Data simulation and analysis of population trends with GLMMs

Supporting documentation for: Unreliable inferences about chinstrap penguin population trends: a statistical critique and reanalysis

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2023-06-19

Purpose

This script simulates population counts over time to test glmer (lme4) and MCMCglmm (MCMCglmm) mixed model specifications. This simulation study shows some of the errors in Krüger (2023)'s MCMCglmm analysis code and show why the results from models used in that paper are not useful. (Citation: Krüger, L. (2023). Decreasing Trends of Chinstrap Penguin Breeding Colonies in a Region of Major and Ongoing Rapid Environmental Changes Suggest Population Level Vulnerability. Diversity, 15(3), 327.)

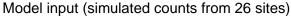
Simulate data

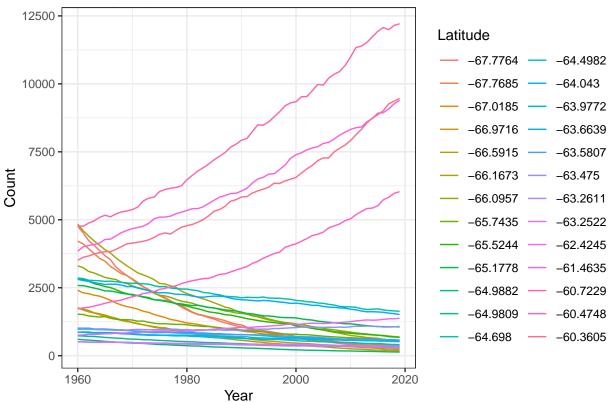
```
# load library
library(tidyverse)
library(lme4)
library(effects)
library(MCMCglmm)
#-----
# Simulate data
#-----
# Simulation based on Chapter 5 from State-Space Models for Population Counts from
# Bayesian Population Analysis using Winbugs by Marc Kery and Michael Schaub
# Make an empty list to save output in
list1 = list() # for population counts
list2 = list() # for lambda of each population
# Set seed for reproducibility
set.seed(1234)
# Choose how many populations and how many years you want to simulate
n.populations = 26 # Number of populations (max = 26)
n.years <- 60 # Number of years
start.year = 1960 # Start year
years = start.year:(start.year+n.years-1) # Year sequence
```

```
# simulate
for(i in 1:n.populations) {
  N1 <- runif(1, 500, 5000) # Initial population size
  mean.lambda <- runif(1, 0.95, 1.02) # Mean annual population growth rate
  sigma2.lambda <- 0.0001 # Process (temporal) variation of the growth rate
  sigma2.y <- 0 # Variance of observation error (0 assumes 100% accurate counts)
  y <- N <- numeric(n.years)
 N[1] \leftarrow N1
  lambda <- rnorm(n.years-1, mean.lambda, sqrt(sigma2.lambda))</pre>
  for (t in 1:(n.years-1)){
   N[t+1] \leftarrow N[t] * lambda[t]
  for (t in 1:n.years){
   y[t] <- rnorm(1, N[t], sqrt(sigma2.y))</pre>
  # Save output in list for each iteration
 list1[[i]] = as.data.frame(y)
 list2[[i]] = as.data.frame(mean.lambda)
# list1
# list2
# Build data frame from simulations of count
df = bind_rows(list1)
names(df) = "count"
# add year to simulated counts
df$year = as.integer(rep(years,n.populations))
# add site to simulated counts
df$site = rep(LETTERS[1:n.populations], each = n.years)
# assign a random latitude to each site
# df$latitude.random = rep(runif(n.populations, -70, -60), each = n.years)
df = as_tibble(df)
# Use list 2 (lambda) to generate a latitude value for each site that
# correlate with the site's growth rate (lambda)
lambda = bind_rows(list2)
lambda$site = LETTERS[1:n.populations]
lambda$noise = runif(n.populations, -1, 1)
df = merge(df, lambda, by = "site")
df$r = df$mean.lambda-1 # convert lambda to growth rate r
df$r100 = df$r * 100
                      # rescale
range(df$r100)
```

```
##
     site
              count year mean.lambda
                                                                   r100
                                          noise
       A 1011.6654 1960
## 1
                            0.993561 -0.3990841 -0.006439042 -0.6439042
## 2
       A 1007.9579 1961
                            0.993561 -0.3990841 -0.006439042 -0.6439042
## 3
       A 1012.3983 1962
                            0.993561 -0.3990841 -0.006439042 -0.6439042
                            0.993561 -0.3990841 -0.006439042 -0.6439042
## 4
       A 982.1316 1963
## 5
       A 980.0222 1964
                            0.993561 - 0.3990841 - 0.006439042 - 0.6439042
## 6
       A 978.6712 1965
                            0.993561 - 0.3990841 - 0.006439042 - 0.6439042
# create one latitude value per site where the mean latitude (-63 degrees S)
# increase or decrease based on the growth rate of the population plus a small
# random component
df = df \%
 group_by(site) %>%
  mutate(latitude = -63 + r100 + noise) %>%
  ungroup()
range(df$latitude)
## [1] -67.77641 -60.36049
# Inspect df: every site should have 1 unique latitude value
df %>%
  group_by(site) %>%
  summarise(count = n_distinct(latitude)) %>%
  summarise(max_sites_per_lat = max(count))
## # A tibble: 1 x 1
   max_sites_per_lat
##
                 <int>
## 1
                     1
# Counts must be positive and integers
df = df \%
  dplyr::filter(count > 0) %>%
  dplyr::select(site, count, year, latitude) %>%
  mutate_at(vars(latitude), round, 4) %>%
 mutate_at(vars(count), round, 0)
# Plot data used for fitting models
ggplot(df, aes(x = year, y = count, color = as.factor(latitude))) +
  geom_line() +
 labs(x = "Year", y = "Count") +
  scale_color_discrete(name = "Latitude")+
  theme_bw()+
  labs(subtitle = "Model input (simulated counts from 26 sites)")
```

