Mixed Models

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```
library(dplyr)
library(ggplot2)
library(nlme)
library(MuMIn)
library(car)
library(glmmTMB)
library(mgcv)
library(MASS)
library(brms)
```

set.seed(3)

Philosophy

The tools we will investigate this week address several related issues.

- Heterogeneity of variance
 - Sometimes this is definitely present, even after building an otherwise good model.
- Nuisance variables
 - Often, we have variables that we know we need to measure and account for, but they are not of primary interest.
- Dependent observations
 - The independence assumption implicit in all of our models thus far is often false.

We do have tools that deal with these issues. If your data are especially nice and your analysis is fairly straightforward, so are the tools for building appropriate models. If you are not so lucky, then things get complicated.

Heterogeneity of variance

Why is the variance heterogenous?

▶ Because of a variable. Hopefully one in your data.

It's possible that the heterogeneity is from not looking at the variables in your model at appropriate scales.

Were the data collected on the same scale that you are using, or have you transformed any variables? Recall that inverting a log-transform changes additive error into multiplicative error. Any nonlinear variable transform does this.

Nuisance variables

There is no set definition of nuisance variable. These are any variables that you know are having an effect on your response but are not what you are trying to investigate.

Be sure you think about why you aren't interested.

Accounting for these variables is essential for establishing appropriate baselines. Sometimes the signal that you are trying to measure is small compared to environmental variation.

 Effect of compost treatment on soil moisture retention is going to be smaller than rainfall, soil characteristics, etc. (Cooper)

Dependent observations

Measurements on the same or similar individuals are not independent.

▶ Individual what? (organism, forest, drainage, ...)



Having dependent observations means that your data set is effectively smaller.

 Sample from enough individuals so that you get a statistically meaningful set of observations. (sufficient power)

Tools

- Mixed effects models (LMM, GLMM, GAMM)
 - Fixed effect variables modify the signal, random effect variables modify the noise.
 - Many packages for this, no clear winner. (lme4 has lmer, glmer and nlmer; nlme has lme; MASS has glmmPQL; glmmTMB has glmmTMB. Bayesian options include brms::brm and MCMCglmm::MCMCglmm.)
 - ▶ Hopefully this will be easier in another decade or so.
- ► Also see **Generalized least squares** (GLS) and **Generalized estimating equations** (GEE).

Many of the tools for mixed modeling also allow the specification of structure to correlation (corStruct) and variance (varStruct).

Owls

Roulin and Bersier (2007) (a running example in Zuur et al. (2009)) investigates begging behavior in nestling barn owls.



Wer die nächste Maus erhält, wird zwischen jungen Schleiereulen mit lauten Schreien ausgehandelt, während die Eltern das Futter suchen. Foto: Karl Weber © Karl Weber

Reproduktion nur mit Quellenangabe «Karl Weber»

