Novel Code

Individual growth rates and size at metamorphosis increase with watershed area in a salamander.

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Simulating Growth Data

To start simulating fake growth data we included 50 initial body sizes drawn from a random uniform distribution with a minimum of 35 mm and a maximum of 115 mm. We then randomly assigned between 5 and 400 days between all initial sizes and five subsequent capture events for each individual. To estimate growth over time we used the Von Bertalanffy (VB) growth function for one individual with at least two captures (Fabens 1965, Eaton and Link 2011):

$$S_t = S_{t-1} + (a - S_{t-1})(1 - e^{-k\Delta t})$$

Where S = size at capture, t = time step, a = asymptotic size, and k = growth rate.

We set $a = 120$ and $k = 0.20$ in order to simulate fake growth data over time for each individual. This allowed us to compare estimated model parameter values to the given ones above to ensure our model was correct.

We also simulated random watershed areas for all individuals with mean = 1.5 and SD = 1, in order to estimate the effect of watershed area on k.

```r
# generate 50 initial sizes with min = 35, max = 115
S1 <- runif(n=50, min=35, max=117)

# generate random time steps (between 5-400 days) for all 50 individuals across 5 captures
t1 <- sample(5:400, 50, replace=FALSE)
t2<-sample(5:400, 50, replace=FALSE)
t3 <- sample(5:400, 50, replace=FALSE)
t4<-sample(5:400, 50, replace=FALSE)
t5 <- sample(5:400, 50, replace=FALSE)

# turn vectors for initial size and time steps into a dataframe
growth_data<-data.frame(t1,t2,t3,t4,t5,S1)

# set asymptotic size and growth rate parameter to simulate subsequent capture sizes
a = 120
k = 0.20

# generate size at capture for five additional capture occasions for all 50 individuals
growth_data <- growth_data %>%
  mutate(S2 = (S1 + (a-S1)*(1-exp(-k*(t1/365))))) %>%
  mutate(S3 = (S2 + (a-S2)*(1-exp(-k*(t2/365))))) %>%
  mutate(S4 = (S3 + (a-S3)*(1-exp(-k*(t3/365))))) %>%
  mutate(S5 = (S4 + (a-S4)*(1-exp(-k*(t4/365))))) %>%
  mutate(S6 = (S5 + (a-S5)*(1-exp(-k*(t5/365)))))

# simulating fake watershed areas for all individuals
area.km2<-abs(rnorm(n=50, mean=1.5, sd=1))
# scale and center area
area <- as.vector(scale(area.km2))

# add watershed area to growth dataframe
growth_data$area.km2 <- area.km2
growth_data$area <- area

# view fake growth data and time steps
head(growth_data)
```

```
##    t1  t2  t3  t4  t5       S1       S2       S3        S4        S5        S6
## 1  27  54 301  34 178 69.44781 70.19020 71.64243  78.99512  79.75197  83.49217
## 2 259 249 279 368 127 60.72553 68.56799 75.12762  81.48893  88.52159  90.63766
## 3 210 389 329  25 153 86.80538 90.41346 96.09306 100.03672 100.30832 101.89188
## 4 260 390 200  37 298 50.30381 59.55827 71.18775  76.25435  77.13232  83.59047
## 5  54 308  51 200 192 93.71809 94.48435 98.44679  99.04076 101.21628 103.09203
## 6 264 253  72 233 333 79.73501 85.15796 89.66826  90.84161  94.33646  98.61680
##   area.km2       area
## 1 1.571352 -0.2800117
## 2 3.139215  1.5192537
## 3 1.986909  0.1968782
## 4 2.206834  0.4492613
## 5 3.287679  1.6896303
## 6 2.435994  0.7122438
```

```
# separate out encounter history
y <- as.matrix(growth_data[,6:11])

# separate out days since last capture
dslc <- as.matrix(growth_data[,1:5])

# set number of individuals
NIND <- nrow(growth_data)
```

