Decreasing trends of chinstrap penguin breeding colonies in a region of major and ongoing environmental change: a statistical critique and reanalysis of Krüger (2023)

Analysis of simulated population counts with GLMMs

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1 Purpose

This script (1) simulates population counts for 26 sites over 60 years; (2) fit different glmer (lme4) and MCMCglmm (MCMCglmm) mixed model specifications to the simulated data; and (3) predict population counts from the fitted models, using various model choices for prediction.

Simulation studies, such as the one we conduct here, are useful to help understand the behavior and adequacy of different statistical models (i.e., to assess how well different models can recover the true relationships between variables). The results show that Krüger (2023)'s MCMCglmm analysis fail to predict population trends (even when the data is strong) and that better modelling choices are required to reproduce the observed data. (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.)

In Supplement 3, we repeat this analysis with sparse observation data.

2 Simulate data

The following line of code sigma2.lambda <- 0.01 controls the annual variation in growth rate. If the value is small (e.g., sigma2.lambda <- 0.0001) the counts at each site increase or decrease relatively smoothly. Annual variation (population increase or decrease) around the modelled trend increase as sigma2.lambda gets larger. Here, we use sigma2.lambda <- 0.0005. In the 'sparse data' analysis, we use # sigma2.lambda <- 0.005.

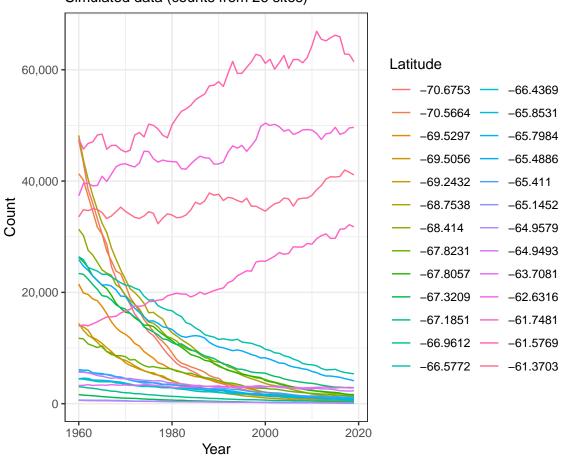
```
#! make sure library plyr / reshape2 (used in Krüger (2023) code) is not loaded!
unload_reshape2_if_loaded <- function() {</pre>
  # Check if the 'reshape2' package is loaded
  if ("package:reshape2" %in% search()) {
    # Unload the 'reshape2' package
    detach("package:reshape2", unload = TRUE)
    message("The 'reshape2' package has been unloaded.")
  } else {
    message("The 'reshape2' package is not loaded.")
}
unload_reshape2_if_loaded()
# load R packages
library(tidyverse)
library(lme4)
library(MCMCglmm)
library(scales)
library(colorspace)
library(gridExtra)
# Set Plotting theme
gg_theme <- function () {</pre>
  theme_bw() %+replace%
    theme(
      axis.text = element_text(colour = "black", size = 11),
      axis.title = element_text(size=13),
```

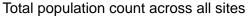
```
axis.ticks = element_line(colour = "black"),
    # panel.grid = element_blank(),
    # strip.background = element_blank(),
     panel.border = element_rect(colour = "black", fill = NA),
      axis.line = element_line(colour = "black"),
   legend.background = element_blank())
}
#-----
# Simulate data
# Simulation based on Chapter 5 from State-Space Models for Population Counts from
# Bayesian Population Analysis using Winbugs by Marc Kery and Michael Schaub
# ISBN: 978-0-12-387020-9
# 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, 50000) # Initial population size
  mean.lambda <- runif(1, 0.92, 1.01) # Mean annual population growth rate
  sigma2.lambda <- 0.0005 # Process (temporal) variation of the growth rate
  sigma2.y <- 0 # Variance of observation error (0 assumes 100% accurate counts)</pre>
  y <- N <- numeric(n.years)
  N[1] <- 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))
  # Save output in list for each iteration
  list1[[i]] = as.data.frame(y)
  list2[[i]] = as.data.frame(mean.lambda)
```

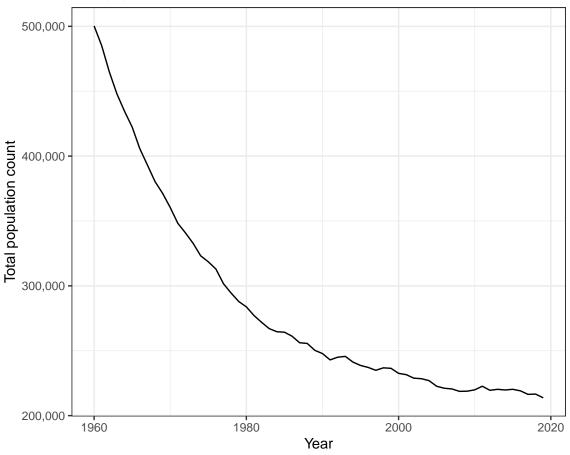
```
# Build data frame from simulations of count
df = bind rows(list1)
names(df) = "count"
# add year to simulated counts
df$year = as.integer(rep(years,n.populations))
# add site to simulated counts
df$site = rep(LETTERS[1:n.populations], each = n.years)
# make df a tibble
df = as_tibble(df)
# Use list 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")
dfr = dfmean.lambda-1 # convert lambda to growth rate r
df$r100 = df$r * 100 # rescale
# 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()
# Inspect df: every site should have 1 unique latitude value
  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
# 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: every sites has a count every year.
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()+
scale_y_continuous(label = comma)+
labs(subtitle = "Simulated data (counts from 26 sites)")
```

Simulated data (counts from 26 sites)







3 glmer (lme4) model fitting

Fit glmm models in a frequentist framework using 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
m_Kr = 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?; Model is nearly unidentifiable: large eigenvalue ratio
## - 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, m_Kr) # Note the AIC difference
##
       df
                 ATC
## m2
       7 38968.18
          38970.19
## m3
        6
## m_Kr 5 3510083.43
summary(m2)
## Generalized linear mixed model fit by maximum likelihood (Laplace
   Approximation) [glmerMod]
## Family: poisson (log)
## Formula: count ~ zyear * zlatitude + (zyear | site)
     Data: df
##
##
##
       AIC
                BIC logLik deviance df.resid
## 38968.2 39005.6 -19477.1 38954.2
                                         1553
##
## Scaled residuals:
       Min
             1Q
                    Median
                                  ЗQ
## -24.8180 -1.7541 -0.0539 1.9760 19.6085
##
## Random effects:
## Groups Name
                    Variance Std.Dev. Corr
## site
          (Intercept) 1.54458 1.24281
                    0.00902 0.09498 0.08
          zyear
## Number of obs: 1560, groups: site, 26
## Fixed effects:
                 Estimate Std. Error z value Pr(>|z|)
                 8.32304 0.24370 34.153 <2e-16 ***
## (Intercept)
## zyear
                 -0.58475
                             0.01864 -31.376
                                             <2e-16 ***
## zlatitude
                 ## zyear:zlatitude 0.42604 0.01864 22.861 <2e-16 ***
```

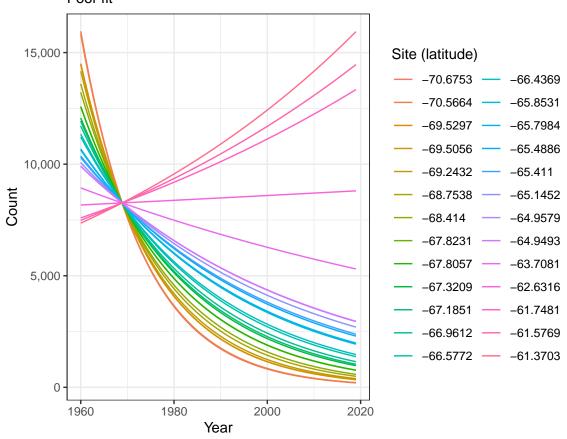
4 glmer (lme4) prediction

4.1 Prediction from m2

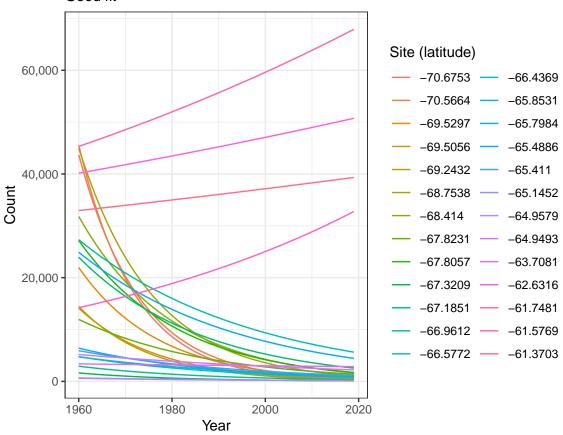
Predictions can be made with, or without, the contribution of random effects. The following plots shows the influence of this choice.

