The evolution of reproductive strategies in turtles

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Abstract

The recorded variation in traits in the egg and clutch among amniotes has led to the idea of an "optimal egg strategy" based on trade-offs, and to hypotheses about general trends. Here we perform an analysis comprising all big clades of living turtles to examine egg and clutch diversity. We include at least one representative of all extant turtle genera. Our goal is to investigate if there are actual trends for reproductive strategies among turtles and to identify factors that influence clutch and egg traits in this amniote clade. Our hypothesis is that turtles have reproductive trends that do not necessarily follow a monophyletic distribution but evolved convergently and in association with specific clades. There are local "optima" correlations between some traits and convergences across phylogeny.

Introduction

Macroevolution researchers have focused in many aspects of the diversity of life, including the study of reproductive patterns of amniotes (Battistella et al., 2019; Murray et al., 2020), that can be approached by investigating the diversity of traits in the egg and clutch (e.g., Kaplan and Salthe 1979; Deeming and Birchard, 2007; Jetz et al., 2008; Deeming and Ruta, 2014).

The idea of an "optimal" egg/clutch-strategy based on trade-offs, similar to K/r strategies, have led to several yet inconclusive discussions (Congdon and Gibbons 1987; Elgar and Heaphy 1989; Godfray et al., 1991; Kuchling, 1999; Li et al., 2017; Yu and Deng, 2020). Optimal egg/clutch size theory assumes that changes ~~of phenotypic traits of~~ oviposition strategies are driven by selection, ~~that~~ results in the best adjustments for the production of the biggest number of offspring with the highest fitness and the lowest resource investment by their progenitors as possible (Brockelman, 1975; Congdon and Gibbons, 1987).

Turtles offer a rich subject of investigation given ~~the~~ ecological diversity ~~of this group in which all species lay eggs~~. Studies focused on turtles have tested many correlations between egg size and both morphological and ecological traits in an effort to explain the variation among species (Elgar and Heaphy, 1989; Iverson, 1992; Iverson et al., 1993; Rowe, 1994). Some authors have argued that the "optimum" egg size is determined by adult body size (Gibbons, 1982); pelvic aperture morphology (Congdon and Gibbons, 1987; Kuchling, 1999), environmental factors (Macip-Ríos et al., 2013) and/or physiology (Bowden et al., 2004). These hypotheses have been largely based on studies of ~~straight~~ correlations of traits (Gibbons, 1982); methods that take phylogeny into account would provide a test to them.

Available evidence supports the idea that big bodied animals tend to produce bigger clutches with small and round eggs (Fig. 1A) while smaller species produce small clutches with big and elongated eggs (Fig. 1B), ~~from now on referred as reproductive strategies~~. Elgar and Heaphy (1989) proposed that spherical eggs are less susceptible to desiccation as the surface/volume ratio is smaller in comparison to elongated eggs. On the other hand, Pritchard (1979) suggested that small species have a tendency to produce bigger and elongated eggs because a small spherical egg would not be capable of producing a functional hatchling as there is not enough space available and that adult body size is a constraint for the egg width. Moll (1979) argued that

spherical eggs are more efficient in occupying limited spaces, therefore larger clutches are supposed to have more spherical eggs.
Although general trends have been identified, a comprehensive analysis comprising all ~~big~~ clades of living turtles in order to explore egg and clutch diversity is still missing. ~~In this study~~ we present ~~several~~ analyzes based on data taken from the literature for at least one representative of all extant turtle genera. Our goal is to examine if there are trends for reproductive strategies among turtles and investigate potential factors that influence clutch and egg traits in this clade. We address the following questions: 1) How do reproductive traits (such as egg size, egg shape, and clutch size) relate to each other within and among turtle clades? 2) How are these reproductive characteristics distributed along turtle phylogeny? 3) Are there "optimal" reproductive strategies? 4) What are the factors that most influence reproductive strategies among turtles? 5) Are there differences on egg/clutch size among turtle families? We hypothesize that although there is variation and ecological factors may affect reproductive traits, these are largely conserved within clades.

Materials & Methods

We collected morphological, ecological and reproductive data for at least one species of each turtle genus (Table 1; Supplemental Information, Appendix S1) using available literature (Supplemental Information, Appendix S2). All statistical and exploratory analyses were conducted in R 3.2.1 (R Core Team 2016; scripts and input files available on Supplemental Information, Appendix S3).

Exploratory analysis

We performed a principal component analysis (PCA) in order to test the correlations among reproductive parameters (e.g., egg size, egg length, adult body size) commonly tested in previous works with smaller datasets (Elgar and Heaphy, 1989; Iverson, 1992; Iverson et al., 1993; Rowe, 1994). Also, in order to evaluate the impact of phylogenetic relationships over these correlations, we performed a phylogenetic PCA. We used the functions imputePCA (package missMDA; Josse and Husson, 2016) and phyl.pca (package phytools; Ravell, 2012) respectively.
For the phylogenetic PCA, we used a super tree reconstructed in Mesquite v. 3.51 (Maddison & Maddison, 2019), including the same taxa as in the database. We followed the phylogenetic hypothesis proposed by Pereira et al. (2017) for the backbone of our tree—which is the hypothesis with the denser taxonomic sampling available—and positioned other species based on other phylogenetic hypotheses: Pelomedusidae (Fritz et al., 2011); Podocnemididae (Vargas-Ramirez et al., 2008; Guillon et al., 2012); Chelidae (Georges et al., 2002; Vargas-Ramirez et al., 2012; Le et al., 2013; Zhang et al., 2017); Geoemydidae (Le et al., 2007; Guillon et al., 2012; Pereira et al., 2017); Testudinidae (Pereira et al., 2017); Emydidae (Fritz et al., 2012; Pereira et al., 2017; Thomson et al., 2018); and Kinosternidae (Iverson et al., 2013).
The resulting topology was used to map characters related to reproductive traits using the contMap function of phytools package (Revell, 2012). This analysis was run three times, using

respectively the following characters: 1) Egg size (ESI): egg length/carapace length; 2) Egg shape (ESH): egg length/egg width; and Fecundity (FEC): maximum number of eggs in a clutch. We also used the phytools package to perform a multivariate analysis using the function phylomorphospace3d, in order to reconstruct the morphospace — which can be defined as the multidimensional distribution of an organism's phenotype (Lloyd, 2018). The incorporation of phylogenetic information (tree topology) provides not only information on phenotypes disparities, but also on the transformation from ancestral to derived conditions, leading to a phylomorphospace (Gerber, 2019) — for turtle phylogeny based on the former proposed characters (ESI, ESH and FEC) as axis. The 3D visualization can be accessed following the R script available on the Supplemental Information (Appendix S3).

Explanatory analysis

In order to address different aspects of reproductive strategies among turtles, we ran two different model selections. In the first one, we used the square root values of the ESI variable as the dependent variable (egg size) to test how the ~~selected~~ independent variables predicted the size of the egg among species (egg size selection). In the second model ~~selection,~~ we used the maximum number of eggs laid in one clutch times the mean number of clutches per year as a proxy for fecundity, to address how the selected independent variables predicted the fecundity of turtle species (fecundity selection).

For the first model selection, we used a dataset containing at least one representative of each genus with a total of 230 species sampled. For the second model selection, we sampled a total of 177 species; the monotypic genus *Notochelys* (Gray, 1863) was the only one not included due to lack of information on number of clutches per year.

We used maximum likelihood to fit general linear mixed models (GLMMs) with Gaussian distribution for the egg size model selection, with egg size as the dependent variable and built every possible combination of models for the five independent variables, without interactions (Table 1). The final set models of the egg size selection contained 31 candidate models besides the null model. The fecundity model selection was performed using maximum likelihood to fit generalized linear mixed models (GLMMs) with log-normal distribution. We used the fecundity as the dependent variable and built every possible combination of models for the four independent variables, without interactions (Table 1; Clutch Size was not included). The final set of candidate models contained 15 candidate models besides the null model. The information about the family each species belongs to was treated as a random effect in all models (1|family), because preliminary analyses show that closed related species have similar egg size and fecundity (ANOVA $p<0.0001$).

Model selections were performed using the function dredge of the MuMIn package (Bartoń, 2015). We ran an all-subset model selection and ranked the models based on Akaike's Information Criterion corrected for small sample size (AICc; Burnham and Anderson, 2002; Symonds and Moussalli, 2011) with the best-supported model having the lowest AICc. When there was no single model strongly supported (Akaike weight > 0.9) we calculated the evidence ratio for the best-supported models (Burnham and Anderson 2002; Johnson and

Omland 2004) and used multimodel inference to understand how independent variables predict the reproductive trait in turtles (Burnham and Anderson 2002; Johnson and Omland 2004; Burnham et al. 2011; Symonds and Moussalli 2011). We used all the candidate models for full model averaging and calculated the relative importance of each independent variable and their respective confidence intervals (85%).

Results

Regular and phylogenetic PCAs (Fig. 2A and B) showed similar correlations among inputs. In both cases, there is a positive correlation between egg size characters (length, width and weight), and a negative correlation between egg size and clutch size. The size of adult animals (e.g., carapace length) have little influence over other parameters, with a weak negative correlation with egg weight present only in the regular PCA. Number of clutches per year is the most divergent parameter when comparing both analyzes.

~~The contMap analysis (Fig. 3A, B and C) allows the easy visualization of characters distribution within the phylogeny.~~ Through the comparison of the plotted trees, it is possible to correlate small and round eggs to species that produce bigger clutches. Such traits evolved independently in several not-directly related families (e.g., Podocnemididae, Cheloniidae, Dermochelyidae, Chelydridae) or even only in bigger bodied representatives in some families (e.g., Testudinidae, Trionychidae). This pattern is also recovered in the phylomorphospace analysis (available on Supplemental Information Fig. S1 on its static view). Species with extreme characters distribution are easily visualized (e.g., *Geoemyda spengleri* and *Glyptemys muhlenbergii* – low FEC, high ESH and ESI; *Lepidochelys olivacea* and *Podocnemis expansa* – high FEC, low ESH and ESI). Although it is possible to visualize some groups of species that fit in "clusters" of extreme character-distribution in the phylomorphospace analysis, most species were positioned close to each other, with average values for all the three characters.

In the egg size model selection, only the best-ranked model (Clutch Size + Habitat) was selected as a plausible model (ΔAICc < 6; weight = 0.979; Likelihood Ratio Test < 0.001; Table 2). The model predicts that the size of the egg in relation to body size decreases with the increase of the mean number of eggs per clutch, and that aquatic and oceanic species of turtles have smaller eggs than terrestrial and semi-aquatic species, respectively (Fig. 4).

In the fecundity model selection, three of the 16 candidate models were selected as best-supported models (ΔAICc < 6; accumulated weight = 98.6%; Table 3). As the first supported model only accounted for 68% of the variation (Table 3), we used all 16 models for multimodel inference through model averaging to calculate the relative importance of each variable to turtle's fecundity (Table 4). Both habitat and diet were the most important factors to predict turtle fecundity (RI = 1.00). Low relative importance values and confidence intervals including zeros suggest that climatic zone and zoogeography are not good predictors for fecundity.

Discussion

The evolutionary history of turtles is marked by a complex pattern of character evolution

regarding breeding biology. The hypothesis that big bodied turtles tend to produce big clutches with comparatively smaller and rounder eggs (group 1) while small bodied species produce small clutches with larger and more elongated eggs (group 2) is supported by the patterns observed in the PCA anlysis, by the contMap analysis and by the egg size model selection.

Evolutionary patterns (evidenced by different colors) in all of the three contMap analyzes tend to interact to each other, suggesting a correlation between the tested characters. These patterns evolved independently and recurrently along the diversification of turtles. This shows that during its evolutionary history, turtles explored different reproductive strategies with several instances of convergent evolution.

Although no clear "optimum" reproductive strategy clusters are formed on the phylomorphospace analysis plot, extreme examples of each of the proposed groups are visible (e.g., *Geoemyda spengleri* and *Lepidochelys olivacea*, as representatives of groups 2 and 1, respectively). The difference on scale of character FEC might be partially responsible for the poor visualization, as most species colonized the same portion of the morphospace (bottom of the Y axis). Nevertheless, even discarding this bias, most species would still be clustered in the middle of the plot as they show average values of both ESH and ESI.

One could either argue that there is a third "optimum" cluster of reproductive strategy with average values or that there are no clusters at all. We advocate that there are major trends on turtle reproductive strategies that one could call "optimum constraints", although they seem to be somewhat relaxed as all reproductive characters are continuous, without any clear break in patterns, especially in the case of average values, where most species are clustered.

As noticed by Elgar and Heaphy (1989: 137), "Terrestrial species lay fewer and larger eggs for their size than freshwater or marine species, but this association is statistically confounded by the fact that chelonian families form ecological groups". The convergent distribution of reproductive traits and the different modifications of these traits across families that occupy unique niches, such as Testudinidae that lives in land and Cheloniidae/Dermochelyidae that lives in the ocean, can be considered evidence for adaptation of an "optimal" reproductive strategy at a specific environment or a constrain of specific clades. Although asserting the adaptive value of these traits can be difficult (see Kluge 2005), the fact that the evolution of these strategies is correlated with the colonization of new environments, provides strong support for a heuristic postulation of its adaptive value (Kluge 2005; Losos 2011). Furthermore, our model selection analysis for egg size (Fig. 4) not only corroborates the patterns described by Elgar and Heaphy (1989), but also brings light to the fact that this pattern is not statistically confounded by chelonian families forming ecological groups, since we used "family" as a random factor.

On the model selection analysis, the "semi-aquatic" group presents slightly bigger relative egg size when compared to the terrestrial species that belong to the Testudinidae (Fig. 4; blue and green lines, respectively). Both groups present bigger relative egg size when compared to oceanic and aquatic species (Fig. 4; red and black lines, respectively). This is evidence that "optimal" reproductive strategies are not correlated to species' phylogenetic distribution (although close related species tend to have similar strategies), but related to their

life/reproductive strategies that converged in different clades. The model selection for fecundity indicates habitat and diet as the most influential characters, highlighting the importance of life history traits for reproductive strategy selection.

Conclusions

Little is known about many aspects of the reproductive behavior within Testudines, and some of them might have a direct correlation with clutch/egg size. As Nussbaum (1987: 38) stated: "The safe harbor hypothesis includes the suggestion that parental care causes the embryonic stage to be the safest harbor, and, therefore, egg size will increase in populations with parental care to decrease the duration of subsequent, higher risk stages". Many species of the Testudinidae are known to care for their eggs (Agha et al., 2013), making the safe harbor hypothesis a good explanation for the comparatively big eggs and, maybe consequently, smaller clutches in this family. Other clades of turtles have historically been considered to lack any forms of parental care, but now we have evidence of the opposite (Ferrara et al., 2013). *Podocnemis expansa* is a good example of "group 1" reproductive strategy, being the biggest South American freshwater turtle and producing many small round eggs in a clutch. In this case, the only described parental care behavior starts after the eggs hatch, providing the safe harbor hypothesis only weak explanatory power. Other factors probably have bigger influence in this case, such as Elgar and Heaphy's (1989) proposition that round eggs should suffer less from desiccation.
Reproductive traits in Testudines evolved independently several times across tree in non-directly related clades, which can be considered an evidence of convergence, and an argument to endorse the existence of adaptive evolution and constraints in reproductive biology, frequently referred as "optimum" reproductive constrains.

Acknowledgements

Dr. Richard Vogt provided important literature on egg/clutch diversity. Danilo Muniz and Diogo Melo helped with statistics.

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Table 1(on next page)

Set of variables included as predictors for variability in each candidate models for model selections

Clutch Size was included only in the ESI selection

1

Variables	Description
Climatic Zone	Climatic zone of distribution (Tropical / Temperate)
Clutch Size	Mean number of eggs per clutch
Diet	Diet type (Carnivore / Herbivore / Omnivore)
Habitat	Main type of habitat (Aquatic / Oceanic / Semi-aquatic / Terrestrial)
Zoogeography	Zoogeographical region of distribution

2

3 **TABLE 1. Set of variables included as predictors for variability in each candidate models for**

4 **model selections.**

5 Clutch Size was included only in the ESI selection.

6

Table 2(on next page)

Coefficients, standard errors, and the 85% confidence interval of the best-support model (Clutch Size + Habitat) in the egg size selection

CI = Confidence interval

1

Variable	Coefficient	Standard Error	Lower CI	Upper CI
Clutch Size	-0.002	0.0003	-0.003	-0.002
Habitat-Aquatic	0.393	0.0190	0.351	0.431
Habitat-Oceanic	0.356	0.0588	-0.084	0.155
Habitat-Semi Aquatic	0.278	0.0338	0.049	0.182
Habitat-Terrestrial	0.289	0.0201	0.064	0.144

2

3 **TABLE 2. Coefficients, standard errors, and the 85% confidence interval of the best-**
4 **support model (Clutch Size + Habitat) in the egg size selection.**

5 CI = Confidence interval.

Table 3(on next page)

Best-supported models (<!--[if !msEquation]--> <!--[if !vml]--> <!--[endif]--><!--[endif]-->AIC_c < 6) predicting fecundity for turtle species

Models are ranked from the lowest to the highest Akaike's Information Criterion corrected for small sample size (AIC_c). See Table 1 for description of the variables

1

Model	df	logLik	AIC_c	ΔAIC_c	weight	Evidence Ratio
Diet + Habitat	8	-983.403	1983.7	0.00	0.687	-
Diet + Habitat + Climatic Zone	9	-983.383	1985.8	2.18	0.231	2.97
Diet + Habitat + Zoogeography	13	-980.024	1988.3	4.62	0.068	10.07

2

3 **TABLE 3. Best-supported models ($\Delta AIC_c < 6$) predicting fecundity in turtle species.**

4 Models are ranked from the lowest to the highest Akaike's Information Criterion corrected for

5 small sample size (AIC_c). See Table 1 for description of the variables.

6

Table 4(on next page)

Relative importance of variables predicting fecundity for turtle species

1

Variable	Relative Importance
Habitat	1.00
Diet	1.00
Climatic Zone	0.24
Zoogeography	0.08

2

3 **TABLE 4. Relative importance for variables predicting fecundity on turtle species**.

4

Figure 1

Different egg and clutch strategies

A) Nest of the giant Amazon river turtle (*Podocnemis expansa*) with many small round eggs; and B) Small clutch with big and elongated eggs of the South American wood turtle (*Rhinoclemmys punctularia*). The carapace length of these species reaches over one meter and 25cm long, respectively.

Figure 2

Correlations among reproductive and body size characteristics of turtles

A) Principal component analysis (PCA) and B) Phylogenetic PCA (PhyPCA). Plastron length was not used on the PhyPCA.