Organizing Data to Run Model in JAGS

We fit a Bayesian VB growth model using Markov chain Monte Carlo (MCMC) methods in JAGS (Plummer 2003).

```
# format data for jags

# NIND = number of individuals
# y = SVL (size) measurements
# f = first capture occasion
# l = last capture occasion

### functions for data manipulation
# determine the occasion of the first capture of each individual
```

```
get.first <- function(x){
  # a function to identify the time period of the first capture from an encounter history matrix
  return( min(which( x != 0 ) ) )
}

# get last occasion of capture for each individual
get.last <- function(x){
  # a function to identify the time period of the first capture from an encounter history matrix
  return( max(which( x != 0 ) ) )
}


fall <- apply( y, 1, get.first )
f <- fall # vector of first cap time step

lall <- apply(y, 1 ,get.last)
l <- lall # vector for which time period has last capture

### get ready to run JAGS
# Define a list of data to be passed to JAGS
growth.data <- list( y = y, NIND = NIND, f= f, l = l, dslc = dslc, area=area)

# set parameters (measurement error, asymptotic size,
# transformed growth rate parameter, effect of area on k) to track in JAGS
growth.parms <- c("tau.eps","a", "mean.k", "area.k")

# set initial values for parameters
sal.inits <- function(){
  list(
    tau.eps = runif( 1, 0, 1 ),
    mean.k = runif( 1, -5, 5 ),
    a = runif( 1, 80, 130 ),
    area.k = runif( 1, -5, 5 )
  )
}

# set up for MCMC run
ni <- 5000 # number of iterations
nt <- 5 # thinning number, e.g. only keeping out of 5 values
nb <- 3000 # burn in
nc <- 3 # number of chains
# total iterations kept = (ni/nb)/nt*nc
```

JAGS Model Script

To run our Bayesian VB growth model we set priors and defined the likelihood below. This initial (simplified) model includes the linear effect of watershed area on k. For this initial model, k is calculated across the entire year equally. We also estimate a parameter, *tau.eps*, that accounts for measurement error.

```
model {

  # Prior Specification (Growth Model)
  a ~ dunif(80,130) # uniform prior for asymptotic size with minimum of 80 and maximum of 130

  tau.eps ~ dgamma(0.001, 0.001)
  # gamma prior for measurement error with shape = 0.001, rate = 0.001

  sd.eps <- 1/sqrt(tau.eps) # measurement error sd

  mean.k ~  dunif(-12,0)
  # coefficient for the log of the active growth rate parameter (limits k between 0 and 1)

  area.k ~ dnorm(0,0.01) # normal prior for the effect of area on mean k

  # Likelihood
  for (i in 1:NIND){ # Loop through individuals
    for (t in f[i]:f[i]){ # First survey

      y[i,t] ~ dnorm(H[i,t],tau.eps) # Measured size is the true size +/- measurement error

      H[i,t] ~ dunif(35,115) # Prior: Expected size at first capture (between 30 and 120)
    }

    for (t in (f[i]+1):l[i]){ # Loop through surveys
      # (1st capture to last survey date for each individual)

      y[i,t] ~ dnorm(H[i,t],tau.eps) # measured size is a fnct of
      # true size plus measurement error

      # Expected size at time t = H.m

      H[i,t] <- H[i,t-1]+(a-H[i,t-1])*

        (1-exp(-k[i,t]*(dslc[i,t-1]/365)))

      log(k[i,t]) <- mean.k + area.k*area[i]

      # log-link function to allow active k to vary in relation to area

    }
  }

}
```

Run Model and View Results

We used the package R2jags (Su and Yajima 2021) to run our JAGS model, and the package bayesplot (Gabry and Mahr 2022) to check for model convergence and view posterior estimates, all in RStudio (Version 1.4.1716; R Development Core Team 2021).