```
# glmer 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, \ldots)
# 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() +
  scale_y_continuous(label = comma)+
 labs(x = "Year", y = "Count") +
  scale color discrete(name = "Site (latitude)")+
  labs(title = "Prediction: no random effects, response scale",
       subtitle = "Poor fit")+
  theme(plot.title = element_text(size = 12))
```

Prediction: no random effects, response scale Poor fit

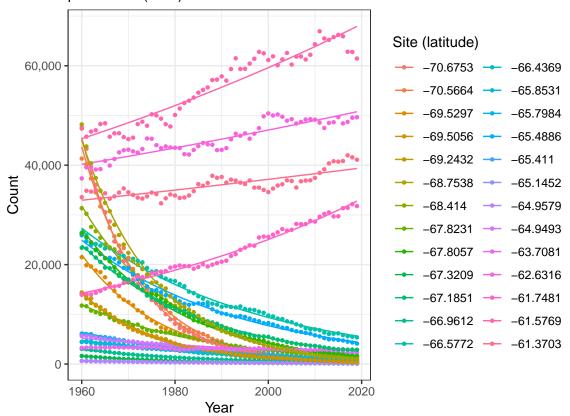


Prediction: random effects, response scale Good fit



```
# now add observed data
ggplot(df, aes(x = year, y = fit.m2, color = as.factor(latitude))) +
  geom_line() + theme_bw() +
  labs(x = "Year", y = "Count") +
  scale_y_continuous(label = comma)+
  scale_color_discrete(name = "Site (latitude)") +
  # add observed data
  geom_point(aes(x = year, y = count, color = as.factor(latitude)), size = 0.9) +
  labs(title = "Prediction: random effects, response scale",
      subtitle = "Good fit: observed data (points) match\npredictions (lines)")+
  theme(plot.title = element_text(size = 12))
```

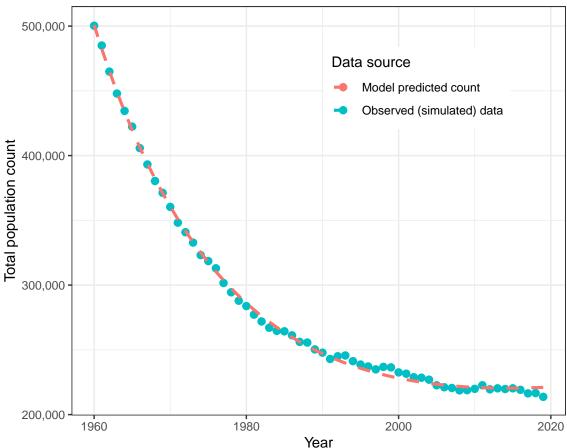
Prediction: random effects, response scale Good fit: observed data (points) match predictions (lines)



```
# calculate total population size predicted (total N across all sites)
pop_predict = df %>%
             group_by(year) %>%
             summarise(total_pred = sum(fit.m2))
# Plot total N observed per year and the predicted total abundance per year
ggplot() +
  geom_point(data = population, aes(x = year, y = totalN,
               color = "Observed (simulated) data"), size = 2.3)+
  geom_line(data = pop_predict, aes(x = year, y = total_pred,
               color = "Model predicted count"), lty = 2, size = 1.1)+
  labs(x = "Year", y = "Total population count") +
  theme_bw()+
  scale_y_continuous(label = comma)+
  labs(subtitle = "Total observed and predicted counts across 26 sites")+
  guides(color=guide_legend(title="Data source"))+
  theme(legend.position = c(0.7, 0.8))
```

```
## Warning: Using 'size' aesthetic for lines was deprecated in ggplot2 3.4.0.
## i Please use 'linewidth' instead.
## This warning is displayed once every 8 hours.
## Call 'lifecycle::last_lifecycle_warnings()' to see where this warning was
## generated.
```

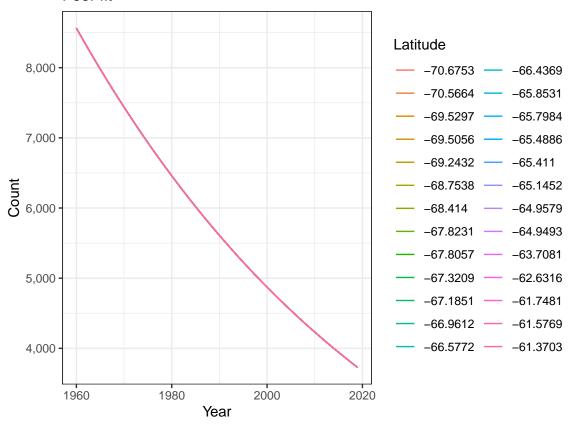




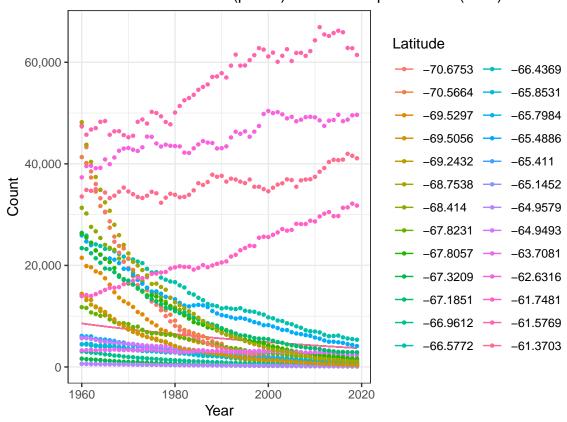
4.2 Prediction from m_Kr (frequentist GLMM syntax similar to Krüger 2023)

This prediction uses GLMM syntax similar to Krüger 2023, and is predicted without random effects (similar to Krüger 2023).

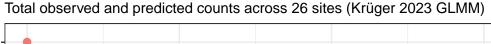
Prediction using Krüger (2023) GLMM: No random effects, response scale Poor fit

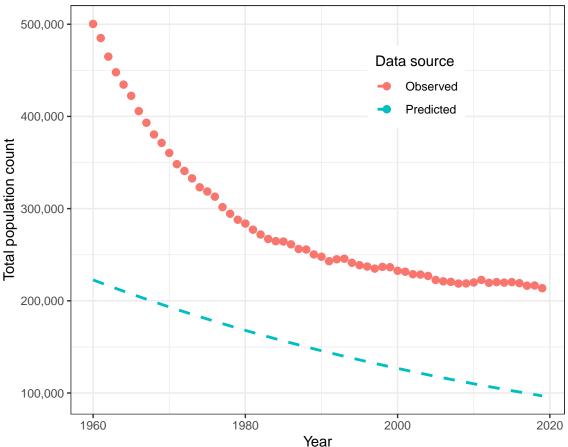


Prediction using Krüger (2023) GLMM: No random effects, response scale Poor fit: observed data (points) don't match predictions (lines)



```
# population prediction from Kruger
pop_predict_Kruger = df %>%
             group_by(year) %>%
             summarise(total_pred = sum(fit.m_Kr))
# Plot total N per year and predicted total count per year
ggplot() +
  geom_point(data = population, aes(x = year, y = totalN, col = "Observed"), size = 2.3)+
  geom_line(data = pop_predict_Kruger, aes(x = year, y = total_pred,
            col = "Predicted"), lty = 2, size = 1)+
  labs(x = "Year", y = "Total population count") +
  theme bw()+
  scale_y_continuous(label = comma)+
  labs(subtitle =
       pasteO("Total observed and predicted counts across 26 sites",
              " (Kr",ds4psy::Umlaut["u"], "ger 2023 GLMM)"))+
  guides(color=guide_legend(title="Data source"))+
  theme(legend.position = c(0.7, 0.8))
```





MCMCglmm model fitting 5

Repeat the analysis with MCMCglmm, comparing the Krüger 2023 model to a new model.