C'est en criant en l'absence des parents, partis chasser, que les jeunes chouettes effraies négocient la prochaine livraison de nourriture.

Photo: Karl Weber © Karl Weber Reproduction autorisée avec mention de l'auteur FONDS NATIONAL SUISSE
SCHWEIZERISCHER NATIONALFONDS
FONDO NAZIONALE SVIZZERO
SWISS NATIONAL SCIENCE FOUNDATION

They ask if vocal

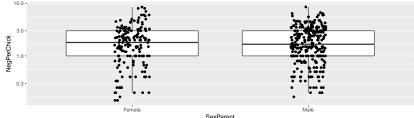
intensity of owl chick begging differs by parent.

Owl data

The data are in the package glmmTMB.

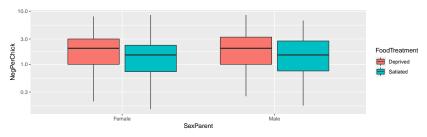
```
head(Owls.3)
           Nest FoodTreatment SexParent ArrivalTime SiblingNegotiation BroodSize
  1 AutavauxTV
                     Deprived
                                   Male
                                              22.25
  2 AutavauxTV
                     Satiated
                                   Male
                                              22.38
  3 AutavauxTV
                    Deprived
                                  Male
                                              22.53
    NegPerChick logBroodSize
             0.8
                    1.609438
             0.0
                   1.609438
## 3
             0.4
                  1.609438
```

Without other predictors, it does not appear that begging frequency depends on the parent.



Food Treatment

Begging behavior is likely affected by the hunger levels in the nest. The researchers imposed this as an experimental treatment to control for unknown variation. Feed some nests extra, deprive others, then swap treatments the following night.



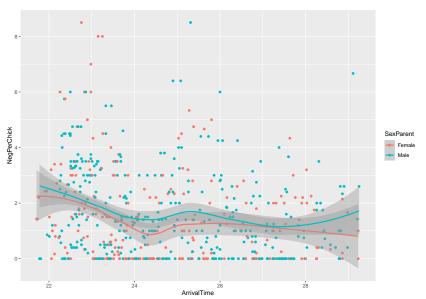
Still no visible difference between parents.

Nest is a nuisance varaible.



Arrival time affects the variance.

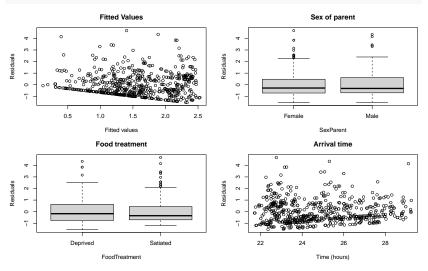
It could also be correlated with the sex of the parent.



Linear model

First thing to try is basic linear regression (ANCOVA).

M.lm <- lm(NegPerChick~SexParent*(FoodTreatment+ArrivalTime),data=Owls)</pre>



Code for those diagnostic plots

From Zuur et al. (2009).

Summary of M.lm

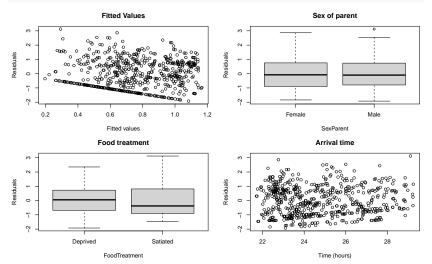
```
##
## Call:
## lm(formula = NegPerChick ~ SexParent * (FoodTreatment + ArrivalTime).
      data = Owls)
##
##
## Residuals:
##
      Min
              10 Median
                                   Max
## -2.3317 -1.0833 -0.4573 0.8630 7.0978
##
## Coefficients:
##
                                    Estimate Std. Error t value Pr(>|t|)
## (Intercept)
                                   6.766988 1.259815 5.371 1.12e-07 ***
## SexParentMale
                                  -0.044492 1.652324 -0.027
                                                                 0.979
## FoodTreatmentSatiated
                                  -0.850112 0.195174 -4.356 1.56e-05 ***
## ArrivalTime
                                   ## SexParentMale:FoodTreatmentSatiated 0.086027 0.254579 0.338 0.736
## SexParentMale: ArrivalTime
                                    0.007349 0.066230 0.111 0.912
## ---
## Signif. codes: 0 '***' 0.001 '**' 0.05 '.' 0.1 ' ' 1
##
## Residual standard error: 1.527 on 593 degrees of freedom
## Multiple R-squared: 0.1134, Adjusted R-squared: 0.1059
## F-statistic: 15.16 on 5 and 593 DF, p-value: 4.941e-14
```

Note the low R^2 .

Log-transform the negotiations per chick

This helps some with the non-normality and heteroscedasticity in variance.