Posterior estimates for a should be around 120 and estimates for k should be around 0.20 if model is set up correctly.

```r
setwd("C:/Users/maddy/Box Sync/HB/Data/growth/")

# run model in R2jags
vbgm.result.area <- R2jags::jags(data=growth.data,
                                 inits = sal.inits,
                                 parameters.to.save=growth.parms,
                                 model.file="vbgm/jags/areamodel.txt",
                                 n.chains=nc,
                                 n.iter=ni,
                                 n.burnin=nb,
                                 n.thin=nt)
```

```
## module glm loaded

## Compiling model graph
##    Resolving undeclared variables
##    Allocating nodes
## Graph information:
##    Observed stochastic nodes: 300
##    Unobserved stochastic nodes: 54
##    Total graph size: 2648
##
## Initializing model
```

```r
# view summary table
vbgm.result.area$BUGSoutput$summary
```

```
##                   mean           sd          2.5%           25%           50%
## a         1.201999e+02 4.611930e-02  1.201134e+02  1.201688e+02  1.201983e+02
## area.k   -1.079936e-05 5.983945e-04 -1.210018e-03 -4.003472e-04 -6.529405e-06
## deviance -6.893532e+02 1.186867e+01 -7.103730e+02 -6.977718e+02 -6.895657e+02
## mean.k   -1.614100e+00 1.261808e-03 -1.616631e+00 -1.614966e+00 -1.614058e+00
## tau.eps   1.707596e+02 1.546906e+01  1.418648e+02  1.600546e+02  1.699286e+02
##                    75%         97.5%     Rhat n.eff
## a         1.202315e+02  1.202929e+02 1.000429  1200
## area.k    3.989197e-04  1.181098e-03 1.000603  1200
## deviance -6.815861e+02 -6.648273e+02 1.001413  1200
## mean.k   -1.613240e+00 -1.611647e+00 1.004775   560
## tau.eps   1.811260e+02  2.028490e+02 1.002558  1200
```

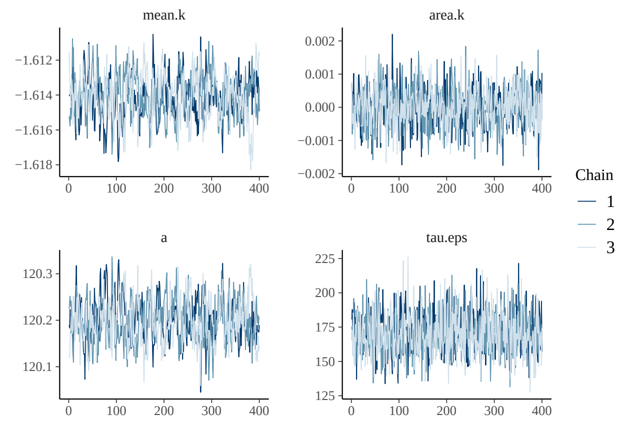
```r
# a parameter estimate should be ~ 120
# area.k parameter estimate should be ~  0
# we want all Rhat values < 1.05

# get an un-transformed estimate of k (should be ~ 0.20 if model worked)
mean.k<-exp(vbgm.result.area$BUGSoutput$sims.list$mean.k)
quantile(mean.k, 0.50) # mean k
```

```
##       50%
## 0.1990782
```

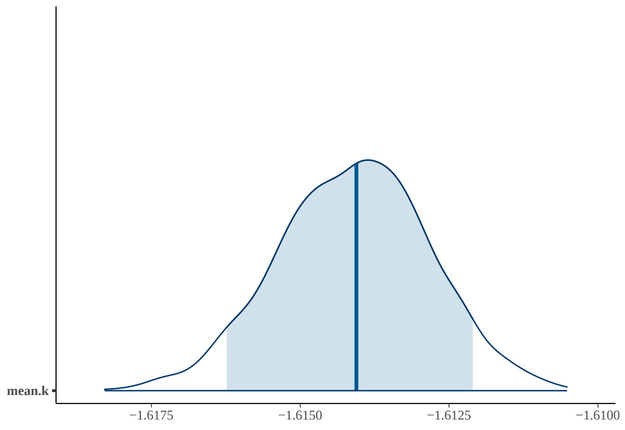
```
# standard deviation of measurement error
tau.eps<-exp(vbgm.result.area$BUGSoutput$sims.list$tau.eps)
mean(1/sqrt(tau.eps)) # should be pretty close to 0
```

```
## [1] 2.480478e-31
```