```
df = as.data.frame(df) # a data frame is expected by MCMCglmm
# Use prior from Kruger (2023) (change 133 to 26)
prior <- list(R = list(V = 1, nu = 0.002),</pre>
              G = list(G1 = list(V = diag(2), nu = 0.002,
                                  alpha.mu = rep(0, 2),
                                  alpha. V= diag(26, 2, 2))))
# Fit model m2 from above
# Works with default prior or with prior specified above
mc2 <- MCMCglmm(count ~ zyear * zlatitude,</pre>
                random = ~us(1 + zyear):site,
                rcov=~units,
                family="poisson",
                data = df,
                mev=NULL,start=NULL,
```

```
# prior=NULL,
prior=prior,
nodes="ALL", scale=TRUE,
nitt=13000, thin=10, burnin=3000, pr=T,
pl=FALSE, verbose=TRUE, DIC=TRUE, singular.ok=FALSE, saveX=TRUE,
saveZ=TRUE, saveXL=TRUE, slice=FALSE, ginverse=NULL, trunc=FALSE)
```

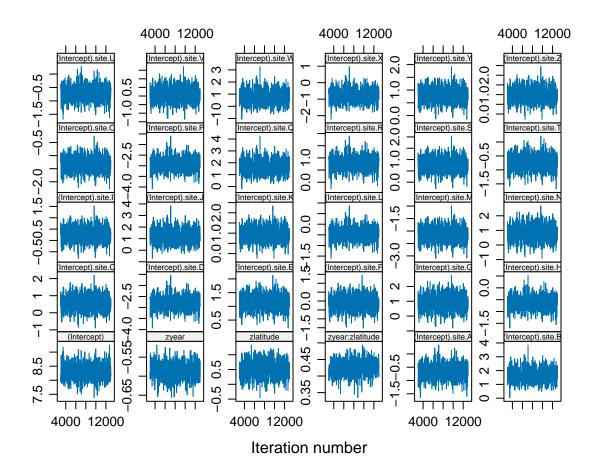
```
##
                           MCMC iteration = 0
##
##
    Acceptance ratio for liability set 1 = 0.000356
##
##
                           MCMC iteration = 1000
##
##
##
    Acceptance ratio for liability set 1 = 0.123172
##
                           MCMC iteration = 2000
##
##
##
    Acceptance ratio for liability set 1 = 0.182665
##
##
                           MCMC iteration = 3000
##
    Acceptance ratio for liability set 1 = 0.213670
##
##
##
                           MCMC iteration = 4000
##
    Acceptance ratio for liability set 1 = 0.204317
##
##
                           MCMC iteration = 5000
##
##
##
    Acceptance ratio for liability set 1 = 0.205298
##
                           MCMC iteration = 6000
##
##
    Acceptance ratio for liability set 1 = 0.204836
##
##
##
                           MCMC iteration = 7000
##
    Acceptance ratio for liability set 1 = 0.205613
##
##
                           MCMC iteration = 8000
##
##
    Acceptance ratio for liability set 1 = 0.205839
##
##
                           MCMC iteration = 9000
##
##
    Acceptance ratio for liability set 1 = 0.205028
##
##
                           MCMC iteration = 10000
##
##
    Acceptance ratio for liability set 1 = 0.204169
##
##
##
                           MCMC iteration = 11000
```

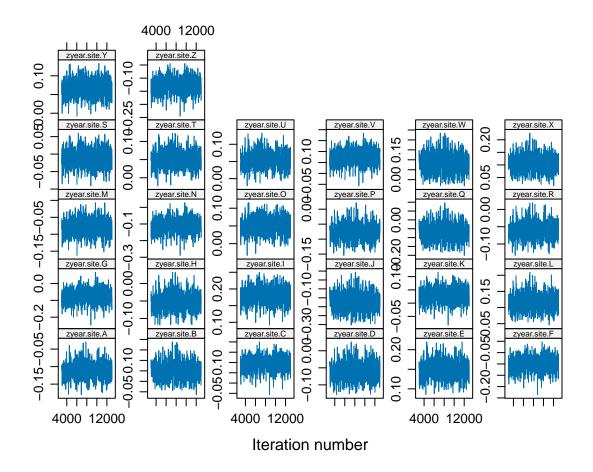
```
##
   Acceptance ratio for liability set 1 = 0.204524
##
##
                          MCMC iteration = 12000
##
##
##
   Acceptance ratio for liability set 1 = 0.205407
##
##
                          MCMC iteration = 13000
##
   Acceptance ratio for liability set 1 = 0.205367
# Now run MCMCglmm 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=13000, thin=10, burnin=3000, pr=T,
              pl=FALSE, verbose=FALSE, DIC=TRUE, singular.ok=FALSE, saveX=TRUE,
              saveZ=TRUE, saveXL=TRUE, slice=FALSE, ginverse=NULL, trunc=FALSE)
summary(mc2)
##
##
   Iterations = 3001:12991
## Thinning interval = 10
## Sample size = 1000
## DIC: 18576.25
##
##
  G-structure: ~us(1 + zyear):site
##
                                post.mean 1-95% CI u-95% CI eff.samp
##
## (Intercept):(Intercept).site 1.89904 0.958886 3.07351
## zyear:(Intercept).site
                                  0.01337 -0.056470 0.07859
                                                                811.4
## (Intercept):zyear.site
                                  0.01337 -0.056470 0.07859
                                                                811.4
## zyear:zyear.site
                                  0.01174 0.006123 0.01945
                                                               1000.0
##
##
  R-structure: ~units
##
##
        post.mean 1-95% CI u-95% CI eff.samp
          0.00143 0.001302 0.001555
## units
  Location effects: count ~ zyear * zlatitude
##
##
##
                   post.mean 1-95% CI u-95% CI eff.samp pMCMC
                   8.323904 7.796944 8.825263
                                                     1000 < 0.001 ***
## (Intercept)
## zyear
                   -0.586120 -0.627885 -0.546343
                                                     1000 <0.001 ***
## zlatitude
                   0.504145 0.002876 1.076979
                                                     1000 0.062 .
                                                    1118 < 0.001 ***
## zyear:zlatitude 0.424806 0.385956 0.466796
```