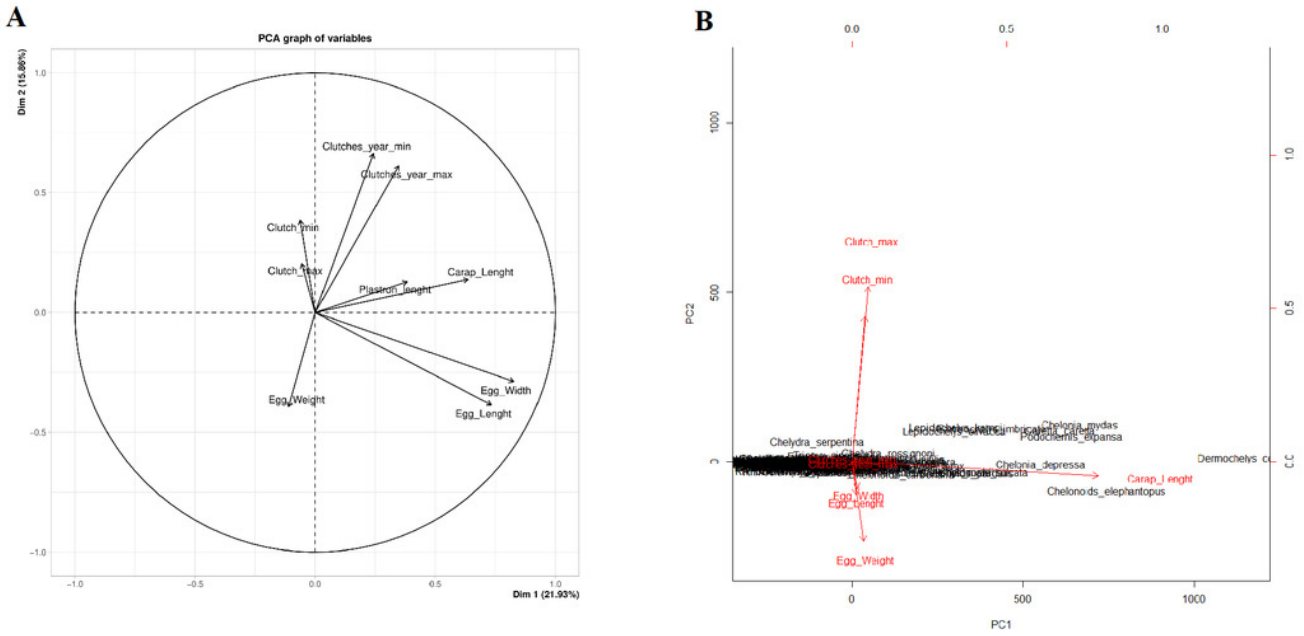


Figure 3

Phylogenetic distribution of Testudines' reproductive characteristics using contMap

A) Egg size (ESI); B) Fecundity (FEC); and C) Egg shape (ESH)

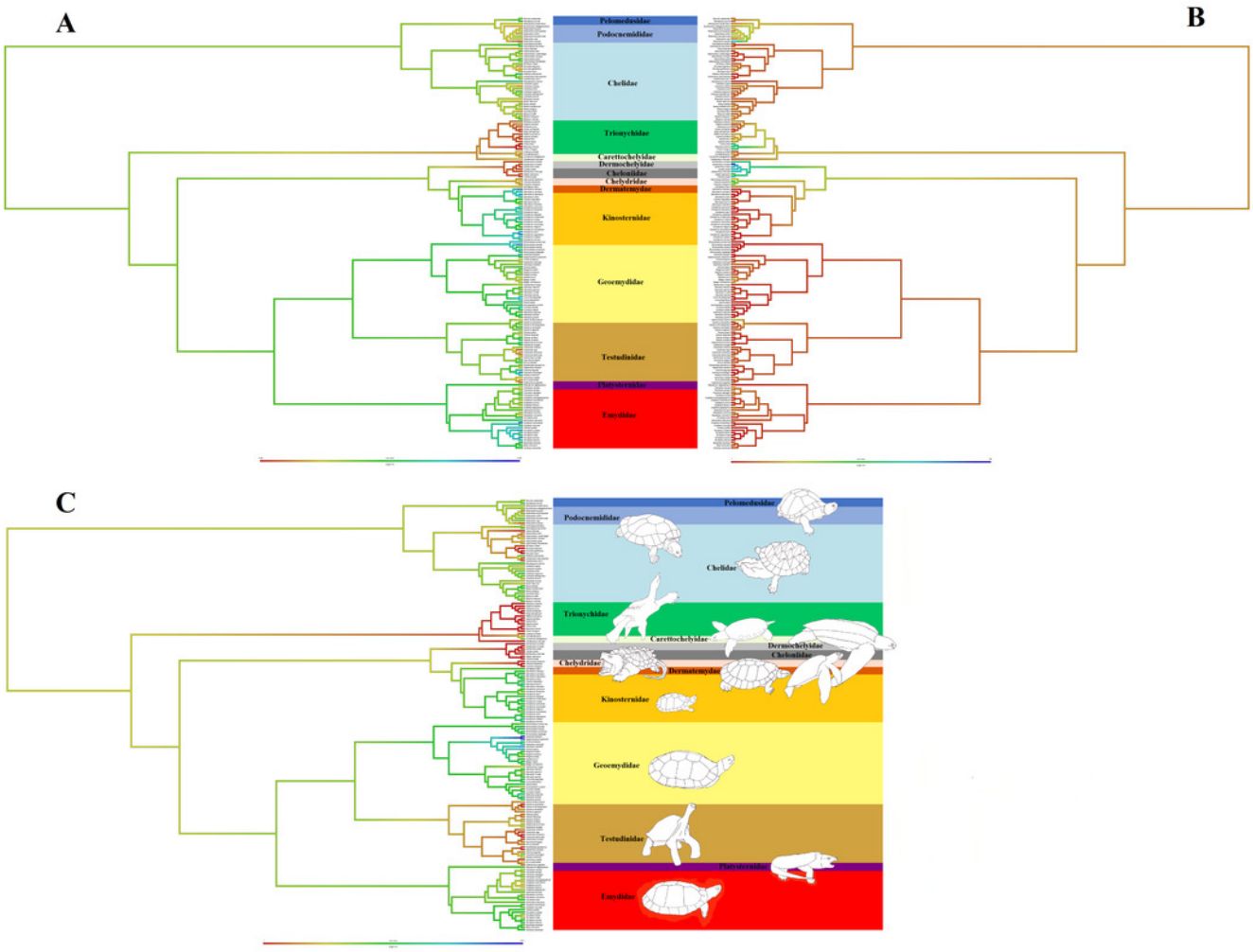
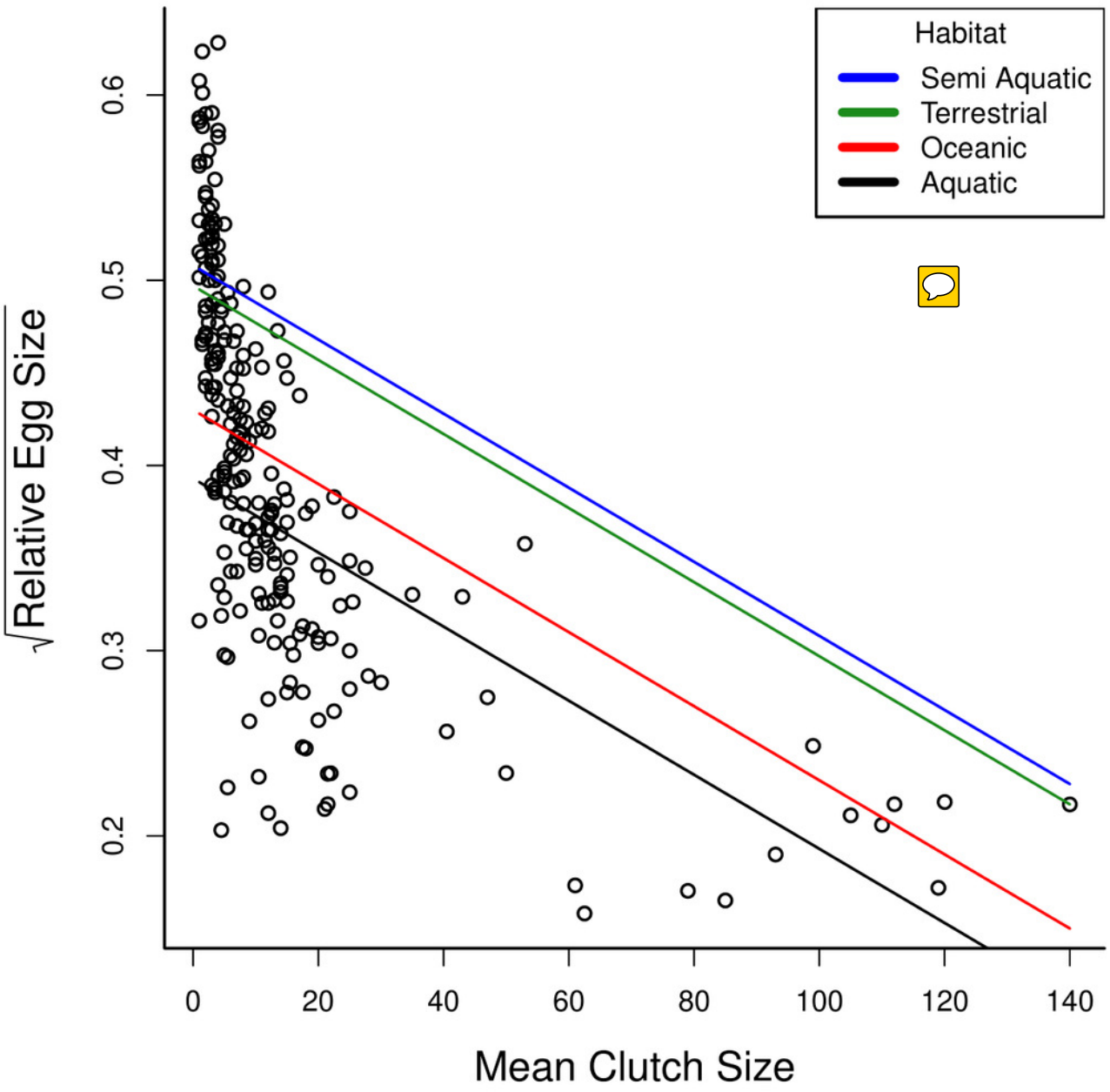


Figure 4

Egg size selection’s best ranked model

Predicts the relationship of square root relative egg size (egg length/carapace length) to mean clutch size (mean number of eggs laid per clutch) for turtle species that occupy different habitats


Habitat
Semi Aquatic
Terrestrial
Oceanic
Aquatic
√Relative Egg Size
0.2
0.3
0.4
0.5
0.6
0
20
40
60
80
100
120
140
Mean Clutch Size

comments

Diogo B. Provete

1/4/2021

Contents


```
R.Version()$version.string; R.Version()$platform
```

```
## [1] "R version 4.0.3 (2020-10-10)"
```

```
## [1] "x86_64-apple-darwin17.0"
```

```
set.seed(1001)#reproducibility
```

#Loading packages

```
library(GGally)
packageVersion("GGally")
```

```
## [1] '2.0.0'
```

```
library(phytools)
packageVersion("phytools")
```

```
## [1] '0.7.70'
```

```
library(nlme)
packageVersion("nlme")
```

```
## [1] '3.1.151'
```

```
library(tidyverse)
packageVersion("tidyverse")
```

```
## [1] '1.3.0'
```

```
library(readr)
packageVersion("readr")
```

```
## [1] '1.4.0'
```

```
library(vcd)
packageVersion("vcd")
```

```
## [1] '1.4.8'
```

```
library(usdm)
packageVersion("usdm")
```

```
## [1] '1.1.18'
```

```
library(treeplyr)
packageVersion("treeplyr")
```

```
## [1] '0.1.10'
```

```
library(cowplot)
packageVersion("cowplot")
```

```
## [1] '1.1.0'
```

```
library(visdat)
packageVersion("visdat")
```

```
## [1] '0.5.3'
```

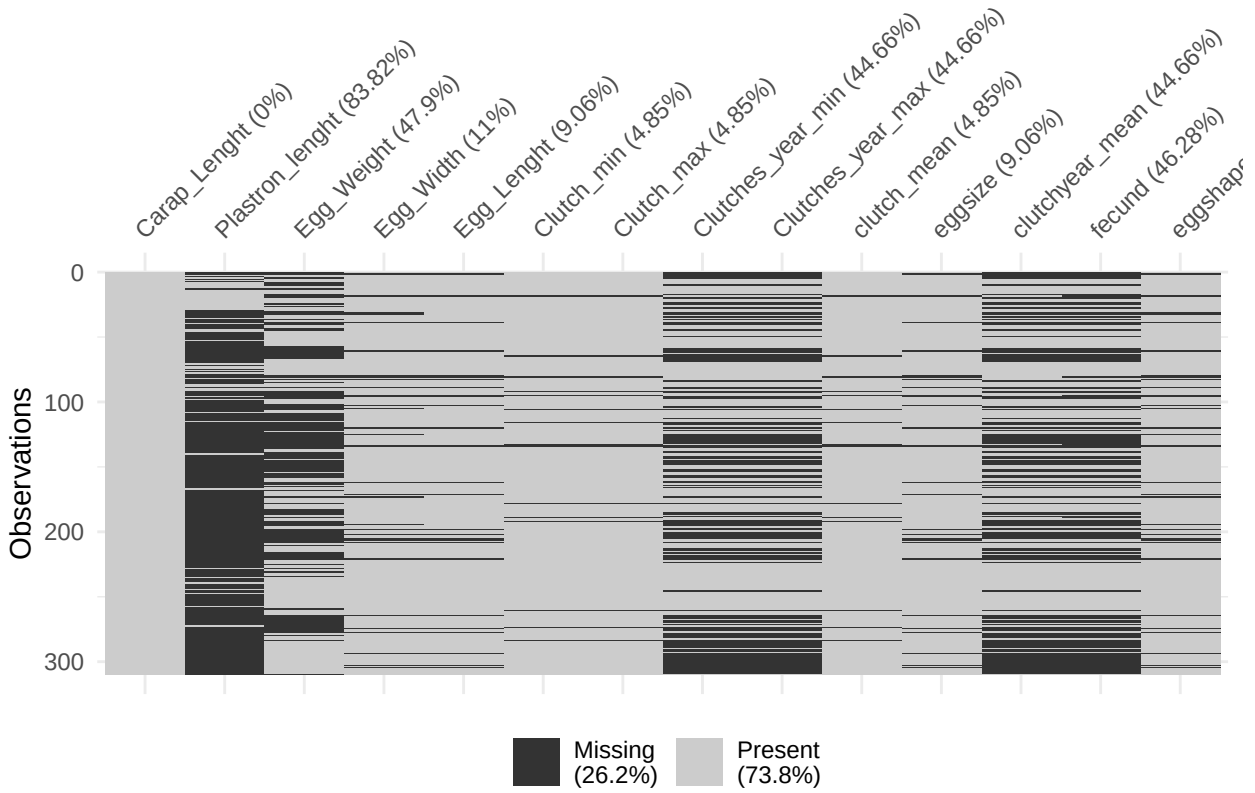
```
library(rr2)
packageVersion("rr2")
```

```
## [1] '1.0.2'
```

```
source("http://ib.berkeley.edu/courses/ib200b/scripts/diagnostics_v3.R")
```

Data input and handling

```
turtdata <- read_delim("turtdata.txt", "\t", escape_double = FALSE, col_types = cols(Plastron_lenght = c

turtdata <- turtdata %>%
       mutate(clutch_mean = (Clutch_max+Clutch_min)/2,
              eggsize = Egg_Lenght/Carap_Lenght,
              clutchyear_mean =  (Clutches_year_max + Clutches_year_min)/2,
              fecund = Clutch_max*clutchyear_mean,
              eggshape = Egg_Lenght/Egg_Width)

vis_miss(turtdata[,-c(1:2)])
```




```
eggsize_dataset <- remove_missing(turtdata, vars = c("eggsize", "clutch_mean"))
eggsize_dataset#270 species
```

```
## # A tibble: 270 x 16
##    Species Family Carap_Lenght Plastron_lenght Egg_Weight Egg_Width Egg_Lenght
##    <chr>   <chr>         <dbl>           <dbl>      <dbl>     <dbl>      <dbl>
##  1 Acanth~ Cheli~          175              NA       NA        23         26
##  2 Acanth~ Cheli~          170             165        8.5      25         27
##  3 Acanto~ Cheli~          295              NA       20        28         30
##  4 Chelod~ Cheli~          248             204       NA        22.2       33.8
##  5 Chelod~ Cheli~          275              NA       12        23.5       36.7
##  6 Chelod~ Cheli~          480             260       18.9      25         37
##  7 Chelod~ Cheli~          178              NA        8        20.6       37.1
##  8 Chelod~ Cheli~          232             174       NA        21         30
##  9 Chelod~ Cheli~          160             125       NA        22         32
## 10 Chelod~ Cheli~          217             168       NA        19         28
## # ... with 260 more rows, and 9 more variables: Clutch_min <int>,
## #   Clutch_max <int>, Clutches_year_min <int>, Clutches_year_max <int>,
## #   clutch_mean <dbl>, eggsize <dbl>, clutchyear_mean <dbl>, fecund <dbl>,
## #   eggshape <dbl>
```

```
fecund_dataset <- remove_missing(turtdata, vars = "fecund")
fecund_dataset#166 species
```

```
## # A tibble: 166 x 16
##    Species Family Carap_Lenght Plastron_lenght Egg_Weight Egg_Width Egg_Lenght
##    <chr>   <chr>         <dbl>           <dbl>      <dbl>     <dbl>      <dbl>
##  1 Chelod~ Cheli~          275              NA       12        23.5       36.7
##  2 Chelod~ Cheli~          480             260       18.9      25         37
##  3 Chelod~ Cheli~          178              NA        8        20.6       37.1
```

```
##  4 Chelod~ Cheli~          232             174       NA        21         30
##  5 Chelod~ Cheli~          320             245       20        26         35
##  6 Chelod~ Cheli~          180              NA       NA        18         30
##  7 Chelus~ Cheli~          381              NA       NA        35         36
##  8 Elseya~ Cheli~          400             330     37.1      34.4       57.5
##  9 Elseya~ Cheli~          500             364      9.9      29.8       52.6
## 10 Elseya~ Cheli~          285             235       23        30         50
## # ... with 156 more rows, and 9 more variables: Clutch_min <int>,
## #   Clutch_max <int>, Clutches_year_min <int>, Clutches_year_max <int>,
## #   clutch_mean <dbl>, eggsize <dbl>, clutchyear_mean <dbl>, fecund <dbl>,
## #   eggshape <dbl>
```

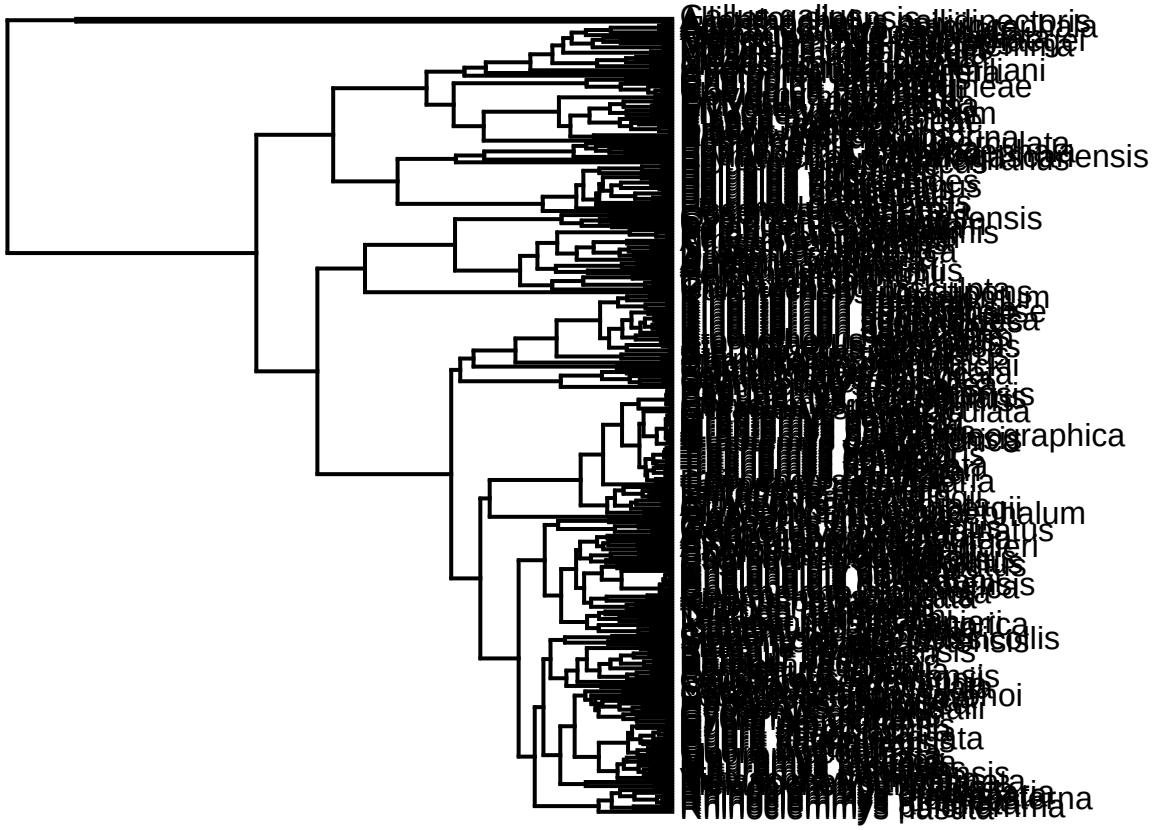
```
dados<- read.csv2("turtles_eggsize.csv", header=T)
head(dados)
```

```
##                         Species   family climatic_zone zoogeography habitat
## 1 Acanthochelys_pallidipectoris Chelidae      Tropical  Neotropical Aquatic
## 2          Acanthochelys_spixii Chelidae      Tropical  Neotropical Aquatic
## 3     Acantochelys_macrocephala Chelidae      Tropical  Neotropical Aquatic
## 4               Chelodina_canni Chelidae      Tropical   Australian Aquatic
## 5             Chelodina_colliei Chelidae      Tropical   Australian Aquatic
## 6             Chelodina_expansa Chelidae     Temperate   Australian Aquatic
##        diet carap egglenght clutchmin clutchmax
## 1 Carnivore   175        26         2         5
## 2 Carnivore   170        27         1         9
## 3 Carnivore   295        30         1         8
## 4 Carnivore   248      33.8         1        10
## 5 Carnivore   275      36.7         9        16
## 6 Carnivore   480        37         5        30
```

