Activity analysis - overall variables - best models selection

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01/03/2021

Introduction

This study aims at developing a methodology to statistically test the effect of potential predictors on ant building activity. The statistical study of ant activity time series is complicated by the effect of colony activity-level shifts on the pattern of activity. Here, we account for these shifts using hidden Markov models (HMM), a widely-used framework in animal movement ecology that identifies different behavioural states within a time series. The individual (or, for us, the colony) switches between states during the course of the recording and each state generates a different distribution of behavioural events: movement speed and direction in the case of movement ecology and nest building rates in our study.

We experimentally record stone deposition rates occurring during nest wall building in *Temnothorax rugatulus* colonies. Four colonies were used for the study. *Temnothorax* nest building has been hypothesised to follow local cues (Franks & Deneubourg, 1997). Here, we study the effect of the variables that are thought to have an influence at a local level (*i.e.*, next to the site of building activity), but for simplicity we limit the analysis to their global effect (*i.e.*, using an average value calculated across building sites). The variables studied are: stone density of the wall under construction, number of ants in the central brood cluster and distance of the building site from the cluster.

This document contains the selection procedure used to identify the best fitting statistical models.

Model selection approach

The predictors used in the analysis are either derived from the existing literature (stone density and distance of the building area from the *centre* of the brood cluster) or influence the others through the experimental setting (the number of ants in the brood cluster influences the total area of the cluster and consequently the distance of the building area to the *edge* of the cluster). We fit single predictor and the three-predictor models and an interaction model that includes the interaction of distance with the n of ants in the cluster. We compare model fit through AIC.

The fitting of each model is iterated over 100 different sets of starting values for the distributions, to check whether the MLE algorithm is reliably converging to the same minimum negative log likelihood (NLL) solution. Lack of convergence indicates numerical instability, which is a symptom of the amount of data being insufficient to fit the model accurately. Here, we use a 50% convergence threshold: if at least half of the iterations have converged to the same best fit, we accept that best convergence point. In case of lack of convergence, we exclude the model from the analysis entirely.

Analysis of deposition activity

Covariate-free model Let us first extract all 100 model fits of the no-covariate model, run from 100different sets of parameter starting values. We look at their NLL to evaluate the reliability of model convergence.

```r
# Load model and plot residuals
fn <- paste0(modelPath, "allm_0.rds")  # load fitted models from rds file
allm.D.0 <- readRDS(fn)  [1:niter]     # the first 100 objects contain the models (the remaining 100 ar

# extract all min neg log likelihood values
allnllk.D.0 <- unlist(lapply(allm.D.0, function(m) m$mod$minimum))
allnllk.D.0
```

```
##   [1]  79.59766  79.59766  79.59766  79.59766  79.69050  79.59766  79.59766
##   [8]  79.59766  79.69050  79.59766  79.59766  79.59766  79.59766 102.23018
##  [15]  79.59766  79.59766  79.59766  79.59766  79.59766  79.59766  79.59766
##  [22]  79.59766  79.69050  79.59766  79.59766  79.59766  79.69050  79.59766
##  [29]  79.59766  79.59766  79.59766  79.59766  79.59766  79.59766  79.59766
##  [36]  79.59766  79.59766  79.59766  79.69050  79.59766  79.69050  79.69050
##  [43]  79.59766  79.59766 102.23018  79.69050  79.69050  79.59766  79.59766
##  [50]  79.59766  79.59766  79.59766 102.23018  79.59766  79.59766  79.59766
##  [57]  79.59766 102.23018  79.59766  79.59766  79.59766  79.59766  79.59766
##  [64] 102.23018  79.59766  79.59766  79.59766  79.59766  79.59766  79.59766
##  [71]  79.59766  79.59766  79.59766  79.59766  79.59766  79.59766  79.59766
##  [78]  79.59766  79.59766  79.59766  79.59766  79.59766  79.69050  79.59766
##  [85] 102.23018  79.59766  79.59766  79.59766  79.59766 102.23018  79.59766
##  [92]  79.59766  79.59766  79.59766  79.59766  79.59766  79.59766  79.59766
##  [99]  79.59766  79.59766
```

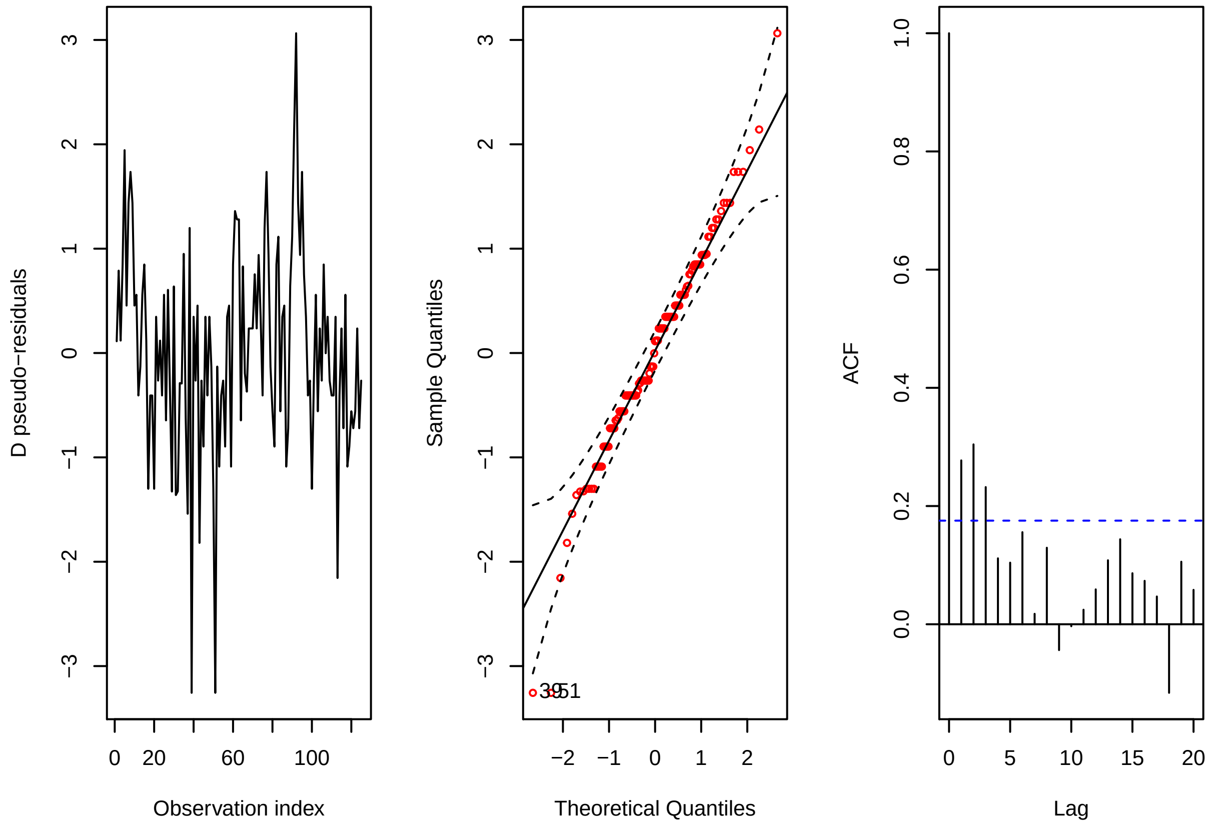
We now count how many iterations converged to the same minimum NLL estimate (with some buffer) out of 100.

```r
minnll.D.0 <- min(allnllk.D.0)
length(which( allnllk.D.0 < minnll.D.0 + 1 & allnllk.D.0 > minnll.D.0 - 1 )) # allow fits that are with
```

```
## [1] 93
```

90% of iterations converged to the same best fit. This is more than enough to think that the algorithm has identified the global best fit for the model. We now look at its residual plots.

```
## Computing pseudo-residuals... DONE
```



Pseudo-residuals are randomly distributed and so are autocorrelation values. The quantiles respect the normality assumption. This is a healthy model.

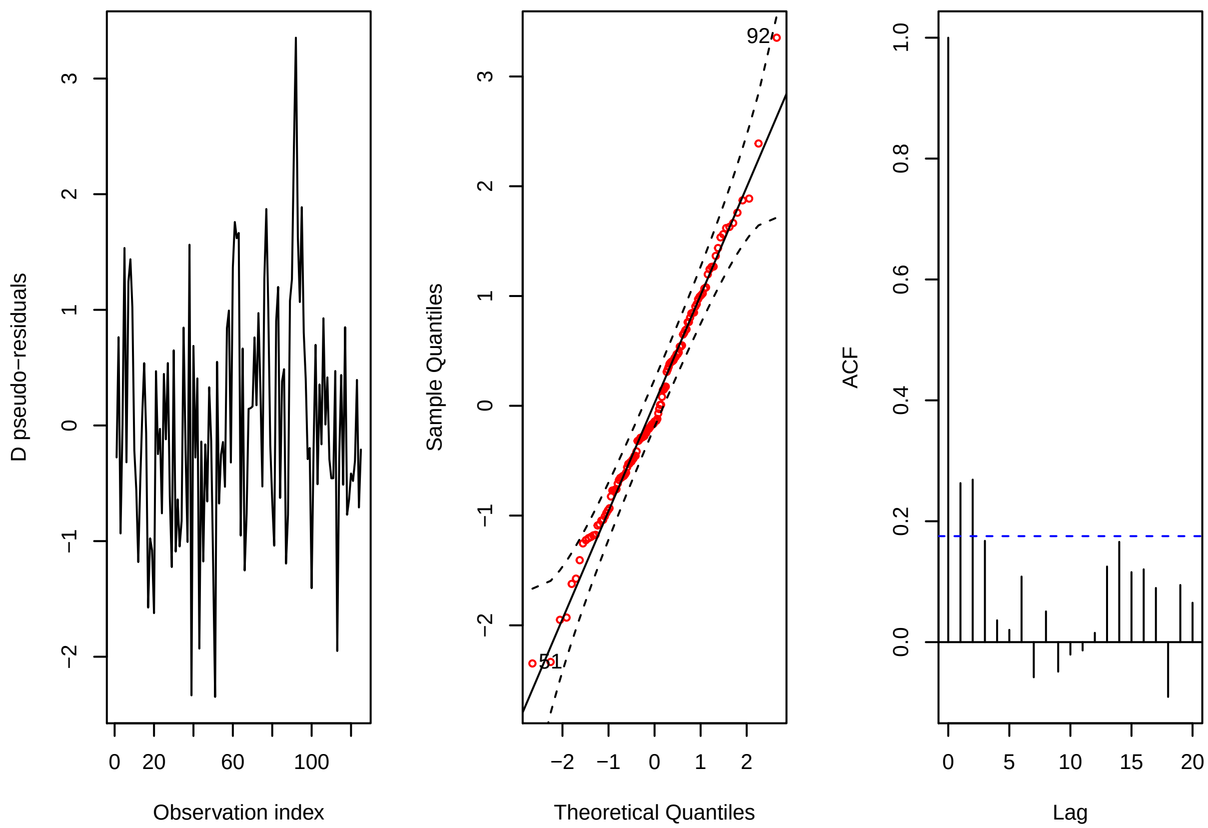
We now do the same for the other models.

stone density + distance * n ants

```
##   [1] 68.19205 68.19205 68.19205 68.19205 68.19226 68.19205 68.19205 68.19205
##   [9] 68.19226 68.19205 68.19205 68.19205 68.19205 87.63999 68.19205 68.19205
##  [17] 68.19205 68.19205 68.19205 68.19205 68.19205 68.19205 68.19226 68.19205
##  [25] 68.19205 68.19205 68.19226 68.19205 68.19205 68.19205 68.19205 68.19205
##  [33] 68.19205 68.19205 68.19205 68.19205 68.19205 68.19205 68.19226 68.19205
##  [41] 68.19226 68.19226 68.19205 68.19205 87.63999 68.19226 68.19226 68.19205
##  [49] 68.19205 68.19205 68.19205 68.19205 87.63999 68.19205 68.19205 68.19205
##  [57] 68.19205 87.63999 68.19205 68.19205 68.19205 68.19205 68.19205 87.63999
##  [65] 68.19205 68.19205 68.19205 68.19205 68.19205 68.19205 68.19205 68.19205
##  [73] 68.19205 68.19205 68.19205 68.19205 68.19205 68.19205 68.19205 68.19205
##  [81] 68.19205 68.19205 68.19226 68.19205 87.63999 68.19205 68.19205 68.19205
##  [89] 68.19205 87.63999 68.19205 68.19205 68.19205 68.19205 68.19205 68.19205
##  [97] 68.19205 68.19205 68.19205 68.19205
```

```
## [1] 93
```

```
## Computing pseudo-residuals... DONE
```