```
## ---
## Signif. codes: 0 '***' 0.001 '**' 0.05 '.' 0.1 ' ' 1
summary(mc_Kr)
##
##
   Iterations = 3001:12991
##
   Thinning interval = 10
   Sample size = 1000
##
##
##
  DIC: 18962.15
##
   G-structure: ~us(1 + zlatitude):site
##
##
##
                                post.mean 1-95% CI u-95% CI eff.samp
                                                      2.895
                                                               900.7
## (Intercept):(Intercept).site
                                  1.7152 0.785217
## zlatitude:(Intercept).site
                                   0.9461 0.147499
                                                      1.811
                                                               437.1
## (Intercept):zlatitude.site
                                                      1.811
                                  0.9461 0.147499
                                                               437.1
## zlatitude:zlatitude.site
                                  0.6077 0.003168
                                                      1.332
                                                               312.3
##
##
  R-structure: ~units
##
##
        post.mean 1-95% CI u-95% CI eff.samp
## units
          0.1949
                   0.1831
                              0.2088
                                         1103
##
   Location effects: count ~ zyear
##
              post.mean 1-95% CI u-95% CI eff.samp pMCMC
## (Intercept)
                 8.2140
                         7.9128
                                    8.5509
                                               1033 <0.001 ***
                 -0.5859 -0.6062 -0.5627
## zvear
                                               1000 < 0.001 ***
## ---
## Signif. codes: 0 '*** 0.001 '** 0.01 '* 0.05 '.' 0.1 ' 1
# Compare the effective sample sizes between mc2 and mc_Kr
# The rvariance components of the Kruger model has MCMC sampling problems
coda::effectiveSize(mc2$VCV)
## (Intercept):(Intercept).site
                                      zyear: (Intercept).site
##
                      1000.0000
                                                    811.4209
##
         (Intercept):zyear.site
                                            zyear:zyear.site
##
                       811.4209
                                                   1000.0000
##
                          units
##
                      1000.0000
coda::effectiveSize(mc_Kr$VCV)
  (Intercept):(Intercept).site
                                  zlatitude:(Intercept).site
##
                                                    437.0647
                       900.7301
##
     (Intercept):zlatitude.site
                                    zlatitude:zlatitude.site
##
                       437.0647
                                                    312.2533
##
                          units
```

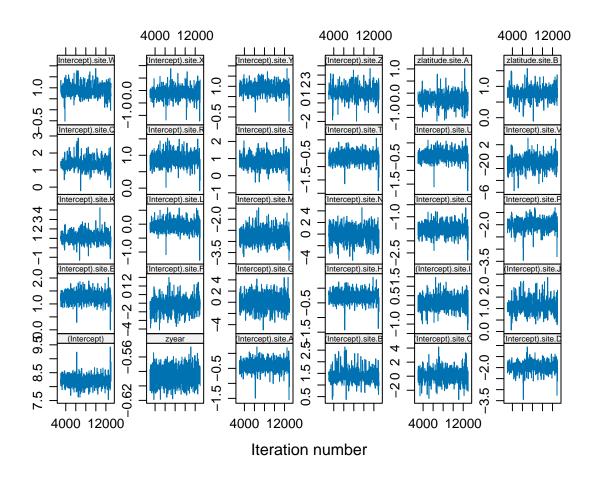
1102.9256

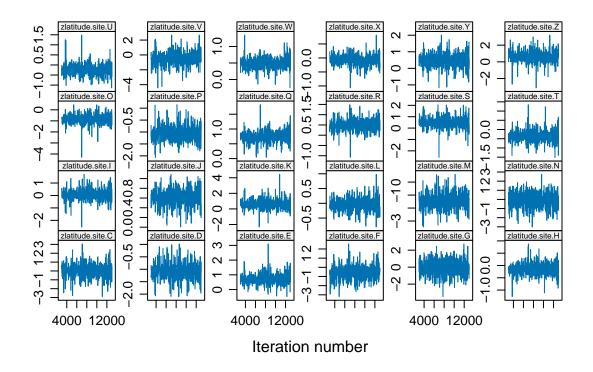
##



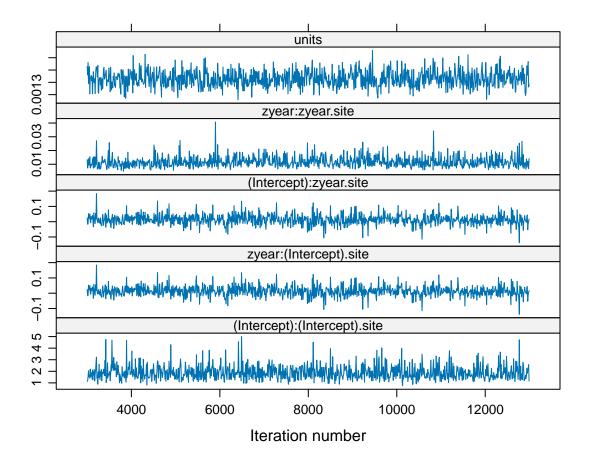


lattice::xyplot(as.mcmc(mc_Kr\$Sol), layout=c(6,5), par.strip.text=list(cex=0.5))

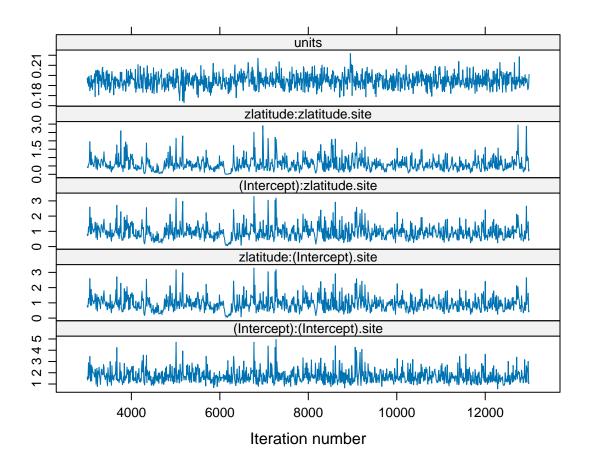




the variance components
lattice::xyplot(as.mcmc(mc2\$VCV), par.strip.text=list(cex=0.8))



lattice::xyplot(as.mcmc(mc_Kr\$VCV), par.strip.text=list(cex=0.8))



6 MCMCglmm predictions

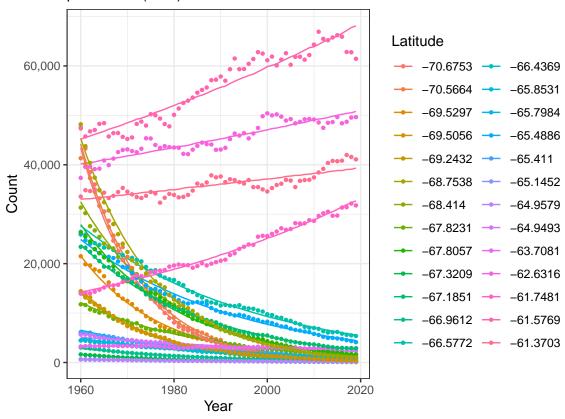
6.1 MCMCglmm predictions with our model specification (mc2)

```
df$fit.mc2 <- pred$fit
df$lwr.mc2 <- pred$lwr
df$upr.mc2 <- pred$upr

# predict with observed data
fit.mc2p = 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") +
    scale_y_continuous(label = comma)+
    # add observed data
    geom_point(aes(x = year, y = count, color = as.factor(latitude)), size = 0.9)+
    labs(title = "MCMCglmm: predict with RE (this study)",
        subtitle = "Observed data (points) match\npredictions (lines)")</pre>
```

MCMCglmm: predict with RE (this study)

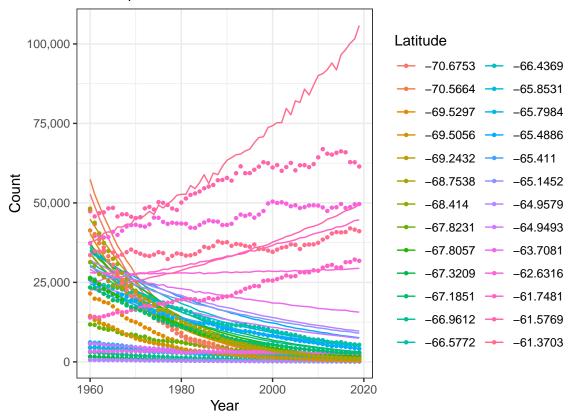
Observed data (points) match predictions (lines)



```
type="response",
                           marginal=mc2$Random$formula,
                           interval="prediction",
                           posterior="all"))
                                               # "all" is better (Kruger 2023 used 'mean')
df$fit.mc2_margin <- pred_margin$fit</pre>
ggplot(df, aes(x = year, y = fit.mc2_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() +
  scale_y_continuous(label = comma)+
  labs(title = "MCMCglmm: prediction with no random effects",
       subtitle = "Relatively poor prediction to sites even with correct\nmodel specification")
```

MCMCglmm: prediction with no random effects

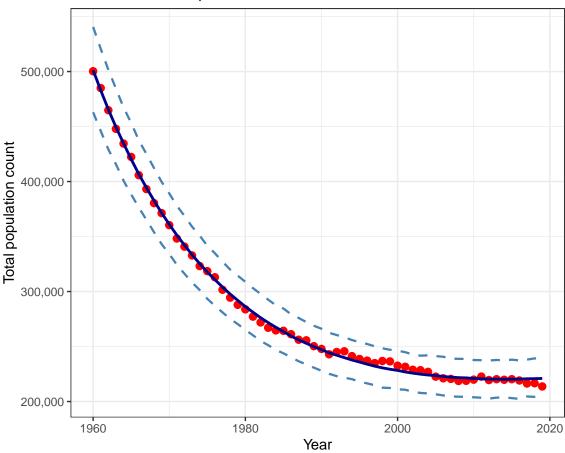
Relatively poor prediction to sites even with correct model specification



```
# while the fit is relatively poor, latitude explain much of the site level variation in this
# simulated data set.
# calculate total population size predicted (total N across all sites)
```

