$ are independently $\mathcal{N}\left(0, \sigma^{2}\right)$-distributed. $\alpha_{1}, \alpha_{2}, \ldots, \alpha_{9}$ are independently $\mathcal{N}\left(0, \sigma_{\alpha}^{2}\right)$-distributed. Mixed-effects: $a$ and $b$ are deterministic, $\alpha_{1}, \alpha_{2}, \ldots, \alpha_{9}$ are random. $[0.5 \mathrm{~cm}]$ To be estimated: $a, b, \sigma_{\alpha}, \sigma$.

```
> library(lme4)
> mmod0 <- lmer(ShannonW~1+NAP+(1|Beach),
+ data=rikz,verbose=TRUE)
    0: -3.0154190: 0.730297
    1: -3.0321775: 0.694973
    2: -3.0321844: 0.694215
    3: -3.0321844: 0.694257
    4: -3.0321844: 0.694257
```

It may be necessary to first install the lme4 package:

```
> install.packages("lme4")
```

This will only work if the R version installed is not too old.

```
> summary (mmod0)
    Linear mixed model fit by REML
    Formula: ShannonW ~ 1 + NAP + (1 | Beach)
        Data: rikz
        AIC BIC logLik deviance REMLdev
        4.968 12.19 1.516 -12.27 -3.032
    Random effects:
        Groups Name Variance Std.Dev.
        Beach (Intercept) 0.017595 0.13264
        Residual 0.036504 0.19106
    Number of obs: 45, groups: Beach, 9
    Fixed effects:
                Estimate Std. Error t value
    (Intercept) 0.46722 0.05366 8.707
    NAP 
    Correlation of Fixed Effects
        (Intr)
    NAP -0.198
```

Why are there $t$-values but no $p$ values?

## REML vs. ML

- ML (Maximum Likelihood): estimate all parameters (here $a, b, \sigma_{\alpha}, \sigma$ ) by maximizing their joint likelihood.
- REML (Restricted Maximum Likelihood): first estimate variance parameters (here $\sigma_{\alpha}, \sigma$ ) from the components of the response space that are orthogonal on components that can be explained by fixed effects. Using these estimates, the coefficients of the fixed effects (here $a$ and $b$ ) are estimated with ML.
- Comparable to estimation of $\sigma^{2}$ from sample $X_{1}, \ldots, X_{n}$ by $\frac{1}{n-1} \sum_{i}\left(\mu_{X}-X_{i}\right)^{2}$ instead of the biased ML estimator $\frac{1}{n} \sum_{i}\left(\mu_{X}-X_{i}\right)^{2}$
- Also for fitting parameters of mixed-effects models, ML estimation is biased and REML is usually preferred.
- ML estimation should be used when a likelihood ratio test shall be applied to models with different fixed effects and the same random effects.


## Why no $p$-values for the $t$-values?

- The $t$-values computed like in the usual linear model, but in the case of mixed-effects models they are in general not $t$-distributed (under the null hypothesis). Thus, it is not clear how to get $p$-values from the $t$-values.
- Some other programs give $p$-values which can be very imprecise.
- Exception: small balanced datasets. Here, $t$-values are approximately $t$-distributed and $|t|>2$ usually indicates significance on the $5 \%$ level.

The computation of confidence ranges in lme4 is based on likelihood ratios. The profiles in the first plots are likelihood ratios.

Vertical lines indicate $50 \%, 80 \%, 90 \%, 95 \%$, and $99 \%$ confidence intervals.

```
> prO <- profile(mmodO)
> xyplot(pr0)
```



Display confidence intervals (per default 95\%).

```
> confint(pr0)
            2.5% 97.5%
.sig01 
(Intercept) 0.3568131 0.5765609
NAP -0.2757402 -0.1540307
```

The next plot shows pairwise confidence ranges (again $50 \%, 80 \%, 90 \%, 95 \%$, and $99 \%$ ).
Panels above the diagonal are in the original scale of the parameters, panels below the diagonal are on the $\sqrt{\text { likelihoodratio scale. }}$


Useful information on methods for getting p values and confidence intervals are given in the R online help page for pvalues in the lme4 package.

According to this, using likelihood profiles might be inaccurate when the number of groups is below 50 (like for the beaches), and using e.g. PBmodcomp package might be preferable in this case.

## 3 How to select a mixed-effects model

## General considerations

- What is the purpose of the model?

