CHAPTER 6

Assessing the effects of environmental variables on nestling growth using non-linear mixed effect models

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Hedlin, E., and A. Franke. 2017. Assessing the effects of environmental variables on nestling growth using non-linear mixed effect models. Pages 113–126 *in* D.L. Anderson, C.J.W. McClure, and A. Franke, editors. Applied raptor ecology: essentials from Gyrfalcon research. The Peregrine Fund, Boise, Idaho, USA.
https://doi.org/10.4080/are.2017/006

6.1 Introduction

6.1.1 Importance of understanding brood rearing

In the context of climate change, understanding how animal populations are affected by changing environmental conditions is of increasing importance. This is particularly true in the Arctic where environmental change is occurring faster than the global average (Kattsov et al. 2005, Trenberth and Josey 2007). For raptors, the brood rearing period is particularly sensitive to environmental conditions due to a combination of nestling vulnerability and increased energetic demands from adults (Dawson and Bortolotti 2002, Robinson et al. 2007), and parameters of breeding success are often used to gauge the vulnerability of populations to changes in the environment (Steenhof et al. 1997, Vincenzi and Mangel 2013, Anctil et al. 2014, Kasprzykowski et al. 2014). Although nestling survival is an important and often used parameter, it is binary (either an individual survives or dies) and simple survival can miss the more subtle responses exhibited by nestlings. For example, sibling competition may not result in mortality, but a brood runt—the smallest sibling in a brood—that survives to fledging will likely grow at reduced rates (Podlas and Richner 2013, Sofaer et al. 2013). In this case, the unique condition experienced by a runt is lost in survival analysis because this individual has survived and is deemed to have "passed" the brood rearing test. Growth analysis can provide further insight by showing how well an individual developed. Not only does this increase the sensitivity of our observations during the brood rearing period, but because nestling condition and fledging mass are correlated to future fitness components such as survival (Lindström 1999, Monaghan 2008, Cam and Aubry 2011, Bowers et al. 2014) and reproductive components such as egg or clutch sizes (Schluter and Gustafsson 1993, Gorman and Nager 2004, Braasch et al. 2009), understanding how well individuals develop may lead to a greater understanding of how well they will function as adults.

6.1.2 Introduction to growth analysis

Growth analysis is the process of regressing body mass, or other biometric measurements, against age. The shape of this regression, otherwise known as a growth curve, reflects adaptive evolution to ecological conditions and is correlated to a number of variables such as adult size, nesting strategy, brood size, parental foraging strategy, and energy sources (Ricklefs 1968). This trajectory is sensitive to conditions at the time of development, and a nestling's growth curve is therefore reflective of its interaction with the environment. As such, studies comparing growth curves within a species have highlighted how factors such as food availability, weather, brood sex-ratio, sibling competition, and nest predation risk underlie variation in growth rates (Ricklefs 1968, Becker and Wink 2003, Pérez et al. 2016).

Estimating growth curves requires that the mass (or other biometric measurement) of multiple individuals be measured several times from hatch through fledging. These weight data are pooled, plotted against age, and then fitted with a growth model. Birds exhibit sigmoidal growth and the most commonly used models for this pattern are the logistic, Richards, Gompertz, and Von Bertalanffy (Gompertz 1825, Winsor 1932, Von Bertalanffy 1957, Richards 1959, Ricklefs 1968). All of the above models are parametric equations that, when fitted to growth data, provide parameter estimates that are specific to the nature of the curve. For example, like the name suggests, a three-parameter logistic model is composed of three parameters: 1) a growth rate constant that indicates the rate at which the slope changes throughout growth, 2) an inflection point that indicates the moment of most rapid growth rate and the moment at which growth rate transitions towards the asymptote, and 3) the asymptote which indicates the final weights reached by the nestlings (Fig. 6.1). By fitting a growth model and obtaining the parametric values, we gain the ability to empirically describe and compare the growth rates of nestlings in two growth rates or populations. We can then use this methodology to investigate specific research hypotheses regarding nestling growth during the brood rearing period.