```
pop_predict_mc2 = df %>%
             group_by(year) %>%
             summarise(total_pred = sum(fit.mc2),
                      min pred = sum(lwr.mc2),
                       max_pred = sum(upr.mc2))
# Plot total N observed per year and the predicted total abundance per year
pop predict mc2p = ggplot() +
  geom_point(data = population, aes(x = year, y = totalN,
               color = "Observed (simulated) data"), color = 'red', size = 2.3)+
  geom_line(data = pop_predict_mc2, aes(x = year, y = total_pred,
              color = "Model predicted count"), color = "darkblue", lty = 1, size = 1)+
    geom_line(data = pop_predict_mc2, aes(x = year, y = min_pred,
               color = "Model predicted count"), color = "steelblue", lty = 2, size = 0.8)+
    geom_line(data = pop_predict_mc2, aes(x = year, y = max_pred,
              color = "Model predicted count"), color = "steelblue", lty = 2, size = 0.8)+
  labs(x = "Year", y = "Total population count") +
  theme_bw()+
  scale_y_continuous(label = comma)+
  labs(subtitle = "Total observed and predicted counts across 26 sites")+
  guides(color=guide legend(title="Data source"))+
  theme(legend.position = c(0.7, 0.8))
pop_predict_mc2p
```

Total observed and predicted counts across 26 sites

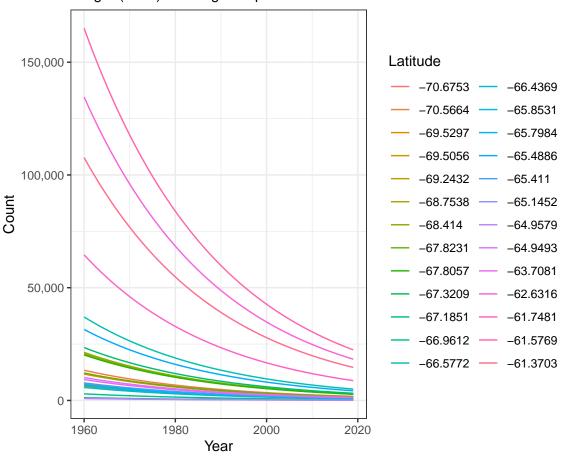


6.2 MCMCglmm predictions with Krüger (2023) model

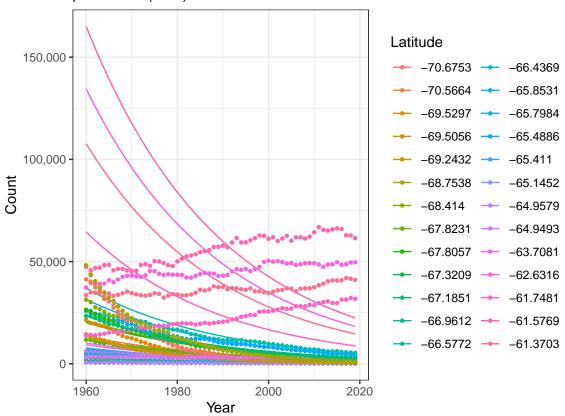
```
# Predict from Kruger (2023) MCMCglmm, using random effects
# and confidence (not prediction) intervals (for comparison with random intercept model)
pred_Kr <- data.frame(predict(mc_Kr,</pre>
                  newdata=df,
                  type="response",
                  marginal=NULL,
                  interval="confidence",
                  posterior="all")) # "all" is better, but Kruger used 'mean'
df$fit.mc_Kr <- pred_Kr$fit</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") +
  theme_bw() +
  scale_y_continuous(label = comma)+
  labs(subtitle = paste0("Kr",
```

```
ds4psy::Umlaut["u"], "ger (2023) MCMCglmm: prediction with random effects"))+
theme(plot.title = element_text(size = 12))
```

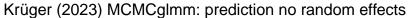
Krüger (2023) MCMCglmm: prediction with random effects

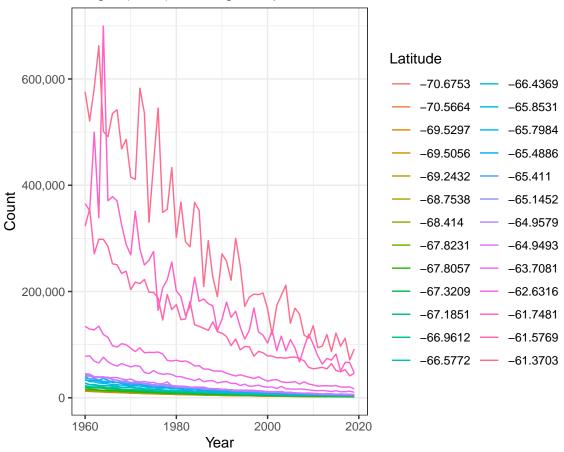


Krüger (2023) MCMCglmm: prediction with random effects Observed data (points) don't match predictions (lines)

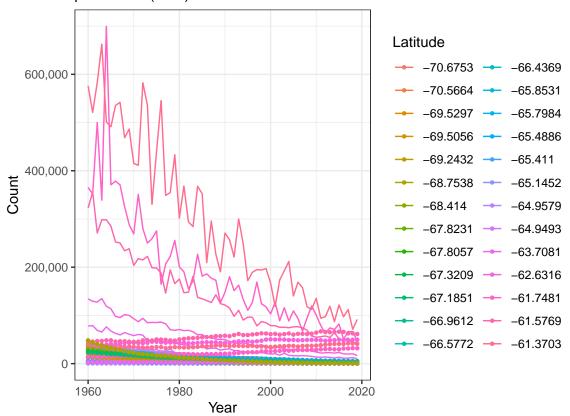


```
# Now predict with maginalised random effects and a prediction interval:
# this is the GLMM and prediction used by Kruger (2023)
pred_margin_Kr <- data.frame(predict(mc_Kr,</pre>
                             newdata=df,
                             type="response",
                             marginal=mc_Kr$Random$formula,
                             interval="prediction",
                             posterior="mean")) # Kruger used mean, but "all" is better
df$fit.mc_Kr_margin <- pred_margin_Kr$fit</pre>
df$lwr.mc_Kr_margin <- pred_margin_Kr$lwr</pre>
df$upr.mc_Kr_margin <- pred_margin_Kr$upr</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") +
  theme_bw() +
  scale_y_continuous(label = comma)+
  labs(title = paste0("Kr",
        ds4psy::Umlaut["u"], "ger (2023) MCMCglmm: prediction no random effects"))+
  theme(plot.title = element_text(size = 12))
```





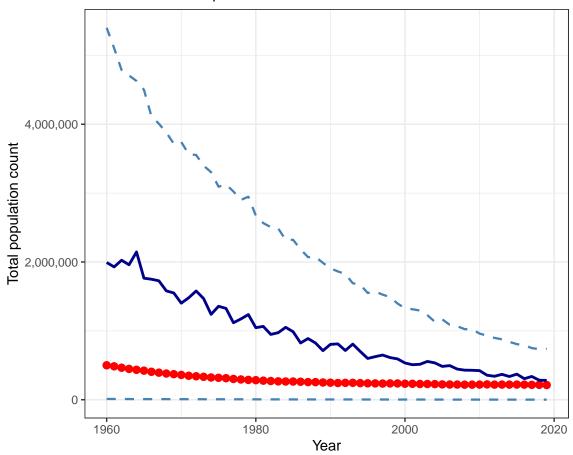
Krüger (2023) MCMCglmm: prediction no random effects Observed data (points) don't match predictions (lines)



```
# calculate total population size predicted (total N across all sites)
pop_predict_Kr = df %>%
             group_by(year) %>%
             summarise(total_pred = sum(fit.mc_Kr_margin),
                       min_pred = sum(lwr.mc_Kr_margin),
                       max_pred = sum(upr.mc_Kr_margin))
# Plot total N observed per year and the predicted total abundance per year
pop_predict_Krp = ggplot() +
  geom point(data = population, aes(x = year, y = totalN,
              color = "Observed (simulated) data"), color = "red", size = 2.3)+
  geom_line(data = pop_predict_Kr, aes(x = year, y = total_pred,
              color = "Model predicted count"), color = "darkblue", lty = 1, size = 1)+
      geom_line(data = pop_predict_Kr, aes(x = year, y = min_pred,
              color = "Model predicted count"), color = "steelblue" , lty = 2, size = 0.8)+
    geom_line(data = pop_predict_Kr, aes(x = year, y = max_pred,
              color = "Model predicted count"), color = "steelblue", lty = 2, size = 0.8)+
  labs(x = "Year", y = "Total population count") +
  theme_bw()+
  scale_y_continuous(label = comma)+
  labs(subtitle = "Total observed and predicted counts across 26 sites")+
  guides(color=guide_legend(title="Data source"))+
  theme(legend.position = c(0.7, 0.8))
```

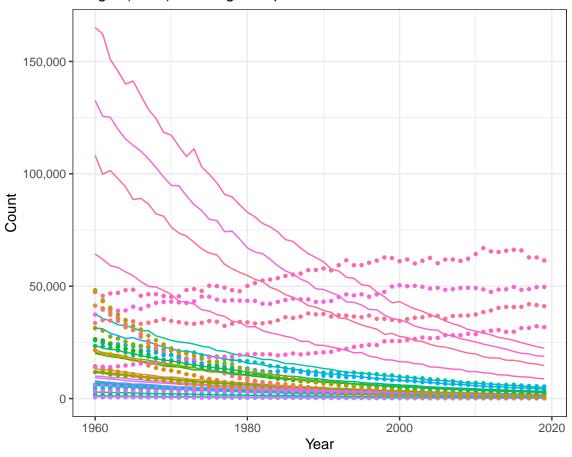
pop_predict_Krp

Total observed and predicted counts across 26 sites

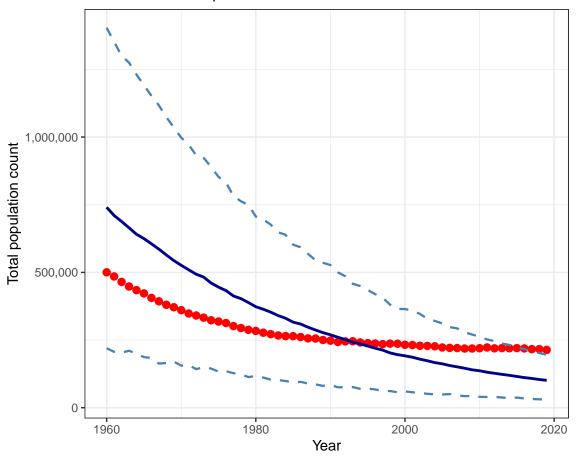