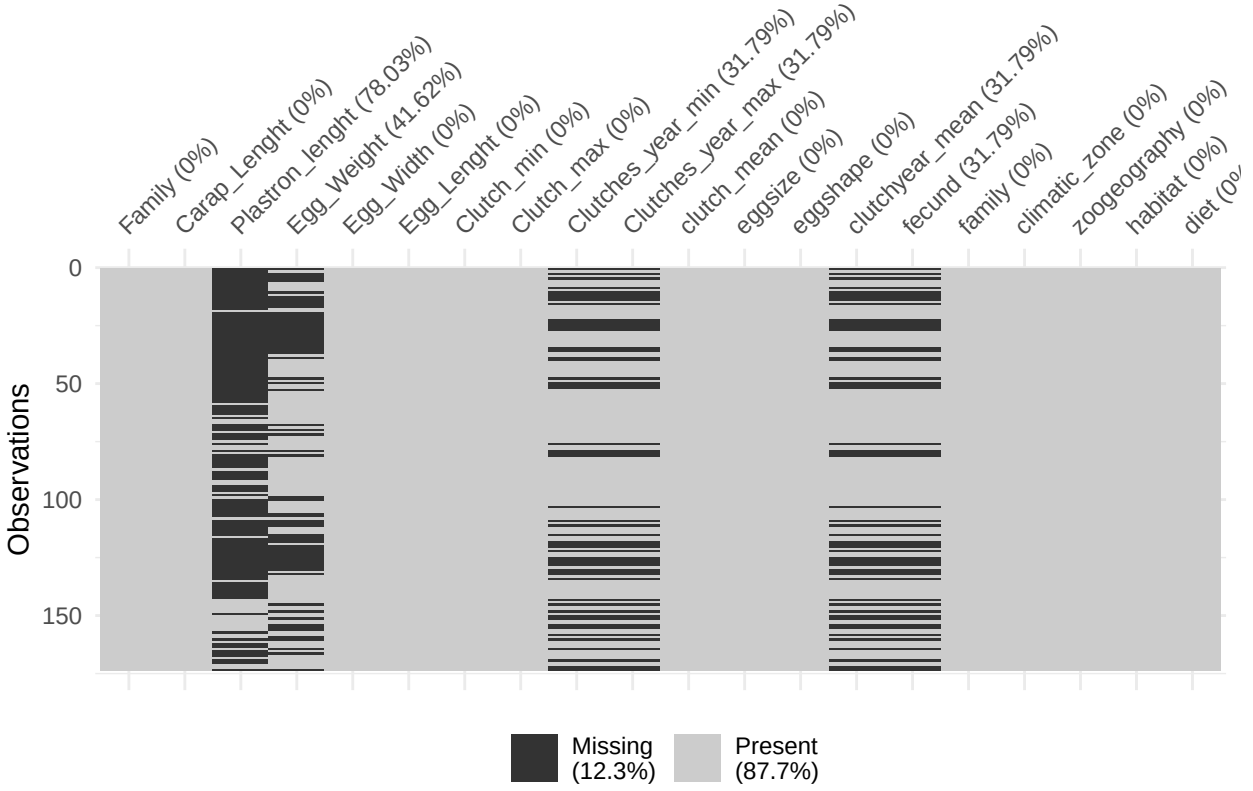
```
full_dataset <- inner_join(eggsize_dataset, dados, by = "Species")

full_dataset <- full_dataset %>%
       dplyr::select(Species, Family, Carap_Lenght, Plastron_lenght, Egg_Weight, Egg_Width,Egg_Lenght,
              Clutch_min, Clutch_max, Clutches_year_min ,
              Clutches_year_max, clutch_mean, eggsize,eggshape,
              clutchyear_mean, fecund, family,
              climatic_zone, zoogeography, habitat, diet)

full_dataset2 <- inner_join(fecund_dataset, dados, by = "Species")

full_dataset2 <- full_dataset2 %>%
       dplyr::select(Species, Family, Carap_Lenght, Plastron_lenght, Egg_Weight, Egg_Width,Egg_Lenght,
                     Clutch_min, Clutch_max, Clutches_year_min ,
                     Clutches_year_max, clutch_mean, eggsize, eggshape,                    clutchyear_m
                     climatic_zone, zoogeography, habitat, diet)
```

Phylogeny

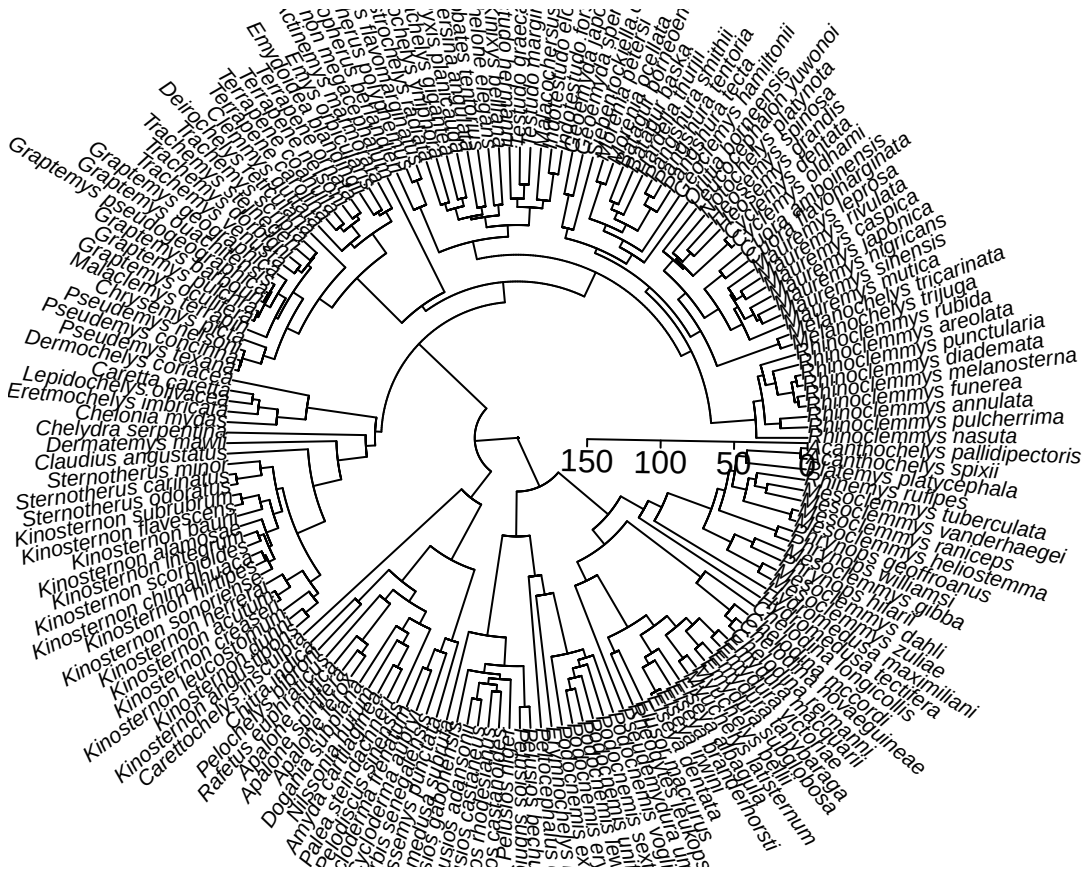
```
phyloPereira <- read.tree('https://ars.els-cdn.com/content/image/1-s2.0-S1055790316304316-mmc2.nwk')#co
plotTree(phyloPereira)
```



```
tidy_data <- make.treedata(phyloPereira, full_dataset)#173 species
vis_miss(tidy_data$dat)
```



```
plot.phylo(tidy_data$phy, cex = 0.7, type = "fan");axisPhylo()
```



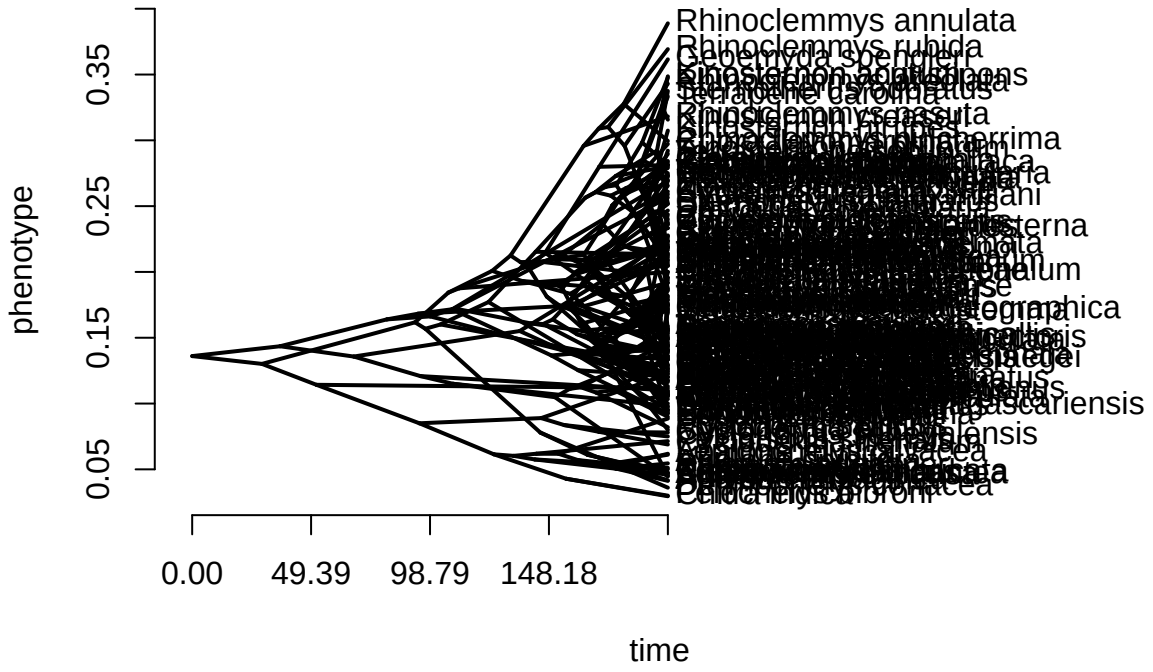

```
tidy_data2 <- make.treedata(phyloPereira, full_dataset2)#118 species
```

Exploratory data analysis

Traitgrams/Phenograms

For univariate traits, this is the best tool for visualizing the data. You cannot make a phylomorphospace with such disparate traits. morphospace, as the name says, only applies to morphological traits that are measured as a series of linear or landmark-based measures in a multivariate space.

```
treedply(tidy_data, phytools::phenogram(phy, getVector(tidy_data, eggsize), spread.labels=FALSE))
```



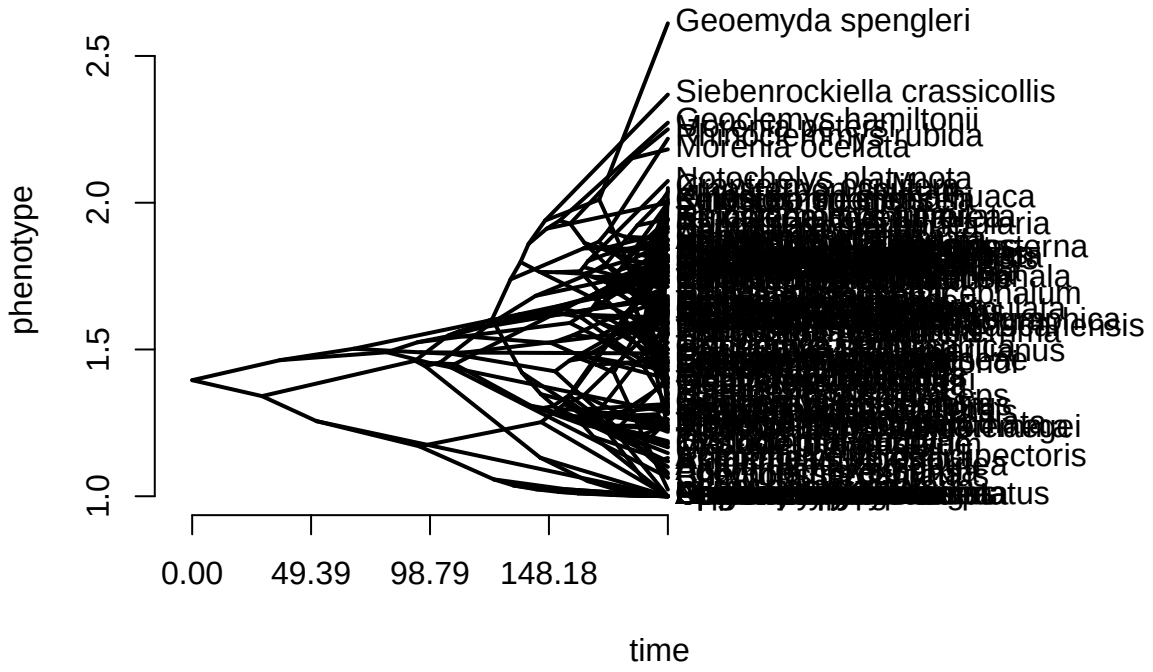

```
##                                  x         y
## Rhinoclemmys_nasuta          197.5709 0.31818182
## Rhinoclemmys_pulcherrima     197.5709 0.29951456
## Rhinoclemmys_annulata        197.5709 0.38888889
## Rhinoclemmys_funerea         197.5709 0.20923077
## Rhinoclemmys_melanosterna    197.5709 0.23333333
## Rhinoclemmys_diademata       197.5709 0.22047244
## Rhinoclemmys_punctularia     197.5709 0.27307692
## Rhinoclemmys_areolata        197.5708 0.34299517
## Rhinoclemmys_rubida          197.5709 0.36927374
## Melanochelys_trijuga         197.5709 0.12467532
## Melanochelys_tricarinata     197.5709 0.26993865
## Mauremys_mutica              197.5709 0.21111111
## Mauremys_sinensis            197.5709 0.18181818
## Mauremys_nigricans           197.5709 0.17843866
## Mauremys_japonica            197.5709 0.15311005
## Mauremys_caspica             197.5709 0.14893617
## Mauremys_rivulata            197.5709 0.17500000
## Mauremys_leprosa             197.5709 0.14400000
## Cuora_flavomarginata         197.5709 0.29722222
## Cuora_amboinensis            197.5709 0.27368421
## Cyclemys_oldhami             197.5709 0.23750000
## Cyclemys_dentata             197.5709 0.25909091
## Heosemys_grandis             197.5709 0.14444444
## Heosemys_spinosa             197.5709 0.27272727
## Notochelys_platynota         197.5709 0.15555556
## Leucocephalon_yuwonoi        197.5709 0.21666667
## Orlitia_borneensis           197.5709 0.10000000
## Geoclemys_hamiltonii         197.5709 0.14285714
## Pangshura_tecta              197.5709 0.17500000
## Pangshura_tentoria           197.5709 0.15498155
## Pangshura_smithii            197.5709 0.19383260
## Hardella_thurjii             197.5709 0.11320755
```

```
## Batagur_baska                 197.5709 0.14074074
## Batagur_borneoensis           197.5709 0.12000000
## Morenia_ocellata              197.5709 0.21818182
## Morenia_petersi               197.5709 0.20454545
## Siebenrockiella_crassicollis 197.5709 0.15000000
## Geoemyda_spengleri            197.5709 0.36153846
## Geoemyda_japonica             197.5709 0.28125000
## Indotestudo_forstenii         197.5708 0.15151515
## Indotestudo_elongata          197.5708 0.17241379
## Malacochersus_tornieri        197.5708 0.26553672
## Testudo_marginata             197.5708 0.09500000
## Testudo_graeca                197.5708 0.15714286
## Testudo_hermanni              197.5708 0.19193548
## Kinixys_belliana              197.5708 0.22325581
## Geochelone_elegans            197.5708 0.21904762
## Psammobates_tentorius         197.5708 0.23622047
## Chersina_angulata             197.5708 0.25161290
## Pyxis_planicauda              197.5708 0.21875000
## Aldabrachelys_gigantea        197.5708 0.04508197
## Astrochelys_yniphora          197.5708 0.11750000
## Astrochelys_radiata           197.5708 0.11627907
## Gopherus_flavomarginatus      197.5708 0.11750000
## Gopherus_polyphemus           197.5708 0.18672199
## Gopherus_berlandieri          197.5709 0.22727273
## Platysternon_megacephalum     197.5709 0.20000000
## Actinemys_marmorata           197.5709 0.20476190
## Emys_orbicularis              197.5709 0.21428571
## Emydoidea_blandingii          197.5709 0.20526316
## Terrapene_ornata              197.5708 0.21232877
## Terrapene_nelsoni             197.5708 0.28965517
## Terrapene_coahuila            197.5708 0.27500000
## Terrapene_carolina            197.5708 0.33333333
## Clemmys_guttata               197.5708 0.28431373
## Deirochelys_reticularia       197.5708 0.24666667
## Trachemys_scripta             197.5709 0.18571429
## Trachemys_stejnegeri          197.5708 0.17916667
## Trachemys_dorbigni            197.5708 0.15653846
## Trachemys_venusta             197.5709 0.09400000
## Graptemys_geographica         197.5709 0.15000000
## Graptemys_ouachitensis        197.5709 0.13333333
## Graptemys_pseudogeographica   197.5709 0.17073171
## Graptemys_barbouri            197.5709 0.13333333
## Graptemys_pulchra             197.5709 0.15555556
## Graptemys_oculifera           197.5709 0.22777778
## Malaclemys_terrapin           197.5709 0.17647059
## Chrysemys_picta               197.5708 0.24000000
## Pseudemys_nelsoni             197.5708 0.12666667
## Pseudemys_concinna            197.5708 0.14000000
## Pseudemys_texana              197.5708 0.10606061
## Dermochelys_coriacea          197.5708 0.03608924
## Caretta_caretta               197.5708 0.04766839
## Lepidochelys_olivacea         197.5708 0.06183206
## Eretmochelys_imbricata        197.5709 0.04712042
## Chelonia_mydas                197.5708 0.04705882
```

```
## Chelydra_serpentina           197.5709 0.12790698
## Dermatemys_mawii              197.5709 0.09538462
## Claudius_angustatus           197.5709 0.21333333
## Sternotherus_minor            197.5709 0.28000000
## Sternotherus_carinatus        197.5709 0.25196850
## Sternotherus_odoratus         197.5709 0.33750000
## Kinosternon_subrubrum         197.5709 0.29213483
## Kinosternon_flavescens        197.5709 0.23596491
## Kinosternon_baurii            197.5709 0.27894737
## Kinosternon_alamosae          197.5709 0.26106195
## Kinosternon_integrum          197.5709 0.18061224
## Kinosternon_scorpioides       197.5709 0.23333333
## Kinosternon_chimalhuaca       197.5709 0.28153846
## Kinosternon_hirtipes          197.5709 0.30740741
## Kinosternon_sonoriense        197.5709 0.18750000
## Kinosternon_herrerai          197.5709 0.21875000
## Kinosternon_acutum            197.5709 0.34864865
## Kinosternon_creaseri          197.5709 0.31570248
## Kinosternon_leucostomum       197.5709 0.20673077
## Kinosternon_dunni             197.5709 0.28125000
## Kinosternon_angustipons       197.5709 0.34782609
## Carettochelys_insculpta       197.5709 0.11168831
## Chitra_indica                 197.5708 0.02956522
## Pelochelys_bibroni            197.5708 0.03000000
## Rafetus_euphraticus           197.5708 0.04600000
## Apalone_mutica                197.5708 0.06111111
## Apalone_spinifera             197.5708 0.05454545
## Apalone_ferox                 197.5708 0.04166667
## Dogania_subplana              197.5708 0.08857143
## Nilssonia_hurum               197.5708 0.05000000
## Amyda_cartilaginea            197.5708 0.04125000
## Palea_steindachneri           197.5708 0.05116279
## Pelodiscus_sinensis           197.5709 0.07142857
## Cycloderma_frenatum           197.5709 0.06889764
## Cycloderma_aubryi             197.5709 0.07800000
## Cyclanorbis_senegalensis      197.5709 0.07500000
## Lissemys_punctata             197.5709 0.12227074
## Pelomedusa_subrufa            197.5709 0.22352941
## Pelusios_gabonensis           197.5708 0.10606061
## Pelusios_adansonii            197.5709 0.13636364
## Pelusios_castaneus            197.5709 0.12280702
## Pelusios_rhodesianus          197.5709 0.14000000
## Pelusios_castanoides          197.5709 0.14545455
## Pelusios_niger                197.5709 0.17142857
## Pelusios_subniger             197.5708 0.12413793
## Pelusios_bechuanicus          197.5708 0.10909091
## Peltocephalus_dumerilianus    197.5709 0.11000000
## Erymnochelys_madagascariensis 197.5709 0.09812500
## Podocnemis_expansa            197.5709 0.04458000
## Podocnemis_erythrocephala     197.5709 0.13593750
## Podocnemis_lewyana            197.5709 0.09000000
## Podocnemis_unifilis           197.5709 0.08200000
## Podocnemis_sextuberculata     197.5709 0.14666667
## Podocnemis_vogli              197.5709 0.14117647
```

```
## Pseudemydura_umbrina          197.5709 0.26923077
## Rheodytes_leukops             197.5709 0.12048193
## Elusor_macrurus               197.5709 0.09259259
## Elseya_dentata                197.5708 0.17543860
## Elseya_irwini                 197.5708 0.13846154
## Elseya_branderhorsti          197.5709 0.10520000
## Elseya_albagula               197.5708 0.14375000
## Myuchelys_latisternum         197.5708 0.10714286
## Myuchelys_bellii              197.5708 0.08000000
## Emydura_subglobosa            197.5709 0.15384615
## Emydura_tanybaraga            197.5709 0.19161677
## Emydura_victoriae             197.5709 0.24375000
## Emydura_macquarii             197.5709 0.10645161
## Chelodina_reimanni            197.5708 0.12903226
## Chelodina_novaeguineae        197.5708 0.20000000
## Chelodina_mccordi             197.5709 0.12931034
## Chelodina_longicollis         197.5709 0.20842697
## Hydromedusa_tectifera         197.5708 0.12000000
## Hydromedusa_maximiliani       197.5709 0.25649718
## Mesoclemmys_zuliae            197.5709 0.12607143
## Mesoclemmys_dahli             197.5709 0.19565217
## Phrynops_hilarii              197.5709 0.09250000
## Mesoclemmys_gibba             197.5709 0.19565217
## Phrynops_williamsi            197.5708 0.13492063
## Phrynops_geoffroanus          197.5708 0.09714286
## Mesoclemmys_heliostemma       197.5708 0.16933333
## Mesoclemmys_raniceps          197.5708 0.10810811
## Mesoclemmys_vanderhaegei      197.5708 0.13358779
## Mesoclemmys_tuberculata       197.5708 0.10333333
## Rhinemys_rufipes              197.5708 0.17407407
## Platemys_platycephala         197.5709 0.28333333
## Acanthochelys_spixii          197.5708 0.15882353
## Acanthochelys_pallidipectoris 197.5708 0.14857143
```

```
treedply(tidy_data, phytools::phenogram(phy, getVector(tidy_data, eggshape), spread.labels=FALSE, quiet=
```