```
Owls$LogNeg<-log(Owls$NegPerChick+1)
M2.lm=lm(LogNeg~SexParent*(FoodTreatment+ArrivalTime),data=Owls)</pre>
```



Summary of M2.1m

```
##
## Call:
## lm(formula = LogNeg ~ SexParent * (FoodTreatment + ArrivalTime),
      data = Owls)
##
##
## Residuals:
##
       Min
                10
                     Median
                                 30
                                        Max
## -1 08353 -0 46500 -0 05645 0 41842 1 74442
##
## Coefficients:
##
                                    Estimate Std. Error t value Pr(>|t|)
                                    2.574961 0.466240 5.523 5.00e-08 ***
## (Intercept)
## SexParentMale
                                   0.176201 0.611502 0.288 0.773336
## FoodTreatmentSatiated
                                  -0.364079 0.072231 -5.040 6.18e-07 ***
## ArrivalTime
                                   ## SexParentMale:FoodTreatmentSatiated 0.006885 0.094216 0.073 0.941767
## SexParentMale: ArrivalTime
                                 -0.003275 0.024511 -0.134 0.893745
## ---
## Signif. codes: 0 '***' 0.001 '**' 0.05 '.' 0.1 ' ' 1
##
## Residual standard error: 0.5649 on 593 degrees of freedom
## Multiple R-squared: 0.1402, Adjusted R-squared: 0.133
## F-statistic: 19.35 on 5 and 593 DF, p-value: < 2.2e-16
```

Still a low R^2 . We are missing most of the signal.

A mixed model with nlme::lme

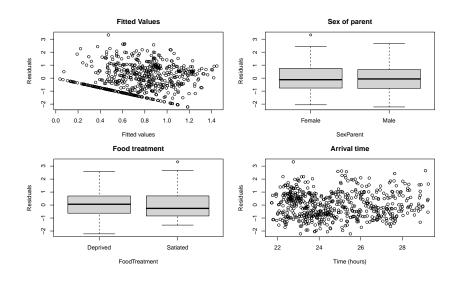
Refit the linear model with nlme::gls so that it can be more easily compared to the mixed model. The fitted model is identical to the one above, but R puts it in a different namespace.

- ► The argument random=~1|Nest in lme indicates that the intercept varies depending on the nest.
- Since observations from the same nest are correlated, the effective number of observations is reduced.
- The anova command carries out a likelihood ratio test since we give it 1me objects.

```
Form <- formula(LogNeg~SexParent*(FoodTreatment+ArrivalTime))
M.gls <- gls(Form, data=Owls)
M1.lme <- lme(Form, random=~1|Nest, data=Owls)
anova(M.gls,M1.lme)
```

```
## Model df AIC BIC logLik Test L.Ratio p-value
## M.gls 1 7 1053.537 1084.233 -519.7683
## M1.lme 2 8 1026.878 1061.959 -505.4390 1 vs 2 28.65875 <.0001
```

Diagnostic plots of the mixed model



Summary of the mixed model

```
## Linear mixed-effects model fit by REML
## Data: Owls
##
         ATC
                 BIC logLik
   1026.878 1061.96 -505.439
##
## Random effects:
## Formula: ~1 | Nest
        (Intercept) Residual
## StdDev: 0.2143996 0.5345205
## Fixed effects: list(Form)
##
                                          Value Std.Error DF t-value p-value
## (Intercept)
                                       2.5872800 0.4495127 567 5.755744 0.0000
## SexParentMale
                                       0.2491715 0.5861657 567 0.425087 0.6709
## FoodTreatmentSatiated
                                      -0.4188292 0.0705245 567 -5.938776 0.0000
## ArrivalTime
                                      -0.0667932 0.0180023 567 -3.710251 0.0002
## SexParentMale:FoodTreatmentSatiated 0.0322772 0.0914373 567 0.352998 0.7242
## SexParentMale: ArrivalTime
                                      -0.0088322 0.0234809 567 -0.376144 0.7070
## Correlation:
                                      (Intr) SxPrnM FdTrtS ArrvlT SPM:FT
##
## SexParentMale
                                     -0.749
## FoodTreatmentSatiated
                                     -0.102 0.080
## ArrivalTime
                                      -0.989 0.746 0.022
## SexParentMale:FoodTreatmentSatiated 0.078 -0.113 -0.756 -0.019
## SexParentMale:ArrivalTime
                                   0 747 -0 994 -0 019 -0 755 0 037
##
## Standardized Within-Group Residuals:
##
                     01
                               Med
                                           03
         Min
                                                     Max
## -2.2182205 -0.7902406 -0.0778161 0.6991138 3.3273193
##
## Number of Observations: 599
## Number of Groups: 27
```

Model selection