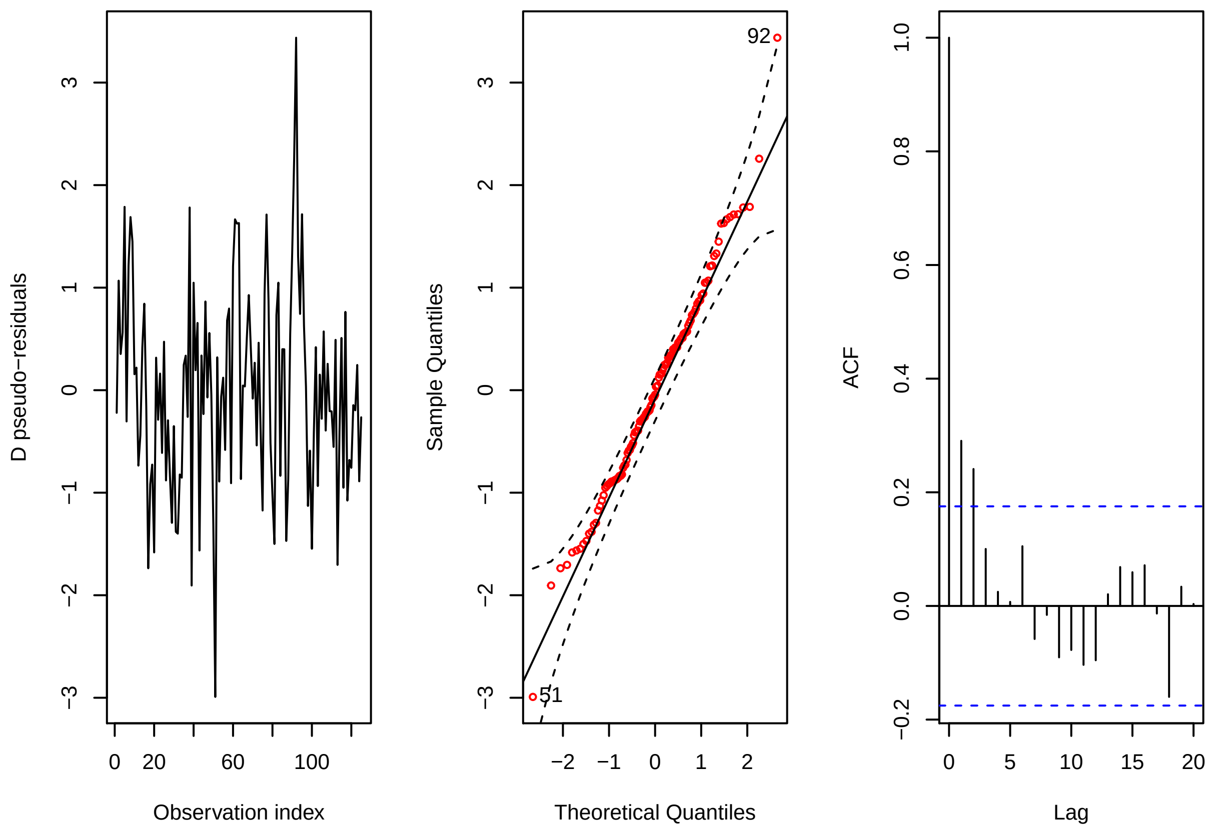


stone density

```
##   [1] 75.70391 97.67821 74.88426 97.67821 75.70391 75.70391 97.67821 74.88426
##   [9] 74.88426 97.67821 75.70391 75.70391 75.70391 75.70391 75.70391 75.70391
##  [17] 97.67821 97.67821 75.70391 75.70391 74.88426 97.67821 75.70391 74.88426
##  [25] 74.88426 74.88426 74.88426 74.88426 75.70391 75.70391 74.88426 74.88426
##  [33] 75.70391 97.67821 75.70391 75.70391 74.88426 97.67821 74.88426 74.88426
##  [41] 75.70391 74.88426 74.88426 74.88426 74.88426 74.88426 74.88426 75.70391
##  [49] 75.70391 74.88426 74.88426 74.88426 75.70391 75.70391 74.88426 75.70391
##  [57] 74.88426 74.88426 74.88426 74.88426 75.70391 74.88426 74.88426 74.88426
##  [65] 74.88426 75.70391 74.88426 75.70391 74.88426 74.88426 97.67821 75.70391
##  [73] 74.88426 75.70391 74.88426 74.88426 75.70391 97.67821 75.70391 74.88426
##  [81] 74.88426 74.88426 75.70391 75.70391 74.88426 74.88426 75.70391 97.67821
##  [89] 75.70391 75.70391 75.70391 75.70391 74.88426 75.70391 74.88426 75.70391
##  [97] 75.70391 75.70391 74.88426 75.70391
```

```
## [1] 88
```

```
## Computing pseudo-residuals... DONE
```



stone density + stone density^2

```
##   [1] 75.28534 75.28534 75.28534 75.28534 75.24953 75.28534 75.24953 75.28534
##   [9] 75.28534 75.28534 75.28534 75.28534 76.30760 75.28534 75.24953 75.28534
##  [17] 75.24953 75.16998 76.30760 75.24953 75.28534 75.16998 75.28534 76.30760
##  [25] 89.95573 75.28534 75.28534 75.24953 75.28534 75.28534 75.24953 75.28534
##  [33] 75.24953 75.28534 75.24953 75.28534 75.28534 75.24953 75.28534 75.28534
##  [41] 75.24953 75.28534 75.28534 76.30760 75.24953 75.24953 75.24953 75.28534
##  [49] 75.28534 75.24953 76.30760 75.28534 75.28534 75.28534 76.30760 75.28534
##  [57] 75.28534 76.30760 75.28534 75.28534 75.16998 75.28534 89.95573 75.28534
##  [65] 75.28534 75.28534 89.95573 76.30760 74.01776 76.30760 75.28534 75.28534
##  [73] 76.30760 75.24953 75.28534 75.24953 75.28534 75.24953 89.95573 75.24953
##  [81] 89.95573 75.28534 75.28534 75.28534 75.28534 89.95573 75.28534 75.16998
##  [89] 75.28534 89.95573 75.24953 75.28534 75.28534 75.28534 75.28534 74.01776
##  [97] 75.24953 75.28534 75.28534 75.28534
```

```
## [1] 2
```

distance

```
##   [1] 75.74740 94.84206 94.84206 75.74740 75.74740 75.74740 75.74740 75.74740
##   [9] 75.74740 75.74740 75.74740 75.74740 75.74740 75.74740 75.74740 94.84206
##  [17] 75.74740 75.88942 75.74779 75.74740 75.74740 75.74740 94.84206 75.74740
##  [25] 75.74740 75.74740 75.75272 75.74740 75.74740 75.74740 75.74740 75.74740
```

```
##  [33] 75.74740 75.74740 75.74740 75.74740 75.74740 75.74740 75.74740 94.84206
##  [41] 75.74740 75.74740 75.74740 75.74740 75.74740 75.74740 75.74740 75.74740
##  [49] 75.74740 75.74740 75.74740 75.74740 75.74740 75.74893 75.74740 75.74740
##  [57] 75.74740 75.74740 75.74740 75.74740 75.74740 75.74740 75.74740 75.74740
##  [65] 75.74740 46.70964 75.74740 75.74740 75.74740 75.74740 75.74740 94.84206
##  [73] 75.74740 75.74740 75.74740 75.74740 75.74740 75.74740 75.74740 75.74740
##  [81] 75.74740 75.74740 75.74740 75.74740 75.74740 75.74740 75.74740 75.74740
##  [89] 75.74740 75.74740 75.74740 75.74740 75.74740 75.74740 75.74740 75.74740
##  [97] 75.74740 75.74740 75.74740 75.74740
```

```
## [1] 1
```

n of ants

```
##   [1] 78.62702 78.62702 79.59168 99.69484 78.62702 78.62702 78.62702 78.62702
##   [9] 78.62702 78.62702 78.62702 78.62702 78.62702 78.62702 78.62702 78.62702
##  [17] 78.62702 78.62702 78.62702 78.62702 78.62702 78.62702 78.62702 78.62702
##  [25] 78.62702 78.62702 78.62702 78.62702 78.62702 99.69484 78.62702 78.62702
##  [33] 78.62702 78.62702 78.62702 78.62702 78.62702 78.62702 78.62702 78.62702
##  [41] 78.62702 78.62702 78.62702 99.69484 78.62702 78.62702 78.62702 78.62702
##  [49] 78.62702 78.62702 78.62702 78.62702 78.62702 78.62702 78.62702 78.62702
##  [57] 78.62702 99.69484 78.62702 78.62702 78.62702 99.69484 78.62702 78.62702
##  [65] 78.62702 78.62702 78.62702 78.62702 78.62702 99.69484 78.62702 78.62702
##  [73] 78.62702 78.62702 51.87707 78.62702 78.62702 78.62702 78.62702 78.62702
##  [81] 78.62702 78.62702 78.62702 78.62702 78.62702 78.62702 78.62702 78.62702
##  [89] 78.62702 78.62702 78.62702 78.62702 78.62702 78.62702 78.62702 99.69484
##  [97] 78.62702 78.62702 78.62702 78.62702
```

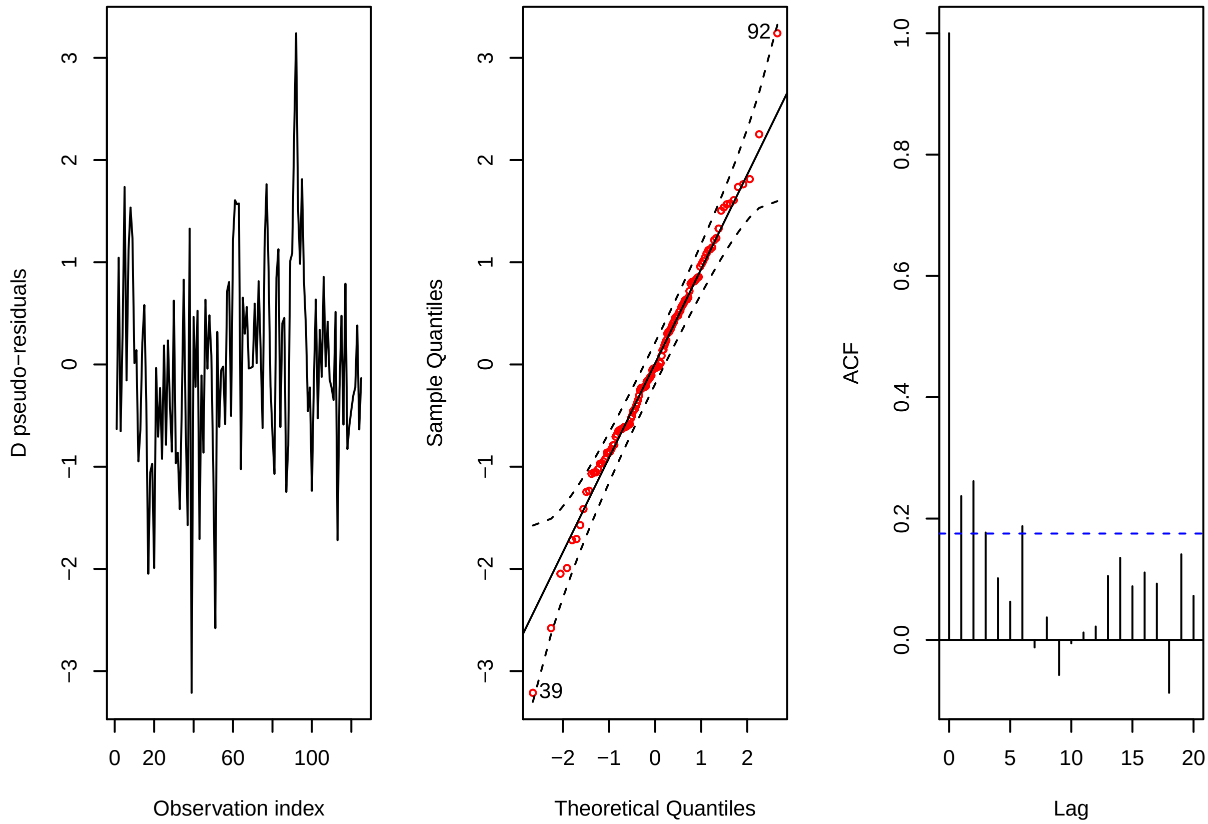
```
## [1] 1
```

stone density + n ants + distance

```
##   [1] 71.64706 71.64706 71.64706 71.64706 71.64706 90.79231 71.64706 71.64706
##   [9] 71.64706 71.64706 71.64706 90.79231 71.64706 71.64706 71.64706 71.64706
##  [17] 71.64706 90.79231 71.64706 71.64706 71.64706 71.64706 71.64706 71.64706
##  [25] 71.64706 71.64706 71.64706 71.64706 71.64706 71.64706 71.64706 71.64706
##  [33] 71.64706 71.64706 71.64706 71.64706 90.79231 71.64706 71.64706 71.64706
##  [41] 71.64706 71.64706 71.64706 71.64706 71.64706 71.64706 71.64706 71.64706
##  [49] 71.64706 71.64706 71.64706 71.64706 71.64706 71.64706 71.64706 90.79231
##  [57] 71.64706 71.64706 71.64706 71.64706 71.64706 71.64706 90.79231 71.64706
##  [65] 71.64706 71.64706 71.64706 71.64706 71.64706 90.79231 71.64706 71.64706
##  [73] 90.79231 71.64706 71.64706 71.64706 71.64706 71.64706 71.64706 71.64706
##  [81] 71.64706 71.64706 71.64706 90.79231 71.64706 71.64706 71.64706 71.64706
##  [89] 71.64706 71.64706 71.64706 71.64706 90.79231 71.64706 71.64706 71.64706
##  [97] 71.64706 71.64706 71.64706 71.64706
```

```
## [1] 90
```

```
## Computing pseudo-residuals... DONE
```