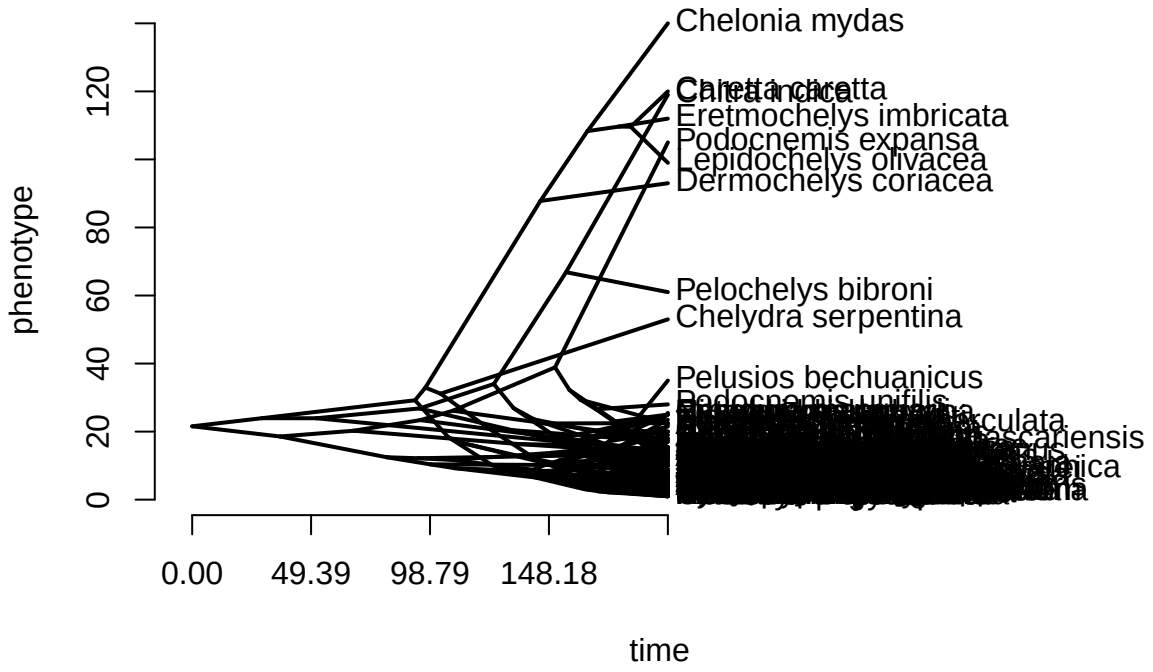

```
##                                x        y
## Rhinoclemmys_nasuta          197.5709 1.842105
## Rhinoclemmys_pulcherrima     197.5709 1.550251
## Rhinoclemmys_annulata        197.5709 1.944444
## Rhinoclemmys_funerea         197.5709 1.942857
## Rhinoclemmys_melanosterna    197.5709 1.842105
## Rhinoclemmys_diademata       197.5709 1.806452
## Rhinoclemmys_punctularia     197.5709 1.918919
## Rhinoclemmys_areolata        197.5708 1.839378
## Rhinoclemmys_rubida          197.5709 2.218121
## Melanochelys_trijuga         197.5709 1.371429
## Melanochelys_tricarinata     197.5709 1.760000
## Mauremys_mutica              197.5709 1.809524
## Mauremys_sinensis            197.5709 1.600000
## Mauremys_nigricans           197.5709 1.846154
## Mauremys_japonica            197.5709 1.454545
## Mauremys_caspica             197.5709 1.750000
## Mauremys_rivulata            197.5709 1.590909
## Mauremys_leprosa             197.5709 1.800000
## Cuora_flavomarginata         197.5709 1.910714
## Cuora_amboinensis            197.5709 1.733333
## Cyclemys_oldhami             197.5709 1.781250
## Cyclemys_dentata             197.5709 1.628571
## Heosemys_grandis             197.5709 1.857143
## Heosemys_spinosa             197.5709 1.875000
## Notochelys_platynota         197.5709 2.074074
## Leucocephalon_yuwonoi        197.5709 1.444444
## Orlitia_borneensis           197.5709 2.000000
## Geoclemys_hamiltonii         197.5709 2.272727
## Pangshura_tecta              197.5709 1.555556
## Pangshura_tentoria           197.5709 1.555556
## Pangshura_smithii            197.5709 1.913043
## Hardella_thurjii             197.5709 1.764706
```

```
## Batagur_baska                 197.5709 1.900000
## Batagur_borneoensis           197.5709 1.800000
## Morenia_ocellata              197.5709 2.181818
## Morenia_petersi               197.5709 2.250000
## Siebenrockiella_crassicollis 197.5709 2.368421
## Geoemyda_spengleri            197.5709 2.611111
## Geoemyda_japonica             197.5709 1.500000
## Indotestudo_forstenii         197.5708 1.219512
## Indotestudo_elongata          197.5708 1.250000
## Malacochersus_tornieri        197.5708 1.620690
## Testudo_marginata             197.5708 1.187500
## Testudo_graeca                197.5708 1.178571
## Testudo_hermanni              197.5708 1.239583
## Kinixys_belliana              197.5708 1.263158
## Geochelone_elegans            197.5708 1.314286
## Psammobates_tentorius         197.5708 1.304348
## Chersina_angulata             197.5708 1.147059
## Pyxis_planicauda              197.5708 1.590909
## Aldabrachelys_gigantea        197.5708 1.100000
## Astrochelys_yniphora          197.5708 1.119048
## Astrochelys_radiata           197.5708 1.000000
## Gopherus_flavomarginatus      197.5708 1.000000
## Gopherus_polyphemus           197.5708 1.000000
## Gopherus_berlandieri          197.5709 1.388889
## Platysternon_megacephalum     197.5709 1.681818
## Actinemys_marmorata           197.5709 1.869565
## Emys_orbicularis              197.5709 1.764706
## Emydoidea_blandingii          197.5709 1.625000
## Terrapene_ornata              197.5708 1.347826
## Terrapene_nelsoni             197.5708 1.555556
## Terrapene_coahuila            197.5708 1.941176
## Terrapene_carolina            197.5708 1.727273
## Clemmys_guttata               197.5708 1.812500
## Deirochelys_reticularia       197.5708 1.608696
## Trachemys_scripta             197.5709 1.500000
## Trachemys_stejnegeri          197.5708 1.653846
## Trachemys_dorbigni            197.5708 1.565385
## Trachemys_venusta             197.5709 1.382353
## Graptemys_geographica         197.5709 1.500000
## Graptemys_ouachitensis        197.5709 1.280000
## Graptemys_pseudogeographica   197.5709 1.590909
## Graptemys_barbouri            197.5709 1.384615
## Graptemys_pulchra             197.5709 1.312500
## Graptemys_oculifera           197.5709 2.050000
## Malaclemys_terrapin           197.5709 1.615385
## Chrysemys_picta               197.5708 1.875000
## Pseudemys_nelsoni             197.5708 1.461538
## Pseudemys_concinna            197.5708 1.555556
## Pseudemys_texana              197.5708 1.346154
## Dermochelys_coriacea          197.5708 1.000000
## Caretta_caretta               197.5708 1.000000
## Lepidochelys_olivacea         197.5708 1.000000
## Eretmochelys_imbricata        197.5709 1.000000
## Chelonia_mydas                197.5708 1.000000
```

```
## Chelydra_serpentina           197.5709 1.064516
## Dermatemys_mawii              197.5709 1.675676
## Claudius_angustatus           197.5709 1.777778
## Sternotherus_minor            197.5709 1.647059
## Sternotherus_carinatus        197.5709 1.777778
## Sternotherus_odoratus         197.5709 1.800000
## Kinosternon_subrubrum         197.5709 1.733333
## Kinosternon_flavescens        197.5709 1.620482
## Kinosternon_baurii            197.5709 1.647668
## Kinosternon_alamosae          197.5709 1.787879
## Kinosternon_integrum          197.5709 1.853403
## Kinosternon_scorpioides       197.5709 1.842105
## Kinosternon_chimalhuaca       197.5709 2.010989
## Kinosternon_hirtipes          197.5709 1.784946
## Kinosternon_sonoriense        197.5709 1.736842
## Kinosternon_herrerai          197.5709 1.944444
## Kinosternon_acutum            197.5709 2.036842
## Kinosternon_creaseri          197.5709 2.000000
## Kinosternon_leucostomum       197.5709 1.592593
## Kinosternon_dunni             197.5709 1.800000
## Kinosternon_angustipons       197.5709 1.818182
## Carettochelys_insculpta       197.5709 1.000000
## Chitra_indica                 197.5708 1.000000
## Pelochelys_bibroni            197.5708 1.000000
## Rafetus_euphraticus           197.5708 1.000000
## Apalone_mutica                197.5708 1.000000
## Apalone_spinifera             197.5708 1.000000
## Apalone_ferox                 197.5708 1.000000
## Dogania_subplana              197.5708 1.000000
## Nilssonia_hurum               197.5708 1.000000
## Amyda_cartilaginea            197.5708 1.000000
## Palea_steindachneri           197.5708 1.000000
## Pelodiscus_sinensis           197.5709 1.000000
## Cycloderma_frenatum           197.5709 1.166667
## Cycloderma_aubryi             197.5709 1.181818
## Cyclanorbis_senegalensis      197.5709 1.800000
## Lissemys_punctata             197.5709 1.000000
## Pelomedusa_subrufa            197.5709 1.727273
## Pelusios_gabonensis           197.5708 1.400000
## Pelusios_adansonii            197.5709 1.666667
## Pelusios_castaneus            197.5709 1.400000
## Pelusios_rhodesianus          197.5709 1.590909
## Pelusios_castanoides          197.5709 1.454545
## Pelusios_niger                197.5709 2.000000
## Pelusios_subniger             197.5708 1.714286
## Pelusios_bechuanicus          197.5708 1.636364
## Peltocephalus_dumerilianus    197.5709 1.486486
## Erymnochelys_madagascariensis 197.5709 1.572621
## Podocnemis_expansa            197.5709 1.074735
## Podocnemis_erythrocephala     197.5709 1.740000
## Podocnemis_lewyana            197.5709 1.022727
## Podocnemis_unifilis           197.5709 1.464286
## Podocnemis_sextuberculata     197.5709 1.629630
## Podocnemis_vogli              197.5709 1.655172
```

```
## Pseudemydura_umbrina          197.5709 1.750000
## Rheodytes_leukops             197.5709 1.428571
## Elusor_macrurus               197.5709 1.400000
## Elseya_dentata                197.5708 1.666667
## Elseya_irwini                 197.5708 1.285714
## Elseya_branderhorsti          197.5709 1.765101
## Elseya_albagula               197.5708 1.671512
## Myuchelys_latisternum         197.5708 1.304348
## Myuchelys_bellii              197.5708 1.523810
## Emydura_subglobosa            197.5709 2.000000
## Emydura_tanybaraga            197.5709 1.230769
## Emydura_victoriae             197.5709 1.772727
## Emydura_macquarii             197.5709 1.434783
## Chelodina_reimanni            197.5708 1.473684
## Chelodina_novaeguineae        197.5708 1.454545
## Chelodina_mccordi             197.5709 1.428571
## Chelodina_longicollis         197.5709 1.800971
## Hydromedusa_tectifera         197.5708 1.285714
## Hydromedusa_maximiliani       197.5709 1.816000
## Mesoclemmys_zuliae            197.5709 1.168874
## Mesoclemmys_dahli             197.5709 1.241379
## Phrynops_hilarii              197.5709 1.000000
## Mesoclemmys_gibba             197.5709 1.406250
## Phrynops_williamsi            197.5708 1.259259
## Phrynops_geoffroanus          197.5708 1.062500
## Mesoclemmys_heliostemma       197.5708 1.227053
## Mesoclemmys_raniceps          197.5708 1.333333
## Mesoclemmys_vanderhaegei      197.5708 1.228070
## Mesoclemmys_tuberculata       197.5708 1.240000
## Rhinemys_rufipes              197.5708 1.119048
## Platemys_platycephala         197.5709 1.821429
## Acanthochelys_spixii          197.5708 1.080000
## Acanthochelys_pallidipectoris 197.5708 1.130435
```

```
treedply(tidy_data, phytools::phenogram(phy, getVector(tidy_data, clutch_mean), spread.labels=FALSE, qu
```