1. Making predictions as precise as possible
2. or to understand what the most influential paramters are?

- In the first case AIC may be appropriate.
- In the second case it may be better to use likelihood-ratio tests and remove all parameters which do not significantly improve the fit.
- Variable selection should not only depend on statistics but also on the relevance of the parameter for the biological question.

We begin with a comparison of two nested models with the same random parameters

```
> B0 <- lmer(ShannonW~1+exposure*NAP+(1|Beach),
+ data=rikz,verbose=TRUE)
0: -3.1079878: 0.730297
    1: -3.9300741: 0.431067
    2: -3.9406377: 0.471682
    3: -3.9424344: 0.460627
    4: -3.9424352: 0.460386
    5: -3.9424352: 0.460388
```

```
> summary(BO)
Linear mixed model fit by REML
Formula: ShannonW ~ 1 + exposure * NAP + (1 | Beach)
    Data: rikz
    AIC BIC logLik deviance REMLdev
    8.058 18.90 1.971 
Random effects:
    Groups Name Variance Std.Dev.
    Beach (Intercept) 0.0069857 0.08358
    Residual 0.0329581 0.18154
Number of obs: 45, groups: Beach, 9
Fixed effects:
            Estimate Std. Error t value
(Intercept) 1.92603 0.44765 4.303
exposure -0.14294 0.04368 -3.272
[..]
> summary(BO)
[..]
Fixed effects:
            Estimate Std. Error t value
\begin{tabular}{lrrr} 
& Estimate & Std. Error t value \\
(Intercept) & 1.92603 & 0.44765 & 4.303 \\
exposure & -0.14294 & 0.04368 & -3.272 \\
NAP & -0.89673 & 0.33620 & -2.667 \\
exposure:NAP & 0.06661 & 0.03270 & 2.037
\end{tabular}
Correlation of Fixed Effects:
            (Intr) exposr NAP
exposure -0.996
NAP -0.233 0.235
exposur:NAP 0.235-0.238-0.996
> B1 <- update(B0,~.-exposure:NAP)
    0: -3.5739227: 0.730297
    1: -4.1112507: 0.00000
    2: -4.1112507: 3.65618e-06
    3: -4.1112511: 0.000144407
    4: -4.1650501: 0.0555603
    5: -4.7984144: 0.246592
    6: -5.0104872: 0.374551
    7: -5.0104967: 0.373651
    8: -5.0104968: 0.373725
    9: -5.0104968: 0.373722
> summary(B1)
Linear mixed model fit by REML
Formula: ShannonW ~ exposure + NAP + (1 | Beach)
    Data: rikz
    AIC BIC logLik deviance REMLdev
    4.99 14.02 2.505 -19.62 -5.01
Random effects:
```

Groups Name Variance Std.Dev.
Beach (Intercept) 0.00509580 .071385
Residual 0.03648470 .191010
Number of obs: 45, groups: Beach, 9

Fixed effects:
Estimate Std. Error t value
(Intercept) $1.711430 .41570 \quad 4.117$
exposure $\quad-0.12166 \quad 0.04053-3.001$
$\begin{array}{llll}\text { NAP } & -0.21555 & 0.02990 & -7.209\end{array}$

Correlation of Fixed Effects:
(Intr) exposr
exposure -0.996
$\begin{array}{llll}\text { NAP } \quad 0.015 & -0.040\end{array}$
> dotplot(ranef(B1, postVar=TRUE))

> qqmath(ranef(B1,postVar=TRUE))


```
> anova(B0,B1)
Data: rikz
Models:
B1: ShannonW ~ exposure + NAP + (1 | Beach)
B0: ShannonW ~ 1 + exposure * NAP + (1 | Beach)
    Df AIC BIC logLik Chisq Chi Df Pr(>Chisq)
B1 5 -9.6222 -0.58886 9.8111
B0 6 -11.5446 -0.70461 11.7723 3.9224 1 0.04765 *
---
Signif. codes: 0 *** 0.001 ** 0.01 * 0.05 . 0.1 1
```

The $p$-value of 0.04765 may be imprecise because REML was used. To get a slighly more reliable $p$-value we fit both models with ML.

```
> B1ML <- update(B1,REML=FALSE)
    0: -16.875166: 0.730297
    1: -19.518802: 0.00000
    2: -19.518802: 3.18807e-06
> BOML <- update(BO,REML=FALSE)
    0: -21.820395: 0.730297
    1: -22.739010: 0.00000
    2: -22.739010: 7.52231e-06
    3: -22.739011: 0.000259128
    4: -22.880262: 0.0868904
    5: -23.616152: 0.288666
    6: -23.703097: 0.366825
    7: -23.703443: 0.361997
    8: -23.703444: 0.362261
    9: -23.703444: 0.362262
```