```
# Finally predict with random effects (should yield a better prediction) and a prediction interval:
pred_Kr_randomeff <- data.frame(predict(mc_Kr,</pre>
                             newdata=df,
                             type="response",
                             marginal=NULL,
                             interval="prediction",
                             posterior="mean")) # Kruger used mean, but "all" is better
df$fit.mc_Kr_randomeff <- pred_Kr_randomeff$fit</pre>
df$lwr.mc_Kr_randomeff <- pred_Kr_randomeff$lwr</pre>
df$upr.mc_Kr_randomeff <- pred_Kr_randomeff$upr</pre>
fit.mc_Kr_randomeff.p =
ggplot(df, aes(x = year, y = fit.mc_Kr_randomeff, color = as.factor(latitude))) +
  geom_line() +
  labs(x = "Year", y = "Count") +
  scale_color_discrete(name = "Latitude") +
  theme_bw() + theme(legend.position="none") +
  scale_y_continuous(label = comma)+
```

Krüger (2023) MCMCglmm: prediction with random effects



Total observed and predicted counts across 26 sites

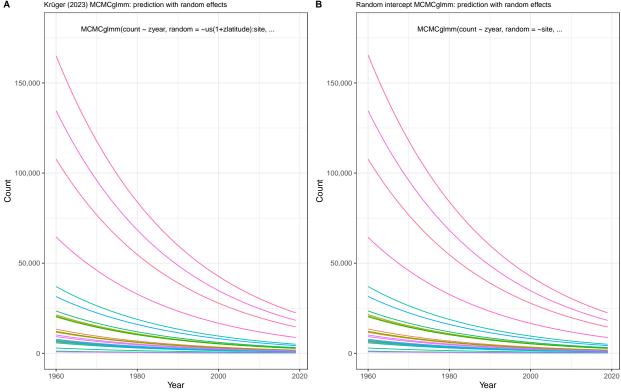


7 Intercept-only MCMCglmm model

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

```
data = df,
mev=NULL,start=NULL,
prior=NULL,
#prior=prior,
nodes="ALL", scale=TRUE,
nitt=13000,
thin=10,
burnin=3000,
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="confidence",
                              posterior="all"))
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 = fit.mc_Kr, 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") +
  scale_y_continuous(label = comma)+
  labs(subtitle = paste0("Kr",
       ds4psy::Umlaut["u"], "ger (2023) MCMCglmm: prediction with random effects")) +
  annotate('text', x = 1990, y = 180000,
        label = "MCMCglmm(count ~ zyear, random = ~us(1+zlatitude):site, ...",
        size=3) +
  theme(plot.subtitle = element_text(size = 9))
# Intercept only model
interc.m = ggplot(df, aes(x = year, y = fit.mc_I, color = as.factor(latitude))) +
  geom_line() +
  labs(x = "Year", y = "Count") +
  scale_color_discrete(name = "Latitude") +
  scale_y_continuous(label = comma)+
  # 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: prediction with random effects")+
  annotate('text', x = 1990, y = 180000,
        label = "MCMCglmm(count ~ zyear, random = ~site, ...",
```



```
## Save Plot
# pdf("./figures/Supp_Kruger_intercept model.pdf",
# useDingbats = FALSE, width = 9, height = 5)
# cowplot::plot_grid(lat_id, interc.m, labels = c('A', 'B'), ncol = 2, label_size = 12)
# dev.off()
```

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

8 Estimating population change from year x to year y

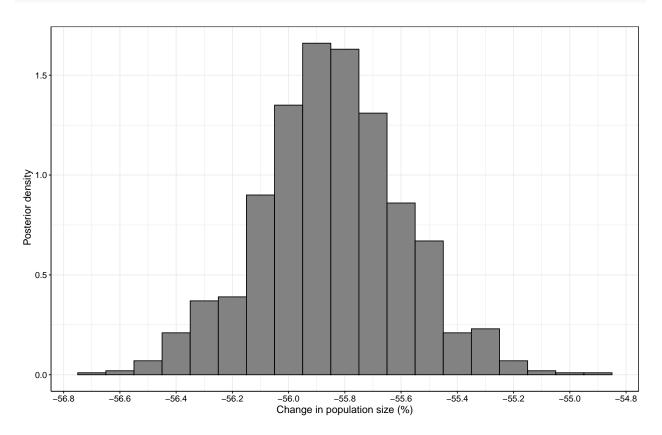
```
# extract posterior draws of fixed effects and random effects
posterior <- as.matrix(mc2$Sol)

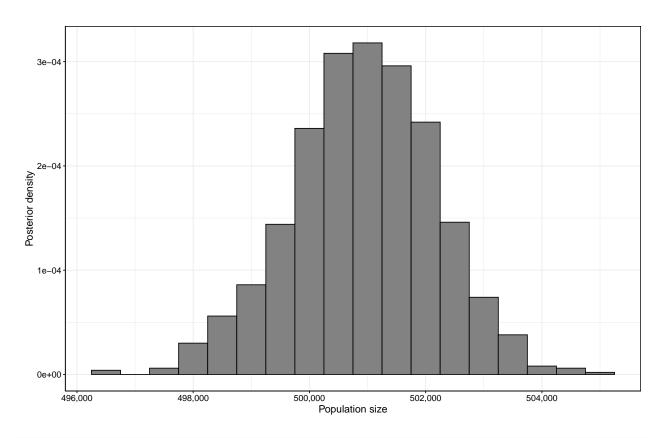
# collect site-level information
site_and_lat <- df %>%
   as_tibble() %>%
   select(site, zlatitude) %>%
   distinct()
site_and_lat
```

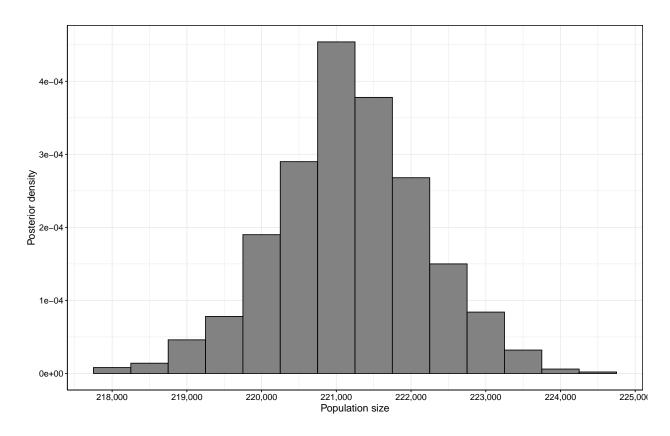
```
## # A tibble: 26 x 2
##
      site zlatitude[,1]
##
      <chr>
                   <dbl>
## 1 A
                   0.215
## 2 B
                   1.42
## 3 C
                  -1.21
## 4 D
                   0.465
## 5 E
                  -0.0818
## 6 F
                  -1.10
## 7 G
                  -1.60
## 8 H
                   0.363
## 9 I
                  -0.557
## 10 J
                   1.91
## # i 16 more rows
# map years which to predict to (standardised scale)
# Here, the first year is 1960 and the last year is 2020 (30 year change)
year1 = 1960
year2 = 2020
first_year <- (year1 - mean(df$year)) / sd(df$year)</pre>
last_year <- (year2 - mean(df$year)) / sd(df$year)</pre>
# define function to predict with or without random effects
get_predictions <- function(posterior,</pre>
                             site_and_lat,
                             first_year,
                             last_year,
                             use_random_effects = FALSE) {
  # matrices for predictions at each site in year 1 (1960) and year 2 (2020)
  # each row is a prediction from a different posterior sample, each column is a site
  pred_pop_per_site.first <- matrix(NA, nrow = nrow(posterior), ncol = nrow(site_and_lat))</pre>
  pred_pop_per_site.last <- matrix(NA, nrow = nrow(posterior), ncol = nrow(site_and_lat))</pre>
  for (s in 1:nrow(posterior)) {
    theta <- posterior[s,]</pre>
    for (j in 1:nrow(site_and_lat)) {
      site <- site_and_lat$site[j]</pre>
      zlatitude <- site_and_lat$zlatitude[j]</pre>
      # predict pop at site j in first year
      lin_pred <- theta["(Intercept)"] +</pre>
        theta["zyear"] * first_year +
        theta["zlatitude"] * zlatitude +
        theta["zyear:zlatitude"] * first_year * zlatitude
      if (use_random_effects) {
        lin_pred <- lin_pred +</pre>
          theta[ str_c("(Intercept).site.",site) ] +
          theta[ str_c("zyear.site.",site) ] * first_year
      pred_pop_per_site.first[s,j] <- exp( lin_pred )</pre>
      # predict pop at site j in last year
```