head(df)





glmer (lme4) analysis

```
# Fit in frequentist framework - lme4
#library(lme4)

# random slope model with interaction between year and latitude that test
# whether latitude influence population trend
m1 = glmer(count ~ year * latitude + (year|site), family = "poisson", data = df)

## Warning: Some predictor variables are on very different scales: consider
## rescaling

## Error in (function (fr, X, reTrms, family, nAGQ = 1L, verbose = 0L, maxit = 100L, : Downdated VtV is
# model convergence problems occur. Can be avoided by scaling variables
# to mean = 0, sd = 1
df$zyear = scale(df$year)
df$zlatitude = scale(df$latitude)

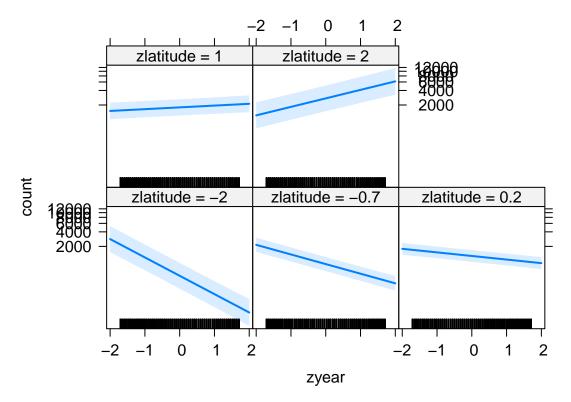
# Refit with scaled predictors variables
m2 = glmer(count ~ zyear * zlatitude + (zyear|site), family = "poisson", data = df)
```

```
# random slope model: assume latitude does not affect overall count (intercepts),
# only the slope of the year effect
m3 = glmer(count ~ zyear + zyear:zlatitude + (zyear|site), family = "poisson", data = df)
# Frequentist representation of the Kruger (2023) model
m4 = glmer(count ~ zyear + (zlatitude|site), family = "poisson", data = df)
## Warning in checkConv(attr(opt, "derivs"), opt$par, ctrl = control$checkConv, : Model is nearly unide:
## - Rescale variables?
# Note the warning message, even with z-standardized covariates
# Are populations nested in latitude? Nested random effects occur when a lower
# level factor appears only within a particular level of an upper level factor.
# How good is the relative fit of the models?
AIC(m2, m3, m4) # Note the AIC difference
              AIC
##
     df
## m2 7 15193.10
## m3 6 15199.14
## m4 5 395741.79
summary(m2)
## Generalized linear mixed model fit by maximum likelihood (Laplace
    Approximation) [glmerMod]
## Family: poisson (log)
## Formula: count ~ zyear * zlatitude + (zyear | site)
     Data: df
##
                BIC
                     logLik deviance df.resid
       ATC
## 15193.1 15230.6 -7589.6 15179.1
##
## Scaled residuals:
              1Q Median
##
      Min
                              3Q
## -4.6649 -0.4108 0.0011 0.4291 3.2434
##
## Random effects:
## Groups Name
                      Variance Std.Dev. Corr
         (Intercept) 0.509685 0.71392
          zyear
                      0.006321 0.07951 0.05
## Number of obs: 1560, groups: site, 26
##
## Fixed effects:
                  Estimate Std. Error z value Pr(>|z|)
                  ## (Intercept)
                             0.01562 -15.051 < 2e-16 ***
## zyear
                  -0.23504
## zlatitude
                  0.42972
                             0.14006
                                      3.068 0.00215 **
## zyear:zlatitude 0.32035
                             0.01561 20.520 < 2e-16 ***
## ---
```

```
## Signif. codes: 0 '*** 0.001 '** 0.01 '* 0.05 '.' 0.1 ' 1
##
## Correlation of Fixed Effects:
##
               (Intr) zyear zlattd
## zyear
               0.051
## zlatitude
               0.000 0.000
## zyear:zlttd 0.000 -0.001 0.051
# significant zyear:zlatitude interaction indicates the count~year regression
# slope is positive when latitude is (more) positive,
# and negative when latitude is (more) negative
#library(effects)
ae = allEffects(m2)
## Warning in Analyze.model(focal.predictors, mod, xlevels, default.levels, : the
## predictors zyear, zlatitude are one-column matrices that were converted to
## vectors
```