> anova(B1ML, B0ML)
Data: rikz
Models:
B1ML: ShannonW ~ exposure + NAP + (1 | Beach)
BOML: ShannonW ~ 1 + exposure * NAP + (1 | Beach)
Df AIC BIC logLik Chisq Chi Df $\operatorname{Pr}(>$ Chisq)
$\begin{array}{lllll}B 1 M L & 5 & -9.5188 & -0.48549 & 9.7594\end{array}$
BOML $6-11.7034-0.8634711 .85174 .184610 .04079$ *
Signif. codes: 0 *** 0.001 ** $0.01 * 0.05$. $0.1 \quad 1$

The model B0 (or B0ML) with interaction between NAP and exposure fits significantly better.
Zuur et al. ${ }^{1}$ recommend the following strategy for the selection of random and fixed parameters.

1. Start with a model that contains as many of the relevant parameters and interactions as possible.
2. First select random parameters. To decide between models which have different random parameters, fit models with REML and choose model of minimal AIC.

[^0]3. Now select fixed parameters. This can be done with the help of AIC or with likelihood ratio tests. If likelihood ratio tests are used, apply ML to fit the models to the data.
4. Never remove covariates that are still involved in interactions.
5. Fit the final model with REML.

```
> B2 <- lmer(ShannonW~1+(exposure+salinity+NAP+humus)^2+(1|Beach),
+ .... [TRUNCATED]
    0: -5.8942807: 0.730297
    1: -5.8978355: 0.838579
    2: -5.9174068: 0.789454
    3: -5.9175376: 0.784845
    4: -5.9175385: 0.785156
    5: -5.9175385: 0.785156
```

> summary (B2)
Linear mixed model fit by REML
Formula: ShannonW ~ $1+$ (exposure + salinity + NAP + humus) ^2
+ (1 | Beach)
Data: rikz
AIC BIC logLik deviance REMLdev
$20.08 \quad 43.57 \quad 2.959 \quad-37.55 \quad-5.918$
Random effects:

| Groups | Name | Variance | Std.Dev. |
| :--- | :--- | :--- | :--- |
| Beach | (Intercept) | 0.015652 | 0.12511 |

Residual 0.0253900 .15934
Number of obs: 45, groups: Beach, 9
Fixed effects:

|  | Estimate |  |  |  | Std. Error | t value |
| :--- | ---: | ---: | ---: | :---: | :---: | :---: |
| (Intercept) | 40.32851 | 21.45346 | 1.880 |  |  |  |
| exposure | -4.16161 | 2.12543 | -1.958 |  |  |  |
| salinity | -1.38750 | 0.74706 | -1.857 |  |  |  |
| NAP | 0.65692 | 0.92037 | 0.714 |  |  |  |
| humus | 40.36916 | 16.33692 | 2.471 |  |  |  |
| exposure:salinity | 0.14522 | 0.07425 | 1.956 |  |  |  |
| exposure:NAP | 0.08357 | 0.03615 | 2.312 |  |  |  |
| exposure:humus | -2.06931 | 0.78148 | -2.648 |  |  |  |
| salinity:NAP | -0.06337 | 0.02639 | -2.401 |  |  |  |
| salinity:humus | -0.67100 | 0.43169 | -1.554 |  |  |  |
| NAP:humus | 1.01589 | 0.59247 | 1.715 |  |  |  |