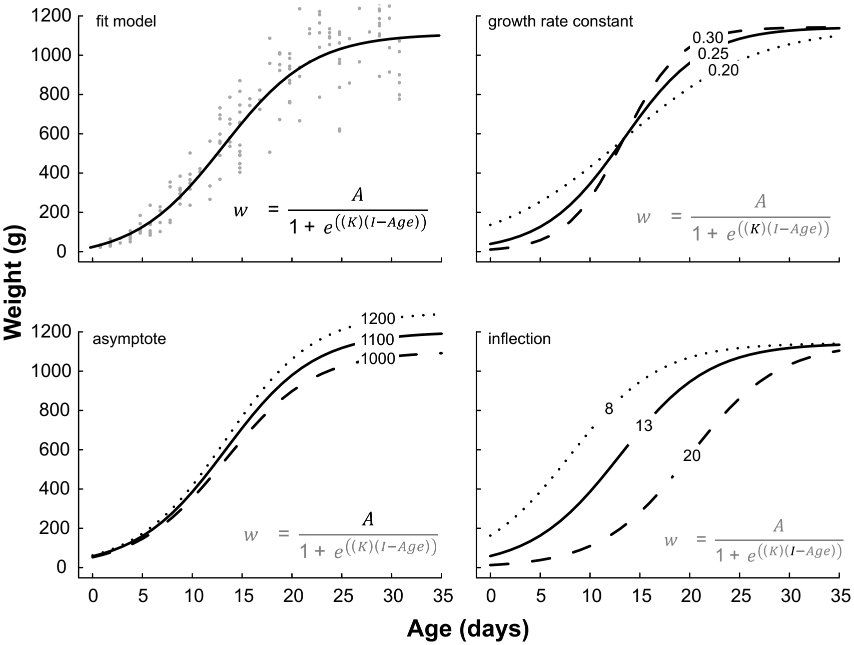

Figure 6.1. To display how each parameter affects the growth trajectory, each example above shows three curves in which two parameters are held constant and the remaining parameter varies. For instance, in the panel titled 'growth rate constant,' the inflection and asymptote values are fixed, while the growth rate constant varies from 0.20 to 0.30.

To illustrate this technique we use a hypothetical example, and test whether Gyrfalcon nestling growth differed between two breeding seasons of sparse and heavy rainfall. In the context of a rapidly changing climate and projected increases in extreme weather in the Arctic (IPCC Working Group 1 et al. 2013), we expect that heavy summer rainfall will play an increasingly prominent role in Gyrfalcon breeding productivity in coming years (Anctil et al. 2014). Pronounced precipitation can lead to alterations in the distribution of prey species, lowered food availability, increased thermoregulatory costs, and adjustments to parental care (Schekkerman et al. 1998, Robinson et al. 2014, Fisher et al. 2015), and we would expect to see such impacts represented in the analysis of nestling growth. Here we use the methodology outlined by Sofaer et al. (2013) to compare nestling growth between two groups using a simulated data set. Our goal was to investigate differences in growth between individuals reared in a year with precipitation amounts below the 30-year average, and individuals reared in a year with precipitation amounts above the 30-year average.

6.2 Analyzing growth of nestlings using non-linear mixed effect models

6.2.1 Formatting data

For this example, we simulated a data set that resembles an intense raptor research project in the Arctic. We assumed nestling weights could be obtained every 5 days, starting at 5 days of age and ending at 30, over a period of 3 years, and have generated data for 150 individuals from 52 broods. This data set was generated by transforming an existing Peregrine Falcon (*Falco peregrinus*) growth data set to resemble Gyrfalcon growth. Obtaining an equivalent sample size may be difficult considering the logistical issues of field work in the Arctic, but this analysis can be applied to smaller data sets. The data table, which was saved in comma-separated value format (.csv), contains all of the variables one needs to model growth. These variables are nestling ID (unique to each individual), nest ID, color, sex, year, yearly conditions (0 = wet, 1 = dry), age, and mass. Considering that this table will be input in to R, it is easiest to create the data table in long format where each variable is represented as a column, and each data point is represented as a row (Table 6.1).