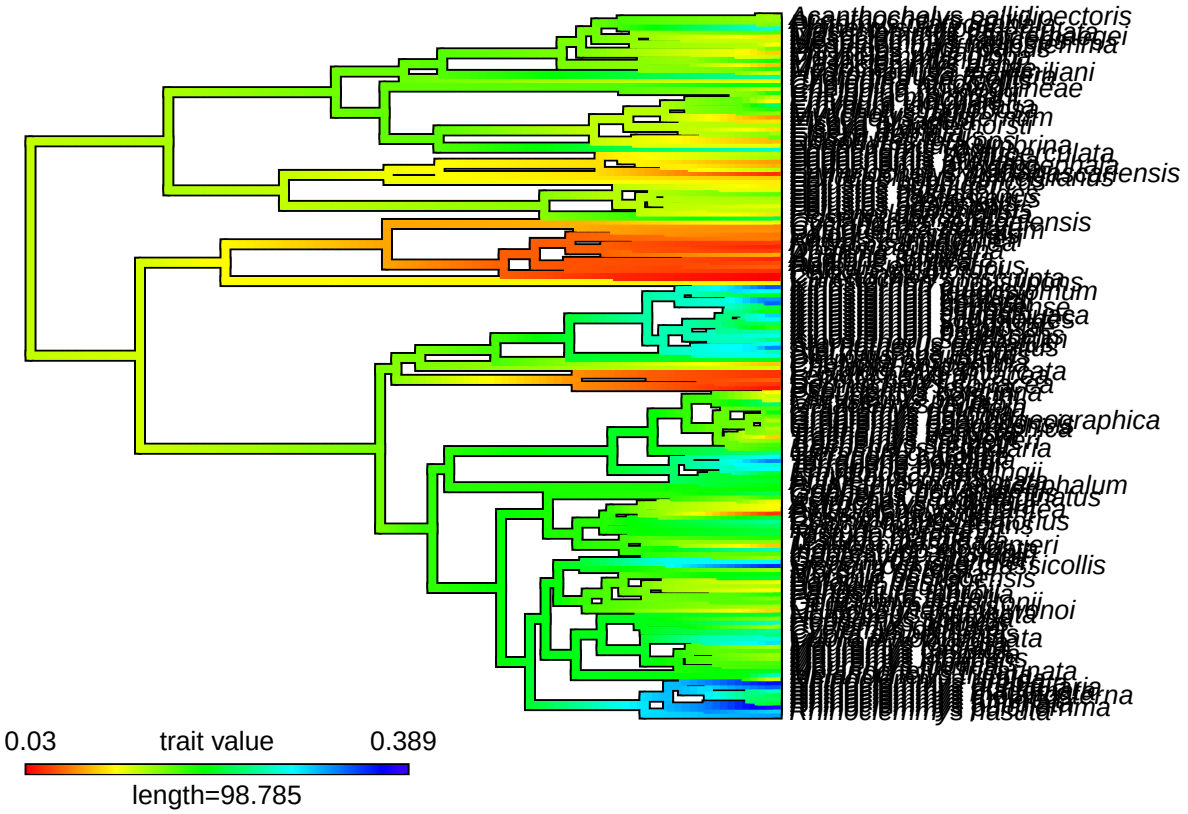

```
##                                 x     y
## Rhinoclemmys_nasuta          197.5709   1.0
## Rhinoclemmys_pulcherrima     197.5709   2.0
## Rhinoclemmys_annulata        197.5709   1.5
## Rhinoclemmys_funerea         197.5709   3.0
## Rhinoclemmys_melanosterna    197.5709   2.0
## Rhinoclemmys_diademata       197.5709   2.0
## Rhinoclemmys_punctularia     197.5709   2.5
## Rhinoclemmys_areolata        197.5708   1.0
## Rhinoclemmys_rubida          197.5709   1.0
## Melanochelys_trijuga         197.5709   5.0
## Melanochelys_tricarinata     197.5709   3.0
## Mauremys_mutica              197.5709   8.0
## Mauremys_sinensis            197.5709   3.0
## Mauremys_nigricans           197.5709   4.0
## Mauremys_japonica            197.5709   6.5
## Mauremys_caspica             197.5709   5.0
## Mauremys_rivulata            197.5709  12.0
## Mauremys_leprosa             197.5709   8.0
## Cuora_flavomarginata         197.5709   2.0
## Cuora_amboinensis            197.5709   3.0
## Cyclemys_oldhami             197.5709   3.0
## Cyclemys_dentata             197.5709   3.0
## Heosemys_grandis             197.5709   6.0
## Heosemys_spinosa             197.5709   2.0
## Notochelys_platynota         197.5709   4.0
## Leucocephalon_yuwonoi        197.5709   1.5
## Orlitia_borneensis           197.5709  13.5
## Geoclemys_hamiltonii         197.5709  19.0
## Pangshura_tecta              197.5709   7.5
## Pangshura_tentoria           197.5709   8.0
## Pangshura_smithii            197.5709   7.0
## Hardella_thurjii             197.5709  14.0
```

```
## Batagur_baska                 197.5709  25.0
## Batagur_borneoensis           197.5709  20.0
## Morenia_ocellata              197.5709   6.5
## Morenia_petersi               197.5709   8.0
## Siebenrockiella_crassicollis  197.5709   3.5
## Geoemyda_spengleri            197.5709   1.5
## Geoemyda_japonica             197.5709   5.0
## Indotestudo_forstenii         197.5708   3.0
## Indotestudo_elongata          197.5708   7.0
## Malacochersus_tornieri        197.5708   1.0
## Testudo_marginata             197.5708  10.5
## Testudo_graeca                197.5708   5.0
## Testudo_hermanni              197.5708   3.0
## Kinixys_belliana              197.5708   7.0
## Geochelone_elegans            197.5708   3.0
## Psammobates_tentorius         197.5708   2.0
## Chersina_angulata             197.5708   1.0
## Pyxis_planicauda              197.5708   1.5
## Aldabrachelys_gigantea        197.5708  12.0
## Astrochelys_yniphora          197.5708   6.0
## Astrochelys_radiata           197.5708  15.0
## Gopherus_flavomarginatus      197.5708   7.0
## Gopherus_polyphemus           197.5708   5.5
## Gopherus_berlandieri          197.5709   4.0
## Platysternon_megacephalum     197.5709   2.0
## Actinemys_marmorata           197.5709   7.0
## Emys_orbicularis              197.5709  10.0
## Emydoidea_blandingii          197.5709  11.0
## Terrapene_ornata              197.5708   4.0
## Terrapene_nelsoni             197.5708   2.5
## Terrapene_coahuila            197.5708   3.0
## Terrapene_carolina            197.5708   4.0
## Clemmys_guttata               197.5708   3.0
## Deirochelys_reticularia       197.5708   8.0
## Trachemys_scripta             197.5709  12.0
## Trachemys_stejnegeri          197.5708   8.5
## Trachemys_dorbigni            197.5708  12.5
## Trachemys_venusta             197.5709  22.0
## Graptemys_geographica         197.5709  14.5
## Graptemys_ouachitensis        197.5709  12.0
## Graptemys_pseudogeographica   197.5709   9.0
## Graptemys_barbouri            197.5709   9.0
## Graptemys_pulchra             197.5709   5.0
## Graptemys_oculifera           197.5709   2.5
## Malaclemys_terrapin           197.5709  11.0
## Chrysemys_picta               197.5708   4.0
## Pseudemys_nelsoni             197.5708  12.0
## Pseudemys_concinna            197.5708  18.0
## Pseudemys_texana              197.5708  11.0
## Dermochelys_coriacea          197.5708  93.0
## Caretta_caretta               197.5708 120.0
## Lepidochelys_olivacea         197.5708  99.0
## Eretmochelys_imbricata        197.5709 112.0
## Chelonia_mydas                197.5708 140.0
```

```
## Chelydra_serpentina           197.5709  53.0
## Dermatemys_mawii              197.5709  17.0
## Claudius_angustatus           197.5709   3.5
## Sternotherus_minor            197.5709   3.0
## Sternotherus_carinatus        197.5709   4.0
## Sternotherus_odoratus         197.5709   4.0
## Kinosternon_subrubrum         197.5709   3.0
## Kinosternon_flavescens        197.5709   4.5
## Kinosternon_baurii            197.5709   3.0
## Kinosternon_alamosae          197.5709   4.0
## Kinosternon_integrum          197.5709   7.5
## Kinosternon_scorpioides       197.5709   4.5
## Kinosternon_chimalhuaca       197.5709   3.5
## Kinosternon_hirtipes          197.5709   3.5
## Kinosternon_sonoriense        197.5709   7.0
## Kinosternon_herrerai          197.5709   5.0
## Kinosternon_acutum            197.5709   3.0
## Kinosternon_creaseri          197.5709   1.0
## Kinosternon_leucostomum       197.5709   3.5
## Kinosternon_dunni             197.5709   2.5
## Kinosternon_angustipons       197.5709   2.0
## Carettochelys_insculpta       197.5709  14.0
## Chitra_indica                 197.5708 119.0
## Pelochelys_bibroni            197.5708  61.0
## Rafetus_euphraticus           197.5708  10.0
## Apalone_mutica                197.5708  18.0
## Apalone_spinifera             197.5708  21.5
## Apalone_ferox                 197.5708  14.0
## Dogania_subplana              197.5708   5.0
## Nilssonia_hurum               197.5708  25.0
## Amyda_cartilaginea            197.5708   4.5
## Palea_steindachneri           197.5708   5.5
## Pelodiscus_sinensis           197.5709  22.5
## Cycloderma_frenatum           197.5709  20.0
## Cycloderma_aubryi             197.5709  25.0
## Cyclanorbis_senegalensis      197.5709  12.0
## Lissemys_punctata             197.5709  10.0
## Pelomedusa_subrufa            197.5709  13.5
## Pelusios_gabonensis           197.5708  12.0
## Pelusios_adansonii            197.5709  15.0
## Pelusios_castaneus            197.5709  15.5
## Pelusios_rhodesianus          197.5709  12.5
## Pelusios_castanoides          197.5709  15.0
## Pelusios_niger                197.5709   8.0
## Pelusios_subniger             197.5708  13.0
## Pelusios_bechuanicus          197.5708  35.0
## Peltocephalus_dumerilianus    197.5709  14.0
## Erymnochelys_madagascariensis 197.5709  17.5
## Podocnemis_expansa            197.5709 105.0
## Podocnemis_erythrocephala     197.5709  10.0
## Podocnemis_lewyana            197.5709  25.0
## Podocnemis_unifilis           197.5709  28.0
## Podocnemis_sextuberculata     197.5709  22.5
## Podocnemis_vogli              197.5709  12.5
```

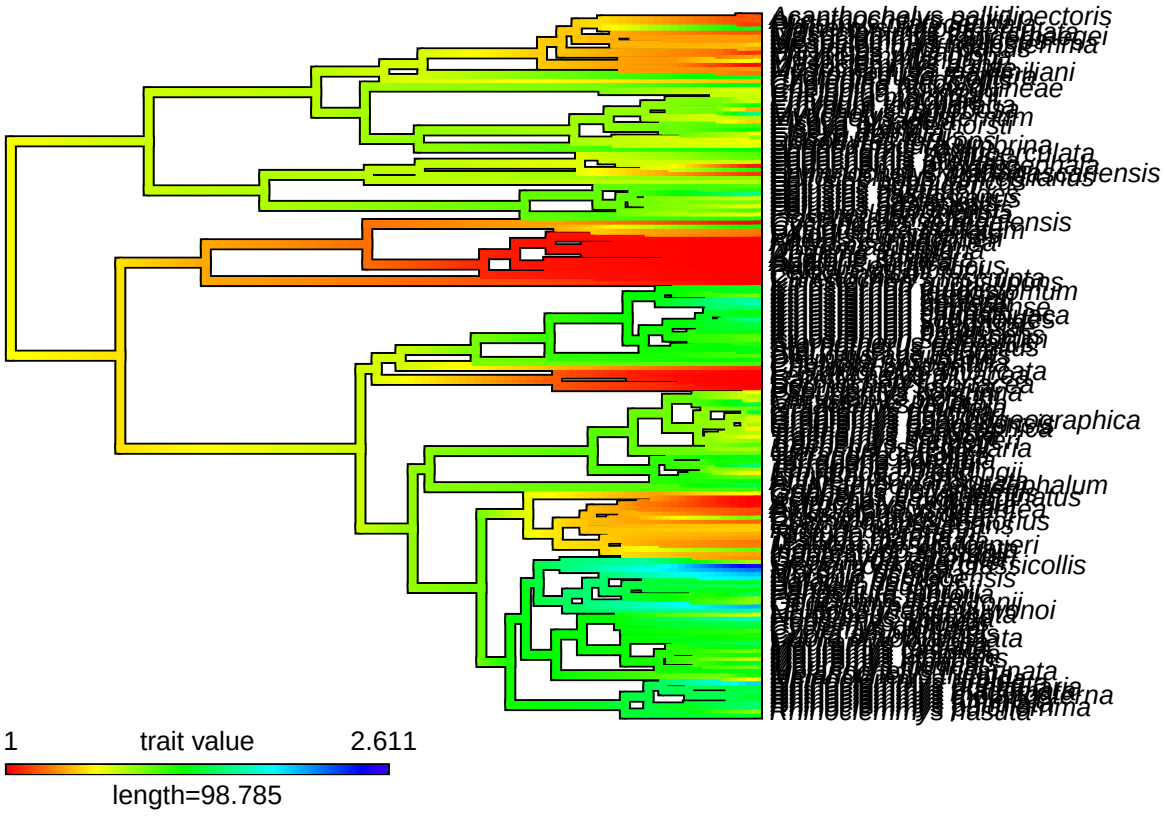
```
## Pseudemydura_umbrina          197.5709   4.0
## Rheodytes_leukops             197.5709  13.0
## Elusor_macrurus               197.5709  13.0
## Elseya_dentata                197.5708  10.0
## Elseya_irwini                 197.5708  12.0
## Elseya_branderhorsti          197.5709  23.5
## Elseya_albagula               197.5708  13.0
## Myuchelys_latisternum         197.5708  13.0
## Myuchelys_bellii              197.5708  15.5
## Emydura_subglobosa            197.5709   7.5
## Emydura_tanybaraga            197.5709  17.0
## Emydura_victoriae             197.5709  12.0
## Emydura_macquarii             197.5709  25.5
## Chelodina_reimanni            197.5708  10.0
## Chelodina_novaeguineae        197.5708  15.0
## Chelodina_mccordi             197.5709  11.5
## Chelodina_longicollis         197.5709  14.5
## Hydromedusa_tectifera         197.5708  10.0
## Hydromedusa_maximiliani       197.5709   2.0
## Mesoclemmys_zuliae            197.5709   8.5
## Mesoclemmys_dahli             197.5709   3.5
## Phrynops_hilarii              197.5709  20.0
## Mesoclemmys_gibba             197.5709   3.0
## Phrynops_williamsi            197.5708   7.0
## Phrynops_geoffroanus          197.5708  19.0
## Mesoclemmys_heliostemma       197.5708   6.5
## Mesoclemmys_raniceps          197.5708   5.0
## Mesoclemmys_vanderhaegei      197.5708   8.5
## Mesoclemmys_tuberculata       197.5708   7.5
## Rhinemys_rufipes              197.5708   7.5
## Platemys_platycephala         197.5709   1.0
## Acanthochelys_spixii          197.5708   9.0
## Acanthochelys_pallidipectoris 197.5708   3.5
```

```
treedply(tidy_data, phytools::contMap(phy, getVector(tidy_data, eggsize), fsize=0.8))
```



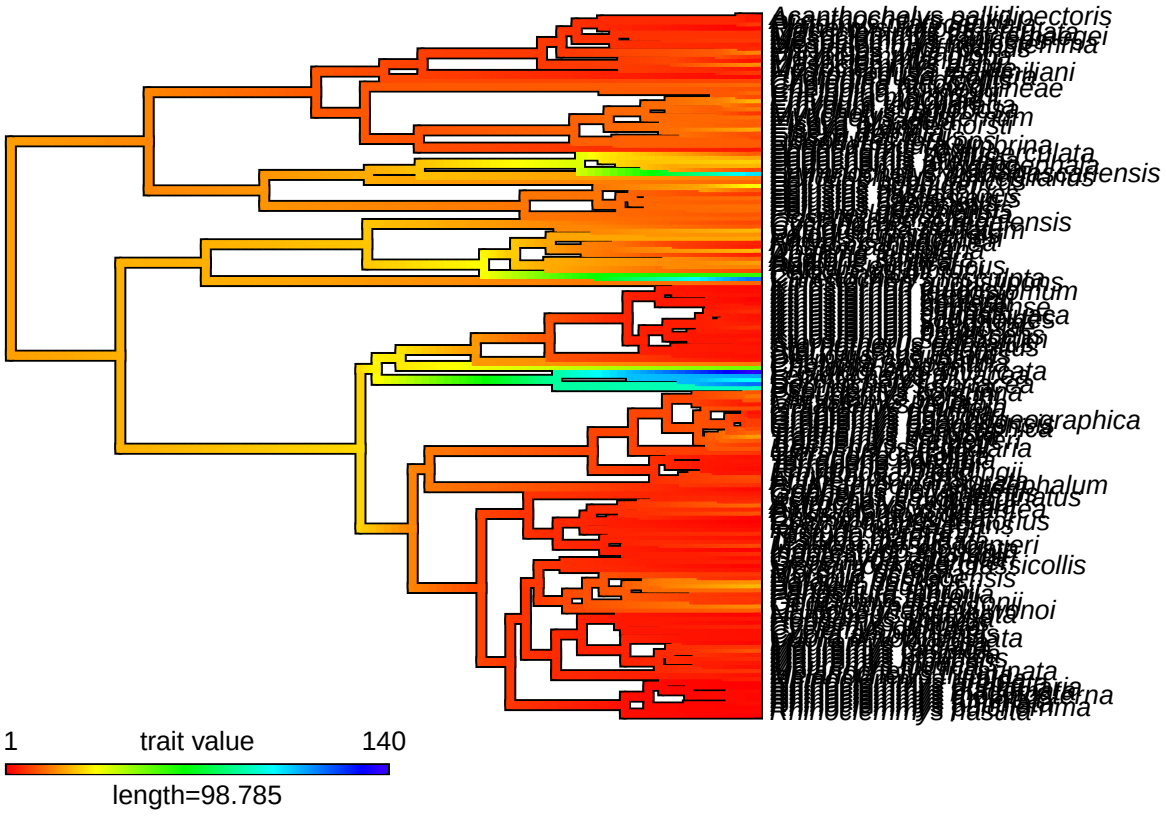

```
## Object of class "contMap" containing:
##
## (1) A phylogenetic tree with 173 tips and 172 internal nodes.
##
## (2) A mapped continuous trait on the range (0.029565, 0.388889).
```

```
treedply(tidy_data, phytools::contMap(phy, getVector(tidy_data, eggshape), fsize=0.8))
```




```
## Object of class "contMap" containing:
##
## (1) A phylogenetic tree with 173 tips and 172 internal nodes.
##
## (2) A mapped continuous trait on the range (1, 2.611111).
```

```
treedply(tidy_data, phytools::contMap(phy, getVector(tidy_data, clutch_mean), fsize=0.8))
```

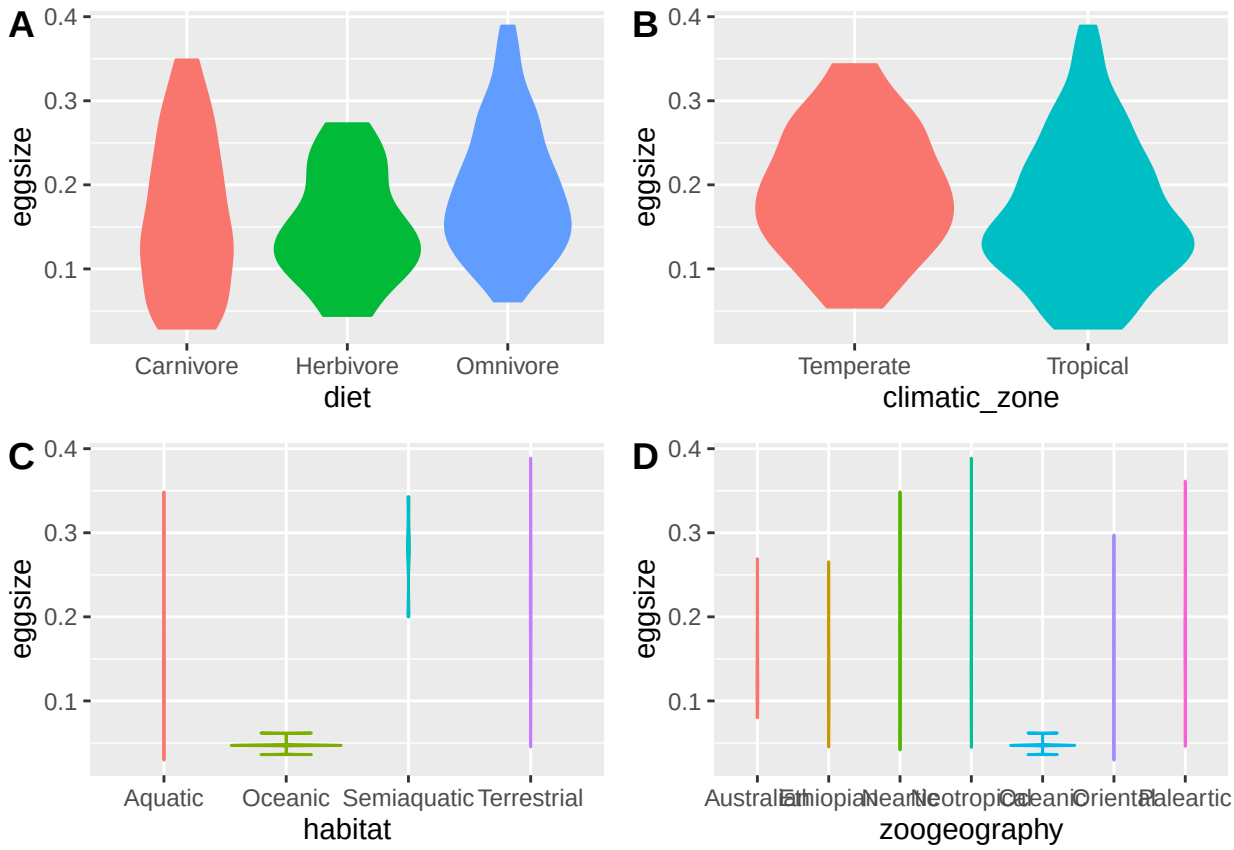



```
## Object of class "contMap" containing:
##
## (1) A phylogenetic tree with 173 tips and 172 internal nodes.
##
## (2) A mapped continuous trait on the range (1, 140).
```