plot(ae)

zyear*zlatitude effect plot

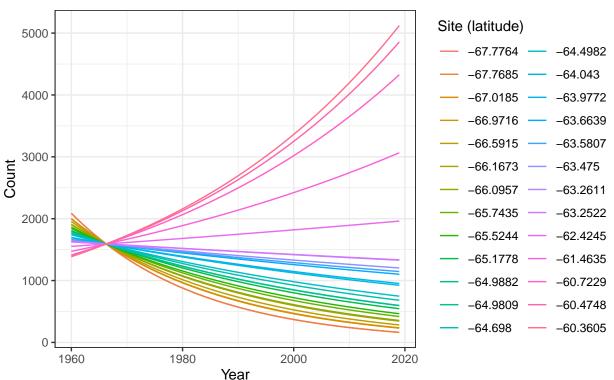


glmer (lme4) prediction

Prediction from m2

```
# qlmer predict function: https://rdrr.io/cran/lme4/man/predict.merMod.html
# predict(object, newdata = NULL, newparams = NULL,
         re.form = NULL, ReForm, REForm, REform,
         random.only=FALSE, terms = NULL,
#
         type = c("link", "response"), allow.new.levels = FALSE,
         na.action = na.pass, ...)
# Predictions can be made with, or without, the contribution of random effects.
# The following plots shows the influence of this choice.
# no random effects, response scale prediction
df$fit.m2_norand <- predict(m2, df, re.form=NA, type = "response")</pre>
ggplot(df, aes(x = year, y = fit.m2\_norand, color = as.factor(latitude))) +
  geom_line() + theme_bw() +
  labs(x = "Year", y = "Count") +
  scale_color_discrete(name = "Site (latitude)")+
  labs(title = "No random effects, response scale prediction",
       subtitle = "Bad fit with no random effects")
```

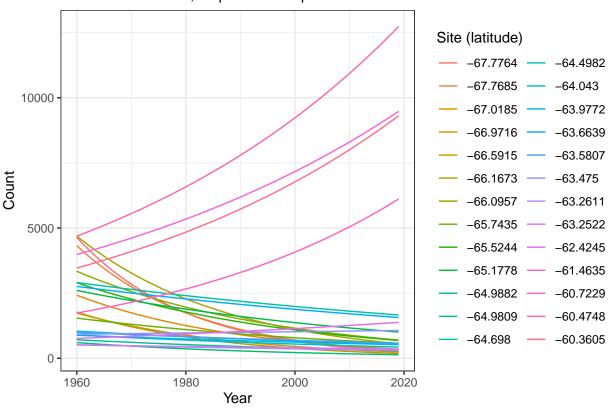
No random effects, response scale prediction Bad fit with no random effects



```
# with random effects, response scale
df$fit.m2 <- predict(m2, df, re.form=NULL, type = "response")

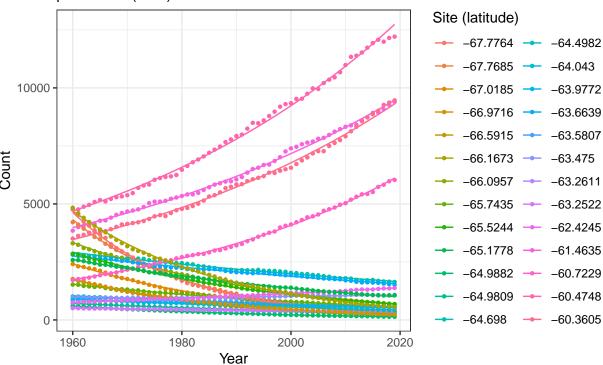
ggplot(df, aes(x = year, y = fit.m2, color = as.factor(latitude))) +
    geom_line() + theme_bw() +
    labs(x = "Year", y = "Count") +
    scale_color_discrete(name = "Site (latitude)") +
    labs(subtitle = "With random effects, response scale prediction")</pre>
```

With random effects, response scale prediction



With random effects, response scale prediction

Observed data (points) match predictions (lines)

