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9 Standard Statistics Revisited

This chapter rapidly reviews much of classical statistics, discussing the underlying likelihood models for procedures such as ANOVA, linear regression, and generalized linear models. It also gives brief pointers to the built-in procedures in **R** that implement these standard techniques. This summary connects maximum likelihood approaches with more familiar classical techniques. If you're already familiar with classical techniques, it may help you understand maximum likelihood better. It also provides a starting point for using efficient, "canned" approaches when they are appropriate for your data. It does not, and cannot, provide full coverage of all these topics. For more details, see Dalgaard (2003), Crawley (2005, 2007), or Venables and Ripley (2002).

9.1 Introduction

So far this book has covered maximum likelihood and Bayesian estimation in some detail. In the course of the discussion I have sometimes mentioned that maximum likelihood analyses give answers equivalent to those provided by familiar, "old-fashioned" statistical procedures. For example, the statistical model $Y \sim \text{Normal}(a + bx, \sigma^2)$ —specifying that Y is a normally distributed random variable whose mean depends linearly on x —underlies ordinary least-squares linear regression. This chapter will briefly review special cases where our general recipe for finding MLEs for statistical models reduces to standard procedures that are built into **R** and other statistics packages.

In the best case, your data will match a classical technique like linear regression exactly, and the answers provided by classical statistical models will agree with the results from your likelihood model. Other models you build may be formally equivalent to a classical model that is parameterized in a different way. Most often, the customized model you build will not be exactly equivalent to any existing classical model, but a similar classical model may be close enough that you wouldn't mind changing your model slightly in order to gain the convenience of using a standard procedure.

For example, in Chapter 6 we used the model

$$Y \sim \text{NegBin}(\mu = a \cdot \text{DBH}^b, k) \quad (9.1.1)$$

to represent cone production by fir trees as a function of diameter at breast height. If we approximated the discrete distribution of cones by a continuous log-normal distribution instead,

$$Y \sim \text{LogNormal}(\mu = a \cdot \text{DBH}^b, \sigma^2), \quad (9.1.2)$$

we could log-transform both sides and fit the linear regression model

$$\log Y \sim \text{Normal}(\log a + b \cdot \log(\text{DBH}), \sigma^2). \quad (9.1.3)$$

Figure 9.1a shows all three models for the DBH–fecundity relationship—power-law with a negative binomial distribution (power/NB), power-law with a log-normal distribution (power/LN), and linear with a normal distribution—fitted to the fir data; all are plausible. Figure 9.1b shows various models for the distribution of cone production, fitted to the individuals with DBH between 6 and 8 cm: a nonparametric density estimate, the negative binomial, lognormal, and normal. The negative binomial is closest to the nonparametric density estimate of the distribution, while the lognormal is more peaked and the normal distribution has an unrealistic negative tail.

Although the power-law/negative binomial is the most realistic model and has a plausible mechanistic interpretation (the data are discrete, positive, and overdispersed; we can imagine individual trees producing cones at an approximately constant rate with variation in fecundity among trees), the difference between the fit of negative binomial and lognormal distributions is small enough that the convenience of linear regression may be worthwhile. When the results of different models are similar on both biological and statistical grounds, you choose among them by balancing convenience, mechanistic arguments, and convention.

Why might you want to use standard, special-case procedures rather than the general MLE approach?

- *Computational speed and stability:* The special-case procedures use special-case optimization algorithms that are faster (sometimes much faster) and less likely to encounter numerical problems. Many of these procedures relieve you of the responsibility of choosing starting parameters.
- *Stable definitions:* The definitions of standard models have often been chosen to simplify parameter estimation. For example, to model a relatively sudden change between two states you could choose between a logistic equation and a threshold model. Both might be equally sensible in terms of the biology, but the logistic equation is easier to fit because it involves smoother changes as parameters change. Similarly, generalized linear models such as logistic or Poisson regression fit parameters on scales (logit- or log-transformed, respectively) that allow unconstrained optimization.
- *Convention:* If you use a standard method, you can just say (e.g.) “we used linear regression” in your Methods section and no one will think twice. If you use a nonstandard method, you need to explain the method carefully and overcome readers’ distrust of “fancy” statistics—even if your model is actually simpler and more appropriate than any standard model. Similarly, it may minimize confusion to use the same models, and the same parameterizations, as previous studies of your system.
- *Varying models and comparing hypotheses:* The machinery built into R and other packages makes it easy to compare a variety of models. For example,