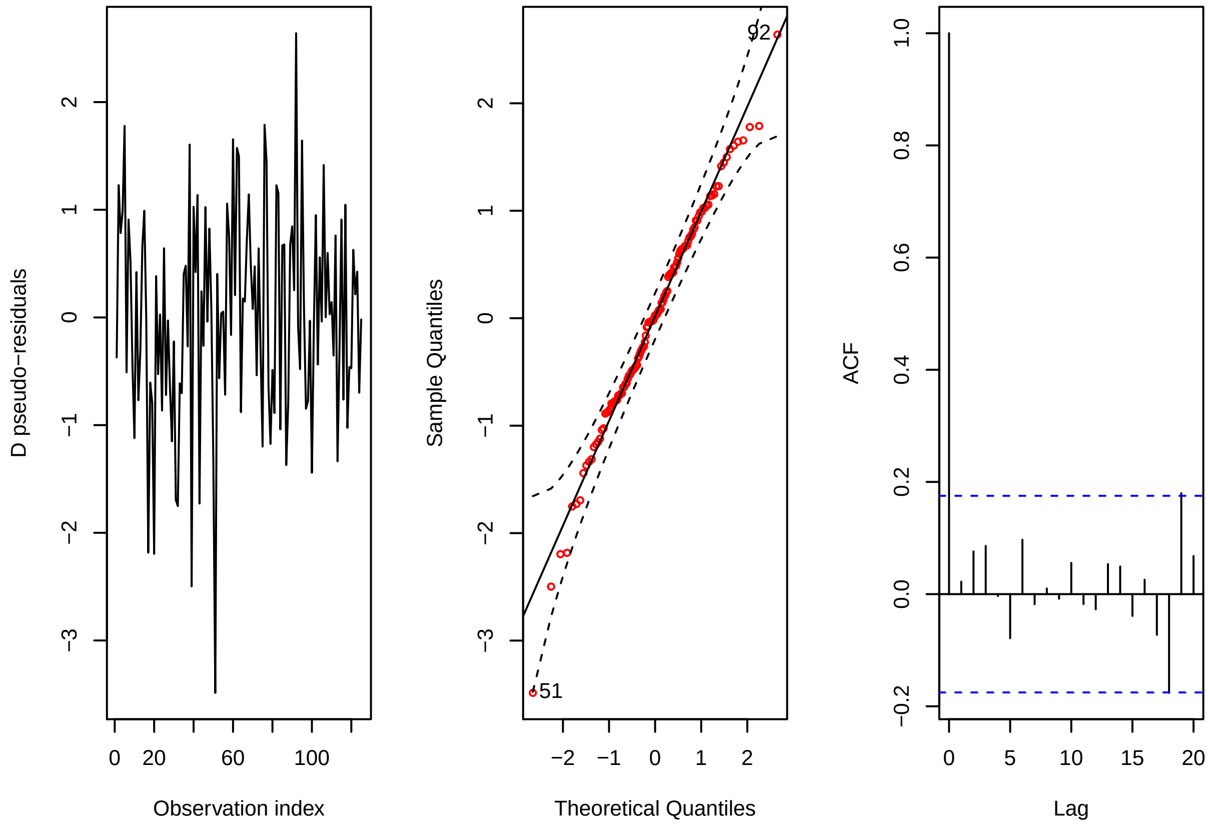


stone density + stone density^2 + n ants + distance

```
##   [1] 63.71512 63.71512 63.71512 63.71512 86.08852 63.71512 86.08852 63.71512
##   [9] 86.08852 63.71512 86.08852 63.71512 86.08852 63.71512 65.00224 63.71512
##  [17] 63.71512 86.08852 63.71512 65.00224 63.71512 63.71512 63.71512 64.99483
##  [25] 64.99483 63.71512 65.00224 63.71512 63.71512 73.02501 65.00224 63.71512
##  [33] 63.71512 63.71512 63.94312 63.71512 63.71512 63.71512 63.71512 63.71512
##  [41] 63.71512 63.71512 63.71512 86.08852 63.71512 63.71512 63.71512 63.71512
##  [49] 63.71512 63.71512 63.71512 63.71512 63.71512 65.00225 86.08852 63.71512
##  [57] 63.71512 63.71512 63.71512 63.71512 63.71512 65.00224 63.71512 65.00224
##  [65] 63.94312 63.71512 86.08852 63.71512 63.71512 65.00225 63.71512 63.71512
##  [73] 63.71512 63.71512 63.71512 63.71512 65.00224 65.00225 63.71512 63.71512
##  [81] 63.71512 63.71512 86.08852 63.71512 65.00224 64.99483 63.71512 65.00224
##  [89] 63.71512 63.94312 63.71512 65.00224 64.99514 65.00226 63.71512 63.71512
##  [97] 63.71512 63.71512 63.71512 63.71512
```

```
## [1] 71
```

```
## Computing pseudo-residuals... DONE
```



We now compare all suitable models, excluding the models that did not converge. We can use Akaike's Information Criterion (AIC) since:

1. priors are flat (frequentist approach)
2. we can assume model parameters to have a multivariate gaussian distribution
3. N » k (where N is sample size and k is the number of parameters in each model).

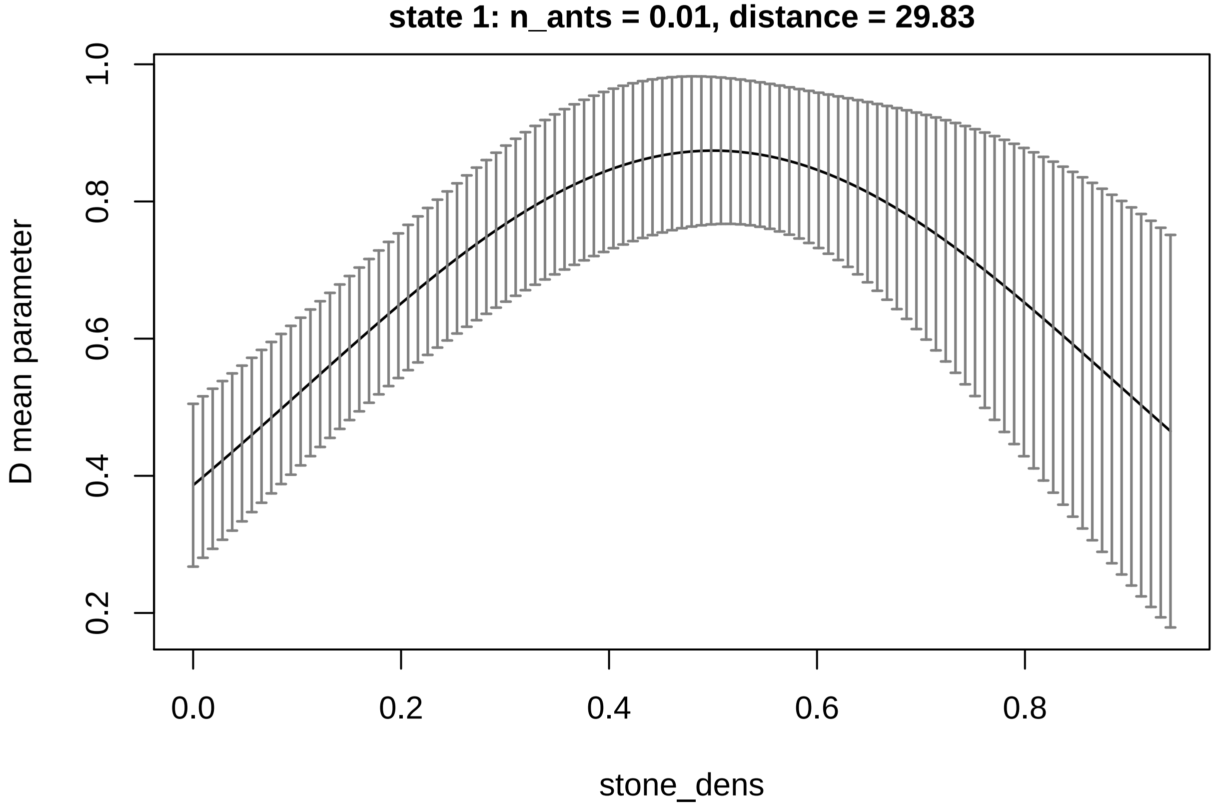
```
AIC(best_model.D.0, best_model.D.nd, best_model.D.s, best_model.D.n.d.s, best_model.D.n.d.s.s2)
```

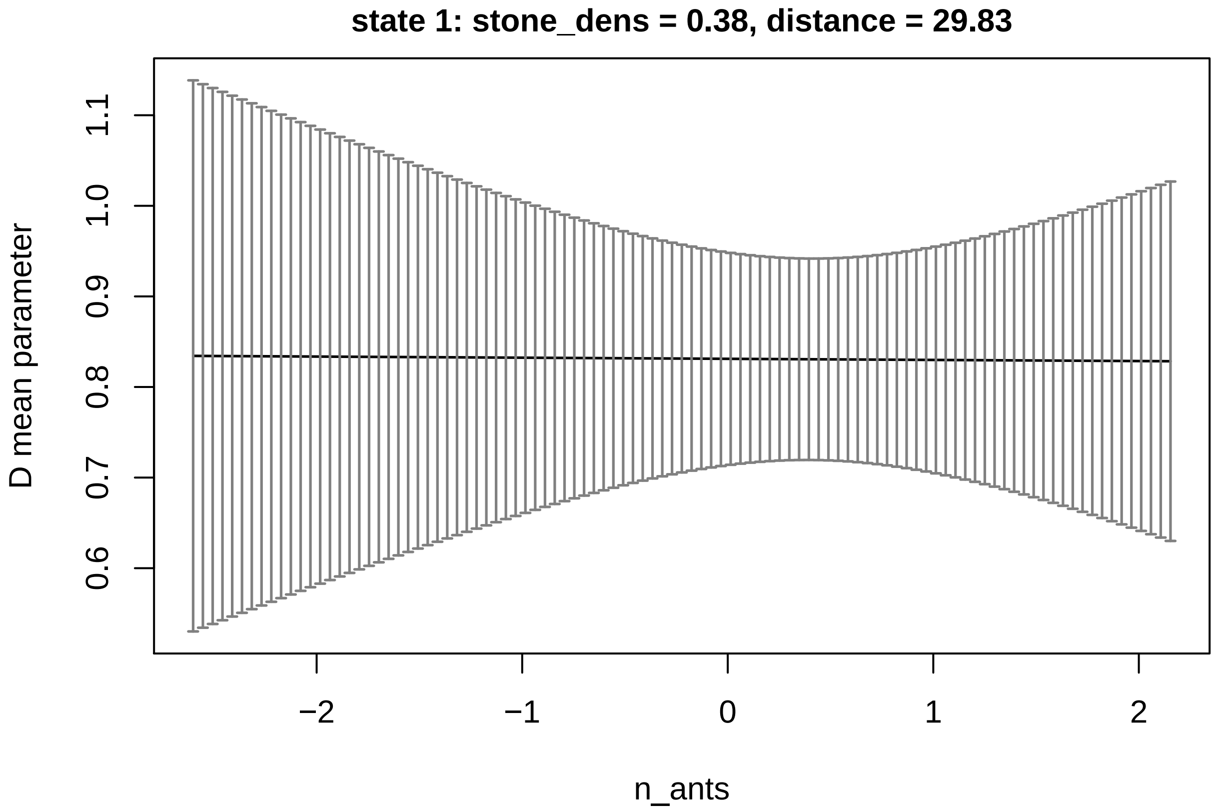
```
##                    Model      AIC
## 1 best_model.D.n.d.s.s2 157.4302
## 2       best_model.D.nd 166.3841
## 3        best_model.D.s 167.7685
## 4    best_model.D.n.d.s 169.2941
## 5        best_model.D.0 173.1953
```