```
M1.lmeML=lme(Form,random=~1|Nest,method="ML",data=Owls)
dredge (M1.lmeML)
## Global model call: lme.formula(fixed = Form, data = Owls, random = ~1 | Nest, method = "ML")
## Model selection table
                  ArT FdT SxP ArT:SxP FdT:SxP df
       (Int)
                                                   logLik AICc delta weight
     2.7200 -0.07137
                                               5 -491.813 993.7 0.00
## 8 2.7030 -0.07191
                                               6 -491.347
                                                           994.8 1.11
                                                                        0.273
                                                           996.7 3.01
## 16 2.5750 -0.06670
                                               7 -491,273
                                                                        0.106
## 24 2.7110 -0.07185
                                            + 7 -491.280
                                                           996.8 3.02
                                                                        0.105
## 32 2 5870 -0 06682
                                               8 -491 211
                                                           998 7 4 94
                                                                        0.040
                                               4 -509.674 1027.4 33.69
## 3 0.9475
                                                                       0.000
## 7 0.9253
                                               5 -509.444 1029.0 35.26
                                                                        0.000
## 23 0.9371
                                               6 -509.354 1030.9 37.12
                                                                       0.000
## 6 2.3950 -0.06804
                                               5 -526.370 1062.8 69.11
                                                                        0.000
## 2 2.4220 -0.06712
                                               4 -527.605 1063.3 69.55
                                                                        0.000
                                               6 -526.346 1064.8 71.11
## 14 2.3170 -0.06488
                                                                        0.000
## 1 0.7604
                                               3 -541.668 1089.4 95.65
                                                                        0.000
                                               4 -540.826 1089.7 95.99 0.000
## 5 0.7189
## Models ranked by AICc(x)
## Random terms (all models):
## '1 | Nest'
```

Sex of the parent is not quite a significant predictor according to AIC. It is close though. Perhaps there is more work to do.

Fit the optimal linear mixed model

Sex of the parent is not a predictor.

```
M1.opt <- lme(LogNeg-FoodTreatment+ArrivalTime,random=-1|Nest,data=Owls) summary(M1.opt)
```

```
## Linear mixed-effects model fit by REML
    Data: Owls
          ATC
                  BIC
                          logLik
##
   1009.241 1031.192 -499.6203
##
## Random effects:
   Formula: ~1 | Nest
          (Intercept) Residual
##
## StdDey: 0.2180265 0.5333704
##
## Fixed effects: LogNeg ~ FoodTreatment + ArrivalTime
##
                              Value Std.Error DF t-value p-value
## (Intercept)
                          2.7219747 0.29697570 570 9.165648
## FoodTreatmentSatiated -0.4031260 0.04597355 570 -8.768650
## ArrivalTime
                         -0.0714293 0.01177156 570 -6.067954
  Correlation:
                         (Intr) FdTrtS
## FoodTreatmentSatiated -0.112
## ArrivalTime
                         -0.984 0.039
## Standardized Within-Group Residuals:
          Min
                        01
                                   Med
                                                03
                                                           Max
## -2.2283609 -0.78307304 -0.07461892 0.68690000 3.29183331
## Number of Observations: 599
## Number of Groups: 27
```

What if we don't use Nest as a random effect?

M1.wrong=lm(LogNeg~SexParent*(FoodTreatment+ArrivalTime)+Nest, data=Owls)
Anova(M1.wrong)