Table 6.1. An example of how the data should be organized. Each column represents one variable, and each row represents one observation. Nestling ID's should be unique for every individual.

ID	NEST	COLOR	SEX	YEAR	COND	AGE	MASS
75r13	31	red	f	2013	0	27	761
75r13	31	red	f	2013	0	24	829
75r13	31	red	f	2013	0	19	631
75r13	31	red	f	2013	0	15	492
75r13	31	red	f	2013	0	10	221
76b14	31	red	f	2013	0	5	76
76b14	72	red	f	2013	0	29	793
76b14	72	red	f	2013	0	22	640
76b14	72	red	f	2013	0	15	258
76b14	72	red	f	2013	0	8	91
76b14	72	red	f	2013	0	2	36
77b14	8	red	f	2013	0	30	920
77b14	8	red	f	2013	0	24	867
77b14	8	red	f	2013	0	16	550
77b14	8	red	f	2013	0	9	218

6.2.2 Introduction to the model

Because Gyrfalcons exhibit reverse sexual size dimorphism, each sex is modeled separately using three-parameter mixed effects logistic models by means of the nlme package (Pinheiro et al. 2016) in R (R Core Team 2016) where w_{t} = mass at time t (g), A = asymptotic mass (g), K = growth rate constant, I = inflection point of the growth curve (days), and t = nestling age (days).

$$w_{\mathrm{t}} = \frac{A}{1 + e^{((K)(I+\mathrm{t}))}} + \varepsilon$$

Variation in nestling growth may be consistent at hierarchical levels, and we can improve the fit of our model by adding random effects (Sofaer et al. 2013). For example, due to similar levels of parental care, asymptotes may be similar among siblings. We can account for this by adding a nest level random effect to the asymptote parameter. Because we initially do not know to what degree, and on which parameter(s), our nestlings show consistent growth, it is necessary to evaluate a number of different random effect structures. We do this by building a set of candidate models that apply one or two random effects to one or more of the parameters. In this example data set, we expected to see two levels of consistent variation and include nest (Ai, Ki, and Ii), and nestling level random effects (Aij, Kij, and Iij) in the candidate models. By doing so, we will account for 1) shared genetic backgrounds and common levels of parental care between siblings, and 2) repeated measurements on individuals.

$$w_{ijk} = \frac{A + \boldsymbol{A_i} + \boldsymbol{A_{ij}}}{1 + e^{((K+\boldsymbol{K_i}+\boldsymbol{K_{ij}})(I+\boldsymbol{I_i}+\boldsymbol{I_{ij}}+t_{ijk}))}} + \varepsilon_{ijk}$$

Ultimately we want to investigate differences in growth between wet and dry years. We can achieve this by including a fixed "wet year" (i.e., X_{con}) effect that denotes the year in which an individual was reared (wet = 0, dry = 1). By adding this effect to each of the three parameters, we can determine if the parameters significantly changed from dry to wet years, and to what degree they changed.

$$w_{ijk} = \frac{A + A_i + A_{ij} + \boldsymbol{A_{con}}}{1 + e^{((K+K_i+K_{ij}+\boldsymbol{K_{con}})(I+I_i+I_{ij}+\boldsymbol{I_{con}} - t))}} + \varepsilon_{ijk}$$

6.2.3 Model fitting in R

The first step in analysis is to assign the logistic function and the derivative of this function to objects. We create a logistic function for growth called parm_diff, which includes a fixed effect for each parameter (Kdiff, middiff, Adiff) that denotes whether the individual was raised in a wet or dry year. If this fixed "condition" effect significantly changes between wet and dry years, the estimate associated with this fixed effect estimate will have a *P*-value < 0.05.

```
# create parm_diff: a logistic function for growth
  parm_diff = function(AGE, COND, Asym, xmid, K, Kdiff,
       middiff, Adiff){(Asym + Adiff * COND) / (1 +
       exp(((xmid + middiff * COND) - AGE) * (K+Kdiff*COND)))
                       }
# p.diff_Deriv derives the logistic function above
# (parm_diff)
  p.diff_Deriv = deriv(body(parm_diff)[[2]], namevec =
       c("Asym", "xmid", "K", "Kdiff", "middiff", "Adiff"),
       function.arg = parm_diff)
```