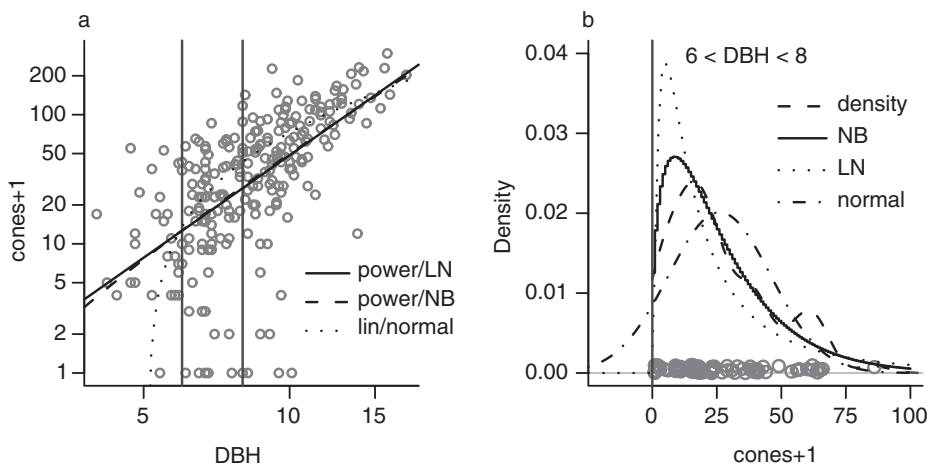


Figure 9.1 Comparing different functional forms for fir fecundity data: power-law with a lognormal (LN) distribution, power-law with a negative binomial (NB) distribution, and linear with a normal distribution. (The linear model appears as a curved line because the data are plotted on a log-log scale.)

when analyzing a factorial growth experiment that manipulates nitrogen (N) and phosphorus (P), you can easily switch between models incorporating the effects of nitrogen only ($\text{growth} \sim N$), phosphorus only ($\text{growth} \sim P$), additive effects of N and P ($\text{growth} \sim N+P$), and the main effects plus interactions between nitrogen and phosphorus ($\text{growth} \sim N \times P$). You can carry out all of these comparisons by hand with your own models, and `mle2`'s formula interface is helpful, but R's built-in functions make the process easy for classical models.

This chapter discusses how a variety of different kinds of models fit together, and how they all represent special cases of a general likelihood framework. Figure 9.2 shows how many of these areas are connected. The chapter also gives *brief* descriptions of how to use them in R; if you want more details on any of these approaches, you'll need to check an introductory (Dalgaard, 2003; Crawley, 2005; Verzani, 2005), intermediate (Crawley, 2002), or advanced (Chambers and Hastie 1992; Venables and Ripley, 2002) reference.

9.2 General Linear Models

General linear models include linear regression, one-way and multiway analysis of variance (ANOVA), and analysis of covariance (ANCOVA); R uses the function `lm` for all of these procedures. SAS implements this with PROC GLM.* While regression, ANOVA, and ANCOVA are often handled differently, and they are usually taught differently in introductory statistics classes, they are all variants of the same basic model. The assumptions of the general linear model are that all observed values are independent and normally distributed with a constant variance (*homoscedastic*),

* This terminology is unfortunate since the rest of the world uses "GLM" to mean *generalized* linear models, which correspond to SAS's PROC GENMOD.