You can't plot fecundity due to many NAs

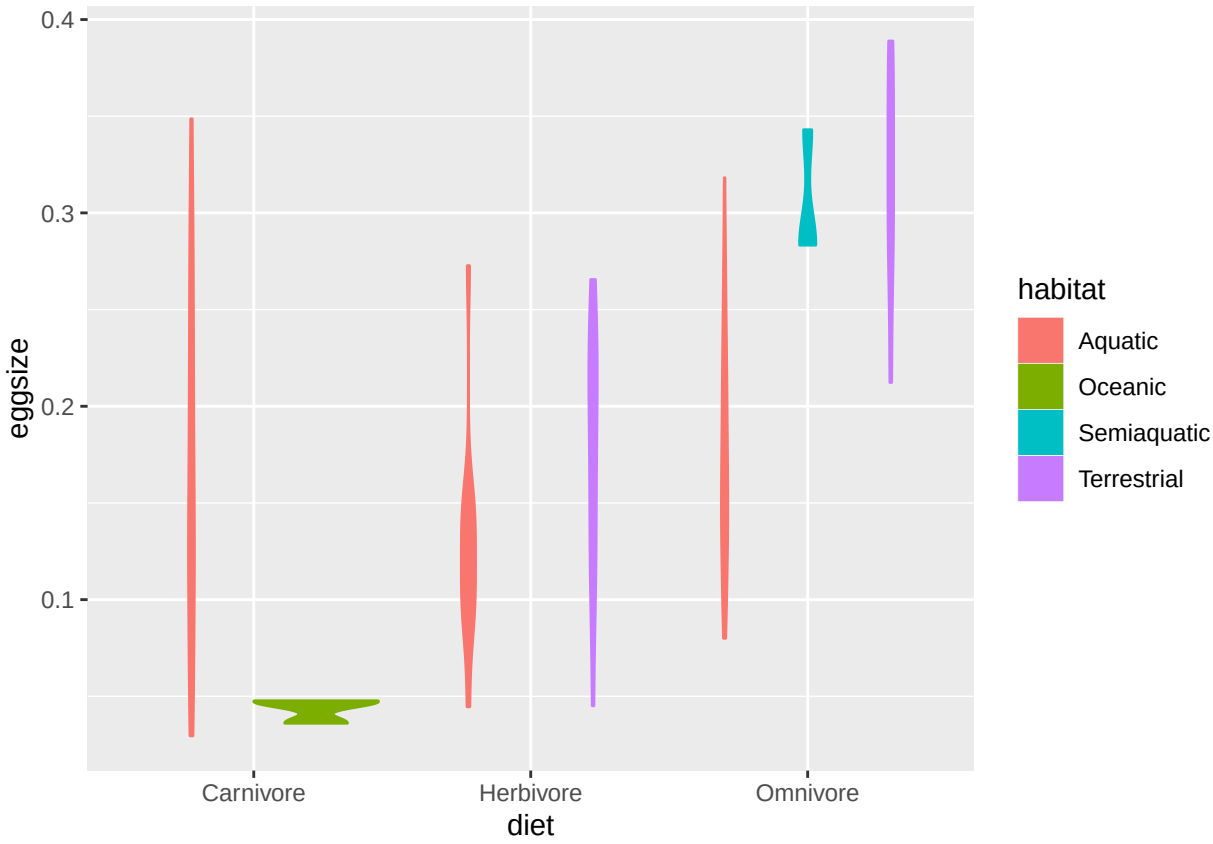
Plotting categorical predictors

```
a <- ggplot(tidy_data$dat, aes(diet, eggsize))+
       geom_violin(aes(col=diet, fill=diet))+
       theme(legend.position = "none")

b <- ggplot(tidy_data$dat, aes(habitat, eggsize))+
       geom_violin(aes(col=habitat, fill=habitat))+
       theme(legend.position = "none")

c <- ggplot(tidy_data$dat, aes(climatic_zone, eggsize))+
       geom_violin(aes(col=climatic_zone, fill=climatic_zone))+
       theme(legend.position = "none")

d <- ggplot(tidy_data$dat, aes(zoogeography, eggsize))+
       geom_violin(aes(col=zoogeography, fill=zoogeography))+
       theme(legend.position = "none")

plot_grid(a,c,b,d, labels = "AUTO")
```



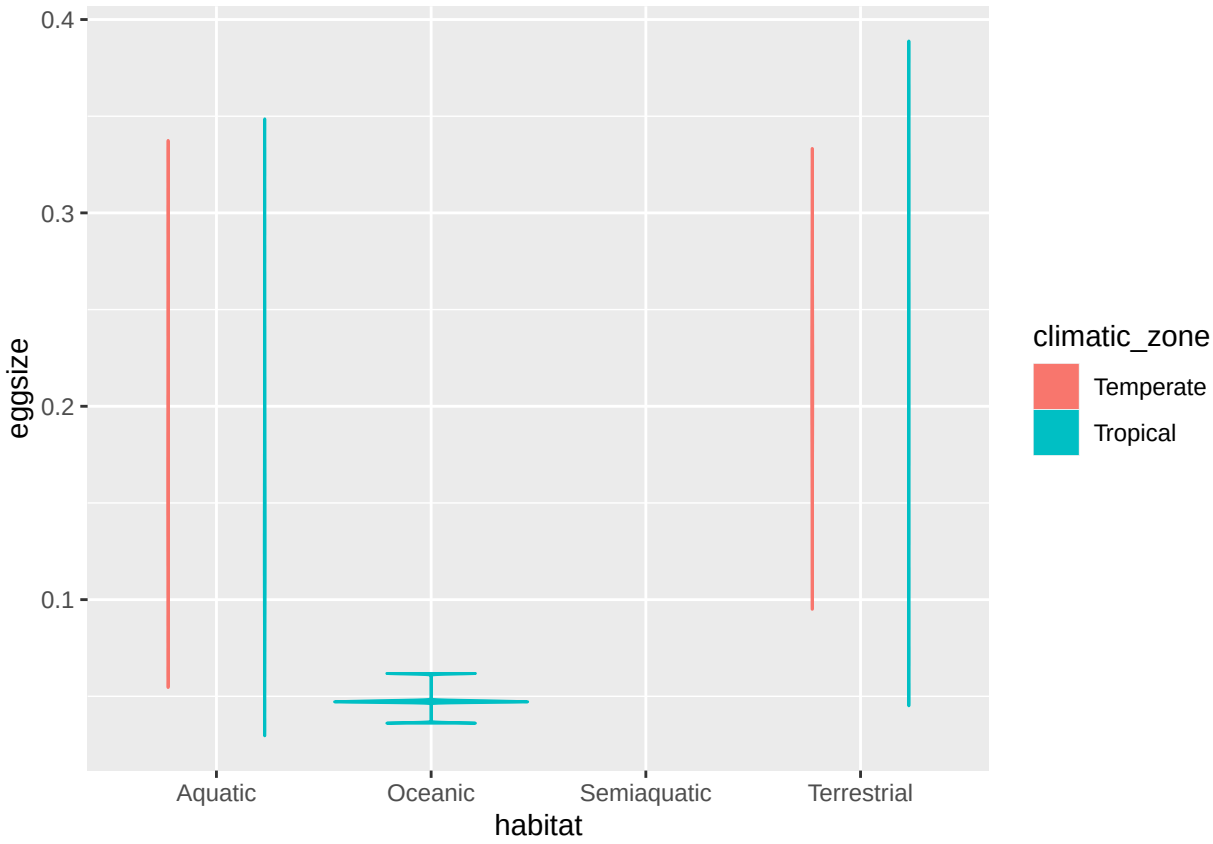
now inclucing the interaction of habitat with other variables

```
ggplot(tidy_data$dat, aes(diet, eggsize))+
       geom_violin(aes(col=habitat, fill=habitat))
```



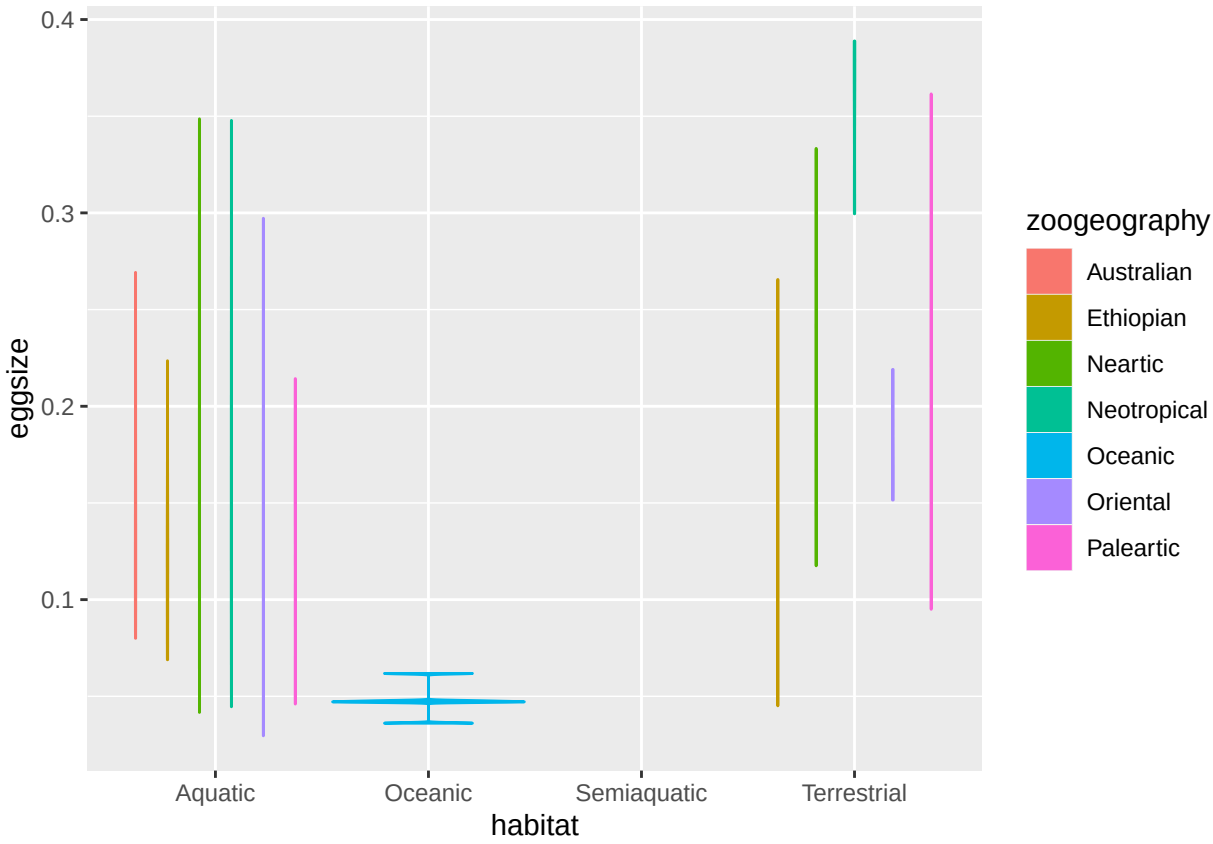
lacks combinations of crossed observation. Carnivores only occur in Aquatic and Oceanic habitats. So, you can't incluse those two variables in the same model

```
ggplot(tidy_data$dat, aes(habitat, eggsize))+
       geom_violin(aes(col=climatic_zone, fill=climatic_zone))
```



same problem here between habitat and climatic zone, you don't have complete crossing of these two factors

```
ggplot(tidy_data$dat, aes(habitat, eggsize))+
       geom_violin(aes(col=zoogeography, fill=zoogeography))
```



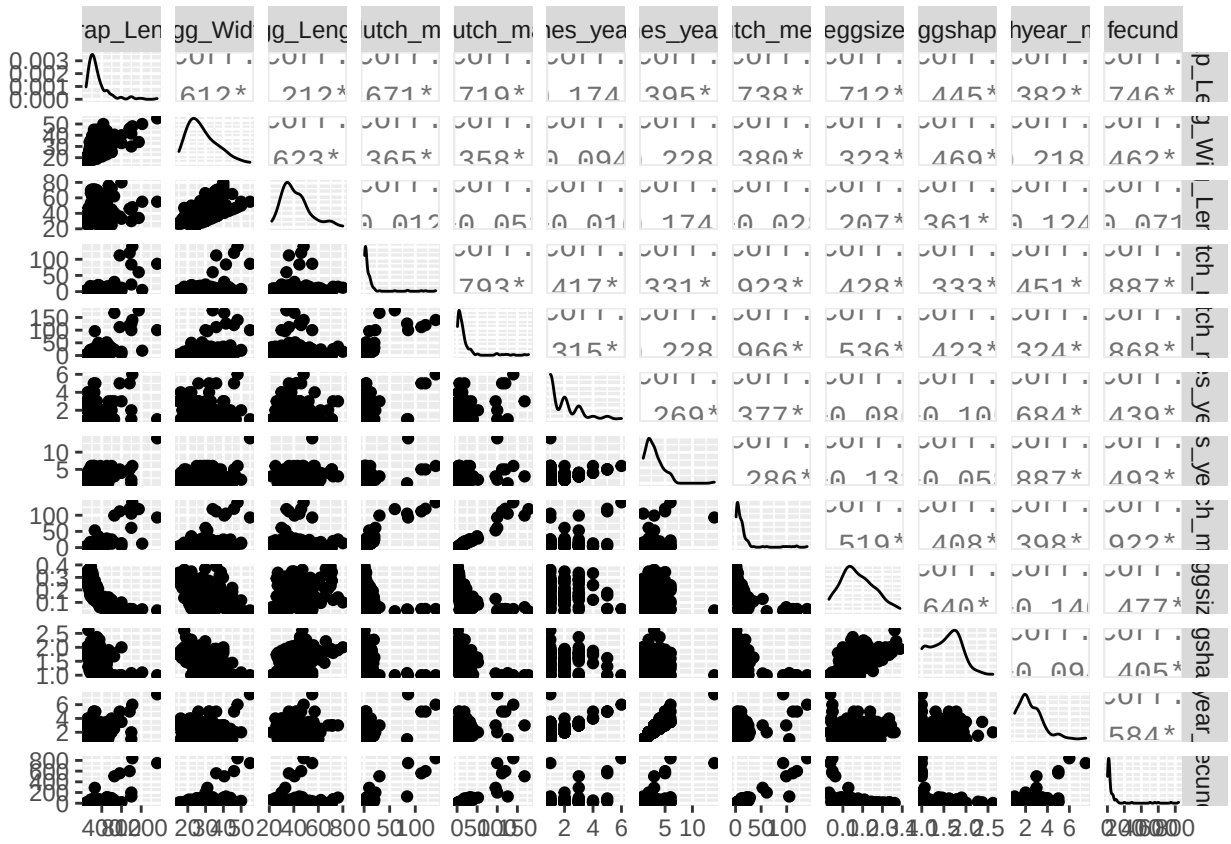
and again, the same problem with zoogeography, you don't have semiaquatic species in any zoogeographical zone.

> actually, the problem is with the "semiaquatic" level of the factor habitat, with only 3 species. You should collapse this level with another level if you want to continue using 'habitat' in your models. See forcats::fct_collapse

Understanding the distribution of the data

Continuous response data

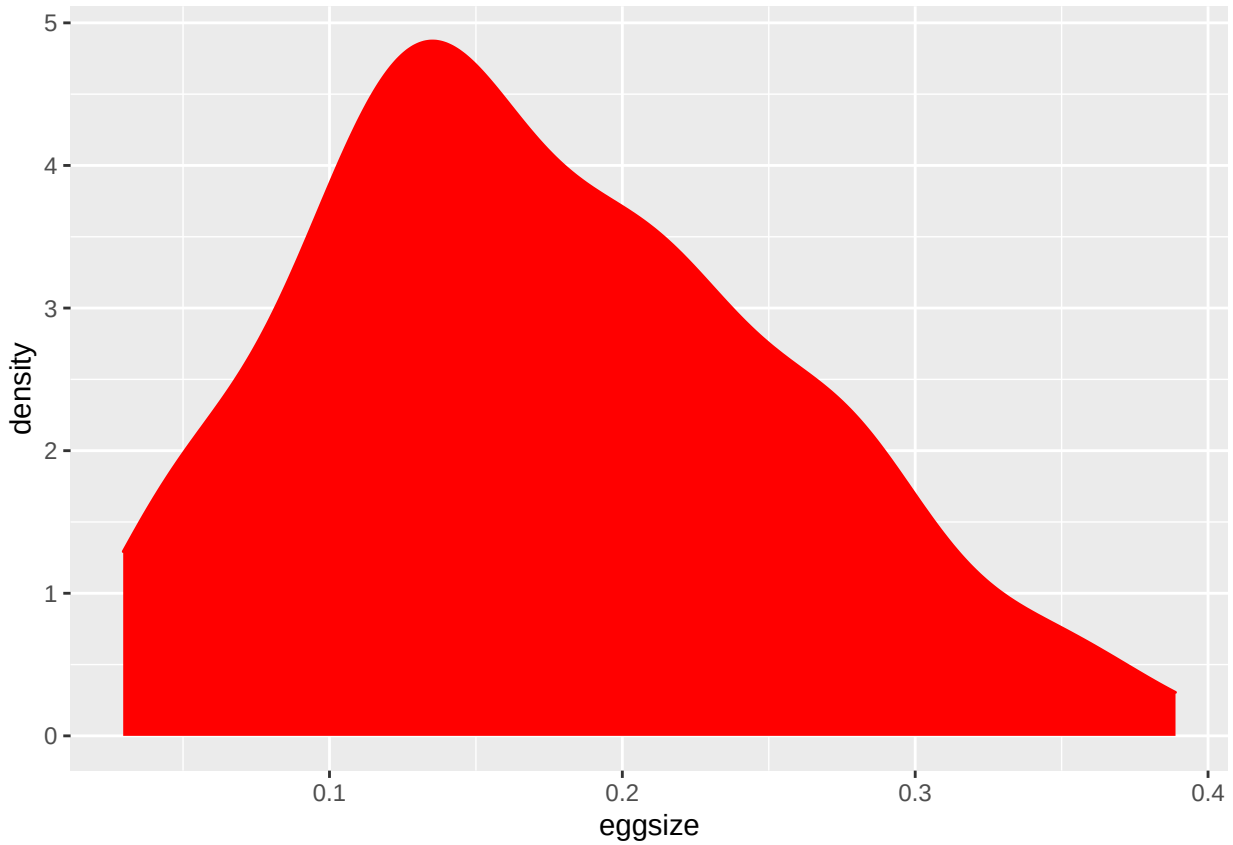
```
ggpairs(tidy_data$dat[,c(2, 5:15)])#with only the quantitative variables
```




```
range(tidy_data$dat$eggsize)
```