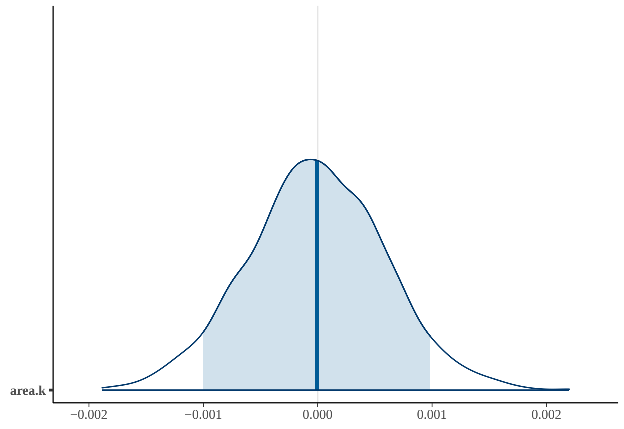
```
# view traceplots to see if chains converged
posterior <- as.array(vbgm.result.area$BUGSoutput$sims.array)
bayesplot::mcmc_trace(posterior, pars = c("mean.k", "area.k","a", "tau.eps"))
```



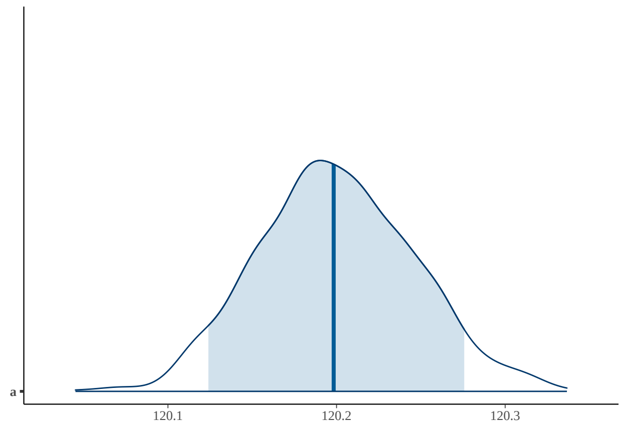
```
# view posterior uncertainty intervals
mcmc_areas(posterior,
           pars = c("mean.k"),
           prob = 0.9) # 90% credible interval
```



```
mcmc_areas(posterior,
           pars = c("area.k"),
           prob = 0.9) # 90% credible interval
```



```
mcmc_areas(posterior,
           pars = c("a"),
           prob = 0.9) # 90% credible interval
```