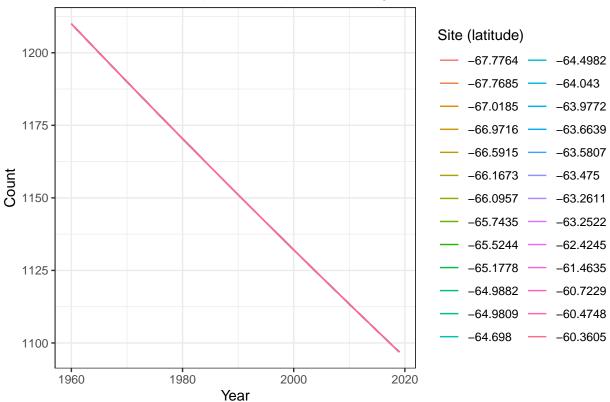


Prediction from m4 (GLMM syntax similar to Krüger 2023)

```
# no random effects, response scale prediction
df$fit.m4_norand <- predict(m4, df, re.form=NA, type = "response")

ggplot(df, aes(x = year, y = fit.m4_norand, color = as.factor(latitude))) +
    geom_line() + theme_bw() +
    labs(x = "Year", y = "Count") +
    scale_color_discrete(name = "Site (latitude)") +
    labs(subtitle = paste0("No random effects, response scale prediction (Kr",ds4psy::Umlaut["u"], "ger (""))</pre>
```

No random effects, response scale prediction (Krüger (2023))

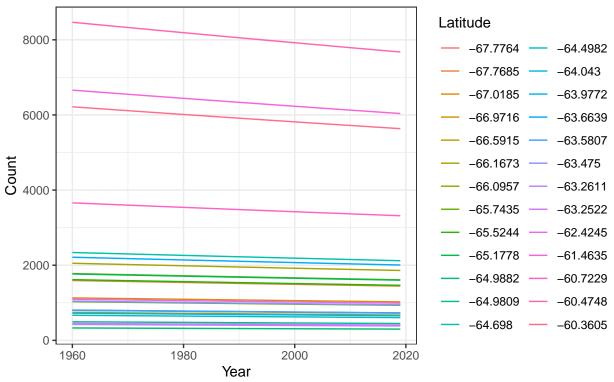


```
# With random effects, response scale prediction
df$fit.m4 <- predict(m4, df, re.form=NULL, type = "response")

ggplot(df, aes(x = year, y = fit.m4, color = as.factor(latitude))) +
    geom_line() +
    labs(x = "Year", y = "Count") +
    scale_color_discrete(name = "Latitude") +
    theme_bw() +
    labs(title = "With random effects, response scale prediction",
        subtitle = paste0("Kr",ds4psy::Umlaut["u"], "ger (2023) model specification (but conditional predictional prediction).")</pre>
```

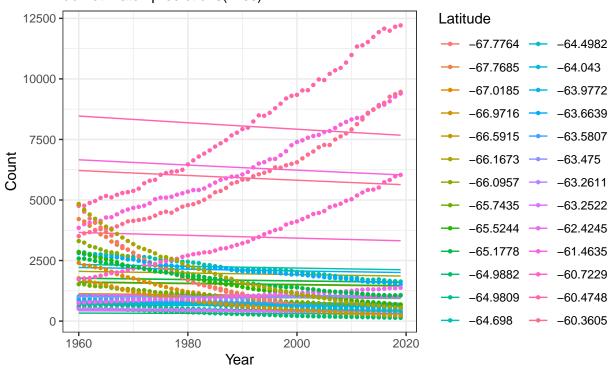
With random effects, response scale prediction

Krüger (2023) model specification (but conditional prediction)



```
# now add observed data
ggplot(df, aes(x = year, y = fit.m4, color = as.factor(latitude))) +
geom_line() +
labs(x = "Year", y = "Count") +
scale_color_discrete(name = "Latitude") +
# add observed data
geom_point(aes(x = year, y = count, color = as.factor(latitude)), size = 0.9)+
theme_bw() +
labs(title = paste0("Best prediction (conditional) based on Kr",ds4psy::Umlaut["u"], "ger (2023) mode
subtitle = "Observed data (points)\ndo not match predictions(lines)")
```

Best prediction (conditional) based on Krüger (2023) model specification Observed data (points) do not match predictions(lines)



MCMCglmm analysis of model m2

```
data = df,
    mev=NULL, start=NULL,
    # prior=NULL,
    prior=prior,
    nodes="ALL", scale=TRUE,
    nitt=20000, thin=10, burnin=5000, pr=T,
    pl=FALSE, verbose=FALSE, DIC=TRUE, singular.ok=FALSE, saveX=TRUE,
    saveZ=TRUE, saveXL=TRUE, slice=FALSE, ginverse=NULL, trunc=FALSE)
```