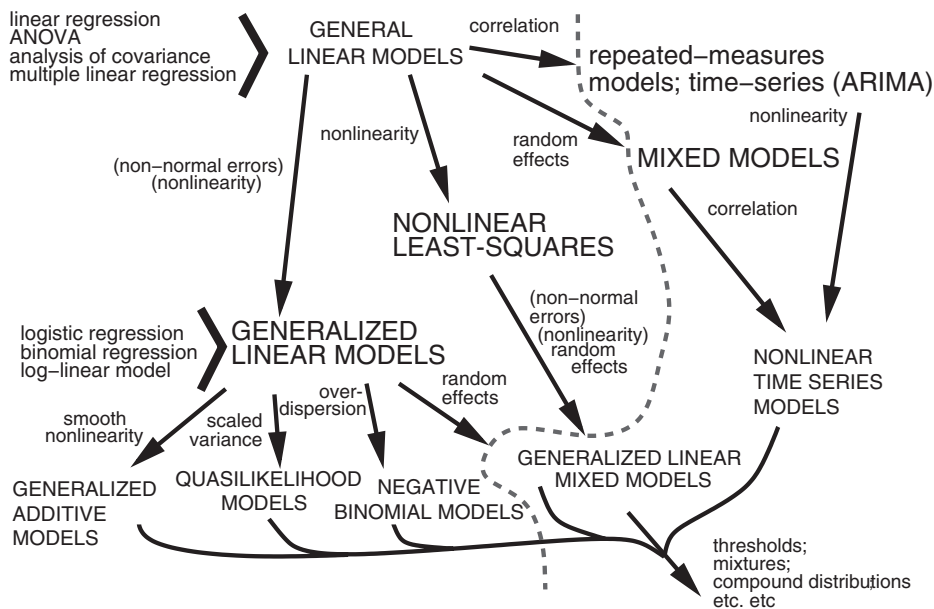


Figure 9.2 All (or most) of statistics. The labels in parentheses (non-normal errors and nonlinearity) imply restricted cases: (non-normal errors) means exponential family (e.g., binomial or Poisson) distributions, while (nonlinearity) means nonlinearities with an invertible linearizing transformation. Models to the right of the gray dashed line involve multiple levels or types of variability; see Chapter 10.

and that any continuous predictor variables (covariates) are measured without error. (Remember that the assumption of normality applies to the variation around the expected value—the residuals—not to the whole data set.)

The “linear” part of “general linear model” means that the models are linear functions of the parameters, not necessarily of the independent variables. For example, quadratic regression

$$Y \sim \text{Normal}(a + bx + cx^2, \sigma^2) \quad (9.2.1)$$

is still linear in the parameters (a, b, c), and thus is a form of multiple linear regression. Another way to think about this is to say that x^2 is just another explanatory variable—if you called it w instead, it would be clear that this model is an example of multivariate linear regression. On the other hand, $Y \sim \text{Normal}(ax^b, \sigma^2)$ is nonlinear: it is linear with respect to a (the second derivative of ax^b with respect to a is zero) but nonlinear with respect to b ($d^2(ax^b)/db^2 = b \cdot (b-1) \cdot ax^{b-2} \neq 0$).

9.2.1 Simple Linear Regression

Simple, or ordinary, linear regression predicts y as a function of a single continuous covariate x . The model is

$$Y \sim \text{Normal}(a + bx, \sigma^2). \quad (9.2.2)$$

The equivalent R code is

```
> lm.reg = lm(y ~ x)
```

The intercept term a is implicit in the R model. If you want to force the intercept to be equal to zero, fitting the model $y \sim \text{Normal}(bx, \sigma^2)$, use `lm(y~x-1)`.

Typing `lm.reg` by itself prints only the formula and the estimates of the coefficients; `summary(lm.reg)` also gives summary statistics (range and quartiles) of the residuals, standard errors and p -values for the coefficients, and R^2 and F statistics for the full model; `coef(lm.reg)` gives the coefficients alone, and `coef(summary(lm.reg))` pulls out the table of estimates, standard errors, t statistics, and p -values. `confint(lm.reg)` calculates confidence intervals. The function `plot(lm.reg)` displays various graphical diagnostics that show how well the assumptions of the model fit and whether particular points have a strong effect on the results; see `?plot.lm` for details. `anova(lm.reg)` prints an ANOVA table for the model.* If you need to extract numeric values of, e.g., R^2 values or F statistics for further analysis, wade through the output of `str(summary(lm.reg))` to find the pieces you need (e.g., `summary(lm.reg)$r.squared`).