[..]
[..]
Correlation of Fixed Effects:
(Intr) exposr salnty NAP humus expsr:s ex:NAP expsr:h sl:NAP
exposure -0.998
salinity $\quad-0.9990 .998$
$\begin{array}{llll}\text { NAP } & -0.079 & 0.062 & 0.074\end{array}$
humus $\quad 0.117-0.142-0.129 \quad 0.152$
expsr:slnty $0.996-0.999-0.998-0.057 \quad 0.155$
exposur:NAP $0.173-0.165-0.177-0.661 \quad 0.067 \quad 0.167$
exposur:hms $-0.285 \quad 0.295 \quad 0.306-0.008-0.694-0.315-0.331$
salinty:NAP $0.005 \quad 0.012 \quad 0.003-0.920-0.224-0.020 \quad 0.316 \quad 0.189$
$\begin{array}{lllllllllll}\text { salinty:hms } & 0.025 & 0.002 & -0.022 & -0.197 & -0.888 & -0.006 & 0.128 & 0.286 & 0.174\end{array}$
$\begin{array}{llllllllll}\text { NAP:humus } & 0.149 & -0.145 & -0.158 & 0.109 & -0.119 & 0.154 & 0.215 & -0.149 & -0.270\end{array}$
slnty:
exposure
salinity
NAP

```
humus
expsr:slnty
exposur:NAP
exposur:hms
salinty:NAP
salinty:hms
NAP:humus 0.266
> B3 <- lmer(ShannonW~1+(exposure+salinity+NAP+humus)^2
+ +(1+NAP|Beach), data=rikz,verbose=TRUE)
    0: -1.5323306: 0.730297 0.700275 0.00000
    1: -5.4597824: 1.16363 0.00000 -0.193541
    2: -5.7892458: 1.04081 4.21403e-06 -0.0735358
    3: -5.9531543: 0.913041 6.58205e-06 -0.188264
[..]
    12: -6.0798268: 0.829521 0.00000 -0.109646
    13: -6.0798268: 0.829519 0.00000 -0.109651
    14: -6.0798268: 0.829519 0.00000 -0.109651
```

Next, we fit a model where there is not only a random intercept for every beach but also a random coefficient of NAP. Again, let $S_{i}$ and $N_{i}$ be the ShannonW and the NAP observed at plot $i$, which is on beach $k$. The model says

$$
S_{i}=a+[\text { fixed effects terms }]+\alpha_{k}+\beta_{k} \cdot N_{i}+\varepsilon_{i} .
$$

$\varepsilon_{1}, \ldots, \varepsilon_{45}$ are independently $\mathcal{N}\left(0, \sigma^{2}\right)$-distributed, and also $\binom{\alpha_{1}}{\beta_{1}}, \ldots,\binom{\alpha_{9}}{\beta_{9}} \sim \mathcal{N}\left(\binom{0}{0},\left(\begin{array}{cc}\sigma_{\alpha}^{2} & \rho_{\alpha \beta} \\ \rho_{\alpha \beta} & \sigma_{\beta}^{2}\end{array}\right)\right)$.
Besides the fixed-effects coefficients we have to estimate the variances $\sigma, \sigma_{\alpha}$ and $\sigma_{\beta}$, and the covariance $\rho_{\alpha \beta}$.

The pairs of $\alpha$ and $\beta$ are independent in the sense that $\binom{\alpha_{i}}{\beta_{i}}$ is independent of $\binom{\alpha_{j}}{\beta_{j}}$ for $i \neq j$ (and independent of all other coefficients).

If we also want independence between $\alpha_{i}$ and $\beta_{i}$, that is $\rho_{\alpha \beta}$ restricted to 0 , we need to replace ( $1+\mathrm{NAP} \mid$ Beach) in the R model formula by
(1+NAP\| Beach) or, equivalently,
(1 $\mid$ Beach $)+(0+$ NAP $\mid$ Beach ) or (1 $\mid$ Beach $)+(N A P-1 \mid$ Beach $)$.
> summary (B3)
[..]
AIC BIC logLik deviance REMLdev
$\begin{array}{llll}23.92 & 51.02 & 3.04 & -37.69\end{array}$-6.08
Random effects:
Groups Name Variance Std.Dev. Corr
Beach (Intercept) 0.017306520 .131554
NAP $0.000208080 .014425-1.000$
Residual 0.025151080 .158591
Number of obs: 45, groups: Beach, 9
Fixed effects:

|  | Estimate |  | Std. Error |
| :--- | ---: | ---: | ---: |
| t value |  |  |  |
| (Intercept) | 40.93936 | 21.72964 | 1.884 |
| exposure | -4.22455 | 2.15239 | -1.963 |
| salinity | -1.40881 | 0.75753 | -1.860 |
| NAP | 0.67896 | 0.93389 | 0.727 |
| humus | 40.42412 | 16.30099 | 2.480 |
| exposure:salinity | 0.14742 | 0.07528 | 1.958 |