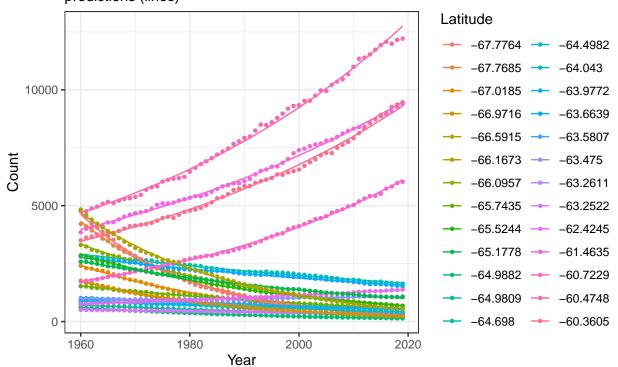
```
##
   Iterations = 5001:19991
##
   Thinning interval = 10
  Sample size = 1500
##
##
  DIC: 14828.51
##
##
   G-structure: ~us(1 + zyear):site
##
                               post.mean 1-95% CI u-95% CI eff.samp
## (Intercept):(Intercept).site 0.634055 0.31215 0.99245
                                                               1500
## zyear:(Intercept).site
                                                               1500
                                0.003924 -0.03058 0.03681
## (Intercept):zyear.site
                                0.003924 -0.03058 0.03681
                                                               1500
## zyear:zyear.site
                                0.008164 0.00408 0.01373
                                                               1050
##
##
   R-structure: ~units
##
        post.mean 1-95% CI u-95% CI eff.samp
##
## units 6.189e-05 4.486e-05 7.878e-05
##
##
   Location effects: count ~ zyear * zlatitude
##
                  post.mean 1-95% CI u-95% CI eff.samp
                                                         pMCMC
                                                  1662 < 7e-04 ***
## (Intercept)
                     7.0533
                              6.7297
                                       7.3508
## zvear
                    -0.2361
                             -0.2690 -0.2009
                                                  1500 < 7e-04 ***
                     0.4299
                                                  1500 0.00667 **
## zlatitude
                              0.1380
                                       0.7316
                     0.3200
                                                  1390 < 7e-04 ***
## zyear:zlatitude
                              0.2848
                                       0.3549
## Signif. codes: 0 '***' 0.001 '**' 0.05 '.' 0.1 ' ' 1
```

Predictions with MCMCglmm mc2

```
# https://www.rdocumentation.org/packages/MCMCglmm/versions/2.34/topics/predict.MCMCglmm
#predict(object, newdata=NULL, marginal=object$Random$formula,
# type="response", interval="none", level=0.95, it=NULL,
# posterior="all", verbose=FALSE, approx="numerical", ...)
# marginal = formula defining random effects to be maginalised.
# You don't want the random effects maginalised, so need to set this to NULL.
```

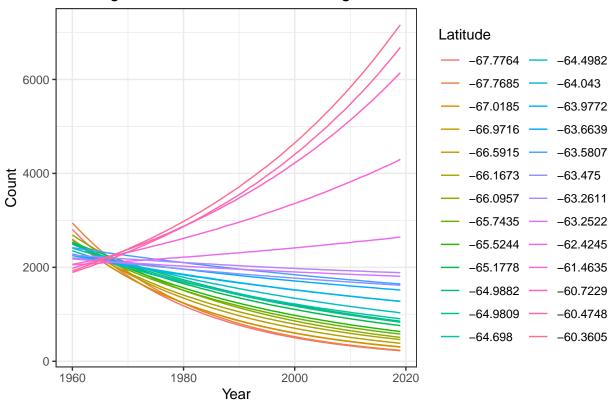
```
# First do a prediction with random effects:
pred <- data.frame(predict(mc2,</pre>
                      newdata=df,
                      type="response",
                      marginal=NULL,
                      interval="prediction",
                      posterior="mean")) # "all" is better, but Kruger used 'mean'
df$fit.mc2 <- pred$fit</pre>
df$lwr.mc2 <- pred$lwr
df$upr.mc2 <- pred$upr</pre>
# predict with observed data
ggplot(df, aes(x = year, y = fit.mc2, color = as.factor(latitude))) +
  geom_line() + theme_bw() +
  labs(x = "Year", y = "Count") +
  scale_color_discrete(name = "Latitude") +
  # add observed data
  geom_point(aes(x = year, y = count, color = as.factor(latitude)), size = 0.9)+
  labs(title = "MCMCglmm with random effects, response scale prediction",
       subtitle = "Observed data (points) match\npredictions (lines)")
```

MCMCglmm with random effects, response scale prediction Observed data (points) match predictions (lines)

