R code PA-CR model

Marwan Naciri

2025-07-10

This code generates the results and the main figures presented in the manuscript "Offspring number, size, and survival: state-dependent optimization of litter size in a long-lived capital breeder" *Ecosphere*

Marwan Naciri, Jon Aars, Magnus Andersen, Marie-Anne Blanchet, Andrew E. Derocher, Marlène Gamelon, Øystein Wiig, and Sarah Cubaynes

A. Run the model

1. Build the model

```
PA CR <- nimbleCode({
 # Length
 for (i in 1:n_coef_mL) {
   alpha[i] ~ dnorm(0, sd = 5)
 sigma_tau ~ dunif(0, 10)
 # Cohort random effect
 for (i in 1:n_cohort) {
   zeta[i] ~ dnorm(0, sd = sigma_zeta)
 sigma_zeta ~ dunif(0, 10)
 # Litter size
 for (i in 1:n_coef_LS) {
   beta[i] ~ dnorm(0, sd = 1.5)
 }
 # Girth
 for (i in 1:n_coef_mG) {
   gamma[i] ~ dnorm(0, sd = 5)
 sigma_xi ~ dunif(0, 10)
 # Cub mass
 for (i in 1:n_coef_M) {
   delta[i] ~ dnorm(0, sd = 5)
 sigma_epsilon ~ dunif(0, 10)
 # Yearly random effects
```

```
for (i in 1:n_year) {
 eta[i] ~ dnorm(0, sd = sigma_eta)
 rho[i] ~ dnorm(0, sd = sigma_rho)
 nu[i] ~ dnorm(0, sd = sigma_nu)
sigma_eta ~ dunif(0, 10)
sigma_rho ~ dunif(0, 10)
sigma nu ~ dunif(0, 10)
# Recapture
for (i in 1:n_coef_p) {
 lambda[i] \sim dnorm(0, sd = 1.5)
# Survival
for (i in 1:n_coef_phi) {
 theta[i] \sim dnorm(0, sd = 1.5)
}
# Yearly random effects on recapture
for (t in 1:(n_year-1)) {
 omega[t] ~ dnorm(0, sd = sigma_omega)
sigma_omega ~ dunif(0, 10)
# length, girth and litter size
for (k in 1:n_litters) {
  # Length
 mu_mL[k] <- alpha[1] * mAgeY[row_litter[k], col_litter[k]] +</pre>
   alpha[2] * mAgeM[row_litter[k], col_litter[k]] +
   alpha[3] * mAgeO[row_litter[k], col_litter[k]] +
   alpha[4] * mSpUnk[row_litter[k]] +
   alpha[5] * mSpPel[row_litter[k]] +
   zeta[cohort[k]]
 mL[row_litter[k], col_litter[k]] ~ dnorm(mu_mL[k], sd = sigma_tau)
  # Litter size
 log(q[k, 1]) \leftarrow 0
 log(q[k, 2]) <- beta[1] * mAgeY[row_litter[k], col_litter[k]] +</pre>
   beta[2] * mAgeM[row_litter[k], col_litter[k]] +
   beta[3] * mAgeO[row_litter[k], col_litter[k]] +
   beta[4] * mL[row_litter[k], col_litter[k]] +
   beta[5] * mL[row_litter[k], col_litter[k]]^2 +
   beta[6] * mAgeY[row_litter[k], col_litter[k]] * DOY[row_litter[k], col_litter[k]] +
   beta[7] * mSpUnk[row_litter[k]] +
   beta[8] * mSpPel[row_litter[k]] +
   eta[col_litter[k]]
 log(q[k, 3]) <- beta[9] * mAgeY[row_litter[k], col_litter[k]] +</pre>
```

```
beta[10] * mAgeM[row_litter[k], col_litter[k]] +
    beta[11] * mAgeO[row_litter[k], col_litter[k]] +
    beta[12] * mL[row_litter[k], col_litter[k]]
 LS[row_litter[k], col_litter[k]] ~ dcat(s[k, 1:3])
 for (i in 1:3) {
    s[k, i] \leftarrow q[k, i]/sum(q[k, 1:3])
 LS1[row_litter[k], col_litter[k]] <- 0.5 * (LS[row_litter[k], col_litter[k]] - 2)*(LS[row_litter[k]