## How about models with less correlation in random effects?

```
> B5b <- lmer(ShannonW~1+(exposure+salinity+NAP+humus)^2+
    (1+NAP|Beach)+(exposure+0|Beach) +(1|Week), data=rikz)
> B5c <- lmer(ShannonW~1+(exposure+salinity+NAP+humus) ^2+
            (1+NAP||Beach)+(exposure+0|Beach)+(1|Week),data=rikz)
> anova(B2,B5b,B5c)
refitting model(s) with ML (instead of REML)
Data: rikz
Models:
B2: ShannonW ~ 1 + (exposure + salinity + NAP + humus) ^2 + (1 | Beach)
B5c: ShannonW ~ 1 + (exposure + salinity + NAP + humus) ~ 2 + ((1 |
B5c: Beach) + (0 + NAP | Beach)) + (exposure + 0 | Beach) + (1 |
B5c: Week)
B5b: ShannonW ~ 1 + (exposure + salinity + NAP + humus)^2 + (1 + NAP |
B5b: Beach) + (exposure + 0 | Beach) + (1 | Week)
    Df AIC BIC logLik deviance Chisq Chi Df Pr(>Chisq)
B2 13 -12.2395 11.247 19.120 -38.240
B5c 16 -9.8246 19.082 20.912 
B5b 17 -7.8246 22.889 20.912 
```

Don't trust the $p$-values on the previous slides! One problem is that the models were fitted with REML. Another problem ist that the null hypotheses (e.g. $\sigma_{\beta}=0$ in the case of $\mathrm{B} 2 / \mathrm{B} 3$ ) are on the boundary of the parameter space. $\sigma_{\beta}$ can only be $\geq 0$, and deviations from $\sigma_{\beta}=0$ are thus only possible in one direction.

The $\chi^{2}$-approximation of likelihood ratio tests are only reliable when deviations from the expectation under the null hypothesis are possible in all directions, for example if the null hypothesis $\theta=0$ is tested for some parameter $\theta$, and estimates of $\theta$ can lead to positive as well as negative values.

Thus, we rather base our decision on the AIC values. This is, of course, also not stringent. However, in our case, all criteria favor model B2.

Now we keep the random effects "(1 | Beach)" and search for a good selection of fixed effects. Here, our aim is to get a simple, understandable model. Therefore apply a strict criterion an remove all variables which do not significantly improve the model fit on the $5 \%$ level.
(If our aim was a model to make good predictions, we would rather take AIC as a criterion, which leaves more parameters in.)

```
> summary(B2)
Linear mixed model fit by REML
Formula: ShannonW ~ 1 + (exposure + salinity + NAP + humus)^2
                                    + (1 | Beach)
[..]
Fixed effects:
\begin{tabular}{lrrr} 
& \multicolumn{1}{c}{ Estimate } & Std. Error & t value \\
(Intercept) & 40.32851 & 21.45346 & 1.880 \\
exposure & -4.16161 & 2.12543 & -1.958 \\
salinity & -1.38750 & 0.74706 & -1.857 \\
NAP & 0.65692 & 0.92037 & 0.714 \\
humus & 40.36916 & 16.33692 & 2.471 \\
exposure:salinity & 0.14522 & 0.07425 & 1.956 \\
exposure:NAP & 0.08357 & 0.03615 & 2.312 \\
exposure:humus & -2.06931 & 0.78148 & -2.648 \\
salinity:NAP & -0.06337 & 0.02639 & -2.401 \\
salinity:humus & -0.67100 & 0.43169 & -1.554 \\
NAP:humus & 1.01589 & 0.59247 & 1.715 \\
[..] & & &
\end{tabular}
\begin{tabular}{cc}
\(>\) & B6 <- update(B2, \(\sim\).-salinity \(:\) humus \()\) \\
\(0:\) & \(-3.3840456: 0.730297\) \\
\(1:\) & \(-3.3848655: 0.748586\) \\
\(2:\) & \(-3.3851681: 0.742306\) \\
\(3:\) & \(-3.3851681: 0.742296\) \\
\(4:\) & \(-3.3851681: 0.742299\) \\
\(5:\) & \(-3.3851681: 0.742299\)
\end{tabular}
```

```
> anova(B6,B2)
Data: rikz
Models:
B6: ShannonW ~ exposure + salinity + NAP + humus + (1 | Beach) +
B6: exposure:salinity + exposure:NAP + exposure:humus + salinity:NAP +
B6: NAP:humus
B2: ShannonW ~ 1 + (exposure + salinity + NAP + humus) ^2 + (1 | Beach)
    Df AIC BIC logLik Chisq Chi Df Pr(>Chisq)
B6 12 -10.720 10.960 17.360
B2 13 -11.553 11.934 18.776 2.8329 1 0.09235 .
--
Signif. codes: 0 *** 0.001 ** 0.01 * 0.05 . 0.1 1
```