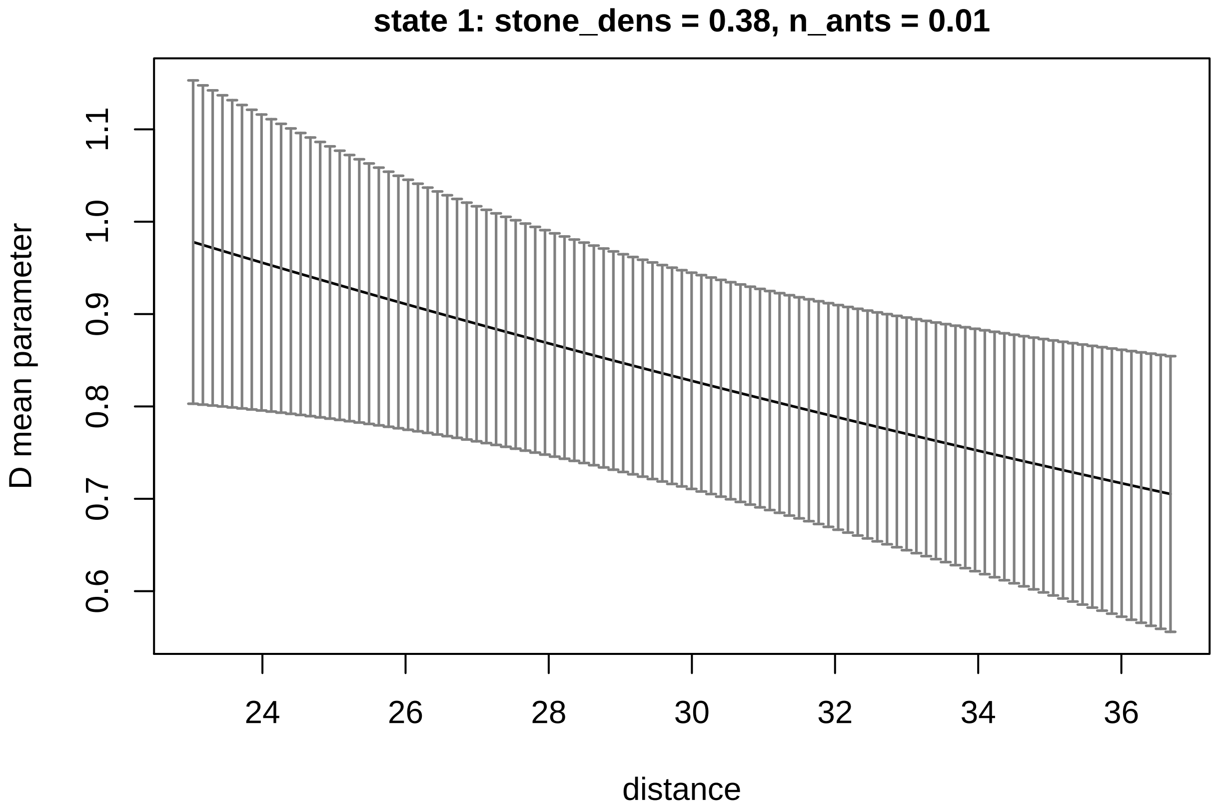
The n model with the squared term and including n ants displays the best weighted fit. Let us have a look at the effect estimates and at the event probability distribution estimate.

Stone density + stone density^2 + n ants + distance

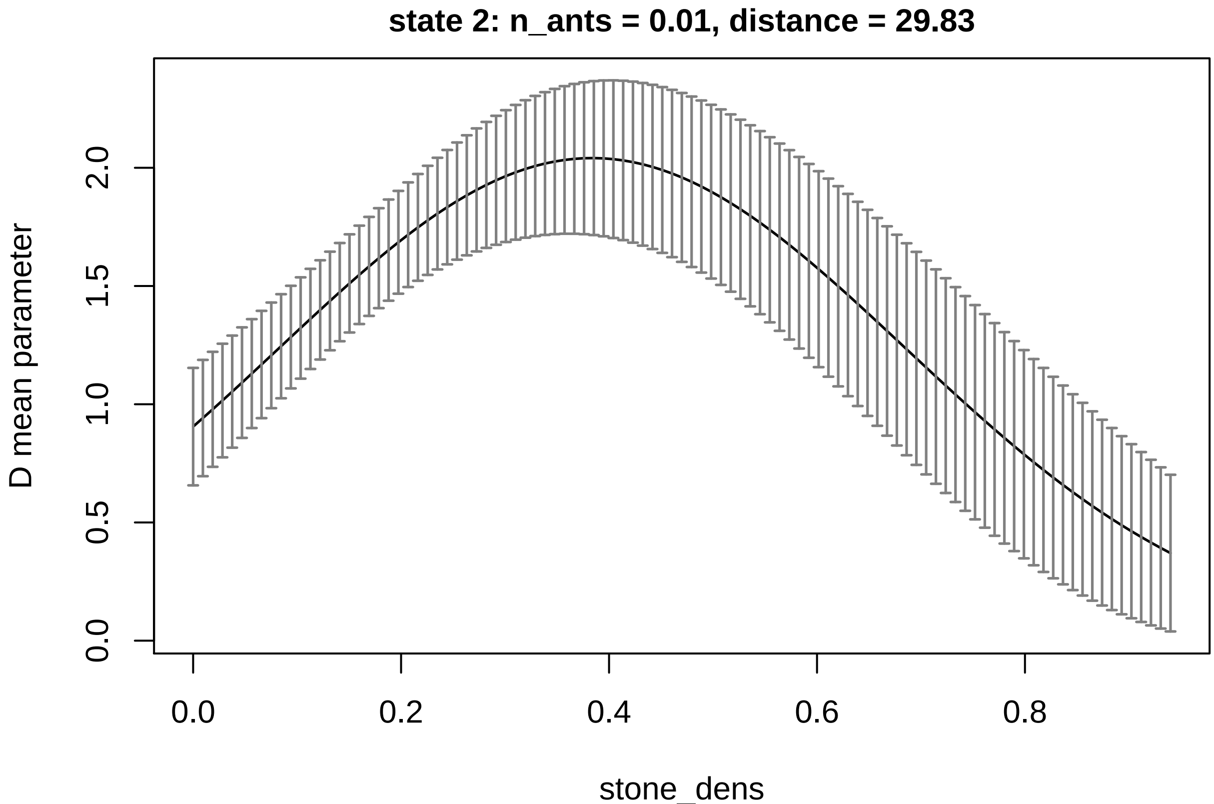
```
## Decoding state sequence... DONE
```


state 1: n_ants = 0.01, distance = 29.83
D mean parameter
1.0
0.8
0.6
0.4
0.2
0.0
0.2
0.4
0.6
0.8
stone_dens

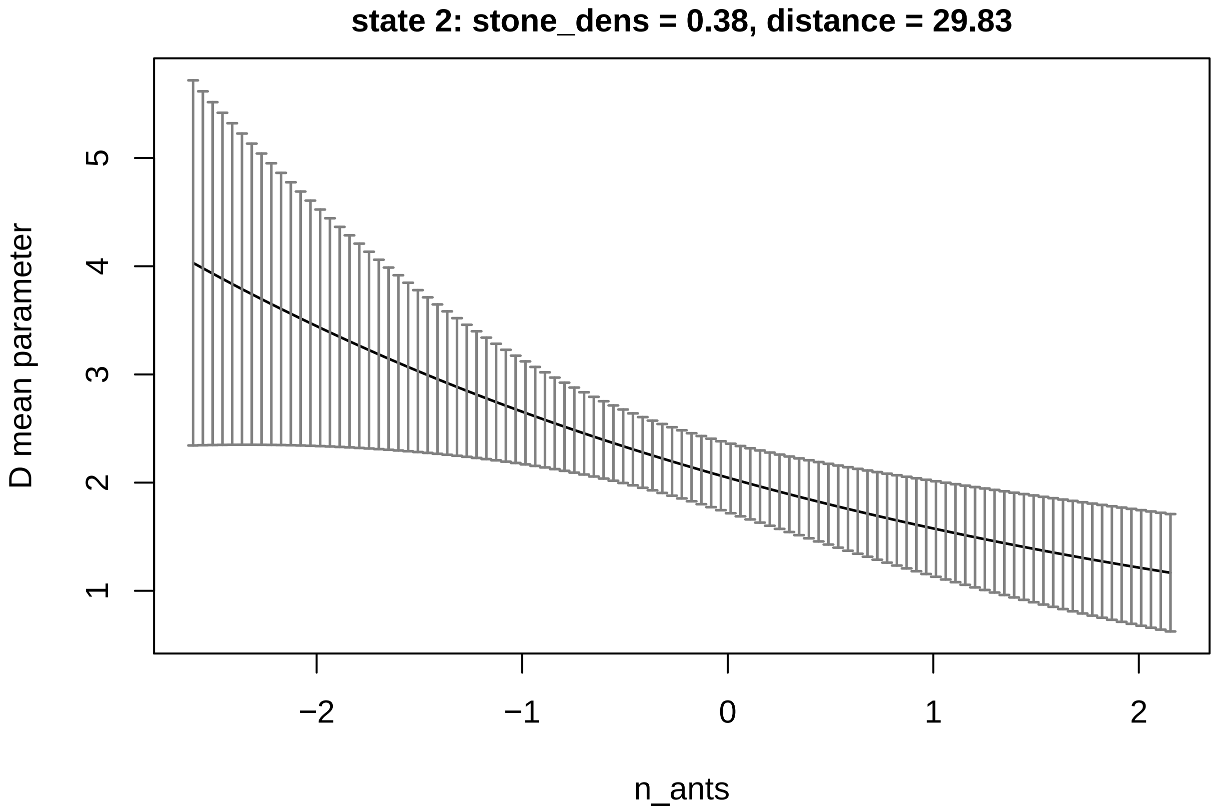

state 1: stone_dens = 0.38, distance = 29.83
D mean parameter
0.6
0.7
0.8
0.9
1.0
1.1
−2
−1
0
1
2
n_ants



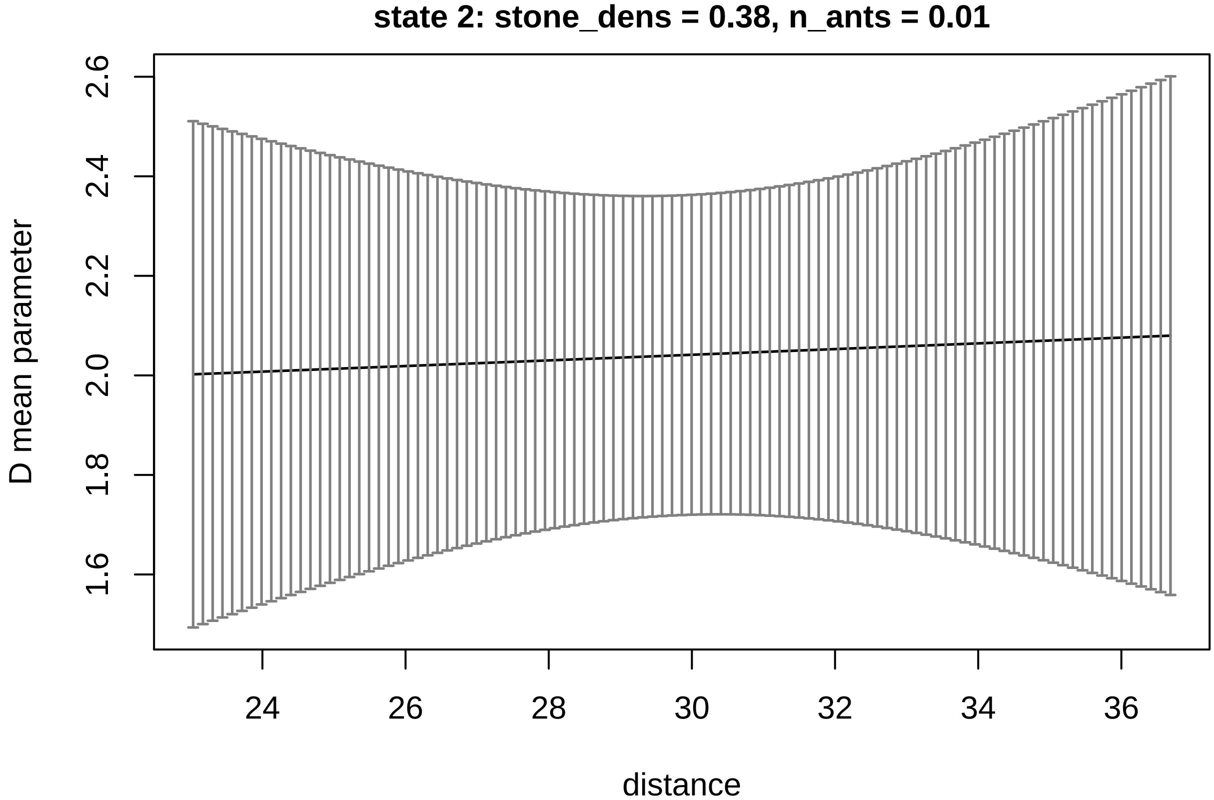
state 1: stone_dens = 0.38, n_ants = 0.01
D mean parameter
1.1
1.0
0.9
0.8
0.7
0.6
24
26
28
30
32
34
36
distance