```
## Anova Table (Type II tests)
##
## Response: LogNeg
##
                          Sum Sq Df F value Pr(>F)
## SexParent
                           0.106 1 0.3745 0.5408
## FoodTreatment
                          22.383 1 79.0186 < 2.2e-16 ***
## ArrivalTime
                          10.865 1 38.3571 1.132e-09 ***
## Nest
                          28.654 26 3.8907 8.526e-10 ***
## SexParent:FoodTreatment
                         0.049 1 0.1716
                                              0.6789
## SexParent:ArrivalTime
                          0.087 1 0.3074
                                              0.5795
## Residuals
                         160,607 567
## ---
## Signif. codes: 0 '***' 0.001 '**' 0.05 '.' 0.1 ' ' 1
```

The result is similar, but it applies *only* to these 27 nests.

Comparison of parameter estimates

2.30446563

##

They are almost identical. The mixed model predicts a 3-6% smaller effect of food treatment.

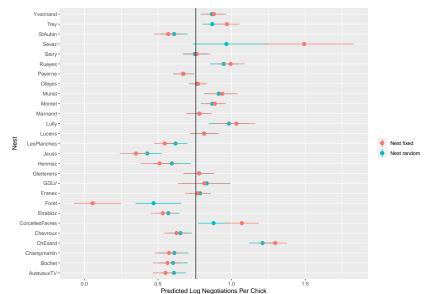
```
intervals (M1.lme) fixed [2:4, c(1.3)]
##
                             lower
                                         upper
## SexParentMale
                       -0.9021498 1.40049288
## FoodTreatmentSatiated -0.5573504 -0.28030806
## ArrivalTime
               -0.1021526 -0.03143379
apply(intervals(M1.lme)fixed[2:4, c(1,3)], 1, diff)
##
          SexParentMale FoodTreatmentSatiated
                                                       ArrivalTime
             2.30264266
                                   0.27704233
                                                        0.07071885
##
confint(M1.wrong)[2:4,]
                             2.5 % 97.5 %
##
## SexParentMale
                  -0.8178743 1.4865913
## FoodTreatmentSatiated -0.5772142 -0.2988176
## ArrivalTime
                   -0.1015671 -0.0308154
apply(confint(M1.wrong)[2:4,], 1, diff)
##
          SexParentMale FoodTreatmentSatiated
                                                       ArrivalTime
```

0.27839658

0.07075168

Comparison of predictions

The model where Nest is a random effect makes predictions that are closer to the overall mean.

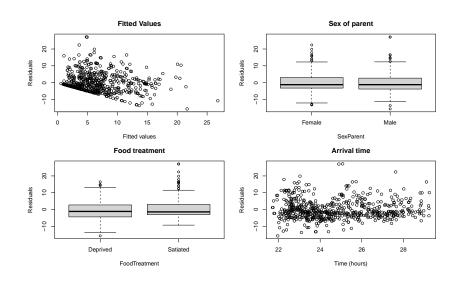


A model built with glmmTMB

Instead of log-transforming the negotiations, we could use a log link and a negative binomial error distribution.

- Include offset(BroodSize) instead of using NegPerChick.
- ▶ Random effect of 1|Nest is included in the main formula.
- ▶ Include zero inflation with zi = ~1. The formula ~1 means that we expect there to be excess zeros in the data but we do not propose a reason for them.

Diagnostic plots of the TMB model



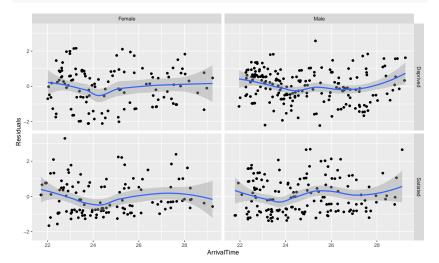
Summary of M1.tmb