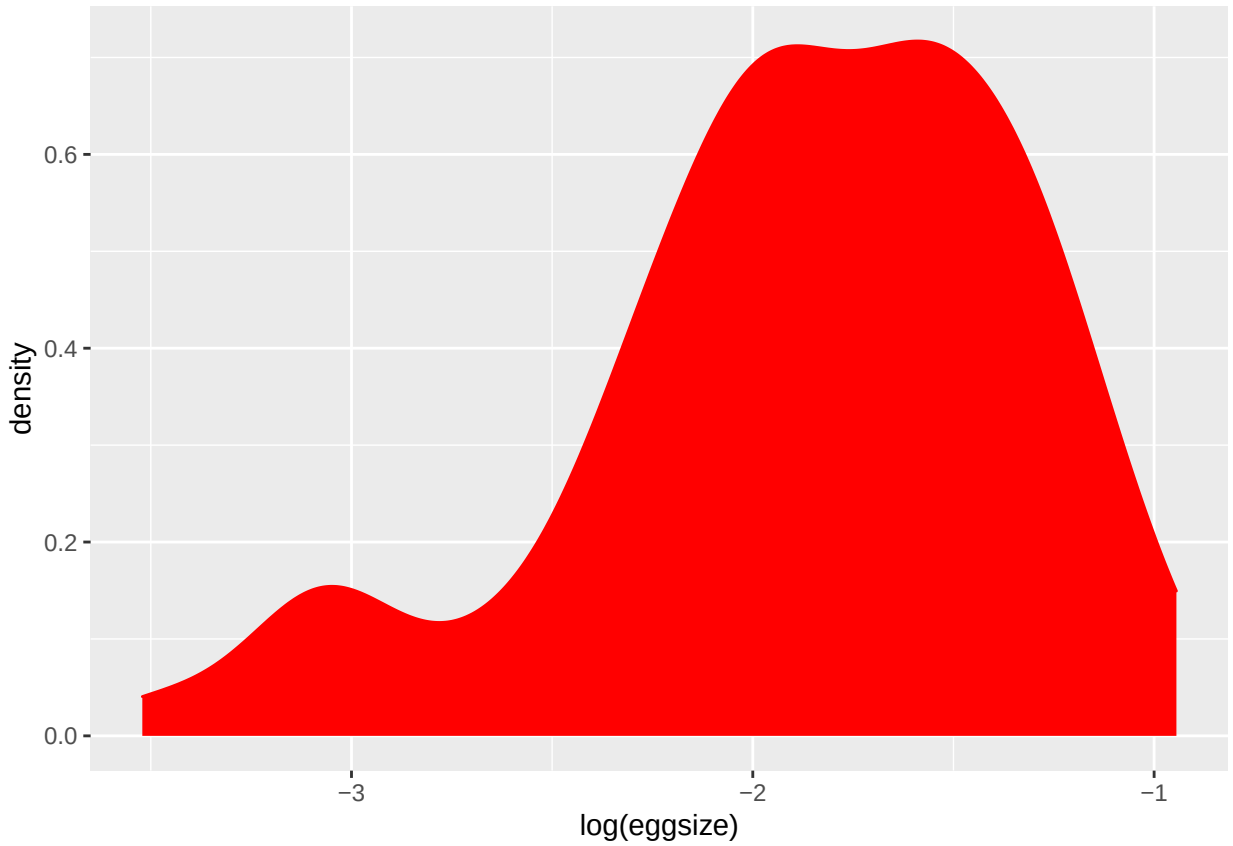
```
## [1] 0.02956522 0.38888889
```

```
ggplot(tidy_data$dat, aes(eggsize))+
       geom_density(col="red", fill="red")
```

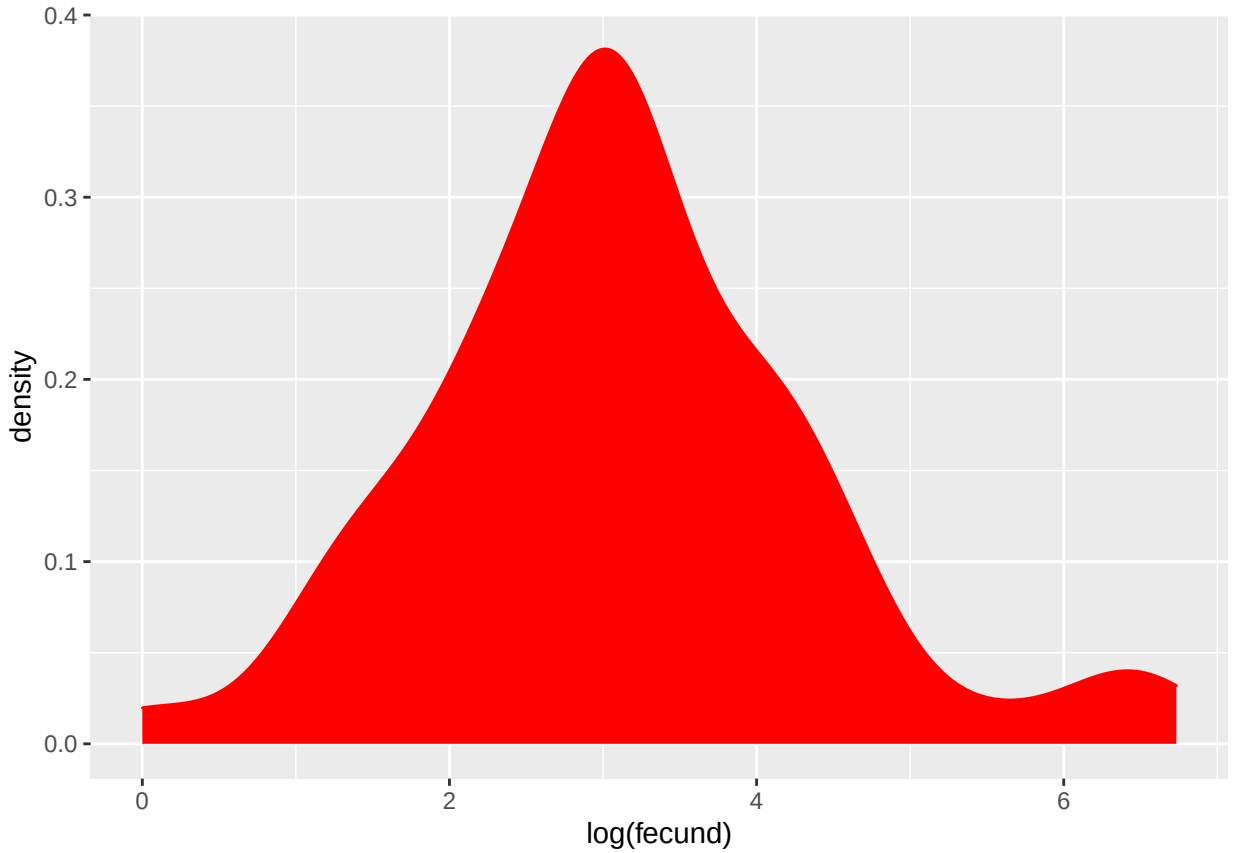


seems pretty Gaussian to me

```
ggplot(tidy_data$dat, aes(log(eggsize)))+
       geom_density(col="red", fill="red")#with log
```

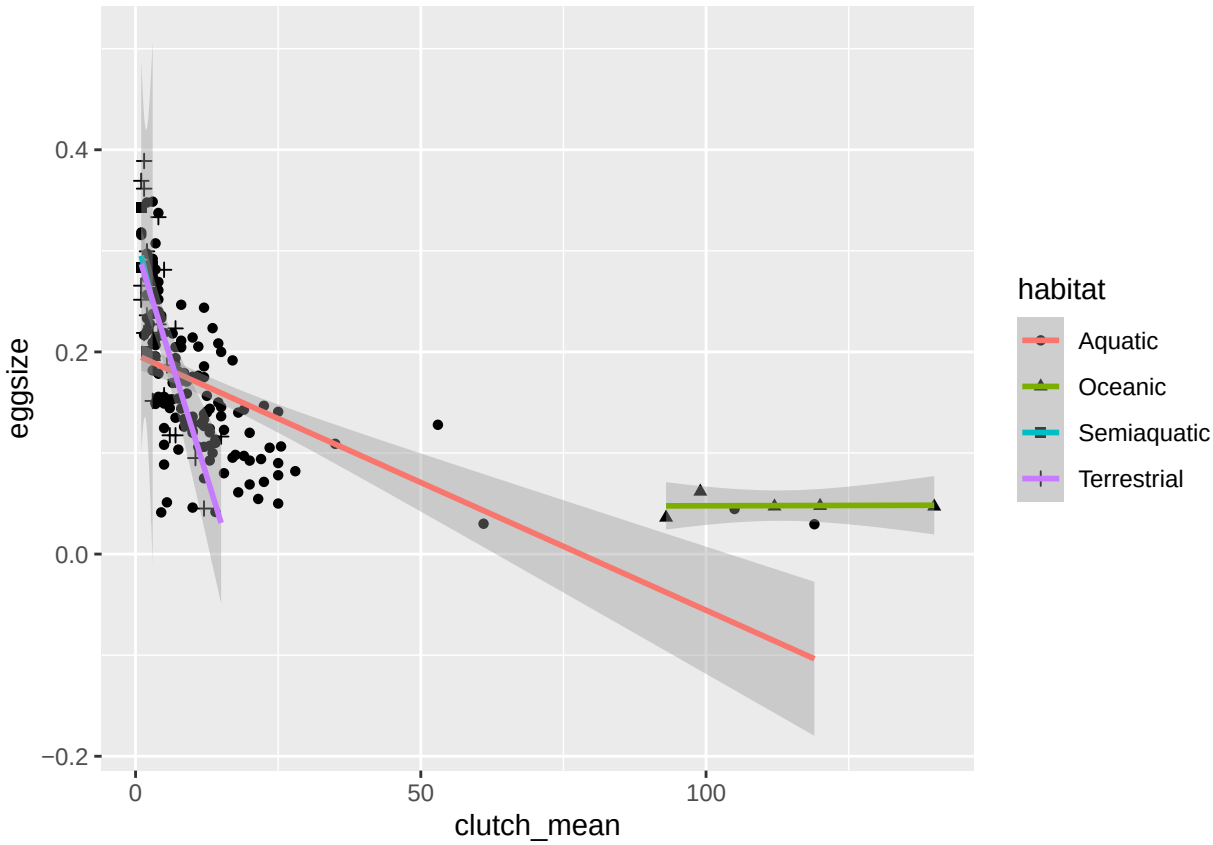



```
ggplot(tidy_data2$dat, aes(log(fecund)))+
       geom_density(col="red", fill="red")
```




```
ggplot(tidy_data$dat, aes(clutch_mean, eggsize))+
  geom_point(aes(shape=habitat)) +
  stat_smooth(method = "lm", aes(col=habitat))
```

```
## `geom_smooth()` using formula 'y ~ x'
```



Inferential data analysis

Building a PGLS for egg size, following Revell (2010)

```
#mod1 <- gls(eggsize ~  climatic_zone + zoogeography + habitat + diet + clutch_mean, data = tidy_data$d
```

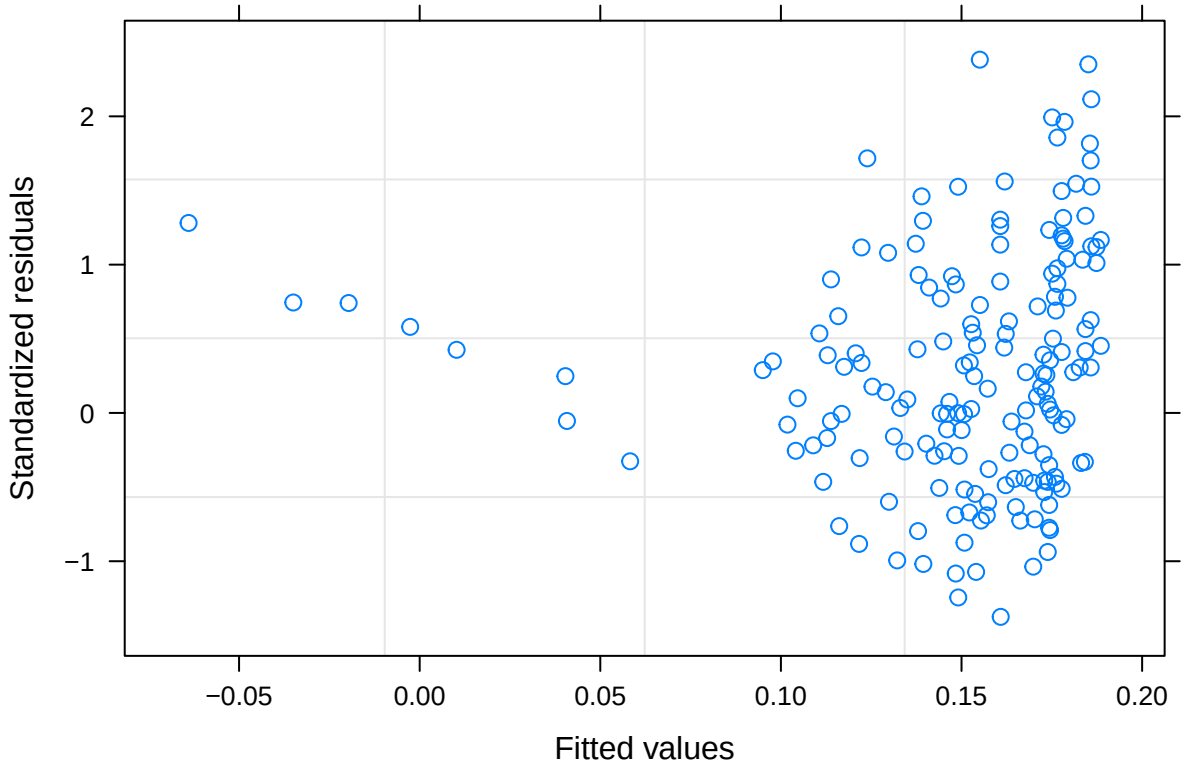
Uncomment this line above and run it. Including habitat makes the model a perfect fit, and returns an error – see why above

```
mod1_n <- gls(eggsize ~  climatic_zone + zoogeography + diet + clutch_mean, data = tidy_data$dat, correl
```

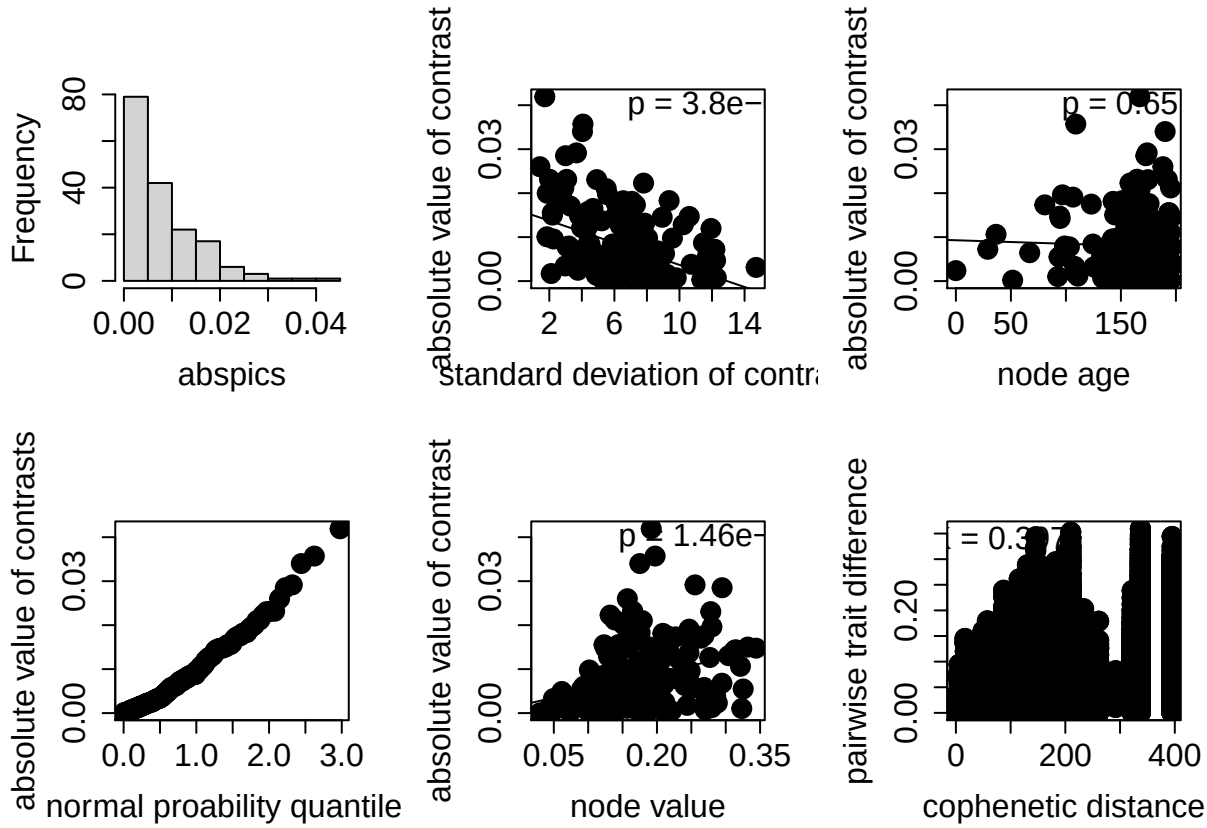
Now it works just fine

Model diagnostics

```
plot(mod1_n)#not good, suggest heteroceidasticity, I'd remove some predictor variables
```

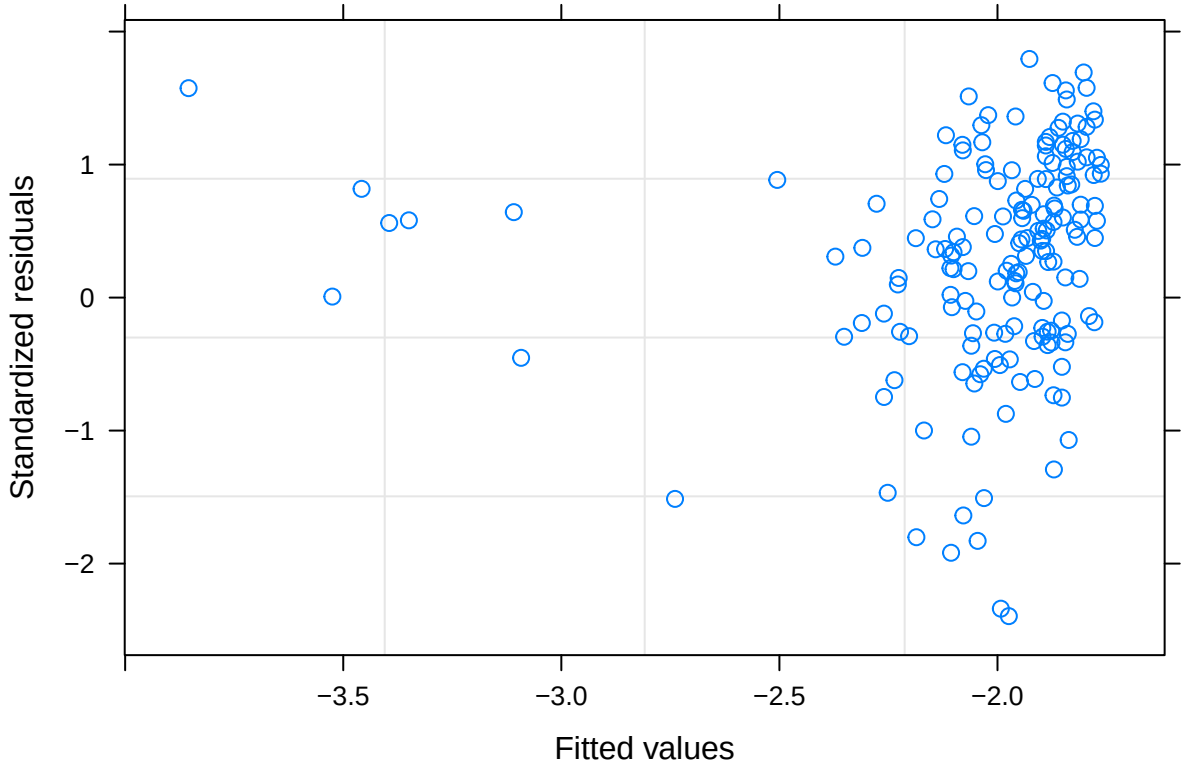



```
diagnostics(tidy_data$dat$eggsize,tidy_data$phy )
```