```
lin_pred <- theta["(Intercept)"] +</pre>
        theta["zyear"] * last_year +
        theta["zlatitude"] * zlatitude +
        theta["zyear:zlatitude"] * last_year * zlatitude
      if (use_random_effects) {
        lin_pred <- lin_pred +</pre>
          theta[ str_c("(Intercept).site.",site) ] +
          theta[ str_c("zyear.site.",site) ] * last_year
      }
      pred_pop_per_site.last[s,j] <- exp( lin_pred )</pre>
    }
  }
  # sum over sites for population level predictions
  pred_pop.first <- rowSums(pred_pop_per_site.first)</pre>
  pred_pop.last <- rowSums(pred_pop_per_site.last)</pre>
  # percent change from year1 to year2
  pred_pop_change <- 100 * ( pred_pop.last - pred_pop.first ) / pred_pop.first</pre>
  # outputs
  predictions <- list(pop_per_site.first = pred_pop_per_site.first,</pre>
                      pop_per_site.last = pred_pop_per_site.last,
                      pop.first = pred_pop.first,
                      pop.last = pred_pop.last,
                      pop_change = pred_pop_change)
 predictions
}
# Make predictions with and without random effects
pred_re <- get_predictions(posterior, site_and_lat, first_year, last_year,</pre>
                            use_random_effects = TRUE)
pred_no_re <- get_predictions(posterior, site_and_lat, first_year, last_year,</pre>
                               use_random_effects = FALSE)
# Plot histogram of population change without random effects in prediction:
\# ggplot(data = data.frame(pred_no_re\$pop_change), aes(x = pred_no_re.pop_change,
                                                         after stat(ndensity)))+
#
   geom_histogram(binwidth = 5, colour = "black", fill = "grey51")+
  gg_theme()+
\# scale_x_continuous(n.breaks = 10) +
  labs(y= "Density (scaled to a maximum of 1)",
         x = "Change in population size (%)")
# Plot histogram of population change using random effects in prediction:
ggplot(data = data.frame(pred_re$pop_change), aes(x = pred_re.pop_change,
                                                       after_stat(density)))+
  geom_histogram(binwidth = 0.1, colour = "black", fill = "grey51")+
  gg_theme()+
  scale_x_continuous(n.breaks = 10)+
```

```
labs(y= " Posterior density",
    x = "Change in population size (%)")
```







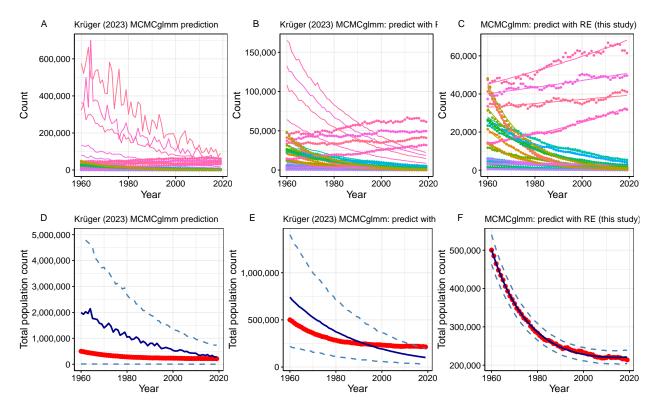
```
# # estimated population size in year1 (no random effects)
# pred_first_noRE = as.data.frame(pred_no_re$pop.first)
# names(pred_first_noRE) = "pred_first"
#
# estimated population size in year2 (no random effects)
# pred_last_noRE = as.data.frame(pred_no_re$pop.last)
# names(pred_last_noRE) = "pred_last"
```

9 Manuscript figures

```
\# cowplot::plot\_grid(fit.mc2p, fit.mc\_Kr\_marginp, labels = c('A', 'B'),
                     ncol = 2, label size = 12)
pop_predict_mc2p =
pop_predict_mc2p +
  gg_theme()+
  labs(subtitle = "MCMCglmm: predict with RE (this study)")+
  theme(legend.position = c(0.7, 0.9))+
    theme(plot.margin = margin(1,1,1,1))
\# geom\_point(data = pred\_first\_noRE, aes(x = year1, y = pred\_first), col = "red") +
 \# geom\_point(data = pred\_last\_noRE, aes(x = year2, y = pred\_last), col = "red") +
\# geom_jitter(data = pred_first, aes(x = year1, y = pred_first),
               col = "black", size = 1, height = 0, width = 0.5,
#
                alpha = 0.1, stroke = NA) +
  geom_jitter(data = pred_last, aes(x = year2, y = pred_last),
#
#
               col = "black", size = 1, height = 0, width = 0.5,
#
                alpha = 0.1, stroke = NA)
pop_predict_Krp =
pop_predict_Krp +
  gg_theme()+
  labs(subtitle = paste0("Kr",ds4psy::Umlaut["u"], "ger (2023) MCMCglmm prediction "))+
  theme(legend.position = c(0.7, 0.9)) +
  scale_y_continuous(label = comma, limits = c(0, 5000000),
                     breaks = seq(0, 5000000, by = 1000000)) +
   theme(plot.margin = margin(1,6,1,1))
\# cowplot::plot_grid(pop_predict_mc2p, pop_predict_Krp, labels = c('A', 'B'),
                     ncol = 2, label_size = 12)
# update:
fit.mc Kr randomeff.p = fit.mc Kr randomeff.p +
                      gg_theme()+
                      labs(title = "",
            subtitle = paste0("Kr",ds4psy::Umlaut["u"], "ger (2023) MCMCglmm: predict with RE"))+
      theme(legend.position="none") +
    theme(plot.margin = margin(1,6,1,1))
pop_predict_Krp_re = pop_predict_Krp_re +
                gg_theme()+
                labs(title = "",
                subtitle = paste0("Kr",ds4psy::Umlaut["u"], "ger (2023) MCMCglmm: predict with RE")) +
            theme(legend.position = c(0.7, 0.9)) +
      theme(plot.margin = margin(1,6,1,1))
library(patchwork)
```