 LS2[row_litter[k], col_litter[k]] <- -1 * (LS[row_litter[k], col_litter[k]] - 1)*(LS[row_litter[k],
 LS3[row_litter[k], col_litter[k]] <- 0.5 * (LS[row_litter[k], col_litter[k]] - 1)*(LS[row_litter[k]
  # Girth
 mu_mG[k] <- gamma[1] * mAgeY[row_litter[k], col_litter[k]] +</pre>
    gamma[2] * mAgeM[row_litter[k], col_litter[k]] +
    gamma[3] * mAgeO[row_litter[k], col_litter[k]] +
    gamma[4] * mL[row_litter[k], col_litter[k]] +
    gamma[5] * DOY[row_litter[k], col_litter[k]] +
    gamma[6] * (-1) * (LS[row_litter[k], col_litter[k]] - 1)*(LS[row_litter[k], col_litter[k]] - 3) +
    gamma[7] * 0.5 * (LS[row_litter[k], col_litter[k]] - 1)*(LS[row_litter[k], col_litter[k]] - 2) +
    gamma[8] * mSpUnk[row_litter[k]] +
   gamma[9] * mSpPel[row_litter[k]] +
   rho[col_litter[k]]
 mG[row_litter[k], col_litter[k]] ~ dnorm(mu_mG[k], sd = sigma_xi)
}
# Cub mass
for (k in 1:n_cubs) {
 mu_M[k] <- delta[1] * LS1[mother[k], col_cub[k]] * mAgeY[mother[k], col_cub[k]] +</pre>
    delta[2] * LS1[mother[k], col_cub[k]] * mAgeM[mother[k], col_cub[k]] +
    delta[3] * LS1[mother[k], col_cub[k]] * mAge0[mother[k], col_cub[k]] +
    delta[4] * LS1[mother[k], col_cub[k]] * mL[mother[k], col_cub[k]] +
    delta[5] * LS1[mother[k], col_cub[k]] * mG[mother[k], col_cub[k]] +
    delta[6] * LS1[mother[k], col_cub[k]] * DOY[mother[k], col_cub[k]] +
    delta[7] * LS1[mother[k], col_cub[k]] * Sex[k] +
    delta[8] * LS1[mother[k], col_cub[k]] * mSpUnk[mother[k]] +
   delta[9] * LS1[mother[k], col_cub[k]] * mSpPel[mother[k]] +
    delta[10] * LS2[mother[k], col_cub[k]] * mAgeY[mother[k], col_cub[k]] +
    delta[11] * LS2[mother[k], col_cub[k]] * mAgeM[mother[k], col_cub[k]] +
    delta[12] * LS2[mother[k], col_cub[k]] * mAge0[mother[k], col_cub[k]] +
    delta[13] * LS3[mother[k], col_cub[k]] * mAgeY[mother[k], col_cub[k]] +
    delta[14] * LS3[mother[k], col_cub[k]] * mAgeM[mother[k], col_cub[k]] +
    delta[15] * LS3[mother[k], col_cub[k]] * mAgeO[mother[k], col_cub[k]] +
    delta[16] * (LS2[mother[k], col_cub[k]] + LS3[mother[k], col_cub[k]]) * mL[mother[k], col_cub[k]]
    delta[17] * (LS2[mother[k], col_cub[k]] + LS3[mother[k], col_cub[k]]) * mG[mother[k], col_cub[k]]
    delta[18] * (LS2[mother[k], col_cub[k]] + LS3[mother[k], col_cub[k]]) * DOY[mother[k], col_cub[k]]
    delta[19] * (LS2[mother[k], col_cub[k]] + LS3[mother[k], col_cub[k]]) * Sex[k] +
```

```
delta[20] * (LS2[mother[k], col_cub[k]] + LS3[mother[k], col_cub[k]]) * mSpUnk[mother[k]] +
    delta[21] * (LS2[mother[k], col_cub[k]] + LS3[mother[k], col_cub[k]]) * mSpPel[mother[k]] +
    nu[col_cub[k]]
 M[k] ~ dnorm(mu_M[k], sd = sigma_epsilon)
}
for (i in 1:n_ind) {
 for (t in f[i]:(n_year-1)) {
    # Survival
    logit(phi[i, t]) <-</pre>
      theta[1] * AgeO[i, t] * mAgeY[mother[i], t] +
      theta[2] * AgeO[i, t] * mAgeM[mother[i], t] +