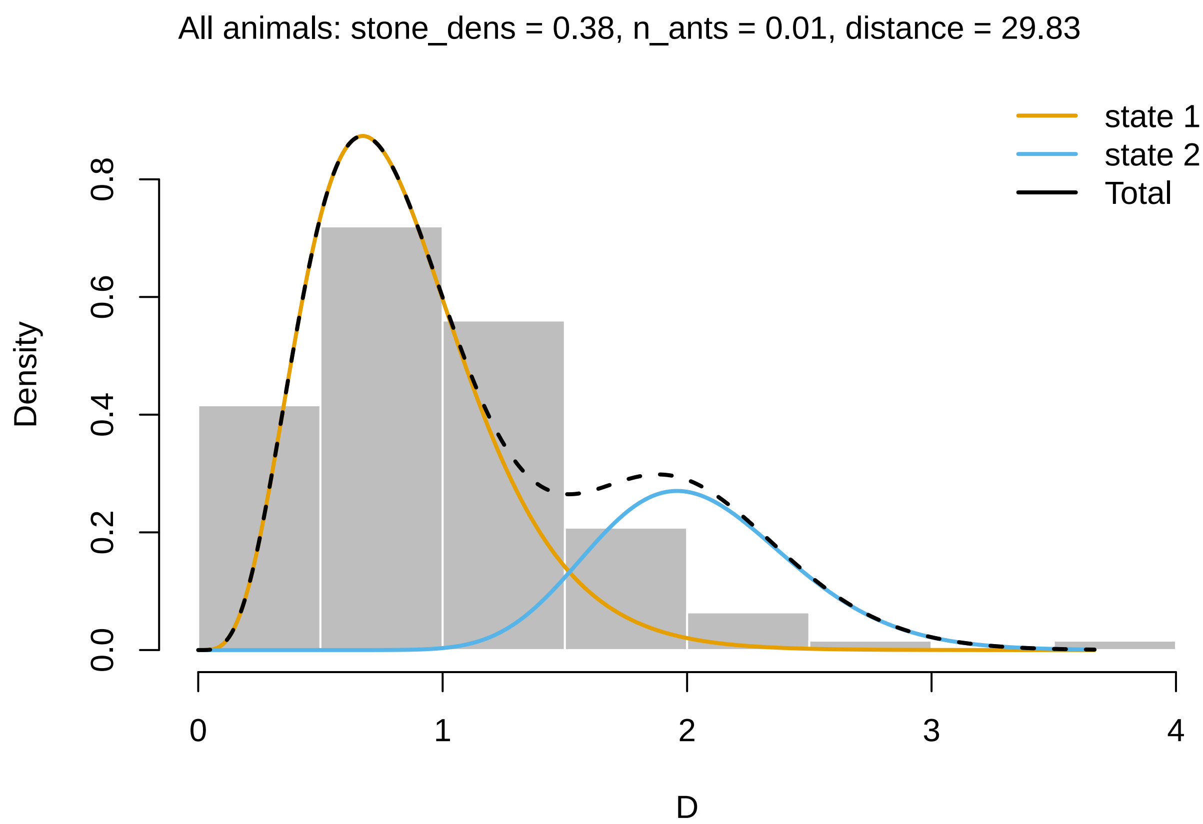
state 2: n_ants = 0.01, distance = 29.83
D mean parameter
0.0
0.5
1.0
1.5
2.0
0.0
0.2
0.4
0.6
0.8
stone_dens



state 2: stone_dens = 0.38, distance = 29.83
D mean parameter
1
2
3
4
5
−2
−1
0
1
2
n_ants



state 2: stone_dens = 0.38, n_ants = 0.01
D mean parameter
2.6
2.4
2.2
2.0
1.8
1.6
24
26
28
30
32
34
36
distance

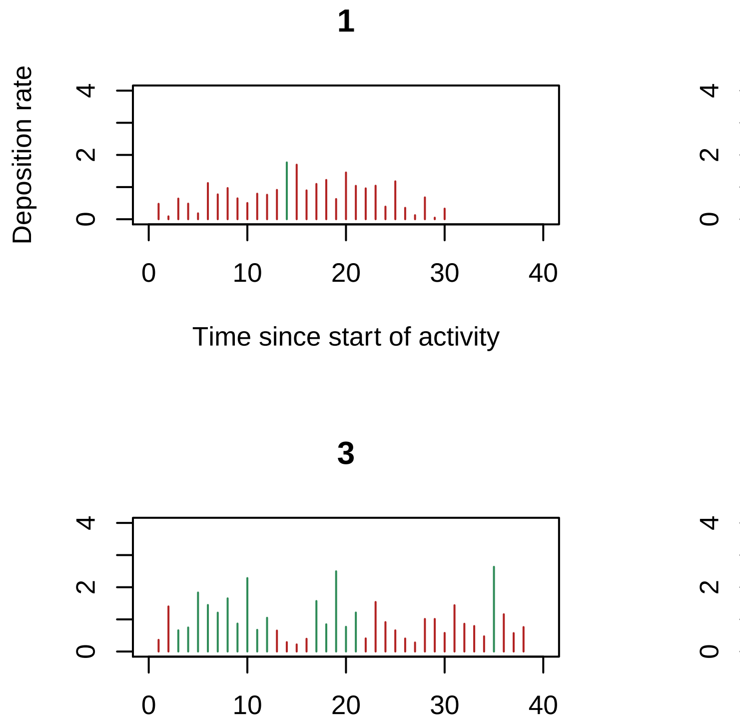



```
## Value of the maximum log-likelihood: -63.71512
##
##
## Regression coeffs for D parameters:
## ----------------------------------
##      mean_1:(Intercept) mean_1:stone_dens mean_1:n_ants mean_1:distance
## [1,]         -0.2369175          3.265312   -0.00148969     -0.02394714
##      mean_1:I(stone_dens^2) mean_2:(Intercept) mean_2:stone_dens mean_2:n_ants
## [1,]              -3.263716         -0.1798989          4.236211     -0.260715
##      mean_2:distance mean_2:I(stone_dens^2) sd_1:(Intercept) sd_2:(Intercept)
## [1,]     0.002787322              -5.518229        -1.015476       -0.8959941
##
## D parameters (based on mean covariate values):
## ----------------------------------------------
##        state 1   state 2
## mean 0.8310959 2.0404264
## sd   0.3622301 0.4082016
##
## Regression coeffs for the transition probabilities:
## ---------------------------------------------------
##                1 -> 2    2 -> 1
## (Intercept) -2.841166 -1.703259
##
## Transition probability matrix:
## -----------------------------
##           state 1    state 2
```

```
## state 1 0.9448602 0.05513977
## state 2 0.1540401 0.84595987
##
## Initial distribution:
## ---------------------
##   state 1   state 2
## 0.7736375 0.2263625
```

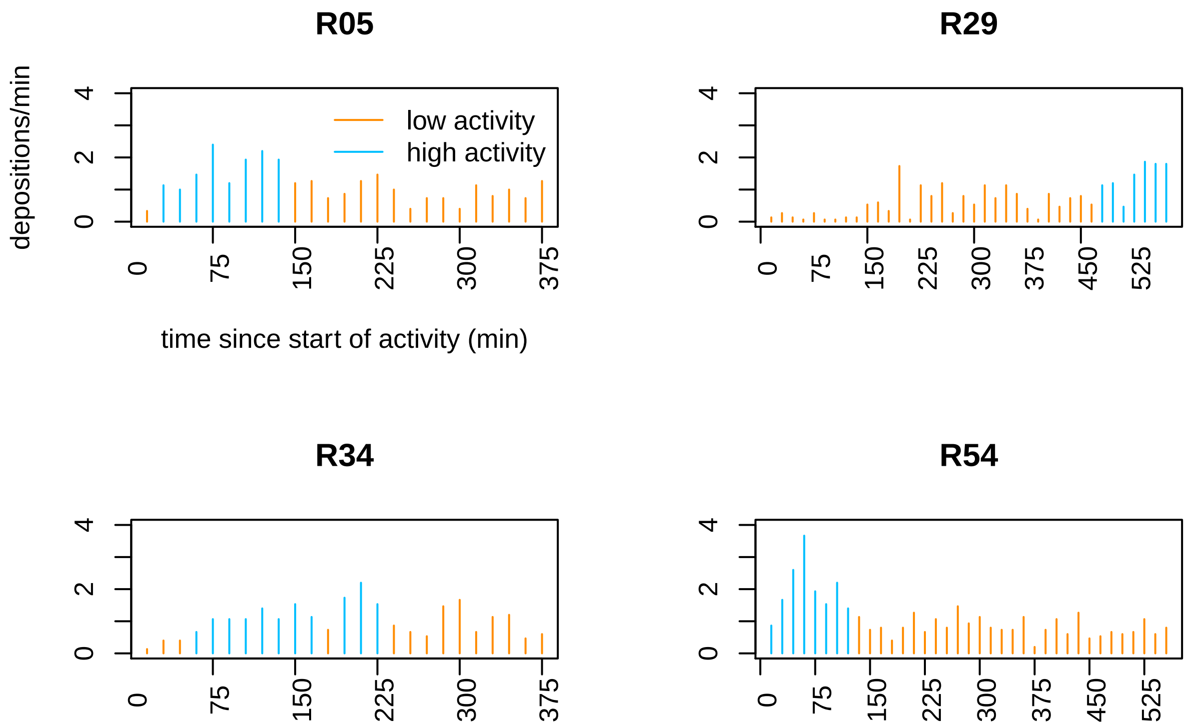
Check model predictions

Let's predict the activity patterns of 4 new colonies based on our best model.



stone density + stone density^2 + n ants + distance

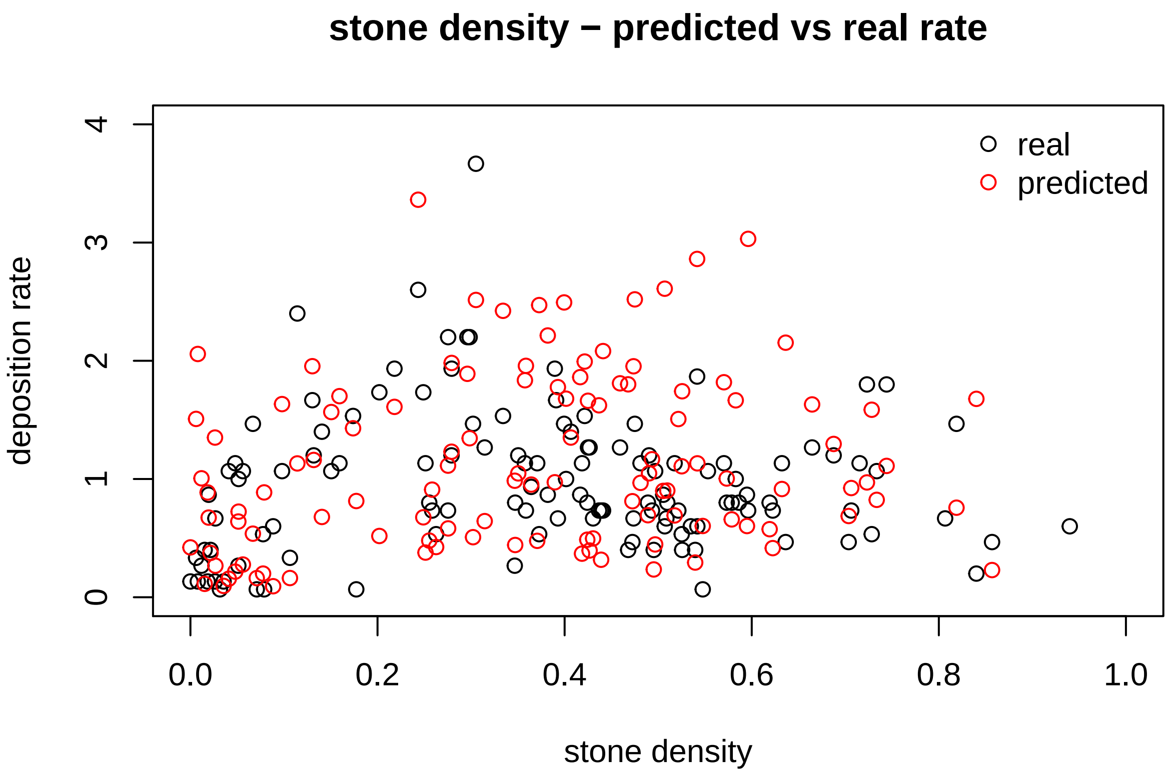
and compare with real data.