Model Validation

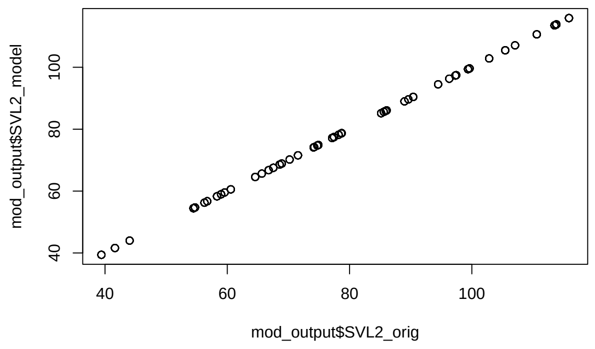
We calculated a Bayesian p-value to make sure our observed data matched our model output.

```
#### posterior predictive check ####
# comparing observed data to posterior predictive distribution
# bayesian p -value = probability that the replicated data could be
# more extreme than the observed data

# posterior distributions
a_output <- vbgm.result.area$BUGSoutput$sims.list$a
area_k_output <- vbgm.result.area$BUGSoutput$sims.list$area.k
mean_k_output <- vbgm.result.area$BUGSoutput$sims.list$mean.k

# create data frame with posterior distributions for all parameters
mod_output <- data.frame(a_output, area_k_output, mean_k_output)

# add in first time step SVL and time to next capture, in addition to discharge co-variates on k
mod_output$original_SVL <- growth_data$S1
```

```r
mod_output$days <- growth_data$t1
mod_output$area <- growth_data$area

# calculate size at next time step based on posterior iterations
mod_output <- mod_output %>%
  mutate(k = exp(mean_k_output + area_k_output*area )) %>%
  mutate(SVL2_model = original_SVL + (a_output - original_SVL)*(1-exp((-k*(days/365)))))

# add in original size at next time step to df
mod_output$SVL2_orig <- growth_data$S2

head(mod_output)
```

```
##   a_output area_k_output mean_k_output original_SVL days       area         k
## 1 120.2113 -0.0003649099     -1.615189     69.44781   27 -0.2800117 0.1988734
## 2 120.2244 -0.0003022885     -1.615434     60.72553  259  1.5192537 0.1987132
## 3 120.1868 -0.0006428329     -1.613985     86.80538  210  0.1968782 0.1990674
## 4 120.1339  0.0007311386     -1.613502     50.30381  260  0.4492613 0.1992542
## 5 120.2778  0.0010810258     -1.616233     93.71809   54  1.6896303 0.1990087
## 6 120.2009 -0.0004563376     -1.615088     79.73501  264  0.7122438 0.1988086
##   SVL2_model SVL2_orig
## 1   70.18913  70.19020
## 2   68.55051  68.56799
## 3   90.41779  90.41346
## 4   59.54386  59.55827
## 5   94.48867  94.48435
## 6   85.15483  85.15796
```

```r
# calculate the proportion of simulated values that are equal to or greater than the original dataset
mod_output <- mod_output %>%
  mutate(greater_than = if_else(SVL2_model >= SVL2_orig, 1,0))

# plot original size compared to modeled size
# want all points on or near 1:1 line
plot(mod_output$SVL2_orig, mod_output$SVL2_model)
```



```
# calculate bayesian p-value
sums<-mod_output%>%
  dplyr::count(greater_than)
sums
```

```
##   greater_than   n
## 1            0 593
## 2            1 607
```

```
sums$n[2]/1200
```

```
## [1] 0.5058333
```

```
# bayesian p-value should be close to 0.5 in order to validate the model
```

Plot Growth Trajectory from Parameter Estimates

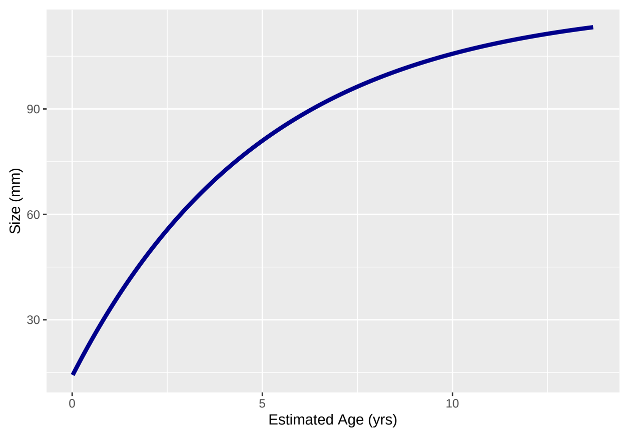
In order to plot growth over time based on posterior parameter estimates we also had to define the initial size of animals as 14 mm based on historic observations. In order to do this we used a different organization of the VB growth function to plot growth over time:

$$S_t = a(1 - be^{-kt})$$

Where S_t = size at age t, a = asymptotic size estimated from model, hatchling size = *a(1-b)*, and k = growth rate parameter estimated from model.

```
# set initial size at time 0
init.size <- 14

# get parameter estimates from model for a and k
mean.a<-vbgm.result.area$BUGSoutput$mean$a
mean.k <-vbgm.result.area$BUGSoutput$mean$mean.k

# create a dataframe with a column for days since hatching
days_vec <- seq(5,5000,by=1)
growth_traj <- data.frame(days_vec)

# project growth across each time step given parameter estimates
growth_traj <- growth_traj%>%
  mutate(k =exp(mean.k))%>%
  mutate(a = mean.a)%>%
  mutate(init.size = init.size)%>%
  mutate(size = init.size + (a-init.size)*(1-exp(-k*(days_vec/365))))

# plot size on y axis and age on x axis
ggplot(data = growth_traj,  aes(x=days_vec/365, y=size)) +
  # set x axis to yrs instead of days
  geom_line(size=1.5, color="darkblue")+
  labs(y="Size (mm)", x = "Estimated Age (yrs)")
```

```
## Warning: Using `size` aesthetic for lines was deprecated in ggplot2 3.4.0.
## i Please use `linewidth` instead.
```



Final JAGS Model Script

Below is the script for our final VB growth model, which includes added complexity (compared to the model described above) when estimating parameters to describe the effect of covariates on *k*. For example, this model includes the relationship between *k* and watershed area, in addition to the effect of fish presence and stream on *k*, and separates out active season verse inactive season growth rates.

```
model {
  # Prior Specification
  a ~ dunif(80,130) # uniform prior on asymptotic size, min = 80, max = 130

  tau.eps ~ dgamma(0.001, 0.001) # gamma prior on measurement error with
  # shape = 0.001, rate = 0.001

  sd.eps <- 1/sqrt(tau.eps) # measurement error sd

  mean.k.active ~  dunif(-12,0)
  # coefficient for the log of the active growth rate parameter (limits k between 0 and 1)

  area.k.active ~ dnorm(0,0.01) # normal prior on linear effect of area on mean k during summer

  fish.k.active ~ dnorm(0,0.01) # normal prior on the effect of fish on k

   for(s in 1:STREAMS){
    k[s] ~ dnorm(0,0.01) # allowing k to vary by stream name
  }

  mean.k.inactive ~ dunif(-12,0)
  # coefficient for the log of the active growth rate parameter (limits k between 0 and 1)

  # Likelihood
  for (i in 1:NIND){ # Loop through individuals

    for (t in f[i]:f[i]){ # First survey

      y[i,t] ~ dnorm(H[i,t],tau.eps) # Measured size is the true size +/- measurement error

      H[i,t] ~ dunif(30,120) # Prior: Expected size at first capture
    }

    for (t in (f[i]+1):l[i]){ # Loop through surveys (1st capture to last
      # survey date for each individual)

      y[i,t] ~ dnorm(H[i,t],tau.eps) # measured size is a fnct of true size plus measurement error

      # Expected size at time t = H.m
      H[i,t] <- H[i,t-1]+(a-H[i,t-1])*
        (1-exp(-k.active[i,t]*(dslc_active[i,t-1]/365)- k.inactive[i,t]*(dslc_inactive[i,t-1]/365)))

      # log-link function to allow active k to vary in relation to area, fish
      log(k.active[i,t]) <- mean.k.active + area.k.active*area[i] +
        fish.k.active*fish[i] + k[stream[i]]

      log(k.inactive[i,t]) <- mean.k.inactive
}}}
```

Literature Cited

Eaton, M. J., and W. A. Link. 2011. Estimating age from recapture data: Integrating incremental growth measures with ancillary data to infer age-at-length. Ecological Applications 21:2487–2497.

Fabens, A. J. 1965. Properties and fitting of the von Bertalanfy growth curve. Growth 29:265–289.

Gabry J, and T. Mahr. 2022. "bayesplot: Plotting for Bayesian Models." R package version 1.9.0.

Plummer, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. Proceedings of the 3rd international workshop on distributed statistical computing 125:1–10.

Su, Y. S., and Yajima, M. 2021. R Package "R2jags: A Package for Running jags from R".