      theta[3] * AgeO[i, t] * mAgeO[mother[i], t] +
      theta[4] * AgeO[i, t] * M[i] +
      theta[5] * Age0[i, t] * (-1 * (LS[mother[i], t] - 1) * (LS[mother[i], t] - 3) + # LS2
      0.5 * (LS[mother[i], t] - 1) * (LS[mother[i], t] - 2)) + # LS3
      theta[6] * AgeO[i, t] * mL[mother[i], t] +
      theta[7] * AgeO[i, t] * mG[mother[i], t] +
      theta[8] * AgeO[i, t] * DOY[mother[i], t] +
      theta[9] * AgeO[i, t] * Sex[i] +
      theta[10] * AgeO[i, t] * mSpUnk[mother[i]] +
      theta[11] * AgeO[i, t] * mSpPel[mother[i]] +
      theta[12] * Age1[i, t] +
      theta[13] * (Age2[i, t] + Age3_4[i, t]) +
      theta[14] * Age5_19[i, t] +
      theta[15] * Age20[i, t] +
      theta[16] * (1 - AgeO[i, t]) * Sex[i] +
                                                                               # Effect of sex = male f
      theta[17] * ((1 - AgeO[i, t]) * (1 - Sex[i]) * mSpUnk[i] +
                                                                            # Effect of space use = NA
                     Age1[i, t] * Sex[i] * mSpUnk[mother[i]]) +
                                                                              # Effect of maternal spac
      theta[18] * ((1 - AgeO[i, t]) * (1 - Sex[i]) * mSpPel[i] +
                                                                       # Effect of space use = pelagic
                     Age1[i, t] * Sex[i] * mSpPel[mother[i]])
                                                                         # Effect of maternal space use
    # Recapture
    logit(p[i, t]) <- lambda[1] +</pre>
      lambda[2] * (mSpUnk[i] * (1 - Sex[i]) +
                                                                                                 # all N
                     mSpUnk[mother[i]] * Sex[i] * (Age1[i, t+1] + Age2[i, t+1])) + # all male depende
      lambda[3] * (mSpPel[i] * (1 - Sex[i]) +
                                                                                                 # all p
                     mSpPel[mother[i]] * Sex[i] * (Age1[i, t+1] + Age2[i, t+1])) + # all male depende
     lambda[4] * Sex[i] * (Age3_4[i, t+1] + Age5_19[i, t+1] + Age20[i, t+1]) +
      omega[t]
    S[1, 1, i, t] <- phi[i, t]
    S[1, 2, i, t] \leftarrow 1 - phi[i, t]
    S[2, 1, i, t] \leftarrow 0
    S[2, 2, i, t] \leftarrow 1
    E[1, 1, i, t] \leftarrow p[i, t]
    E[1, 2, i, t] \leftarrow 1 - p[i, t]
```

```
E[2, 1, i, t] <- 0
    E[2, 2, i, t] <- 1
}

for(i in 1:n_ind){
    chi[i, f[i], 1] <- 1
    chi[i, f[i], 2] <- 0

for(t in f[i]:(n_year-1)){
    chi[i, t+1, 1] <- inprod(chi[i, t, 1:2], S[1:2, 1, i, t]) * E[1, CH[i, t+1], i, t]
    chi[i, t+1, 2] <- inprod(chi[i, t, 1:2], S[1:2, 2, i, t]) * E[2, CH[i, t+1], i, t]
}

lik[i] <- sum(chi[i, n_year, 1:2])
    ones[i] ~ dbin(lik[i], freq[i])
}
</pre>
```