The predictions show a good match between the activity state and the deposition rate - even if some intervals with high rate are classified as low activity.

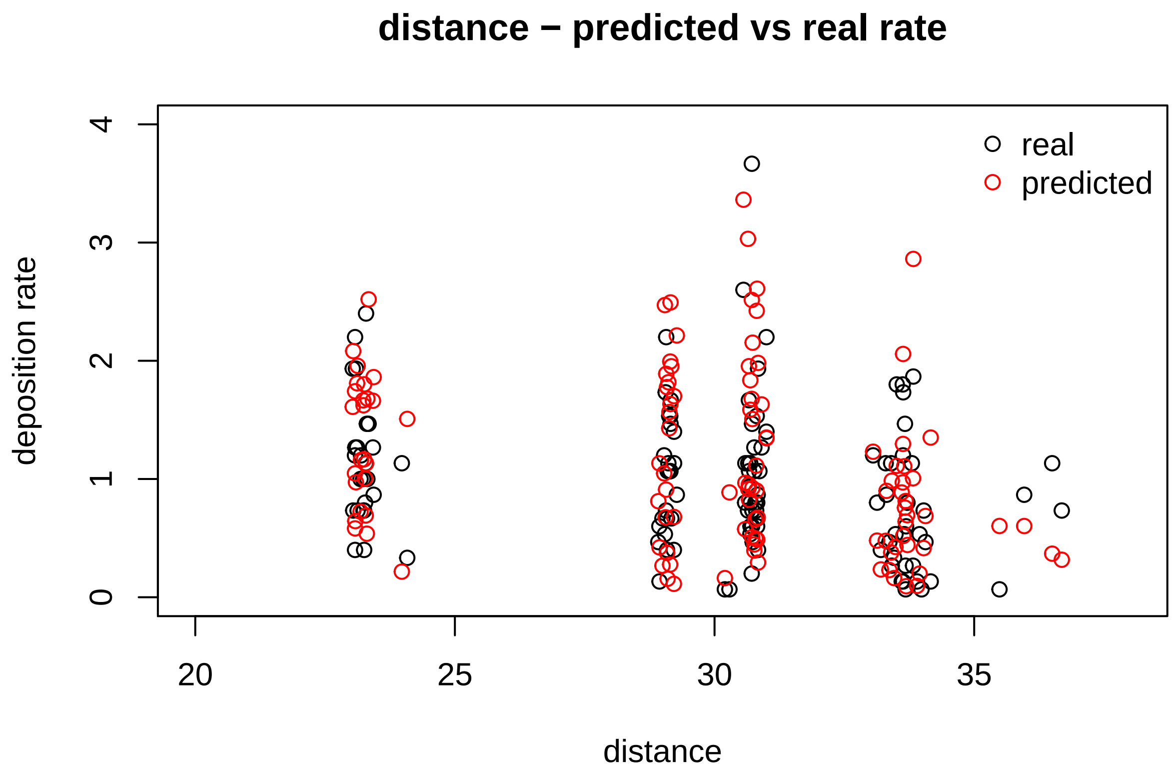
Let's now plot the predictions made by this model over the predictors, to check for unusual patterns that might indicate issues.

Activity over stone density



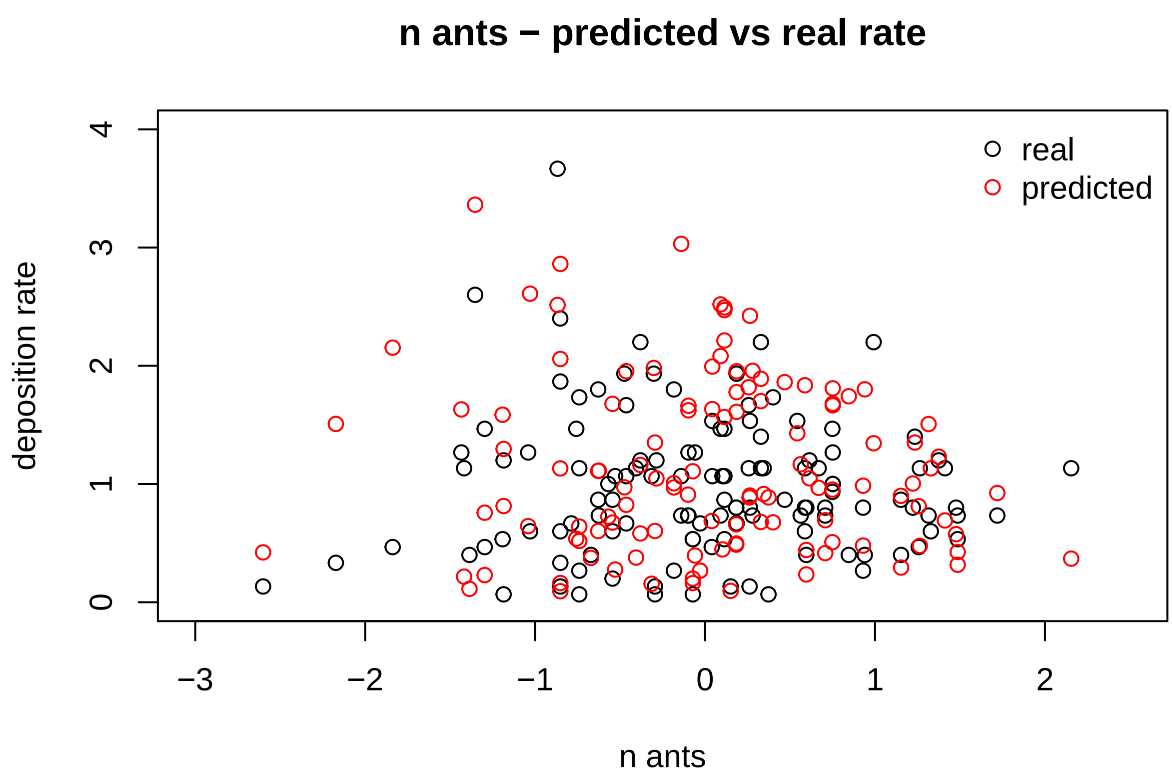
The model overestimates deposition rate at very low stone density values and generally seems to tend towards intermediate deposition rates.

Activity over distance



Not so good for high distance values, but otherwise pretty good.

Activity over n of ants in cluster



Seems to be a good fit.

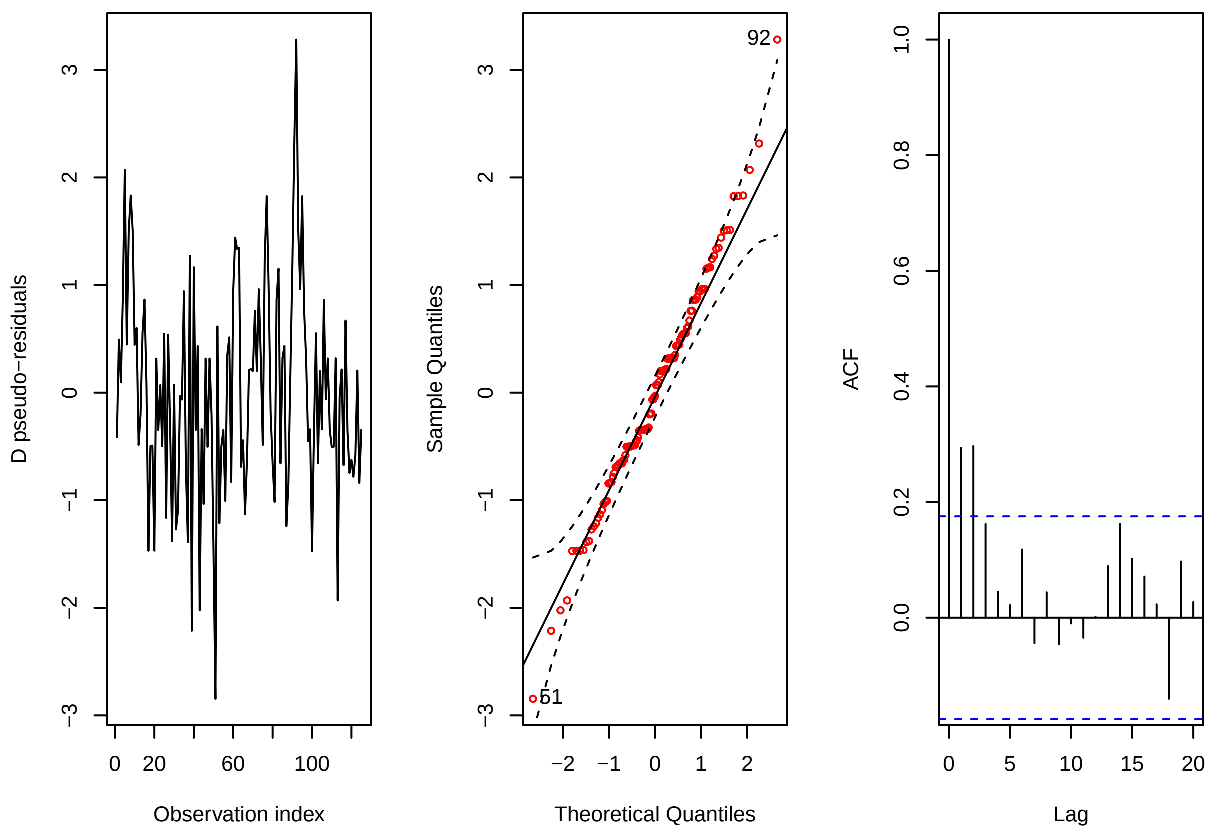
Based on current models of cyclic behaviour in ants, worker interactions might underlie the activity cycles. Interactions become more likely as n of ants in the colony increases. Because change in n of workers engaged in building or otherwise in the building area is inversely proportional to the change in n of ants in the brood cluster, we can use this latter variable to check the effect on transition probabilities. Let's fit a model where transition probabilities between states depend on n of ants in the brood cluster.

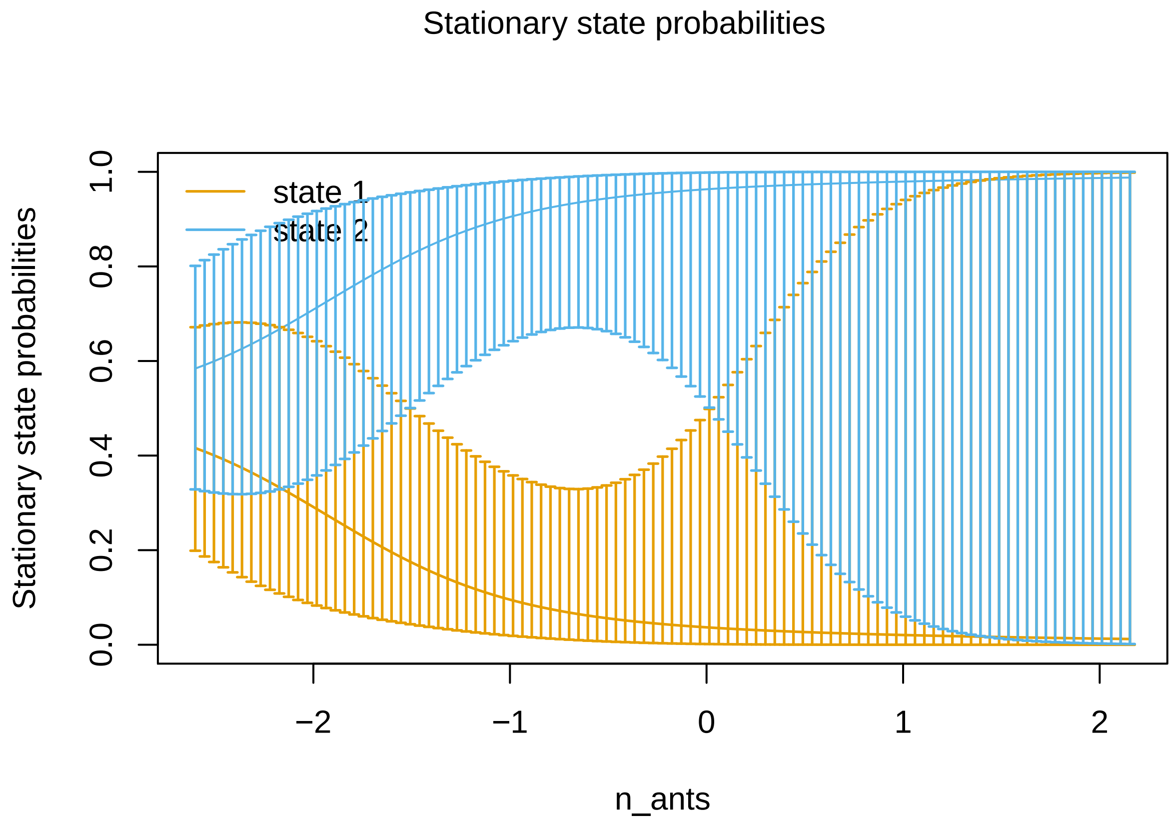
Effect of n of ants on probability of transition between states

```
# Load model and plot residuals
fn <- paste0(modelPath, "allm_trans_n.rds")  # load fitted models from rds file
allm.trans.n <- readRDS(fn)  [1:niter]      # the first 25 objects contain the models (the remaining 25

# extract all min neg log likelihood values
allnllk.trans.n <- unlist(lapply(allm.trans.n, function(m) m$mod$minimum))
allnllk.trans.n
```