To do linear regression by brute force with `mle2`, you could write this negative log-likelihood function:

```
> linregfun = function(a, b, sigma) {
+   Y.pred = a + b * x
+   -sum(dnorm(Y, mean = Y.pred, sd = sigma, log = TRUE))
+ }
```

or use the formula interface:

```
> mle2(Y ~ dnorm(mean = a + b * x, sd = sigma), start = ...)
```

When using `mle2` you must explicitly fit a standard deviation term σ , which is implicit in the `lm` approach.

9.2.2 Multiple Linear Regression

It's easy to extend the simple linear regression model to multiple continuous predictor variables (covariates). If the extra covariates are powers of the original variable (x^2, x^3, \dots), the model is called *polynomial* regression (*quadratic* if just the x^2 term is added):

$$Y \sim \text{Normal}(a + b_1x + b_2x^2, \sigma^2). \quad (9.2.3)$$

Or you can use completely separate variables (x_1, x_2, \dots):

$$Y \sim \text{Normal}(a + b_1x_1 + b_2x_2 + b_3x_3, \sigma^2) \quad (9.2.4)$$

As with simple regression, the intercept a and the coefficients of the different covariates (b_1, b_2) are implicit in the R formula:

```
> lm.poly = lm(y ~ x + I(x^2))
```

* `anova` gives so-called *sequential sums of squares*, which SAS calls “type I” sums of squares. If you need SAS-style “type III” sums of squares, you can use the `Anova` function in the `car` package. However, be aware that type III sums of squares are problematic, and indeed controversial (Venables, 1998).

(surround x^2 and other powers of x with $I()$, meaning “as is”) or

```
> lm.mreg = lm(y ~ x1 + x2 + x3)
```

You can add interactions among covariates, testing whether the slope with respect to one covariate changes linearly as a function of another covariate—e.g., $Y \sim \text{Normal}(a + b_1x_1 + b_2x_2 + b_{12}x_1x_2, \sigma^2)$; in R, `lm.intreg = lm(y~x1*x2)`.

Use the `anova` function with `test="Chisq"` to perform Likelihood Ratio tests on a nested series of multivariate linear regression models (e.g., `anova(lm1,lm2,lm3,test="Chisq")`). If you wonder why `anova` is a test for regression models, remember that regression and analyses of variance are just different subsets of the general linear model.

While multivariate regression is conceptually simple, models with many terms (e.g., models with many covariates or with multiway interactions) can be difficult to interpret. Blind fitting of models with many covariates can get you in trouble (Whittingham et al., 2006). If you absolutely must go on this kind of fishing expedition, you can use `step`, or `stepAIC` in the `MASS` package, to do stepwise modeling, or `regsubsets` in the `leaps` package to search for the best model.

9.2.3 One-Way Analysis of Variance (ANOVA)

If the predictor variables are discrete (factors) rather than continuous (covariate), the general linear model becomes an analysis of variance. The basic model is

$$Y_i \sim \text{Normal}(\alpha_i, \sigma^2); \quad (9.2.5)$$

in R it is

```
> lm.1way = lm(y ~ f)
```

where `f` is a factor. If your original data set has names for the factor levels (e.g., {N,S,E,W} or {high,low}), then R will automatically transform the treatment variable into a factor when it reads in the data. However, if the factor levels look like numbers to R (e.g., you have site designations 101, 227, and 359, or experiments numbered 1 to 5), R will interpret them as continuous rather than discrete predictors and will fit a linear regression rather than doing an ANOVA—not what you want. Use `v=factor(v)` to turn a numeric variable `v` into a factor, and then fit the linear model.

Executing `anova(lm.1way)` produces a basic ANOVA table; `summary(lm.1way)` gives a different view of the model, testing the significance of each parameter against the null hypothesis that it equals 0.

When fitting regression models, the parameters of the model are easy to interpret—they’re just the intercept and the slopes with respect to the covariates. When you have factors in the model, however—as in ANOVA—the parameterization becomes trickier. By default, R parameterizes the model in terms of the differences between the first group and subsequent groups (*treatment contrasts*) rather than in terms of the mean of each group, although you can tell it to fit the means of each group by putting a `-1` in the formula (e.g., `lm.1way = lm(y~f-1)`).