2. Process the data

3. Run the model

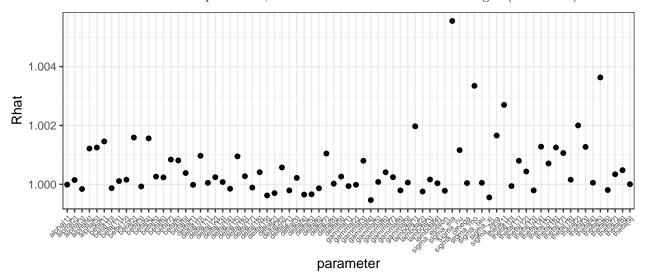
The model takes >5 hours to run on a cluster. The output of the model (fit_PA_CR) is provided in the repository as a .RData file.

B. Inspect the results

1. Diagnostic plots

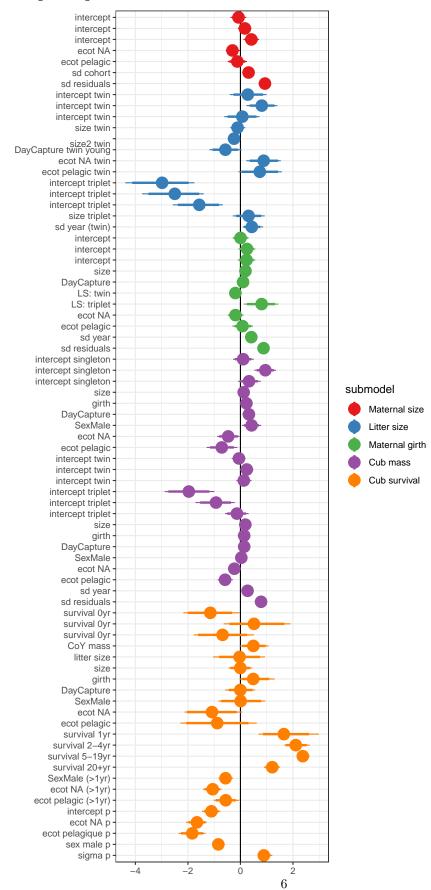
2. Rhat

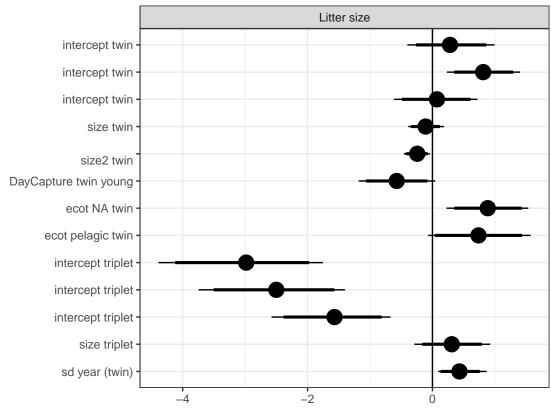
Calculate the Rhat value of each parameter, to make sure the chains have converged (Rhat < 1.1)

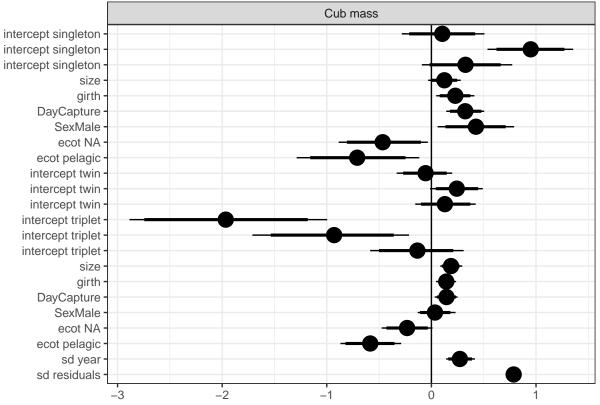


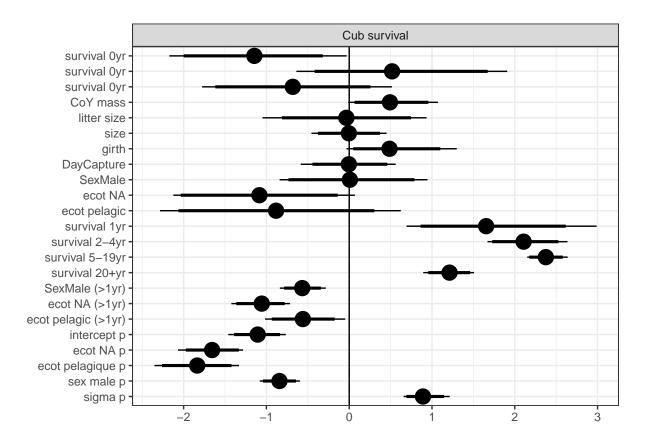
All Rhat are < 1.1

3. Caterpillar plots









C. Compute residuals

The residuals computed here will be used to plot the observations corrected for variables other than that on the x axis for the figures.