```
(fit.mc_Kr_marginp | fit.mc_Kr_randomeff.p | fit.mc2p) /
(pop_predict_Krp | pop_predict_Krp_re | pop_predict_mc2p) +
   plot_annotation(tag_levels = 'A') &
   theme(plot.tag.position = c(0.1, 0.9), # Adjust position (x, y)
        plot.tag = element_text(size = 12, hjust = 0, vjust = 0))
```

Warning: Removed 2 rows containing missing values ('geom_line()').



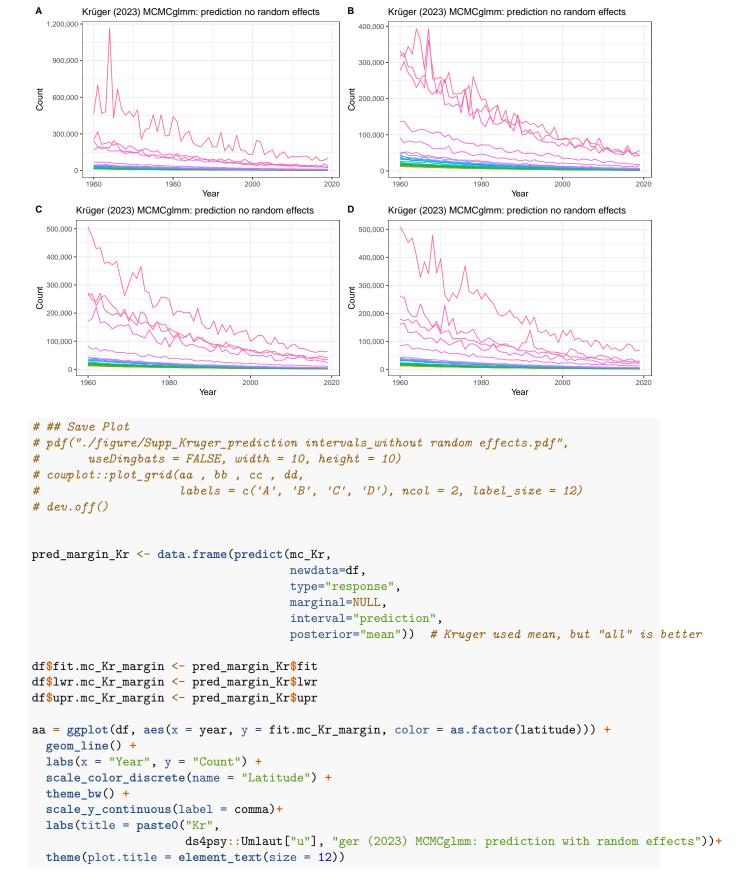
```
# Save Plot
# pdf("./figure/Figure2.pdf",
       useDingbats = FALSE, width = 13, height = 9)
# (fit.mc_Kr_marginp | fit.mc_Kr_randomeff.p | fit.mc2p) /
# (pop_predict_Krp | pop_predict_Krp_re | pop_predict_mc2p) +
   plot_annotation(tag_levels = 'A') &
    theme(plot.tag.position = c(0.1, 0.9), # Adjust position (x, y)
          plot.tag = element_text(size = 12, hjust = 0, vjust = 0))
# dev.off()
#
# # Save as PNG
 ggsave("./figure/Figure2.png",
         (fit.mc_Kr_marginp | fit.mc_Kr_randomeff.p | fit.mc2p) /
# (pop_predict_Krp | pop_predict_Krp_re | pop_predict_mc2p) +
   plot_annotation(tag_levels = 'A') &
    theme(plot.tag.position = c(0.1, 0.9), # Adjust position (x, y)
          plot.tag = element_text(size = 12, hjust = 0, vjust = 0)),
# \ width = 13, \ height = 9, \ dpi = 2000)
```

10 Supplement 5 figures

In Figure S5.2 we show why we did not use posterior predictive simulation (interval="prediction") to compare the 'intecept' model (Figure S5.1.). When prediction intervals and marginalized random effects are specified (this was the syntax implemented by Krüger (2023)) the predictions are highly variable ('wriggly') (see Figure S5.2). Also, note that the predictions differ each time we predict using the same GLMM as object (Figure S5.2). Most (but not all) of this variation is removed when we specify prediction intervals but include random effects in the prediction (Figure S5.3).

```
pred_margin_Kr <- data.frame(predict(mc_Kr,</pre>
                                      newdata=df,
                                      type="response",
                                      marginal=mc_Kr$Random$formula,
                                      interval="prediction",
                                      posterior="mean")) # Kruger used mean, but "all" is better
df$fit.mc_Kr_margin <- pred_margin_Kr$fit</pre>
df$lwr.mc_Kr_margin <- pred_margin_Kr$lwr</pre>
df$upr.mc_Kr_margin <- pred_margin_Kr$upr</pre>
aa = 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") +
  theme bw() +
  scale_y_continuous(label = comma)+
  labs(title = paste0("Kr",
                       ds4psy::Umlaut["u"], "ger (2023) MCMCglmm: prediction no random effects"))+
  theme(plot.title = element_text(size = 12))
pred_margin_Kr <- data.frame(predict(mc_Kr,</pre>
                                      newdata=df,
                                      type="response",
                                      marginal=mc Kr$Random$formula,
                                      interval="prediction",
                                      posterior="mean")) # Kruger used mean, but "all" is better
df$fit.mc_Kr_margin <- pred_margin_Kr$fit</pre>
df$lwr.mc_Kr_margin <- pred_margin_Kr$lwr</pre>
df$upr.mc Kr margin <- pred margin Kr$upr
bb = 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") +
  theme_bw() +
  scale_y_continuous(label = comma)+
  labs(title = paste0("Kr",
                       ds4psy::Umlaut["u"], "ger (2023) MCMCglmm: prediction no random effects"))+
  theme(plot.title = element_text(size = 12))
pred_margin_Kr <- data.frame(predict(mc_Kr,</pre>
                                      newdata=df,
```

```
type="response",
                                      marginal=mc_Kr$Random$formula,
                                      interval="prediction",
                                      posterior="mean")) # Kruger used mean, but "all" is better
df$fit.mc_Kr_margin <- pred_margin_Kr$fit</pre>
df$lwr.mc_Kr_margin <- pred_margin_Kr$lwr</pre>
df$upr.mc_Kr_margin <- pred_margin_Kr$upr</pre>
cc = 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") +
  theme_bw() +
  scale_y_continuous(label = comma)+
  labs(title = paste0("Kr",
                      ds4psy::Umlaut["u"], "ger (2023) MCMCglmm: prediction no random effects"))+
  theme(plot.title = element_text(size = 12))
pred_margin_Kr <- data.frame(predict(mc_Kr,</pre>
                                      newdata=df,
                                      type="response",
                                      marginal=mc_Kr$Random$formula,
                                      interval="prediction",
                                      posterior="mean")) # Kruger used mean, but "all" is better
df$fit.mc_Kr_margin <- pred_margin_Kr$fit</pre>
df$lwr.mc_Kr_margin <- pred_margin_Kr$lwr</pre>
df$upr.mc_Kr_margin <- pred_margin_Kr$upr</pre>
dd = 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") +
  theme bw() +
  scale_y_continuous(label = comma)+
 labs(title = paste0("Kr",
                      ds4psy::Umlaut["u"], "ger (2023) MCMCglmm: prediction no random effects"))+
 theme(plot.title = element text(size = 12))
aa = aa + theme(legend.position="none")
bb = bb + theme(legend.position="none")
cc = cc + theme(legend.position="none")
dd = dd + theme(legend.position="none")
cowplot::plot_grid(aa , bb , cc , dd,
                    labels = c('A', 'B', 'C', 'D'), ncol = 2, label_size = 12)
```



```
pred_margin_Kr <- data.frame(predict(mc_Kr,</pre>
                                      newdata=df,
                                      type="response",
                                      marginal=NULL,
                                      interval="prediction",
                                      posterior="mean")) # Kruger used mean, but "all" is better
df$fit.mc_Kr_margin <- pred_margin_Kr$fit</pre>
df$lwr.mc_Kr_margin <- pred_margin_Kr$lwr</pre>
df$upr.mc_Kr_margin <- pred_margin_Kr$upr</pre>
bb = 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") +
  theme_bw() +
  scale_y_continuous(label = comma)+
  labs(title = paste0("Kr",
                       ds4psy::Umlaut["u"], "ger (2023) MCMCglmm: prediction with random effects"))+
  theme(plot.title = element text(size = 12))
pred_margin_Kr <- data.frame(predict(mc_Kr,</pre>
                                      newdata=df,
                                      type="response",
                                      marginal=NULL,
                                      interval="prediction",
                                      posterior="mean")) # Kruger used mean, but "all" is better
df$fit.mc_Kr_margin <- pred_margin_Kr$fit</pre>
df$lwr.mc_Kr_margin <- pred_margin_Kr$lwr</pre>
df$upr.mc_Kr_margin <- pred_margin_Kr$upr</pre>
cc = 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") +
 theme_bw() +
  scale_y_continuous(label = comma)+
 labs(title = paste0("Kr",
                      ds4psy::Umlaut["u"], "ger (2023) MCMCglmm: prediction with random effects"))+
 theme(plot.title = element_text(size = 12))
pred_margin_Kr <- data.frame(predict(mc_Kr,</pre>
                                      newdata=df,
                                      type="response",
                                      marginal=NULL,
                                      interval="prediction",
                                      posterior="mean")) # Kruger used mean, but "all" is better
df$fit.mc_Kr_margin <- pred_margin_Kr$fit</pre>
```

```
df$lwr.mc_Kr_margin <- pred_margin_Kr$lwr</pre>
df$upr.mc_Kr_margin <- pred_margin_Kr$upr</pre>
dd = 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") +
  theme bw() +
  scale_y_continuous(label = comma)+
  labs(title = paste0("Kr",
                         ds4psy::Umlaut["u"], "ger (2023) MCMCglmm: prediction with random effects"))+
  theme(plot.title = element_text(size = 12))
aa = aa + theme(legend.position="none")
bb = bb + theme(legend.position="none")
cc = cc + theme(legend.position="none")
dd = dd + theme(legend.position="none")
cowplot::plot_grid(aa , bb , cc , dd,
                      labels = c('A', 'B', 'C', 'D'), ncol = 2, label_size = 12)
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```

```
# ## Save Plot
# pdf("./figure/Supp_Kruger_prediction intervals_with random effects.pdf",
# useDingbats = FALSE, width = 10, height = 10)
# cowplot::plot_grid(aa , bb , cc , dd,
# labels = c('A', 'B', 'C', 'D'), ncol = 2, label_size = 12)
```

dev.off()