```
## Family: nbinom1 (log)
## Formula:
## SiblingNegotiation ~ SexParent * (FoodTreatment + ArrivalTime) +
      (1 | Nest) + offset(BroodSize)
## Zero inflation:
                                    ~1
## Data: Owls
##
##
               BIC logLik deviance df.resid
       ATC:
  3394 1 3433 6 -1688 0 3376 1
##
## Random effects:
##
## Conditional model:
## Groups Name
              Variance Std.Dev.
## Nest (Intercept) 1.157 1.076
## Number of obs: 599, groups: Nest, 27
##
## Overdispersion parameter for nbinom1 family (): 5.01
##
## Conditional model:
                                   Estimate Std. Error z value Pr(>|z|)
##
## (Intercept)
                                   0.86649 0.85366 1.015 0.310092
## SexParentMale
                                   0.57261 1.04563 0.548 0.583950
                                  -0.94619 0.13788 -6.862 6.77e-12 ***
## FoodTreatmentSatiated
                                   -0.11557 0.03400 -3.399 0.000676 ***
## ArrivalTime
## SexParentMale:FoodTreatmentSatiated 0.28153 0.17318 1.626 0.104017
                               -0.02681 0.04294 -0.624 0.532409
## SexParentMale: ArrivalTime
## Signif. codes: 0 '***' 0.001 '**' 0.05 '.' 0.1 ' ' 1
##
## Zero-inflation model:
             Estimate Std. Error z value Pr(>|z|)
## ---
## Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
```

The effect of arrival time is not linear

SexParent-FoodTreatment combinations show residual patterns.

```
Owls$Eopt <- resid(M1.opt,type="normalized")
ggplot(Owls, aes(ArrivalTime, Eopt))+ geom_point()+geom_smooth()+
  facet_grid(FoodTreatment~SexParent)+ylab("Residuals")</pre>
```



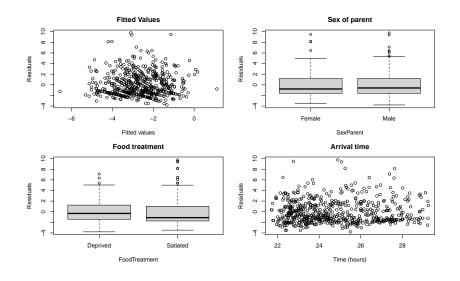
GAMM

A generalized additive mixed model gives flexibility to include nonlinear effects.

- ► A black-box smooth function relating ArrivalTime to SiblingNegotiation is created with s().
- Including by=SexParent substitutes for the interaction.
- Random effects go in a list.
- Negative binomial errors aren't an option so we use Poisson.

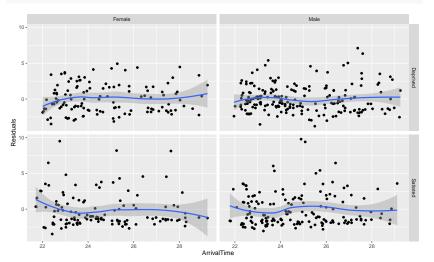
```
##
## Maximum number of PQL iterations: 20
```

Diagnostic plots of the generalized additive mixed model



Using a GAMM straightens out the residuals

```
Owls$Egamm <- resid(M.gamm,type="normalized")
ggplot(Owls, aes(ArrivalTime, Egamm))+ geom_point()+geom_smooth()+
  facet_grid(FoodTreatment~SexParent)+ylab("Residuals")</pre>
```



Summary of M.gamm\$gam

```
##
## Family: poisson
## Link function: log
##
## Formula:
## SiblingNegotiation ~ offset(BroodSize) + SexParent * FoodTreatment +
##
      s(ArrivalTime, by = SexParent)
##
## Parametric coefficients:
##
                                    Estimate Std. Error t value Pr(>|t|)
                                   -2.17039 0.23417 -9.268 <2e-16 ***
## (Intercept)
## SexParentMale
                                   -0.00743 0.04830 -0.154 0.8778
                                   -0.68125 0.05721 -11.908 <2e-16 ***
## FoodTreatmentSatiated
## SexParentMale:FoodTreatmentSatiated 0.14333 0.07172 1.998 0.0461 *
## Signif. codes: 0 '***' 0.001 '**' 0.05 '.' 0.1 ' ' 1
##
## Approximate significance of smooth terms:
##
                                 edf Ref.df F p-value
## s(ArrivalTime):SexParentFemale 8.324 8.324 24.82 <2e-16 ***
## s(ArrivalTime):SexParentMale 8.096 8.096 35.85 <2e-16 ***
## ---
## Signif. codes: 0 '***' 0.001 '**' 0.05 '.' 0.1 ' ' 1
##
## R-sq.(adj) = -16.2
## Scale est = 1 n = 599
```

Baby Owl says, "Hey Papa, bring us another mouse! The one the scientists left for us smells funny."

F tests on the GAMM