The way R arrives at the best fitting model (i.e., the parameter values within the logistic equation that best fit the growth data) is by sequentially working through potential parameter values. To prevent errors and endless searching, we can assign parameter "start values" that we believe, based on experience, are within the range of normal values. R will then use these start values as guidance, and search within the proximity of the start values.

```
# start values for males (PEFA)
  startmal = c(Asym = 700, xmid = 3, K = .05, Kdiff = 0,
       middiff = 0, Adiff = 0)

# start values for females (PEFA)
  startfem = c(Asym = 700, xmid = 3, K = .05, Kdiff = 0,
       middiff = 0, Adiff = 0)
```

With a derived logistic function and approximate parameter values, we can start fitting models to our data. For this process, we fit a number of candidate models that incorporate different random effects structures, and determine which random structure is most parsimonious with regard to describing nestling growth within our population. Here is an example model for the males that incorporates a nest-level random effect on the asymptote. This model is therefore accounting for similar asymptote values within each brood due to genetic and parental care similarities among siblings. Note that we use the dataframe growth_mal which is the subset of the data containing only males. We also rounded some of the output for simplicity. See the online code for this chapter for more details.

```
# model with NEST-level random effect on the ASYMPTOTIC
# MASS
  r.n_f.a._males = nlme(WEIGHT ~ p.diff_Deriv
       (AGE, COND, Asym, xmid, K, Kdiff, middiff, Adiff),
       fixed = Asym + xmid + K + Kdiff + middiff + Adiff ~ 1,
       random = Asym ~ 1 | NEST, data = growth_mal, start =
       startmal)

# returns a summary of the model
  summary(r.n_f.a._males)
```

Examining the summary output, we see the following:

```
Nonlinear mixed-effects model fit by maximum likelihood
  Model: WEIGHT ~ p.diff_Deriv(AGE, COND, Asym, xmid, K,
Kdiff, middiff, Adiff)
 Data: growth_mal
       AIC      BIC    logLik
  5563.907 5597.026 -2773.953

Random effects:
 Formula: Asym ~ 1 | NEST
        Asym     Residual
StdDev: 88.65756 89.83508
```

```
Fixed effects: Asym + xmid + K + Kdiff + middiff + Adiff ~ 1
         Value      Std.Error   DF     t-value    p-value
Asym     1142.56    25.63       429    44.58      0.00
xmid     13.35      0.28        429    49.85      0.00
K        0.22       0.01        429    19.97      0.00
Kdiff    0.01       0.01        429    0.77       0.44
middiff -0.17       0.33        429   -0.51       0.61
Adiff    71.72      25.80       429    2.78       0.01
 Correlation:
         Asym     xmid      K        Kdiff     middff
xmid     0.549
K       -0.498   -0.519
Kdiff    0.404    0.416   -0.800
middiff -0.451   -0.814    0.422    -0.512
Adiff   -0.611   -0.536    0.489    -0.623     0.688

Standardized Within-Group Residuals:
Min         Q1         Med        Q3         Max
-5.65e+00 -4.23e-01  6.85e-05  5.74e-01  5.28e+00

Number of Observations: 464
Number of Groups: 30
```

This represents one model fitting, thus, we refrain from making conclusions about differences in growth between treatment groups until it becomes clear which random effect structure best fits our growth data, but all the needed information can be seen in this summary. For this particular model, we can see the values associated with each parameter in the "Fixed Effects" section. For example, a typical male (median) reached an asymptote (Asym) of 1142.6 grams ± 25.6, was inflecting (xmid) at 13.3 days of age ± 0.3, and had a growth rate constant (K) of 0.22 ± 0.01. No significant differences were found between wet and dry years in regards to the growth rate constant and inflection point (p = 0.4 and 0.6 respectively), but the asymptote values increased significantly by 71.7 grams in years of less precipitation (p = 0.006). Model fit diagnostics appear at the top (AIC, BIC, and Log Likelihood) and we use these to rank the candidate models. To complete this analysis, one should run the full set of candidate models to find the one of best fit, and then examine the significance of the fixed condition effects within that model. For more examples of models with varying random effect structures see the code for this chapter online.