Remember that we should better use ML instead of REML if we want to apply likelihood ratio tests!

```
> B2ML <- update(B2,REML=FALSE)
    0: -37.815253: 0.730297
    1: -38.227458: 0.520323
```

```
    -38.238951: 0.555035
    -38.239535: 0.548840
    -38.239535: 0.548745
    -38.239535: 0.548714
    -38.239535: 0.548724
> B6ML <- update(B6,REML=FALSE)
    0: -34.786862: 0.730297
    -35.481002: 0.455308
    -35.502068: 0.503911
    -35.503579: 0.494055
    -35.503579: 0.493868
    -35.503579: 0.493857
    -35.503579: 0.493844
    -35.503579: 0.493844
> anova(B6ML,B2ML)
Data: rikz
Models:
B6ML: ShannonW ~ exposure + salinity + NAP + humus + (1 | Beach) +
B6ML: exposure:salinity + exposure:NAP + exposure:humus + salinity:NAP +
B6ML: NAP:humus
B2ML: ShannonW ~ 1 + (exposure + salinity + NAP + humus)^2 + (1 | Beach)
    Df AIC BIC logLik Chisq Chi Df Pr(>Chisq)
B6ML 12 -11.504 10.176 17.752
B2ML 13-12.239 11.247 19.120 2.736 1 0.09811.
---
Signif. codes: 0 *** 0.001 ** 0.01*0.05 . 0.1 1
```

On Ben Bolker's GLMM FAQ:
"Consider not testing the significance of random effects. If the random effect is part of the experimental design, this procedure may be considered sacrificial pseudoreplication (Hurlbert 1984). Using stepwise approaches to eliminate non-significant terms in order to squeeze more significance out of the remaining terms is dangerous in any case."

## References

[1] Ben Bolker et al. (2020) GLMM FAQhttps://bbolker.github.io/mixedmodels-misc/glmmFAQ.html
[2] Hurlbert, S. (1984) Pseudoreplication and the Design of Ecological Field Experiments. Ecological Monographs 54: 187211.

## Further reading

## References

[1] lme4 online help page on p values (online available e.g. on https://rdrr.io/cran/lme4/man/pvalues. html)
[2] B.M. Bolker, M.E. Brooks, C.J. Clark, S.W. Geange, J.R. Poulsen, M.H.H. Stevens, J.-S.S. White (2009) Generalized linear mixed models: a practical guide for ecology and evolution Trends in ecology \& evolution 24:127-135
[3] Allegue, H., Araya-Ajoy, Y.G., Dingemanse, N.J., Dochtermann N.A., Garamszegi, L.Z., Nakagawa, S., Rale, D., Schielzeth, H. and Westneat, D.F. (2016) SQuID - Statistical Quantification of Individual Differences: an educational and statistical tool for understanding multi-level phenotypic data in linear mixed models. Methods in Ecology and Evolution 8:257-267.

## Some of the publications by Douglas Bates

## References

[1] D. Bates, M. Mächler, B.M. Bolker, S.C. Walker (2015) Fitting linear mixed-effects models using lme4 Journal of Statistical Software 67: 1-48https://www.jstatsoft.org/v067/i01
[2] D. Bates, R. Kliegl, S. Vasishth, H. Baayen (2015) Parsimonious mixed models https://arxiv.org/ abs/1506. 04967
[3] H. Matuschek, R. Kliegl, S. Vasishth, H. Baayen, D. Bates (2017) Balancing Type I error and power in linear mixed models Journal of Memory and Language 94: 305-315 http://dx.doi.org/10.1016/j. jml.2017.01.001

## Some of what you should be able to explain

- Assumpitions of mixed-effects models
- Why random-effect factors are sometimes better than fixed-effect factors
- How to translate an lme4 mixed-effects model formula into a precise mathematical model specification and vice versa
- When to use REML and when using ML
- Parametric bootstrapping
- Possible approaches and problems of model selection, also with random-effect factors


[^0]:    ${ }^{1}$ A.F. Zuur, E.N. Ieno, N.J. Walker, A.A. Saveliev, G.M. Smith (2009) Mixed effects models and extensions in ecology with $R$. Springer.