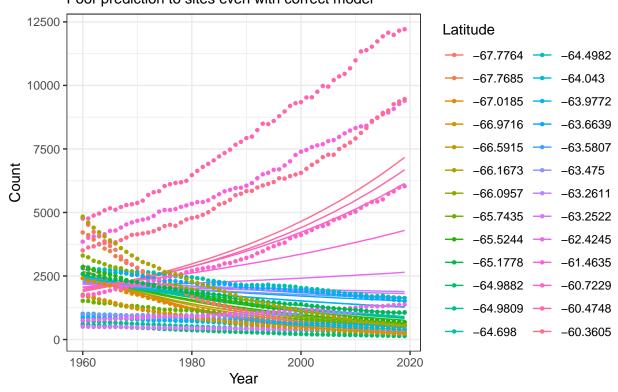


```
# Kruger (2023) maginalised the random effects.
# Let's also do that to show what the impact is on this data set.
# Now predict with maginalised random effects (Kruger (2023)):
```

MCMCglmm with random effects marginalised



MCMCglmm with random effects marginalised Poor prediction to sites even with correct model



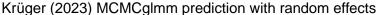
MCMCglmm analysis (Krüger 2023 model)

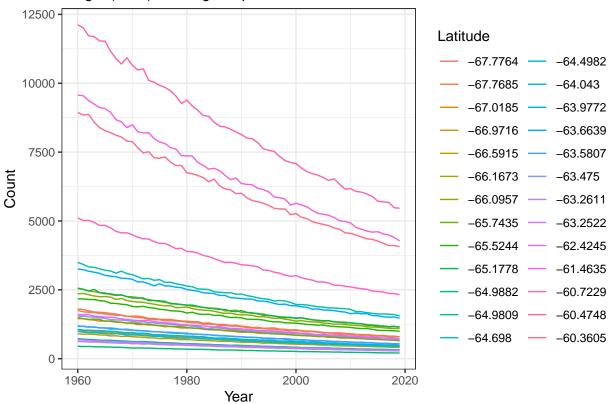
```
# Now run MCMCglmm using Kruger (2023) model formulation
mc_Kr <- MCMCglmm(count ~ zyear,</pre>
              random = ~us(1+zlatitude):site,
              rcov=~units,
              family="poisson",
              data = df,
              mev=NULL,start=NULL,
              # prior=NULL,
              prior=prior,
              nodes="ALL", scale=TRUE,
              nitt=20000,
              thin=10,
              burnin=5000,
              pr=T,
              pl=FALSE, verbose=FALSE, DIC=TRUE, singular.ok=FALSE, saveX=TRUE,
              saveZ=TRUE, saveXL=TRUE, slice=FALSE, ginverse=NULL, trunc=FALSE)
\# Compare the effective sample sizes between mc2 and mc_Kr
summary(mc2)
```

```
##
##
   Iterations = 5001:19991
   Thinning interval = 10
   Sample size = 1500
##
##
##
  DIC: 14828.51
##
##
  G-structure: ~us(1 + zyear):site
##
##
                                post.mean 1-95% CI u-95% CI eff.samp
## (Intercept):(Intercept).site 0.634055 0.31215 0.99245
                                                                1500
## zyear:(Intercept).site
                                 0.003924 -0.03058 0.03681
## (Intercept):zyear.site
                                                                1500
                                 0.003924 -0.03058 0.03681
## zyear:zyear.site
                                 0.008164 0.00408 0.01373
                                                                1050
##
##
   R-structure: ~units
##
##
         post.mean 1-95% CI u-95% CI eff.samp
## units 6.189e-05 4.486e-05 7.878e-05
                                          114.8
##
   Location effects: count ~ zyear * zlatitude
##
##
                   post.mean 1-95% CI u-95% CI eff.samp
                                                          pMCMC
                      7.0533
                               6.7297
                                        7.3508
                                                   1662 < 7e-04 ***
## (Intercept)
                             -0.2690 -0.2009
                                                   1500 < 7e-04 ***
## zyear
                     -0.2361
## zlatitude
                     0.4299
                               0.1380
                                        0.7316
                                                   1500 0.00667 **
## zyear:zlatitude
                      0.3200
                               0.2848
                                        0.3549
                                                   1390 < 7e-04 ***
## Signif. codes: 0 '*** 0.001 '** 0.01 '* 0.05 '.' 0.1 ' 1
summary(mc_Kr)
##
##
   Iterations = 5001:19991
   Thinning interval = 10
##
   Sample size = 1500
##
  DIC: 16973.07
##
##
   G-structure: ~us(1 + zlatitude):site
##
##
                                post.mean 1-95% CI u-95% CI eff.samp
                                   0.6219 0.287928
## (Intercept):(Intercept).site
                                                     1.0786
                                                              1044.5
## zlatitude:(Intercept).site
                                   0.2925 0.076589
                                                     0.6130
                                                               502.9
## (Intercept):zlatitude.site
                                   0.2925 0.076589
                                                     0.6130
                                                               502.9
## zlatitude:zlatitude.site
                                   0.1655 0.001637
                                                     0.3804
                                                               398.2
##
##
   R-structure: ~units
##
        post.mean 1-95% CI u-95% CI eff.samp
##
## units
           0.1104
                     0.1023
                              0.1179
                                         1713
##
  Location effects: count ~ zyear
##
```