9.2.4 Multiway ANOVA

Multiway ANOVA models Y as a function of two or more different categorical variables (factors). For example, the full model for two-way ANOVA with interactions is

$$Y_{ij} \sim \text{Normal}(\alpha_i + \beta_j + \gamma_{ij}, \sigma^2) \quad (9.2.6)$$

where i is the level of the first treatment/group, and j is the level of the second. The R code using `lm` is

```
> lm.2way = lm(Y ~ f1 * f2)
```

(`f1` and `f2` are factors). As before, `summary(lm.2way)` gives more information, testing whether the parameters differ significantly from zero; `confint(lm.2way)` computes confidence intervals; `anova(lm.2way)` generates a standard ANOVA table; `plot(lm.2way)` shows diagnostic plots. If you want to fit just the main effects without the interactions, use `lm(Y ~ f1 + f2)`; use `f1:f2` to specify an interaction between `f1` and `f2`.

A negative log-likelihood function for `mle2` could look like this:

```
> aov2fun = function(m11, m12, m21, m22, sigma) {
+   intval = interaction(f1, f2)
+   Y.pred = c(m11, m12, m21, m22)[intval]
+   -sum(dnorm(Y, mean = Y.pred, sd = sigma, log = TRUE))
+ }
```

(`interaction(f1,f2)` defines a factor representing the interaction of `f1` and `f2` with levels in the order (1.1, 2.1, 1.2, 2.2)). Using the formula interface:

```
> mle2(Y ~ dnorm(mean = m, sd = sigma),
+   parameters = list(m ~ f1 * f2))
```

For a multiway model, R's parameters are again defined in terms of contrasts. If you construct a two-way ANOVA with factors `f1` (with levels A and B) and `f2` (with levels I and II), the first ("intercept") parameter will be the mean of individuals in level A of the first factor and level I of the second (`m11`); the second parameter is the difference between A,II and A,I (`m12-m11`); the third is the difference between B,I and A,I (`m21-m11`); and the fourth, the interaction term, is the difference between the mean of B,II and its expectation if the effects of the two factors were additive (`m22-(m11+(m12-m11)+(m21-m11)) = m22-m12-m21+m11`).

9.2.5 Analysis of Covariance (ANCOVA)

Analysis of covariance defines a statistical model that allows for different intercepts and slopes with respect to a covariate x in different groups:

$$Y_i \sim \text{Normal}(\alpha_i + \beta_i x, \sigma^2). \quad (9.2.7)$$

In R:

```
> lm(Y ~ f * x)
```

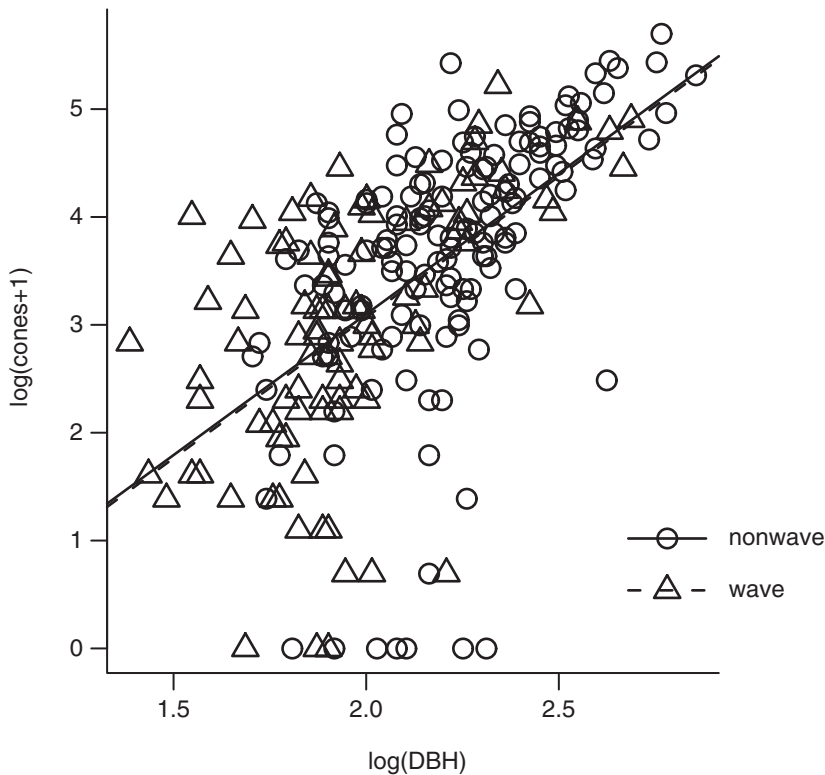



Figure 9.3 General linear model fit to fir fecundity data (analysis of covariance): $\text{lm}(\log(\text{TOTCONES}+1) \sim \log(\text{DBH}) + \text{WAVE_NON}, \text{data} = \text{firdata})$. (Lines are practically indistinguishable between groups.)

where f is a factor and x is a covariate (the formula $Y \sim f + x$ would specify parallel slopes, $Y \sim f$ would specify zero slopes but different intercepts, $Y \sim x$ would specify a single line). Figure 9.3 shows the fit of the model $\text{lm}(\log(\text{TOTCONES}+1) \sim \log(\text{DBH}) + \text{WAVE_NON})$ to the fir data. As suggested by the figure, there is a strong effect of DBH but no significant effect of population (wave vs. nonwave).

As with other models, use `summary`, `confint`, `plot`, and `anova` to analyze the model. The parameters are now the intercept of the first factor level; the slope with respect to x for the first factor level; the differences in the intercepts for each factor level other than the first; and the differences in the slopes for each factor level other than the first.

A negative log-likelihood function for ANCOVA:

```
> ancovafun = function(i1, i2, slope1, slope2, sigma) {
+   int = c(i1, i2)[f]
+   slope = c(slope1, slope2)[f]
+   Y.pred = int + slope * x
+   -sum(dnorm(Y, mean = Y.pred, sd = sigma, log = TRUE))
+ }
```

9.2.6 More Complex General Linear Models

You can add factors (grouping variables) and interactions between factors in different ways to make multiway ANOVA, covariates (continuous independent variables) to make multiple linear regression, and combinations to make different kinds of analysis of covariance. R will automatically interpret formulas based on whether variables are factors or numeric variables.

9.3 Nonlinearity: Nonlinear Least Squares

Nonlinear least-squares models relax the requirement of linearity but keep the requirements of independence and normal errors. Two common examples are the power-law model with normal errors

$$Y \sim \text{Normal}(ax^b, \sigma^2) \quad (9.3.1)$$

and the Ricker model with normal errors

$$Y \sim \text{Normal}(axe^{-rx}, \sigma^2). \quad (9.3.2)$$

Before computers were ubiquitous, the only practical way to solve these problems was to *linearize* them by finding a transformation of the parameters (e.g., log-transforming x and y to do power-law regression). A lot of ingenuity went into developing transformation methods to linearize common functions. However, transforming variables changes the distribution of the error as well as the shape of the dependence of y on x . Ideally we'd like to find a transformation that simultaneously produces a linear relationship and makes the errors normally distributed with constant variance, but these goals are often incompatible. If the errors are normal with constant variance, they won't be after you transform the data to linearize $f(x)$.

The modern way to solve these problems without distorting the error structure, or to solve other models that cannot be linearized by transforming them, is to minimize the sums of squares (equivalent to minimizing the negative log-likelihood) computationally, using quasi-Newton methods similar to those built into `optim`. Restricting the variance model to normally distributed errors with constant variance allows the use of specific numeric methods that are more powerful and stable than the generalized algorithms that `optim` uses.

In R, use the `nls` command, specifying a nonlinear formula and the starting values (as a list); e.g., for the power model

```
> n1 = nls(y ~ a * x^b, start = list(a = 1, b = 1))
```

As usual, `summary(n1)` shows values of parameters and standard errors; `anova(n1, ...)` does likelihood ratio tests for nested sequences of nonlinear fits; and `confint(n1)` computes profile confidence limits which are more accurate than the confidence limits suggested by `summary(n1)`. (Unfortunately, `plot(n1)` does nothing.) Figure 9.4 shows the fit of a nonlinear least-squares model (`nls(TOTCONES ~ a*DBH^b)`) to the fir fecundity data set, along with the log-log fit (equivalent to a power-law fit with lognormal errors) calculated above. The power-lognormal model