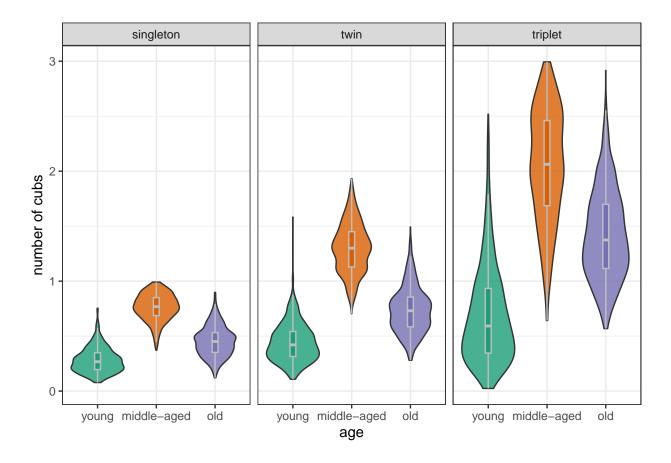
- a. Cub mass for Fig. 2A
- b. Cub mass for Fig. 2B
- c. Cub mass for Fig. 2C

D. Predict number of surviving cubs

Let's predict the number of surviving cubs by litter size and maternal age

We need to account for the fact that females who produce singleton/twin/triplet litters are not the same size on average. Let's compute the size of females corrected for the cohort random effect and the effect of the space-use strategy:

- ## 'summarise()' has grouped output by 'iteration'. You can override using the
 ## '.groups' argument.
 ## 'summarise()' has grouped output by 'iteration'. You can override using the
 ## '.groups' argument.
- ## 'summarise()' has grouped output by 'iteration'. You can override using the
- ## '.groups' argument.



E. Compute probabilities of direction (pd)

1. Pd and effect sizes

a. Maternal length

- ## [1] 178 214
- ## [1] 1.598916
- ## 2.5% 97.5%
- ## -0.1957341 3.3576141
- ## [1] 0.9593333
- ## [1] 1.534974
- **##** 2.5% 97.5%
- ## -0.5585596 3.6183635
- ## [1] 0.9257778
- ## [1] 3.13389
- ## 2.5% 97.5%
- ## 0.874069 5.344517
- ## [1] 0.9966667
- ## [1] -0.3062836
- ## 2.5% 97.5%

- ## -0.58484200 -0.02190895
- ## [1] 0.9828889
- ## [1] -0.1228604
- ## 2.5% 97.5%
- ## -0.4915318 0.2399341
- ## [1] 0.7393333
- ## [1] 0.1063801
- ## 2.5% 97.5%
- ## 0.01520452 0.26450646
- b. Litter size
- ## [1] 1.685039
- ## [1] 0.5290126
- ## [1] 0.1181196
- ## 2.5% 97.5%
- ## -0.0329391 0.2706840
- ## [1] 0.9348889
- ## [1] 0.2001149
- ## 2.5% 97.5%
- ## 0.02470783 0.36702402
- ## [1] 0.9882222
- ## [1] -0.06871656
- ## 2.5% 97.5%
- ## -1.610856e-01 -1.350053e-05
- ## [1] 0.9748889
- ## [1] 0.0819953
- **##** 2.5% 97.5%
- ## -0.1057886 0.2676468
- ## [1] 0.8068889
- ## [1] -0.07026202
- **##** 2.5% 97.5%
- ## -0.163690840 0.001204978
- ## [1] 0.9733333
- ## [1] -0.2393557
- ## 2.5% 97.5%
- ## -0.45221461 -0.03318619
- ## [1] 0.9884444
- ## [1] 0.9715556
- ## [1] 0.9968889

- ## [1] 0.9635556
- ## [1] 0.2275493
- ## 2.5% 97.5%
- ## 0.008774673 0.737457806

c. Maternal girth

- ## [1] 94 135
- ## [1] 1.822906
- ## 2.5% 97.5%
- ## -0.1261582 3.7908947
- ## [1] 0.9662222
- ## [1] 0.2249699
- ## 2.5% 97.5%
- ## -2.099811 2.532180
- ## [1] 0.5797778
- ## [1] 1.597936
- ## 2.5% 97.5%
- ## -0.8217357 3.9966875
- ## [1] 0.9022222
- ## [1] 1.393393
- ## 2.5% 97.5%
- ## -0.4038563 3.1819140
- ## [1] 0.9366667
- ## [1] -5.798155
- **##** 2.5% 97.5%
- ## -10.6329135 -0.9102755
- ## [1] 0.9902222
- ## [1] 0.9991111
- ## [1] 0.9304444
- ## [1] 0.876
- ## [1] 0.66
- ## [1] 0.183741
- ## 2.5% 97.5%
- ## 0.0589552 0.3937363