##

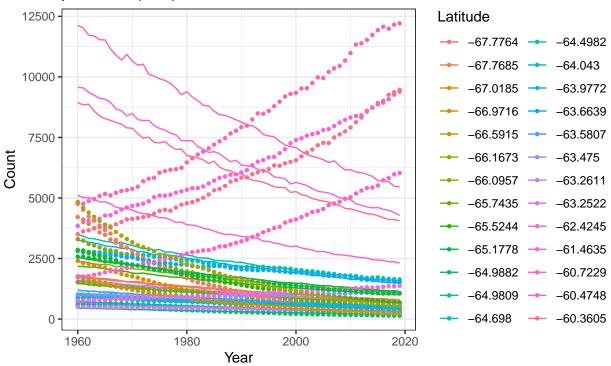
```
##
               post.mean 1-95% CI u-95% CI eff.samp pMCMC
## (Intercept)
                6.9104 6.6583
                                   7.1080
                                            1500 <7e-04 ***
                -0.2346 -0.2500 -0.2181
                                               1500 <7e-04 ***
## zyear
## ---
## Signif. codes: 0 '*** 0.001 '** 0.01 '* 0.05 '.' 0.1 ' 1
# The random effect structure of the Kruger model has MCMC sampling problems
coda::effectiveSize(mc2$VCV)
## (Intercept):(Intercept).site
                                      zyear: (Intercept).site
##
                      1500.0000
                                                    1500.0000
                                            zyear:zyear.site
##
         (Intercept):zyear.site
##
                      1500.0000
                                                    1050.1442
##
                          units
##
                       114.7672
coda::effectiveSize(mc_Kr$VCV)
## (Intercept):(Intercept).site
                                 zlatitude:(Intercept).site
##
                      1044.5172
                                                    502.8578
##
     (Intercept):zlatitude.site
                                    zlatitude:zlatitude.site
##
                       502.8578
                                                     398,2386
##
                          units
##
                      1713.0864
# Predict from model akin to Kruger (2023) MCMCglmm, using random effects
pred_Kr <- data.frame(predict(mc_Kr,</pre>
                  newdata=df,
                  type="response",
                  marginal=NULL,
                  interval="prediction",
                  posterior="mean")) # "all" is better, but Kruger used 'mean'
df$fit.mc_Kr <- pred_Kr$fit</pre>
df$lwr.mc_Kr <- pred_Kr$lwr</pre>
df$upr.mc_Kr <- pred_Kr$upr</pre>
# Without observed data
ggplot(df, aes(x = year, y = fit.mc_Kr, color = as.factor(latitude))) +
  geom_line() +
 labs(x = "Year", y = "Count") +
 scale_color_discrete(name = "Latitude") +
  # add observed data
 # geom_point(aes(x = year, y = count, color = as.factor(latitude)), size = 0.9)+
 theme bw() +
  labs(subtitle = paste0("Kr",ds4psy::Umlaut["u"], "ger (2023) MCMCglmm prediction with random effects"
```





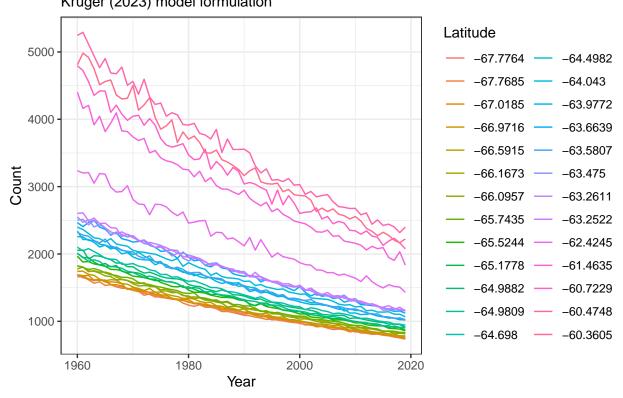
Krüger (2023) MCMCglmm prediction with random effects

Observed data (points) don't match predictions (lines)