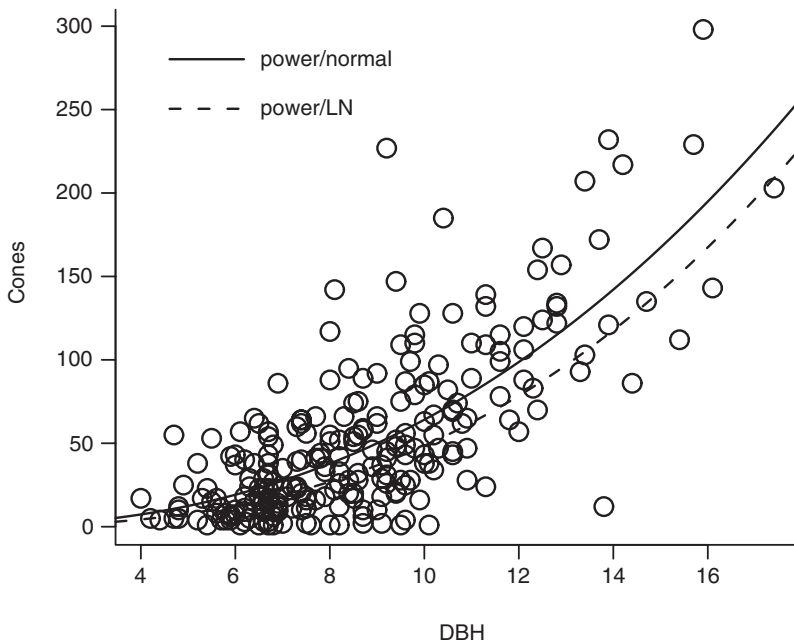


Figure 9.4 A nonlinear least-squares fit to the fir fecundity data (`nls(TOTCONES~a*DBH^b,...)`); the linear model fit to the log-log data (equivalent to a power-law fit with lognormal errors) is also shown.

is better from a biological point of view, since the normal distribution allows negative values, but both models are reasonable.

Fitting models with both nonlinear covariates and categorical variables (the nonlinear analogue of ANCOVA—e.g., fitting different a and b parameters for wave and nonwave populations) is more difficult, but two functions from the `nls` package, `nlsList` and `gnls` (generalized nonlinear least squares), can handle such models. `nlsList` does completely separate fits for separate groups—for example,

```
> nlsList(TOTCONES ~ a * DBH^b | WAVE_NON, data = firdata,
+         start = list(a = 0.1, b = 2.7))
```

would fit separate a and b parameters for wave and nonwave populations—all parameters will vary among groups. The `gnls` command can fit models with only a subset of the parameters differing among groups—for example,

```
> gnls(TOTCONES ~ a * DBH^b, data = firdata, start = c(0.1,
+             2.7, 2.7), params = list(a ~ 1, b ~ WAVE_NON))
```

will fit different b parameters but the same a parameter for wave and nonwave populations.

The numerical methods that `nls` uses are similar to `mle2`'s in that (1) you must specify starting values and (2) if the starting values are unrealistic, or if the problem is otherwise difficult, the numerical optimization may get stuck. Errors such as

```
step factor [] reduced below 'minFactor' of ...
```

number of iterations exceeded maximum of ...

or

Missing value or an infinity produced when evaluating the model

indicate numerical problems. To solve these problems try to find better starting conditions, reparameterize your model, or adjust the control options of `nls` (see `?nls.control`).

As with ML models, you can often use simpler, more robust approaches like linear models to get a first estimate for the parameters (e.g., estimate the initial slope of a Michaelis-Menten function from the first 10% of the data and the asymptote from the last 10%, or estimate the parameters by linear regression based on a linearizing transformation). R includes some “self-starting” functions that do these steps automatically. The functions `SSlogis` and `SSmicmen`, for example, provide self-starting logistic and Michaelis-Menten functions. To fit a self-starting Michaelis-Menten model to the tadpole data with asymptote `a` and half-maximum `b`:

```
> data(ReedfrogFuncresp)
> nls(Killed ~ SSmicmen(Initial, a, b),
+     data = ReedfrogFuncresp)
```

Use `apropos("SS", ignore.case=FALSE)` to see a more complete list of self-starting models. The names are cryptic, so check the help system for information about each model.