```
anova (M.gamm$gam)
##
## Family: poisson
## Link function: log
##
## Formula:
## SiblingNegotiation ~ offset(BroodSize) + SexParent * FoodTreatment +
       s(ArrivalTime, by = SexParent)
##
##
## Parametric Terms:
##
                          df
                                   F p-value
## SexParent
                               0.024 0.8778
                           1 141.794 <2e-16
## FoodTreatment
## SexParent:FoodTreatment 1
                               3.994 0.0461
##
## Approximate significance of smooth terms:
##
                                   edf Ref.df
                                                  F p-value
## s(ArrivalTime):SexParentFemale 8.324 8.324 24.82 <2e-16
## s(ArrivalTime):SexParentMale 8.096 8.096 35.85 <2e-16
```

Summary of M.gamm\$lme

summary(M.gamm\$lme) includes the correlation matrix.

- Highly correlated parameters may warrant an explanation.
- ► Intercept is often highly correlated with slope for variables in linear models that are not centered.
- Interaction terms tend to be correlated with the interacting variables.

```
sml <- summary(M.gamm$lme)
colnames(sml$corFixed) <- abbreviate(colnames(sml$corFixed), minlength=8)
rownames(sml$corFixed) <- abbreviate(rownames(sml$corFixed), minlength=8)
round(sml$corFixed,3)</pre>
```

```
##
            X(Intrc) XSxPrntM XFdTrtmS XSPM:FTS X(AT):SPF X(AT):SPM
## X(Intrc)
               1.000
                      -0.130
                               -0.092
                                        0.069
                                                  0.007
                                                           0.001
                                                 -0.043
## XSxPrntM
              -0.130
                     1.000
                                0.457
                                       -0.569
                                                          -0.090
## XFdTrtmS
              -0.092
                     0.457 1.000
                                       -0.769
                                                  0.093
                                                          -0.001
                     -0.569
                              -0.769
                                                 -0.067
                                                           0.034
## XSPM:FTS
             0.069
                                       1.000
## X(AT):SPF
             0.007
                      -0.043
                                0.093
                                       -0.067
                                                  1.000
                                                           0.003
## X(AT):SPM
              0.001
                      -0.090
                               -0.001
                                        0.034
                                                  0.003
                                                           1,000
```

AIC and significance of SexParent

Fitting a model without SexParent gives a much higher AIC.

```
M2.gamm <- gamm(SiblingNegotiation~offset(BroodSize)+
               SexParent+FoodTreatment+s(ArrivalTime, by=SexParent),
               random=list(Nest=~1), data=Owls, family=poisson)
M3.gamm <- gamm(SiblingNegotiation~offset(BroodSize)+
               SexParent*FoodTreatment+s(ArrivalTime),
               random=list(Nest=~1), data=Owls, family=poisson)
M4.gamm <- gamm(SiblingNegotiation~offset(BroodSize)+
               SexParent+FoodTreatment+s(ArrivalTime).
               random=list(Nest=~1), data=Owls, family=poisson)
M5.gamm <- gamm(SiblingNegotiation~offset(BroodSize)+
               FoodTreatment+s(ArrivalTime).
               random=list(Nest=~1), data=Owls, family=poisson)
AIC(M.gamm, M2.gamm, M3.gamm, M4.gamm, M5.gamm)
##
          df
                  ATC
## M.gamm 9 3107.012
## M2.gamm 8 3105.906
## M3.gamm 7 3179.468
## M4.gamm 6 3179.027
## M5.gamm 5 3177.889
```

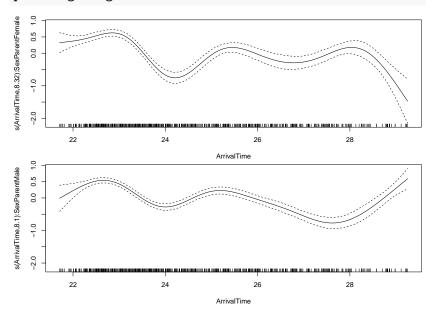
Summary of M2.gamm\$gam