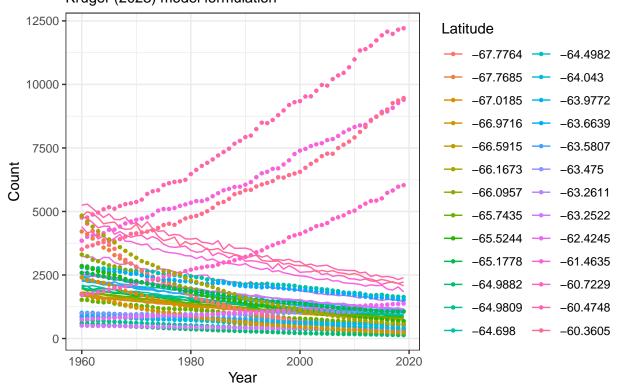


```
# Now predict with maginalised random effects (Kruger (2023)):
# This is the prediction used by Kruger (2023)
pred_margin_Kr <- data.frame(predict(mc_Kr,</pre>
                                newdata=df,
                                type="response",
                                marginal=mc_Kr$Random$formula,
                                interval="prediction",
                                posterior="mean")) # "all" is better
df$fit.mc_Kr_margin <- pred_margin_Kr$fit</pre>
ggplot(df, aes(x = year, y = fit.mc_Kr_margin, color = as.factor(latitude))) +
 geom_line() +
  labs(x = "Year", y = "Count") +
  scale color discrete(name = "Latitude") +
  # add observed data
 # geom_point(aes(x = year, y = count, color = as.factor(latitude)), size = 0.9)+
 theme bw() +
  labs(title = "MCMCglmm random effects marginalised",
       subtitle = paste0("Kr",ds4psy::Umlaut["u"], "ger (2023) model formulation"))
```

MCMCglmm random effects marginalised Krüger (2023) model formulation



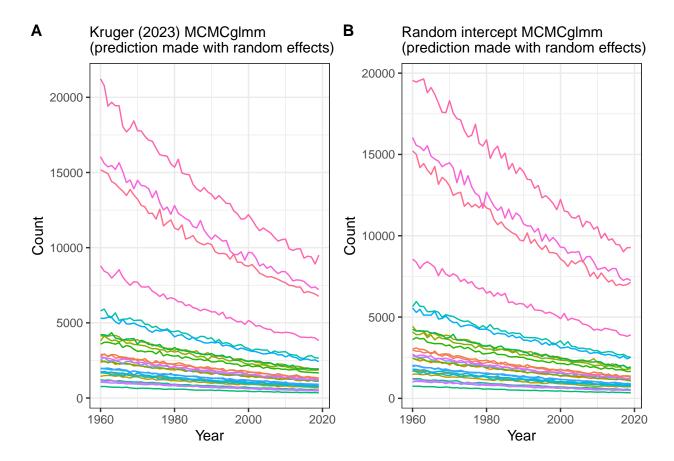
MCMCglmm random effects marginalised Krüger (2023) model formulation



Run intercept-only MCMCglmm model to show equivalency to Krüger (2023) model

```
# Now run MCMCglmm intercept only model, using the default prior
mc_I <- MCMCglmm(count ~ zyear,</pre>
                   random = ~site,
                   rcov=~units,
                   family="poisson",
                   data = df,
                   mev=NULL,start=NULL,
                   prior=NULL,
                   #prior=prior,
                   nodes="ALL", scale=TRUE,
                   nitt=20000,
                   thin=10,
                   burnin=5000,
                   pr=T,
                   pl=FALSE, verbose=FALSE, DIC=TRUE, singular.ok=FALSE, saveX=TRUE,
                   saveZ=TRUE, saveXL=TRUE, slice=FALSE, ginverse=NULL, trunc=FALSE)
# Predict from intercept model (include random site)
pred_I <- data.frame(predict(mc_I,</pre>
```

```
newdata=df,
                              type="response",
                              marginal=NULL,
                              interval="prediction",
                              posterior="mean"))
df$fit.mc_I <- pred_I$fit</pre>
df$lwr.mc_I <- pred_I$lwr</pre>
df$upr.mc_I <- pred_I$upr</pre>
# figure (from above) with Lat as a random effect
lat_id = ggplot(df, aes(x = year, y = upr.mc_Kr, color = as.factor(latitude))) +
  geom_line() +
 labs(x = "Year", y = "Count") +
 scale_color_discrete(name = "Latitude") +
  # add observed data
  \# geom_point(aes(x = year, y = count, color = as.factor(latitude)), size = 0.9)+
 theme_bw() + theme(legend.position="none") +
 labs(subtitle = "Kruger (2023) MCMCglmm\n(prediction made with random effects)")
# Intercept only model
interc.m = ggplot(df, aes(x = year, y = upr.mc_I, color = as.factor(latitude))) +
 geom_line() +
 labs(x = "Year", y = "Count") +
 scale_color_discrete(name = "Latitude") +
  # add observed data
  # qeom_point(aes(x = year, y = count, color = as.factor(latitude)), size = 0.9)+
  theme_bw() + theme(legend.position="none") +
  labs(subtitle = "Random intercept MCMCglmm\n(prediction made with random effects)")
cowplot::plot_grid(lat_id, interc.m, labels = c('A', 'B'), label_size = 12)
```



The two models produce the same estimates for 'fit'.