All the information needed to make conclusions about nestling growth is in the model output, but it helps if we can visualize growth between wet and dry conditions (Fig. 6.2). This visualization helps us understand exactly how changes in growth parameters affect the overall growth curve.

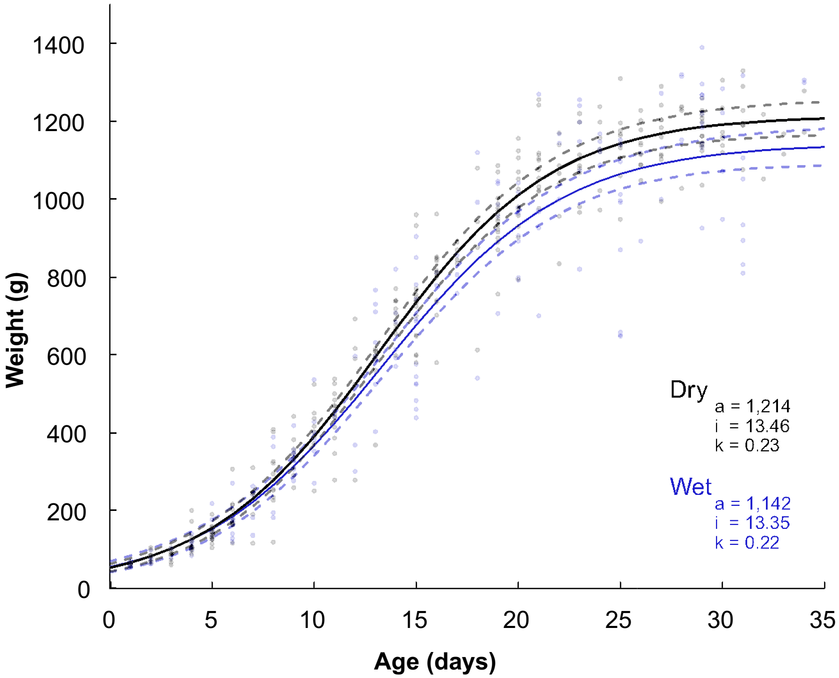

Figure 6.2. A visualization of growth in male Gyrfalcons across wet and dry years where asymptotes varied randomly across nests. In this model, only asymptotes changed significantly across conditions (p = 0.006).

```
# manually save the parameter estimates to objects (values
# obtained from model summary)
  Asym_est     =  1142.557
  xmid_est     =  13.3460
  K_est        =  0.2242
  Kdiff_est    =  0.0109
  middiff_est = -0.1663
  Adiff_est    =  71.7208

# create a matrix of the model's variance covariance
  sigma = matrix(vcov(r.n_f.a._males), nrow = 6, ncol = 6)

# vector of ages spanning 0 to 35 days
  age_vec = seq(0, 35, by = 1)
```

```
# growth in wet conditions
  Mass_wet = Asym_est / (1 + exp((xmid_est - age_vec) *
       K_est))

# growth in dry conditions
  Mass_dry = (Asym_est + Adiff_est)/(1 +
       exp(((xmid_est+middiff_est) - age_vec) *
       (K_est+Kdiff_est)))

# treatment
  wet = 0
  dry = 1

# standard error for growth in wet conditions
  se_wet.mass = sqrt(deltavar((Asym_est + Adiff_est * wet)/
       (1 + exp(((xmid_est + middiff_est * wet) -
       age_vec) * (K_est + Kdiff_est * wet))), meanval =
       c(Asym_est = Asym_est, xmid_est = xmid_est, K_est =
       K_est, Kdiff_est = Kdiff_est, middiff_est =
       middiff_est, Adiff_est =
       Adiff_est), Sigma=sigma ))

# calculate upper and lower confidence intervals from the SE
# for growth in wet conditions
  wet_ucl = Mass_wet + 1.96 * se_wet.mass
  wet_lcl = Mass_wet - 1.96 * se_wet.mass

# standard error for growth in dry conditions
  se_dry.mass = sqrt(deltavar((Asym_est + Adiff_est *
       dry) / (1 + exp(((xmid_est+middiff_est * dry) -
       age_vec) * (K_est+Kdiff_est * dry))), meanval =
       c(Asym_est = Asym_est, xmid_est = xmid_est, K_est =
       K_est, Kdiff_est = Kdiff_est, middiff_est =
       middiff_est, Adiff_est = Adiff_est), Sigma=sigma ))

# calculate upper and lower confidence intervals from the SE
# for growth in dry conditions
  dry_ucl = Mass_dry + 1.96 * se_dry.mass
  dry_lcl = Mass_dry - 1.96 * se_dry.mass