```
##
## Family: poisson
## Link function: log
##
## Formula:
## SiblingNegotiation ~ offset(BroodSize) + SexParent + FoodTreatment +
##
      s(ArrivalTime, by = SexParent)
##
## Parametric coefficients:
##
                      Estimate Std. Error t value Pr(>|t|)
## (Intercept) -2.20314 0.23392 -9.418 <2e-16 ***
## SexParentMale
                     0.04768 0.03977 1.199 0.231
## FoodTreatmentSatiated -0.59379 0.03659 -16.230 <2e-16 ***
## ---
## Signif. codes: 0 '***' 0.001 '**' 0.05 '.' 0.1 ' ' 1
##
## Approximate significance of smooth terms:
##
                                 edf Ref.df F p-value
## s(ArrivalTime):SexParentFemale 8.309 8.309 24.93 <2e-16 ***
## s(ArrivalTime):SexParentMale 8.093 8.093 35.91 <2e-16 ***
## ---
## Signif. codes: 0 '***' 0.001 '**' 0.05 '.' 0.1 ' ' 1
##
## R-sq.(adi) = -16.5
## Scale est. = 1 n = 599
```

Or, maybe Papa Owl and Mama Owl just visit at different times.

The smooth approximators

plot(M.gamm\$gam)



Questioning the result

The p-value for SexParent:FoodTreatmentSatiated is just barely significant at the $\alpha=0.05$ level, and removing it gives a small improvement in AIC, so we should definitely temper our enthusiasm.

- Are we overfitting?
- Is the effect size large enough to care about?

Cross validation and simulation could help answer these questions.

Enough owl models already

Roulin and Bersier (2007) finds that the sex of the parent *is* significant without going further than a linear mixed model.

The analysis there seems to hinge on the variable amount of time in nestbox which is missing from the data provided in Zuur et al. (2009) (which is the source of the data in glmmTMB::Owls).

Mixed model formula cheatsheet

Y is the response variable, X is a fixed effect variable, S and T are random effect variables. Random terms b are normally distributed with parameters determined by the variables in the subscript.

Modeling goal	Formula specification	Mathematical specification $Y \sim$
fixed effect only model random group intercept random slope of X within group with correlated intercept	NA (1 group) (x group) = (1+x group)	$ \begin{vmatrix} \beta_{0} + \beta_{1}X + \epsilon \\ (\beta_{0} + b_{0S}) + \beta_{1}X + \epsilon \\ (\beta_{0} + b_{0S}) + (\beta_{1} + b_{1S})X + \epsilon \end{vmatrix} $
random slope of X within group, no variation in intercept	(0+x group) = (-1+x group)	$\beta_0 + (\beta_1 + b_{1S})X + \epsilon$
intercept varying among sites and among blocks within sites (nested random effects)	<pre>(1 site/block) = (1 site)+(1 site:block)</pre>	$(\beta_0 + b_{0S} + b_{0ST}) + \beta_1 X + \epsilon$
intercept varying among crossed random effects (e.g. site, year)	(1 group1)+(1 group2)	$(\beta_0 + b_{0S} + b_{0T}) + \beta_1 X + \epsilon$

References

```
Roulin, Alexandre, and Louis-Felix Bersier. 2007. "Nestling Barn Owls Beg More Intensely in the Presence of Their Mother Than in the Presence of Their Father." Animal Behaviour 74 (4): 1099–1106. https://doi.org/https://doi.org/10.1016/j.anbehav.2007.01.027.
```

Zuur, A., E. N. Ieno, N. Walker, A. A. Saveliev, and G. M. Smith. 2009. *Mixed Effects Models and Extensions in Ecology with r.* Statistics for Biology and Health. Springer New York. https://books.google.com/books?id=vQUNprFZKHsC.