d. Cub mass

- ## [1] 3.00 31.25
- ## [1] 1.198992
- ## 2.5% 97.5%
- ## 1.096946 1.309545

- ## [1] 1
- ## [1] 1.463102
- ## 2.5% 97.5%
- ## 1.270121 1.680392
- ## [1] 1
- ## [1] 1.220944
- ## 2.5% 97.5%
- ## 1.076283 1.386007
- ## [1] 0.9993333
- ## [1] 1.312661
- ## 2.5% 97.5%
- ## 1.146553 1.497552
- ## [1] 1
- ## [1] 1.228099
- ## 2.5% 97.5%
- ## 1.057121 1.416323
- ## [1] 0.9964444
- ## [1] 1.072236
- ## 2.5% 97.5%
- ## 0.9242601 1.2358751
- ## [1] 0.812
- ## [1] 1.102309
- ## 2.5% 97.5%
- ## 1.028914 1.179866
- ## [1] 0.9971111
- ## [1] 1.038721
- ## 2.5% 97.5%
- ## 0.9548766 1.1258012
- ## [1] 0.8042222
- ## [1] 1.062718
- ## 2.5% 97.5%
- ## 0.9673298 1.1656765
- ## [1] 0.8955556
- ## [1] 0.1994588
- ## 2.5% 97.5%
- ## 0.03175342 0.37281896
- ## [1] 0.9895556
- ## [1] 0.1910185

- ## 2.5% 97.5%
- ## -0.0006108203 0.3885421931
- ## [1] 0.9744444
- ## [1] 0.008440393
- ## 2.5% 97.5%
- ## -0.1753051 0.1970066
- ## [1] 0.5386667
- ## [1] 0.9351111
- ## [1] 0.9995556
- ## [1] 0.9917778
- ## [1] 0.998
- ## [1] 0.9997778
- ## [1] 0.9966667
- ## [1] 1.147383
- ## 2.5% 97.5%
- ## 1.024216 1.282927
- ## [1] 1
- ## [1] 0.9873333
- ## [1] 0.9708889
- ## [1] 0.9924444
- ## [1] 1
- ## [1] 0.9917778
- ## [1] 0.6566667
- ## [1] 0.07836786
- ## 2.5% 97.5%
- ## 0.01959861 0.17793266
- e. Litter mass
- ## singleton twin triplet
- ## 15.27660 25.49816 31.43350
- ## [1] 1.671562
- ## 2.5% 97.5%
- ## 1.527249 1.823244
- ## [1] 1
- ## [1] 1.233621
- ## 2.5% 97.5%
- ## 1.082246 1.393686
- ## [1] 0.9993333

f. Cub survival

- ## [1] 0.9666667
- ## [1] 0.3651858
- ## 2.5% 97.5%
- ## 0.1070290 0.6157603
- ## [1] 0.9966667
- ## [1] 0.2731349
- **##** 2.5% 97.5%
- ## -0.0009016138 0.5448867798
- ## [1] 0.9733333
- ## [1] -0.09205086
- ## 2.5% 97.5%
- ## -0.3391568 0.1318436
- ## [1] 0.7783333
- ## [1] 0.54
- ## [1] -0.04333147
- ## [1] 0.505
- ## [1] -0.004916966
- ## [1] 0.9633333
- ## [1] 0.5033333
- ## [1] 0.5116667
- ## [1] 0.9566667
- ## [1] 0.8816667

g. Recapture probability

- ## [1] 0.2497323
- ## 0.1886972 0.3187844
- ## [1] 0.06095235
- ## 2.5% 97.5%
- ## 0.03825788 0.09017166
- ## [1] 0.05131676
- ## 2.5% 97.5%
- ## 0.02832574 0.08375710
- ## [1] 0.1262124
- ## 2.5% 97.5%
- ## 0.09053871 0.16843799
- ## [1] 0.8926378

```
## 2.5% 97.5%
## 0.6492742 1.2203507
```