```

```
# plot the curves
  graphics.off()
  windows(4.5,4.5)
  par(mgp = c(1.5,0.5,0))
  plot (age_vec, Mass_wet, type = “n”, cex.lab = 0.6,
       cex.axis = 0.75, xlab = “Age (days)”, tck = 0.01,
       font.lab = 2,ylab = ‘Weight (g)’, las = 1, ylim =
       c(0,1500), xaxs = “i”, yaxs = “i”, bty = “l”,
       cex.lab = 1,axes=T)
  lines(age_vec, Mass_wet, lty = 1, lwd = 1, col =
       rgb(0.1,0.1,0.8,1))
  lines(age_vec, wet_ucl,  lty = 2, lwd = 1, col =
       rgb(0.1,0.1,0.8,0.5))
  lines(age_vec, wet_lcl,  lty = 2, lwd = 1, col =
       rgb(0.1,0.1,0.8,0.5))
  lines(age_vec, Mass_dry, lty = 1, lwd = 1, col =
       rgb(0,0,0,1))
  lines(age_vec, dry_ucl,  lty = 2, lwd = 1, col =
       rgb(0,0,0,0.5))
  lines(age_vec, dry_lcl,  lty = 2, lwd = 1, col =
       rgb(0,0,0,0.5))
  points(growth_mal$WEIGHT[growth_mal$COND==0]~
       growth_mal$AGE[growth_mal$COND==0], pch = 19,col =
       rgb(0.1,0.1,0.8,0.2),cex = 0.2)
  points(growth_mal$WEIGHT[growth_mal$COND==1]~
       growth_mal$AGE[growth_mal$COND==1], pch = 19,col =
       rgb(0,0,0,0.2), cex = 0.2)
  legend(25,600, bty = “n”, legend = “Dry”, text.col =
       rgb(0,0,0,1),cex = 0.75)
  legend(28,525, bty = ”n”, legend = “a = 1,214”,cex = 0.5)
  legend(28,475, bty = “n”,legend = “i  = 13.46”, cex = 0.5)
  legend(28,425, bty = “n”,legend = “k = 0.23”, cex = 0.5)
  legend(25,350, bty = “n”, legend = “Wet”, text.col =
       rgb(0.1,0.1,0.8,1),cex = 0.75)
  legend(28,275, bty = “n”, legend = “a = 1,142”, text.col =
       rgb(0.1,0.1,0.8,1),cex = 0.5)
  legend(28,225, bty = “n”, legend = “i  = 13.35”, text.col =
       rgb(0.1,0.1,0.8,1),cex = 0.5)
  legend(28,175, bty = “n”, legend = “k = 0.22”, text.col =
       rgb(0.1,0.1,0.8,1),cex = 0.5)
```

Once completed in full, this analysis will provide us with detailed inference on how nestling growth changes across years of varying precipitation. We chose precipitation as our variable of comparison due to the predicted increases in extreme Arctic weather and the documented effects of heavy rainfall on raptor breeding productivity (IPCC Working Group 1 et al. 2013, Anctil et al. 2014, Fisher et al. 2015), but any two-level variable could be used in its place (i.e., growth between two different populations or growth in years of differing prey abundance; see Chapter 8 this volume).

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