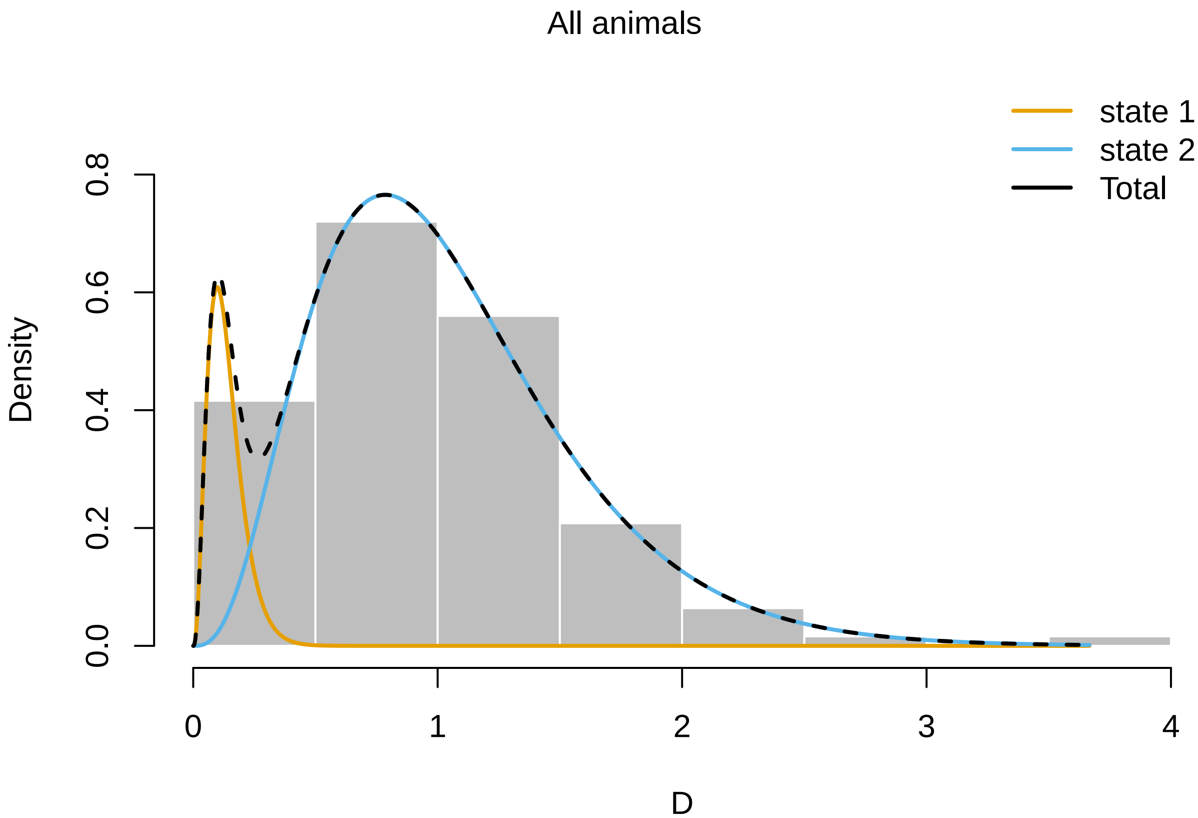
```
##   [1]  78.20521  78.20521  78.20521  78.20521  78.20521  78.20521  78.20521
##   [8]  78.20521  78.20521  78.20521  78.20521  78.20521  78.20521 102.23018
##  [15]  78.20521  78.20521  78.20521  78.20521  78.20521  78.20521  78.20521
```

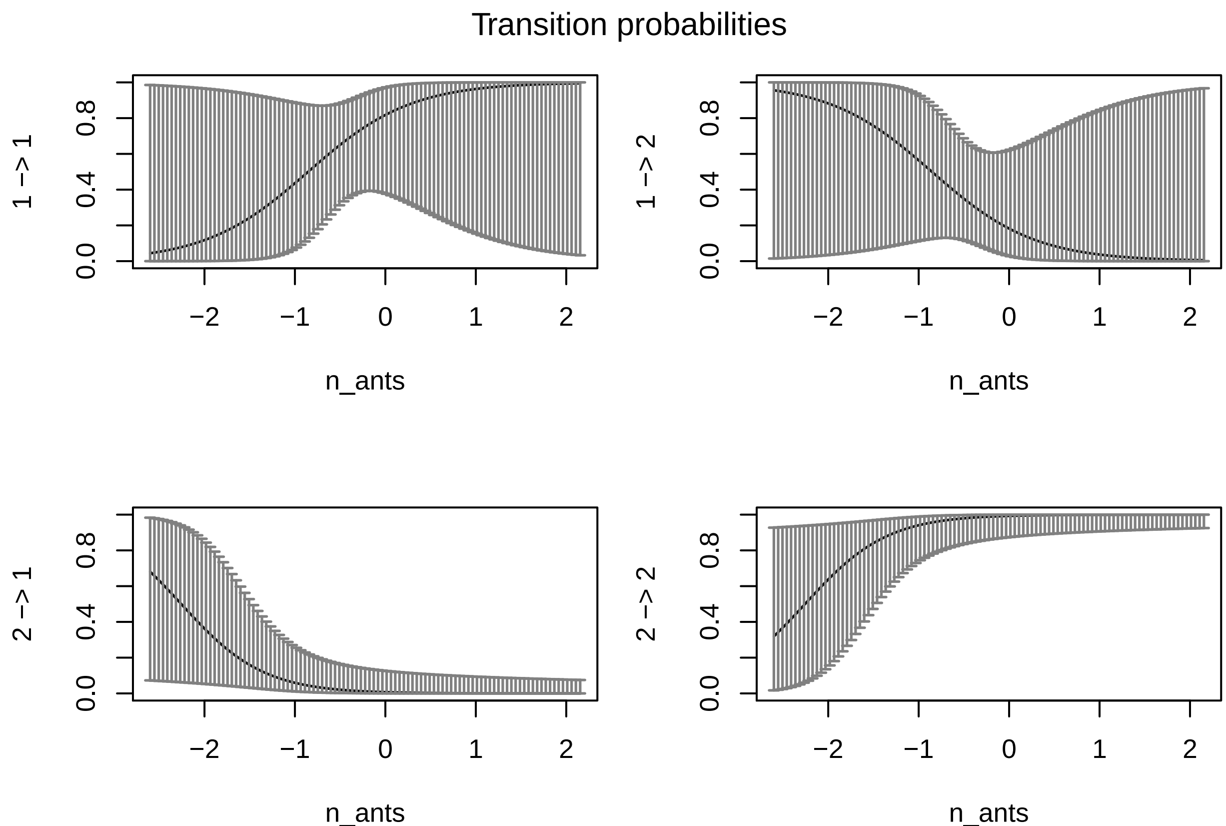
```
## [22]  78.20521  78.20521  78.20521  78.20521  78.20521  78.20521  78.20521
## [29]  78.20521  78.20521  78.20521  78.39689  78.20521  78.20521  78.20521
## [36]  78.20521  78.20521  78.20521  78.20521  78.20521  78.20521  78.20521
## [43]  78.20521  78.20521 102.23018  78.20521  78.20521  78.20521  78.20521
## [50]  78.20521  78.20521  78.20521 102.23018  78.20521  78.20521  78.20521
## [57]  78.20521 102.23019  78.20521  79.36821  78.20521  78.20521  78.20521
## [64] 102.23018  78.20521  78.20521  78.20521  78.20521  78.20521  78.39689
## [71]  79.36821  78.20521  78.20521  78.20521  78.20521  78.20521  78.20521
## [78]  78.20521  78.20521  78.20521  78.39689  78.20521  78.20521  78.20521
## [85] 102.23018  78.20521  78.20521  78.20521  78.20521 102.23018  78.20521
## [92]  78.20521  78.20521  78.20521  78.20521  78.20521  78.20521  78.20521
## [99]  78.20521  78.20521

## [1] 91

## Computing pseudo-residuals... DONE
```






```
## Decoding state sequence... DONE
```


All animals
state 1
state 2
Total
Density
0.0
0.2
0.4
0.6
0.8
0
1
2
3
4
D




```
## Value of the maximum log-likelihood: -78.20521
##
##
## D parameters:
## -------------
##         state 1   state 2
## mean 0.13595121 1.0526229
## sd   0.07170166 0.5301595
##
## Regression coeffs for the transition probabilities:
## ---------------------------------------------------
##                1 -> 2    2 -> 1
## (Intercept) -1.501032 -4.959768
## n_ants      -1.758446 -2.197959
##
## Transition probability matrix (based on mean covariate values):
## ---------------------------------------------------------------
##             state 1   state 2
## state 1 0.820463081 0.1795369
## state 2 0.006807926 0.9931921
##
## Initial distribution:
## ---------------------
##   state 1   state 2
## 0.3794686 0.6205314
```

Colonies that are active are more likely to stay active when there are more ants in the central brood cluster, contrary to predictions.

Effect of stone density on probability of transition between states

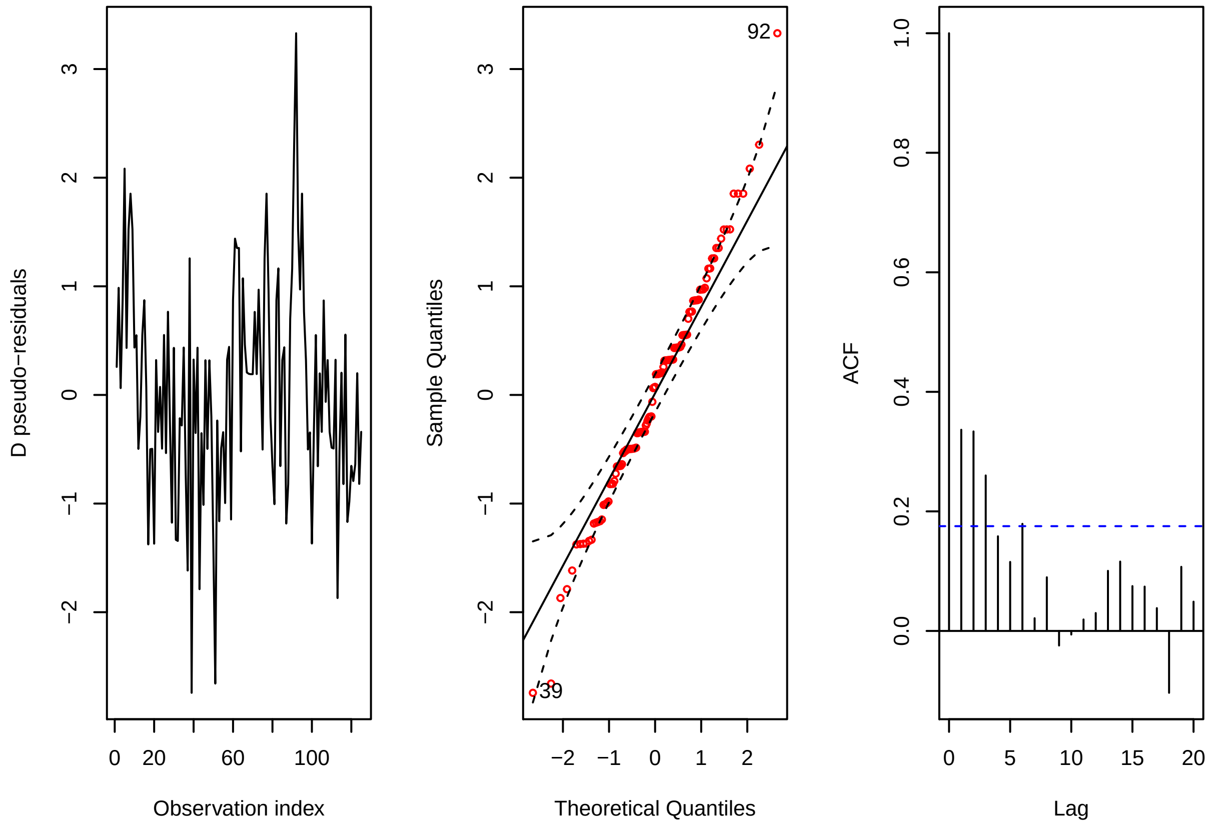
Because in the F&D model deposition probability is affected by local stone density, we check whether stone density also affects transition between states.

```
# Load model and plot residuals
fn <- paste0(modelPath, "allm_trans_s.rds")  # load fitted models from rds file
allm.trans.s <- readRDS(fn)  [1:niter]     # the first 25 objects contain the models (the remaining 25

# extract all min neg log likelihood values
allnllk.trans.s <- unlist(lapply(allm.trans.s, function(m) m$mod$minimum))
allnllk.trans.s
```