Trying log transformation

```
mod1_nlog <- gls(log(eggsize) ~  climatic_zone + zoogeography + diet + clutch_mean, data = tidy_data$da

plot(mod1_nlog)#not good, suggest heteroceidasticity. log transforming doesn't solve the problem
```



###Inference

```
summary(mod1_n)
```

```
## Generalized least squares fit by REML
##   Model: eggsize ~ climatic_zone + zoogeography + diet + clutch_mean
##   Data: tidy_data$dat
##         AIC       BIC   logLik
##   -428.1973 -388.0586 227.0987
##
## Correlation Structure: corPagel
##  Formula: ~1
##  Parameter estimate(s):
##    lambda
## 0.8286825
##
## Coefficients:
##                                Value  Std.Error   t-value p-value
## (Intercept)                0.18555364 0.05058301  3.668300  0.0003
## climatic_zoneTropical      0.00038288 0.01173744  0.032620  0.9740
## zoogeographyEthiopian     -0.01581689 0.04902075 -0.322657  0.7474
## zoogeographyNeartic       -0.00258257 0.04649313 -0.055547  0.9558
## zoogeographyNeotropical   -0.00762118 0.04476729 -0.170240  0.8650
## zoogeographyOceanic        0.00433869 0.07960488  0.054503  0.9566
## zoogeographyOriental      -0.02961000 0.04840410 -0.611725  0.5416
## zoogeographyPaleartic     -0.03767108 0.04887156 -0.770818  0.4419
```

```
## dietHerbivore           -0.02918845 0.02268577 -1.286642  0.2001
## dietOmnivore             0.00921903 0.01827596  0.504435  0.6146
## clutch_mean             -0.00160761 0.00037161 -4.326051  0.0000
##
##  Correlation:
##                         (Intr) clmt_T zggrpE zggrphyNr zggrphyNt zggrphyOc
## climatic_zoneTropical   -0.159
## zoogeographyEthiopian   -0.655 -0.055
## zoogeographyNeartic     -0.689  0.062  0.823
## zoogeographyNeotropical -0.661 -0.089  0.819  0.913
## zoogeographyOceanic     -0.365 -0.100  0.495  0.534     0.536
## zoogeographyOriental    -0.650 -0.115  0.865  0.860     0.856     0.543
## zoogeographyPaleartic   -0.666  0.044  0.838  0.872     0.837     0.507
## dietHerbivore           -0.207 -0.011  0.081  0.117     0.093     0.143
## dietOmnivore            -0.204 -0.002  0.126  0.094     0.066     0.107
## clutch_mean             -0.102  0.077 -0.015 -0.014    -0.034    -0.479
##                         zggrphyOr zggrpP dtHrbv dtOmnv
## climatic_zoneTropical
## zoogeographyEthiopian
## zoogeographyNeartic
## zoogeographyNeotropical
## zoogeographyOceanic
## zoogeographyOriental
## zoogeographyPaleartic    0.904
## dietHerbivore            0.123     0.118
## dietOmnivore             0.124     0.088  0.566
## clutch_mean             -0.057    -0.017 -0.120 -0.039
##
## Standardized residuals:
##        Min         Q1        Med         Q3        Max
## -1.3750449 -0.3047387  0.2481882  0.8452372  2.3820883
##
## Residual standard error: 0.08667411
## Degrees of freedom: 173 total; 162 residual
```

```
anova(mod1_n)#diet and clutch mean are significant
```

```
## Denom. DF: 162
##               numDF   F-value p-value
## (Intercept)       1 16.865510  0.0001
## climatic_zone     1  0.038219  0.8452
## zoogeography      6  1.585702  0.1544
## diet              2  3.026165  0.0513
## clutch_mean       1 18.714721  <.0001
```

```
R2(mod1_n)#35% of explanation
```

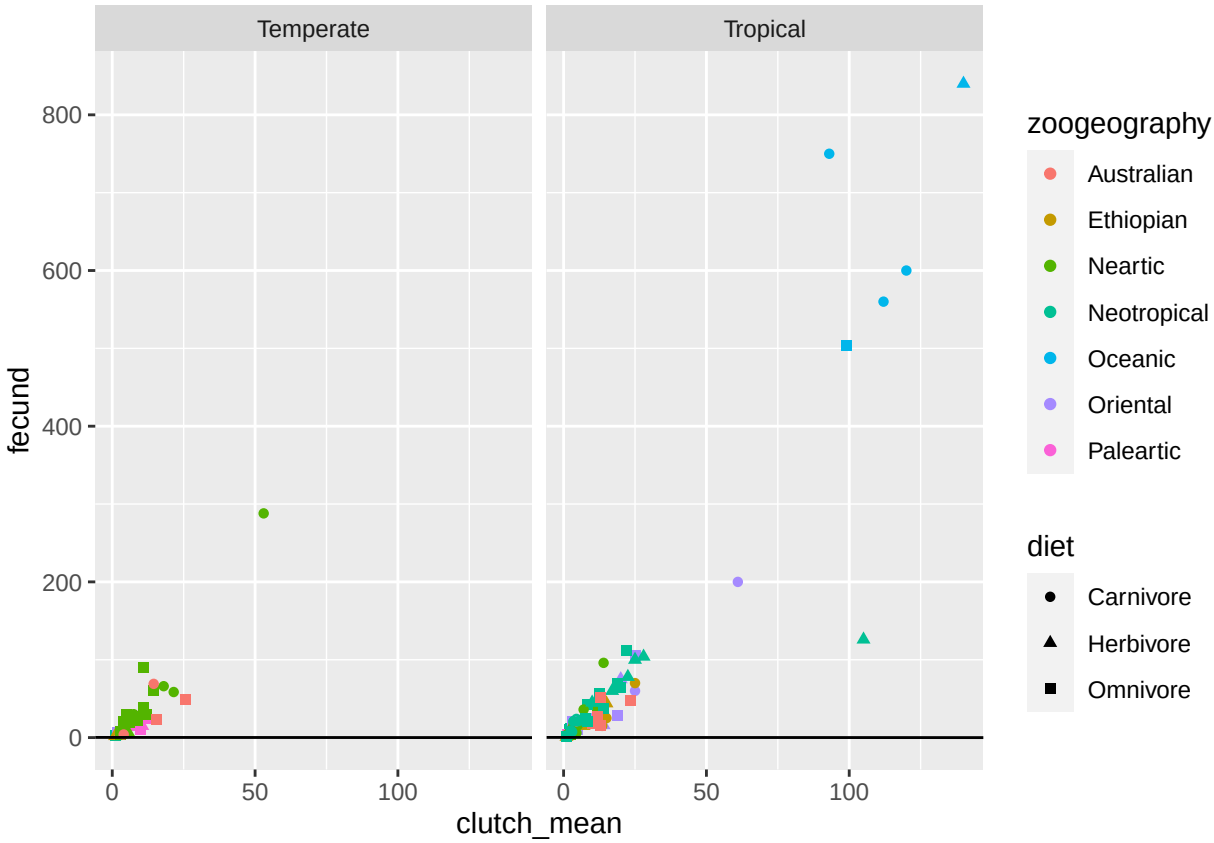
```
##    R2_lik  R2_resid   R2_pred
## 0.3507843 0.6214566 0.6270314
```

Visualizing the results

```
tidy_data$dat$predlm <-  predict(mod1_n)
```

```
ggplot(tidy_data$dat, aes(clutch_mean, fecund))+
       geom_point(aes(col=zoogeography, shape=diet))+
       geom_abline(slope = coef(mod1_n)[[11]], intercept = coef(mod1_n)[[1]])+#predicted by the PGLS
       facet_wrap(vars(climatic_zone))
```

```
## Warning: Removed 55 rows containing missing values (geom_point).
```

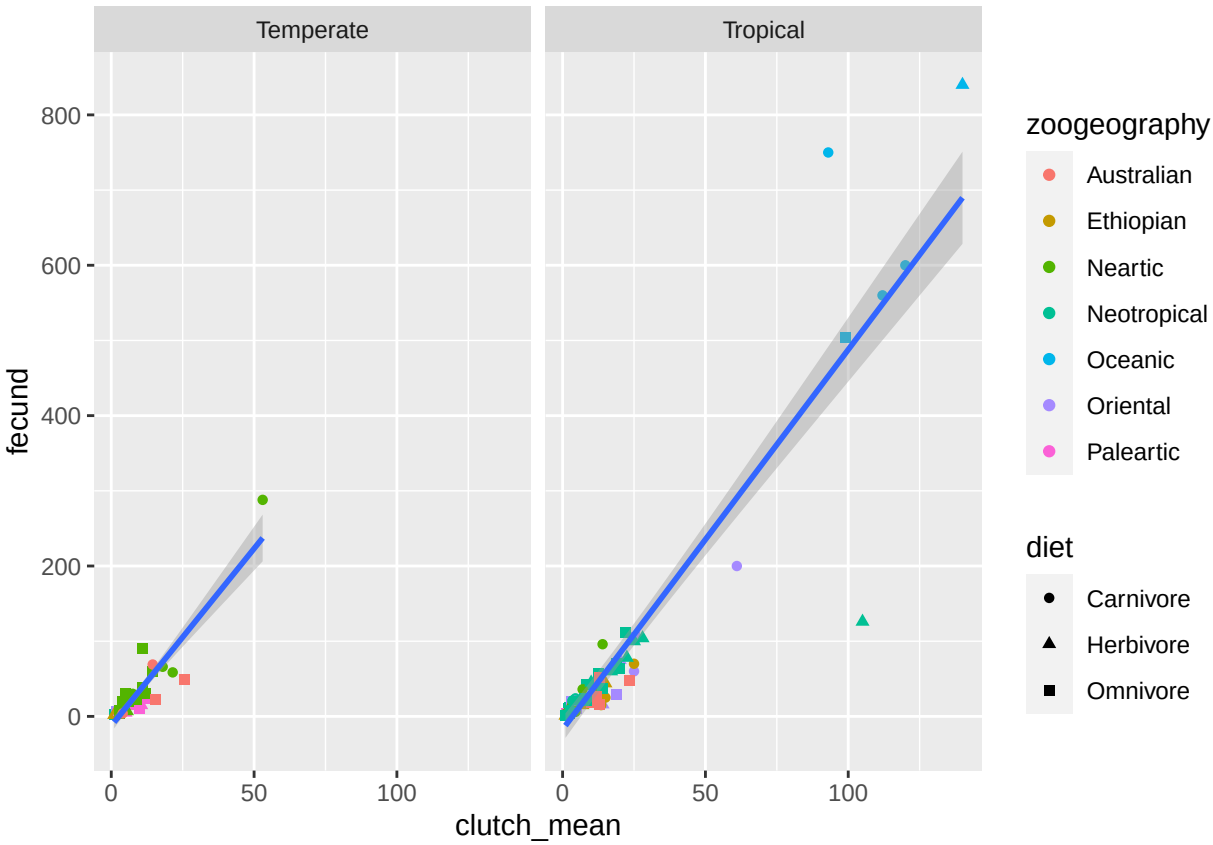



```
ggplot(tidy_data$dat, aes(clutch_mean, fecund))+
       geom_point(aes(col=zoogeography, shape=diet))+
       stat_smooth(method = "lm")+#linear model
       facet_wrap(vars(climatic_zone))
```

```
## `geom_smooth()` using formula 'y ~ x'
```

```
## Warning: Removed 55 rows containing non-finite values (stat_smooth).
```

```
## Warning: Removed 55 rows containing missing values (geom_point).
```



If you want a effect size measure, assuming BM though, results will be different

```
summary(geomorph::procD.pgls(eggsize ~  climatic_zone + zoogeography + diet + clutch_mean, data = tidy_
```

```
##
## Preliminary Model Fit...
##
##
## Coefficients estimation: 1000 permutations.
##   |                                                                                                 |
```

```
## Total         172 0.0210539
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## Call: procD.lm(f1 = f1, iter = iter, seed = seed, RRPP = TRUE, SS.type = SS.type,
##     effect.type = effect.type, int.first = int.first, Cov = Cov,
##     data = data, print.progress = print.progress)
```

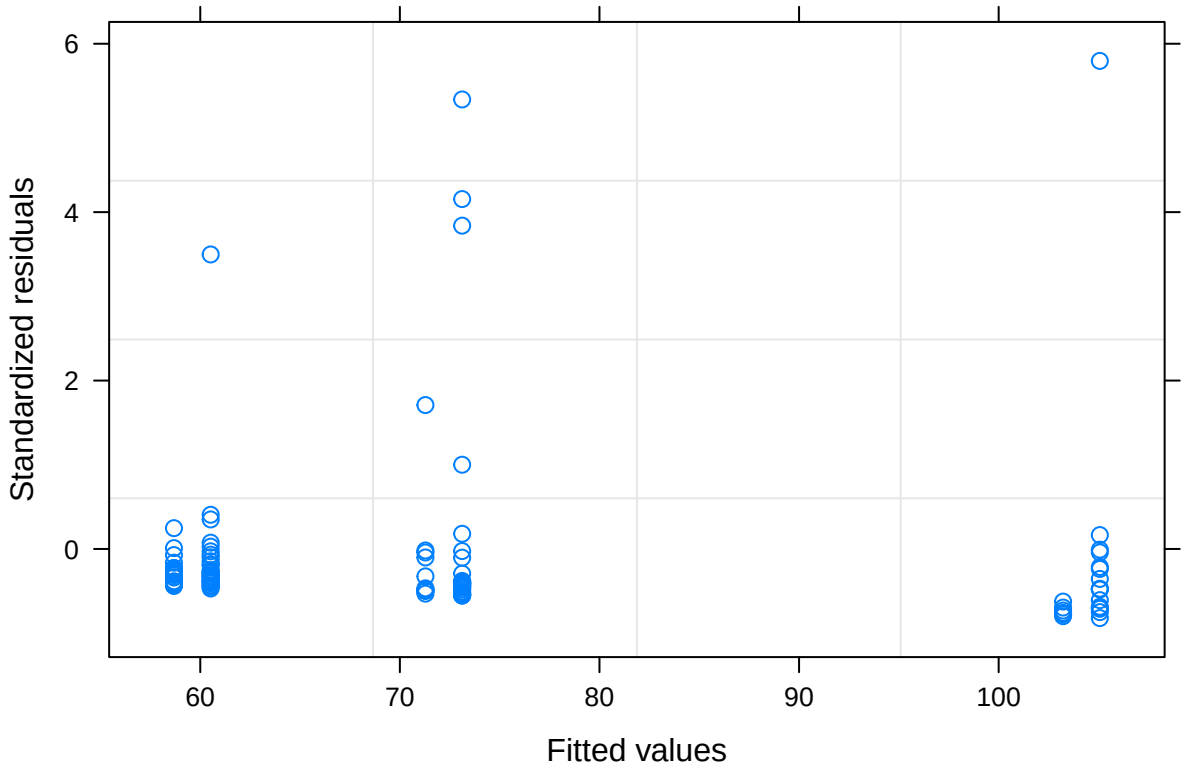
Model building for the fecundity

```
mod_fecund <- gls(fecund ~  climatic_zone +  diet, data = tidy_data2$dat, correlation = corPagel(1, tid
```

Including zoogeography in the model returns an error, see explanation why down below.

Diagnostics

```
plot(mod_fecund)
```



Inference

```
anova(mod_fecund)#zoogeography significant
```

```
## Denom. DF: 114
##                numDF   F-value p-value
## (Intercept)        1 2.1278144  0.1474
## climatic_zone      1 0.0322028  0.8579
```

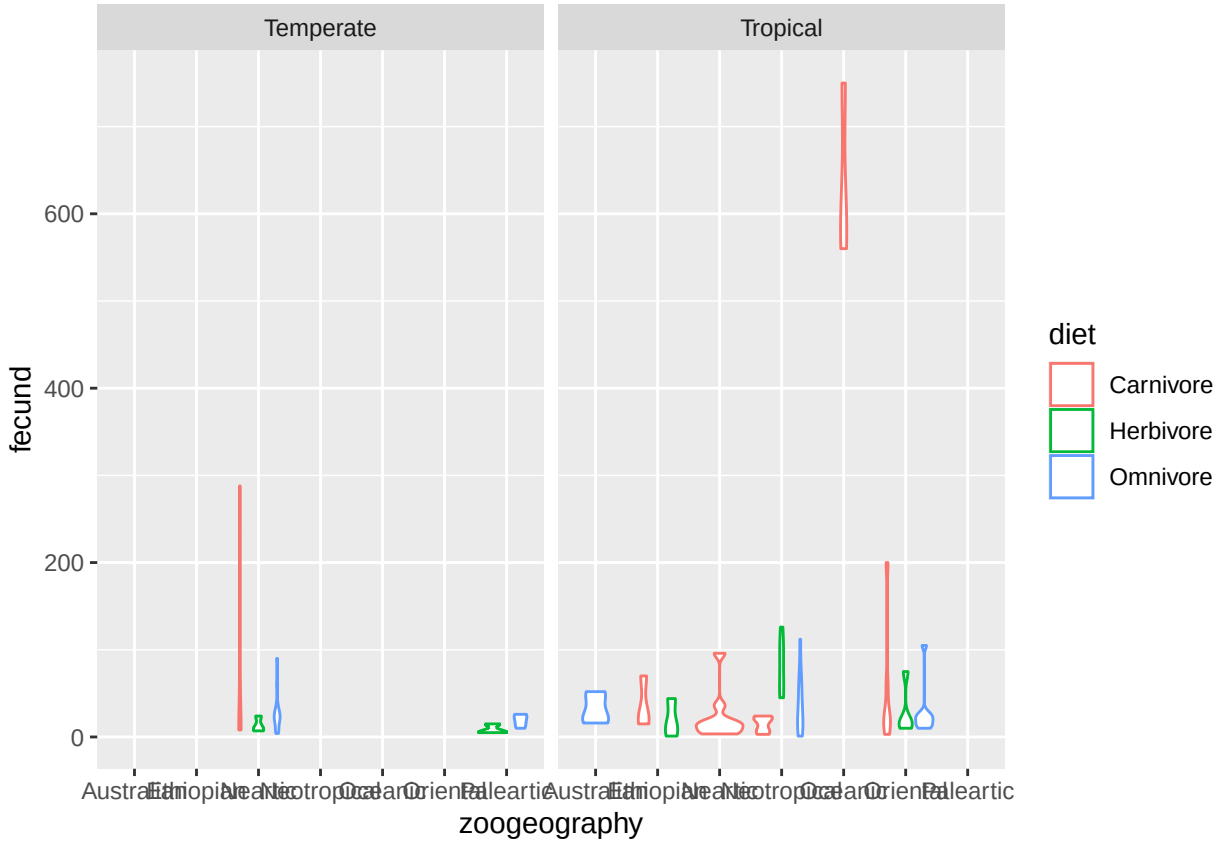
```
## diet              2 1.2479105  0.2910
```

```
R2(mod_fecund)#95% of explanation
```

```
##    R2_lik  R2_resid   R2_pred
## 0.8744505 0.8093160 0.8489848
```

Visualizing results

```
ggplot(tidy_data2$dat, aes(zoogeography, fecund))+
       geom_violin(aes(col=diet))+
       facet_wrap(vars(climatic_zone))
```



Again you have certain factor levels without replicates in both temperate and tropical. This makes very much sense since some zoogeographical areas only exist in the temperate realm, while other are fully tropical. So consider removing either of those factors from your model.