h. Productivity by litter size

```
## [1] 0.1594975
```

2.5% 97.5%

-0.1042502 0.4668759

[1] 0.8733333

[1] 0.5401565

2.5% 97.5%

0.2262592 0.8736775

[1] 0.9983333

[1] 0.2818197

2.5% 97.5%

-0.04483155 0.65873897

[1] 0.9466667

[1] -0.2499186

2.5% 97.5%

-1.2074287 0.3266533

[1] 0.7133333

[1] -0.7425002

2.5% 97.5%

-1.32186771 0.07086852

[1] 0.97

[1] -0.6865163

2.5% 97.5%

-1.3766590 -0.2153653

[1] 1

2. Variance explained by model

[1] 0.1232103

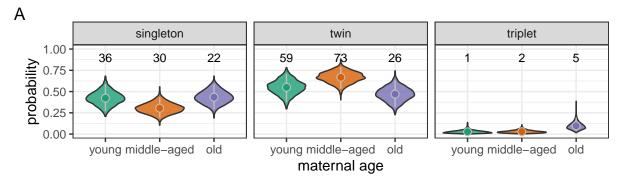
[1] 0.2195112

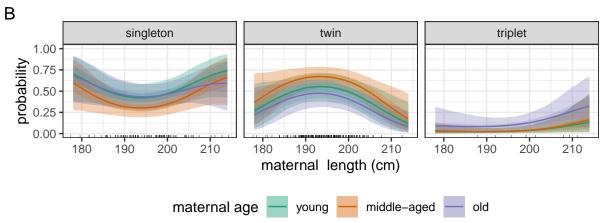
[1] 0.379511

F. Plot main figures

1. Figure 2: Effects on litter size

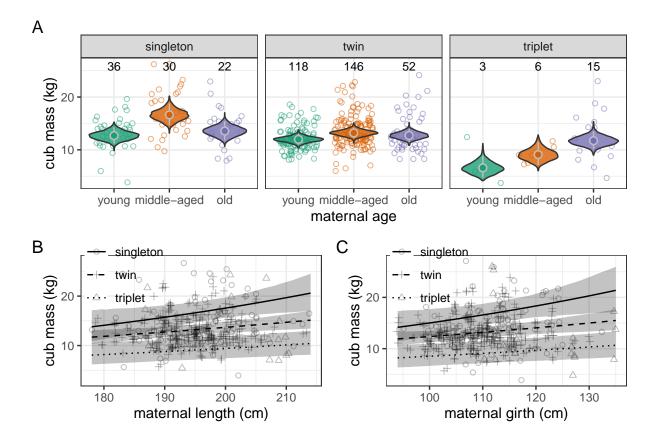
'summarise()' has grouped output by 'var', 'litter_size'. You can override
using the '.groups' argument.





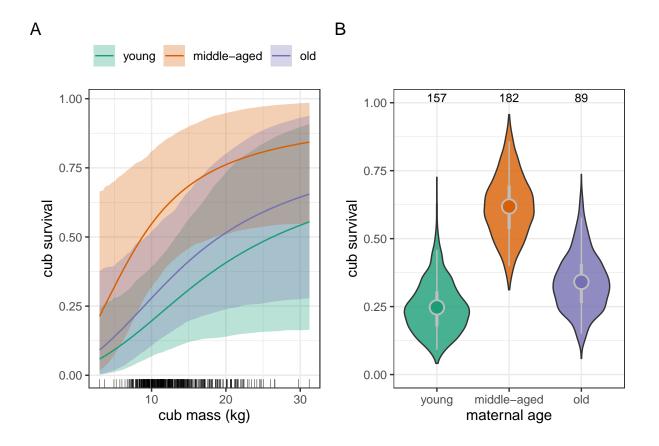
2. Figure 3: Determinants of cub mass

- ## 'summarise()' has grouped output by 'var'. You can override using the '.groups'
 ## argument.
- ## Warning: A numeric 'legend.position' argument in 'theme()' was deprecated in ggplot2
 ## 3.5.0.
- ## i Please use the 'legend.position.inside' argument of 'theme()' instead.
- ## This warning is displayed once every 8 hours.
- ## Call 'lifecycle::last_lifecycle_warnings()' to see where this warning was
- ## generated.
- ## 'summarise()' has grouped output by 'var'. You can override using the '.groups'
- ## argument.



3. Figure 4: Determinants of cub survival

'summarise()' has grouped output by 'var'. You can override using the '.groups'
argument.



4. Figure 6: Productivity by litter size