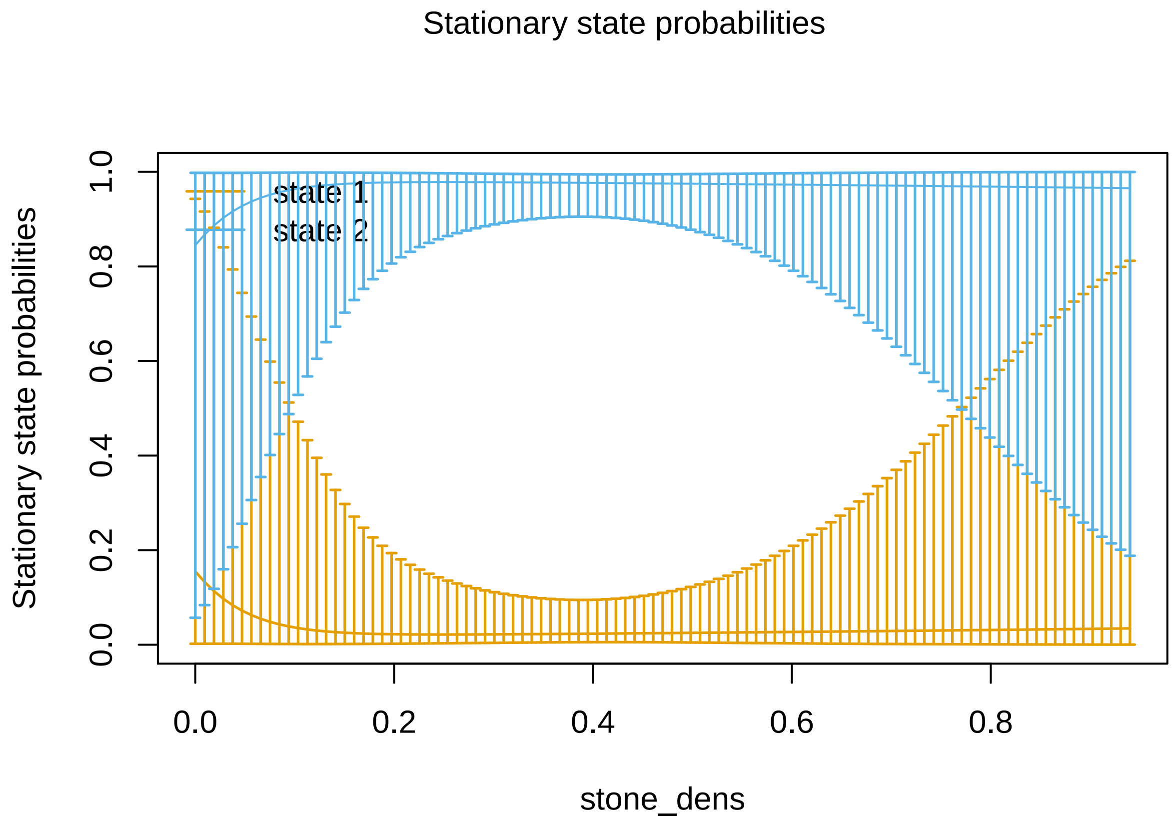
```
##   [1]  77.19044  77.49385  77.19044  77.49385  77.19044  77.19044  77.19044
##   [8]  77.19044  77.19044  77.19044  77.19044  77.49385  77.49385 102.23018
##  [15]  77.19044  77.19044  77.49384  79.47134  77.19044  77.19044  77.19044
##  [22]  77.19044  77.19044  77.19044  77.19044  77.19044  77.49385  77.49385
##  [29]  77.19044  77.19044  77.49385  79.47134  77.19044  77.19044  77.19044
##  [36]  77.19044  79.47134  77.19044  77.19044  79.47134  77.19044  77.19044
##  [43]  77.19044  77.49385 102.23018  77.19044  77.49384  77.19044  77.49385
##  [50]  77.19044  77.19044  79.47134 102.23018  77.49381  77.19044  79.47134
##  [57]  77.19044 102.23018  79.47134  79.47134  77.19044  77.49385  77.19044
##  [64] 102.23018  77.19044  77.19044  77.19044  77.49385  77.19044  79.47134
##  [71]  79.47134  77.19044  77.19044  77.49385  77.19044  77.19044  77.19044
##  [78]  77.19044  77.19044  77.19044  77.19044  77.49384  77.49383  77.19044
##  [85] 102.23018  77.49385  77.19044  77.19044  77.19044 102.23018  77.19044
##  [92]  77.19044  77.19044  77.49385  77.19044  77.19044  77.19044  77.49385
##  [99]  77.19044  77.49385
```

```
## [1] 83
```

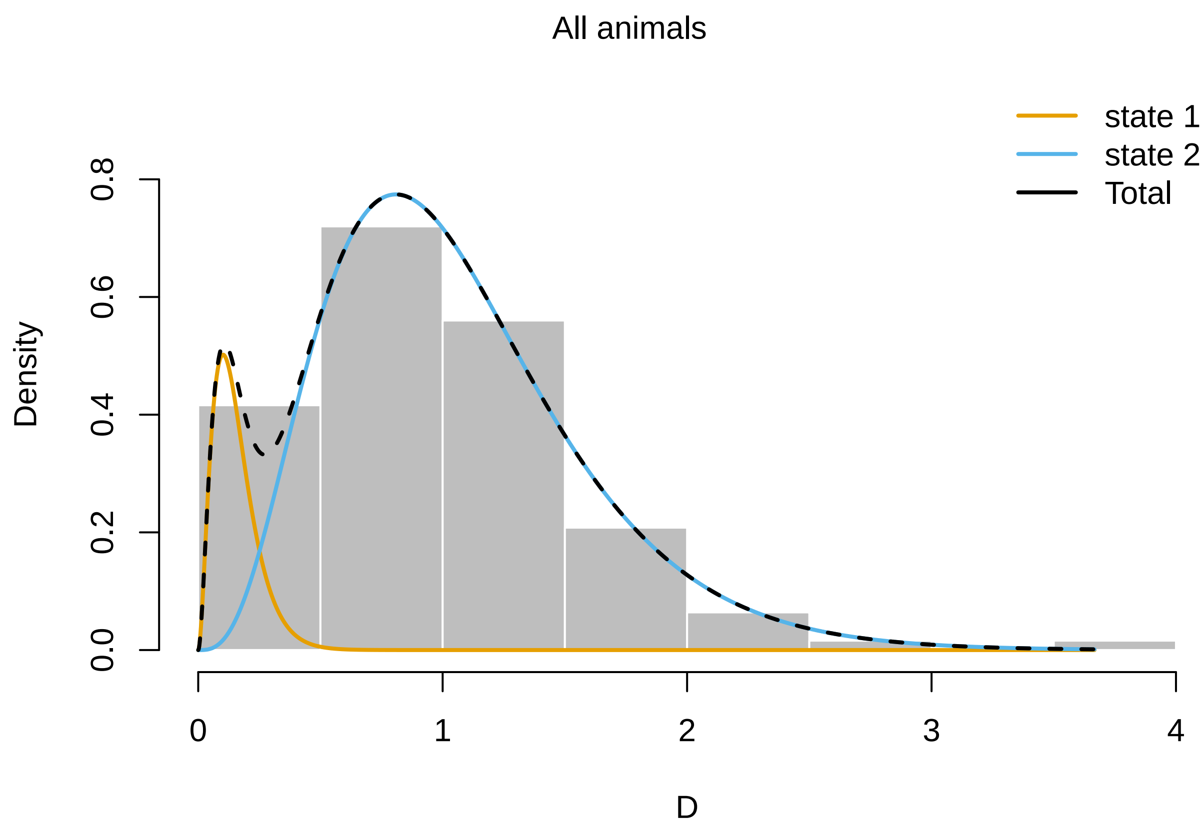
```
## Computing pseudo-residuals... DONE
```

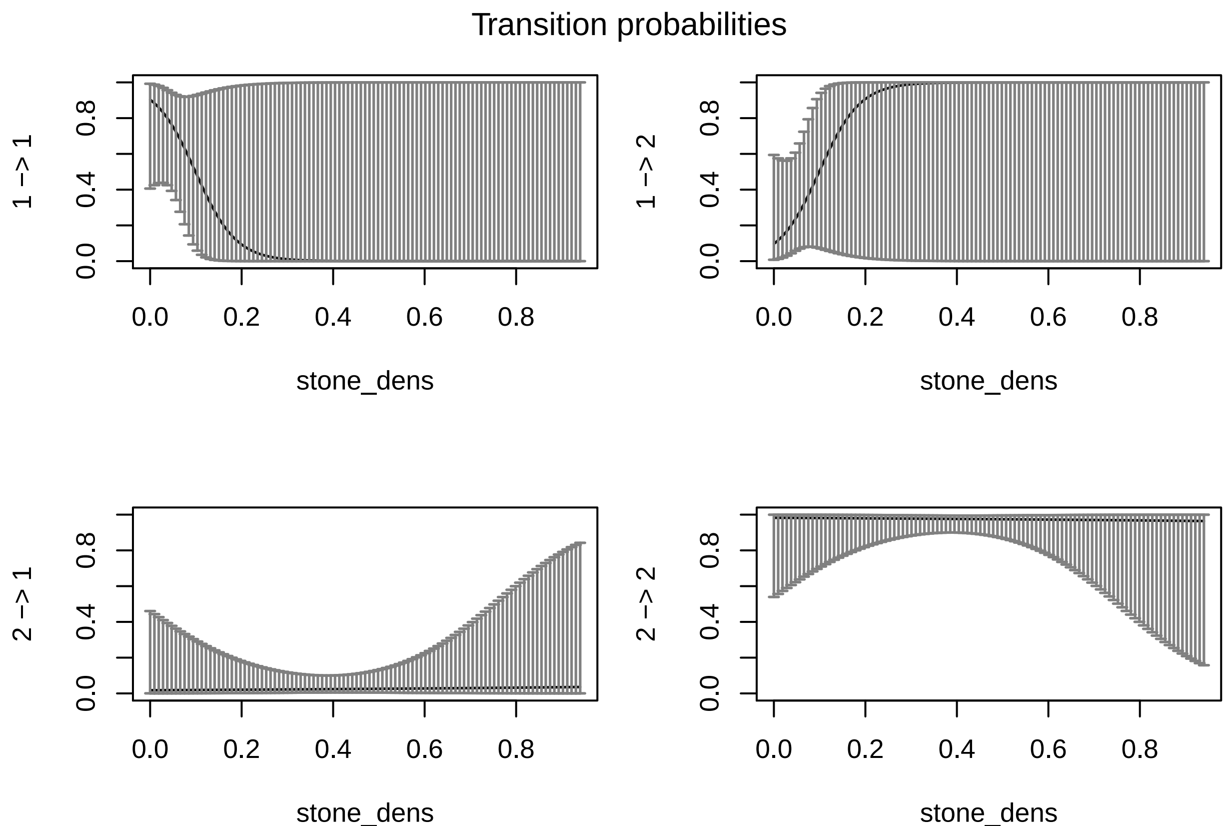


D pseudo−residuals
Observation index
Sample Quantiles
Theoretical Quantiles
92
39
ACF
Lag




```
## Decoding state sequence... DONE
```


All animals
state 1
state 2
Total
Density
0.0
0.2
0.4
0.6
0.8
0
1
2
3
4
D




```
## Value of the maximum log-likelihood: -77.19044
##
##
## D parameters:
## -------------
##         state 1   state 2
## mean 0.15419341 1.0632829
## sd   0.09005455 0.5202762
##
## Regression coeffs for the transition probabilities:
## ---------------------------------------------------
##                1 -> 2    2 -> 1
## (Intercept) -2.238371 -4.016540
## stone_dens  22.586978  0.769253
##
## Transition probability matrix (based on mean covariate values):
## ---------------------------------------------------------------
##             state 1   state 2
## state 1 0.001925828 0.9980742
## state 2 0.023489496 0.9765105
##
## Initial distribution:
## ---------------------
##   state 1   state 2
## 0.6850447 0.3149553
```

Colonies that are active are very likely to remain active at intermediate values of stone density - but not at extreme ones. At very low stone density, inactive colonies are unlikely to become active until stone density has increased.