Further reading: Bates and Watts (1988), Pinheiro and Bates (2000).

9.4 Nonnormal Errors: Generalized Linear Models

Generalized linear models (not to be confused with general linear models) allow you to analyze models that have a particular kind of nonlinearity and particular kinds of nonnormally distributed (but still independent) errors.

Generalized linear models can fit any nonlinear relationship that has a *linearizing transformation*. That is, if $y = f(x)$, there must be some function F such that $F(f(x))$ is a linear function of x . The procedure for fitting generalized linear models uses the function F to fit the data on the linearized scale ($F(y) = F(f(x))$) while calculating the expected variance on the untransformed scale in order to correct for the distortions that linearization would otherwise induce. In generalized-linear-model jargon F is called the *link* function. For example, when f is the logistic curve ($y = f(x) = e^x / (1 + e^x)$), the link function F is a the logit function ($F(y) = \log(y / (1 - y)) = x$; see p. 83 for the proof that the logit is really the inverse of the logistic). R knows about a variety of link functions including the log ($x = \log(y)$, which linearizes $y = e^x$); square root ($x = \sqrt{y}$, which linearizes $y = x^2$); and inverse ($x = 1/y$, which linearizes $y = 1/x$): see `?family` for more possibilities.

The class of nonnormal errors that generalized linear models can handle is called the *exponential family*. It includes Poisson, binomial, Gamma and normal distributions, but not negative binomial or beta-binomial distributions. Each distribution has a standard link function: the log link is standard for a Poisson, a logit link is standard

for a binomial distribution, etc. The standard link functions make sense for typical applications. For example, the logit transformation converts unconstrained values into values between 0 and 1, which are appropriate as probabilities in a binomial model. However, **R** does allow you some flexibility to change these associations for specific problems.

GLMs are fit by a process called *iteratively reweighted least squares*, which overcomes the basic problem that transforming the data to make them linear also changes the variance. The key is that given an estimate of the regression parameters, and knowing the relationship between the variance and the mean for a particular distribution, one can calculate the variance associated with each point. With this variance estimate, one reestimates the regression parameters weighting each data point by the inverse of its variance; the new estimate gives new estimates of the variance; and so on. This procedure quickly and reliably fits the models, without the user needing to specify starting points.

Generalized linear models combine a range of nonnormal error distributions with the ability to work with some reasonable nonlinear functions. They also use the same simple model specification framework as **lm**, allowing us to explore combinations of factors, covariates, and interactions among variables. GLMs include logistic and binomial regression and log-linear models. They use terminology that should now be familiar to you; they estimate log-likelihoods and test the differences between models using the LRT.

The **glm** function implements generalized linear models in **R**. By far the two most common GLMs are Poisson regression, for count data, and logistic regression, for survival/failure data.

- Poisson regression: log link, Poisson error ($Y \sim \text{Poisson}(ae^{bx})$):

```
> glm1 = glm(y ~ x, family = "poisson")
```

The equivalent likelihood function is

```
> poisregfun = function(a, b) {
+   Y.pred = exp(a + b * x)
+   -sum(dpois(y, lambda = Y.pred, log = TRUE))
+ }
```

- Logistic regression: logit link, binomial error ($Y \sim \text{Binom}(p = \exp(a + bx) / (1 + \exp(a + bx)), N)$):

```
> glm2 = glm(cbind(y, N - y) ~ x, family = "binomial")
```

or

```
> logistregfun = function(a, b) {
+   p.pred = exp(a + b * x) / (1 + exp(a + b * x))
+   -sum(dbinom(y, size = N, prob = p.pred, log = TRUE))
+ }
```

(You could also say `p.pred=plogis(a+b*x)` in the first line of `logistregfun`.)

GLMs can also fit models of exponentially decreasing survival, $Y \sim \text{Binom}(p = \exp(a + bx), N)$. Strong et al. (1999) modeled the survival probability of ghost

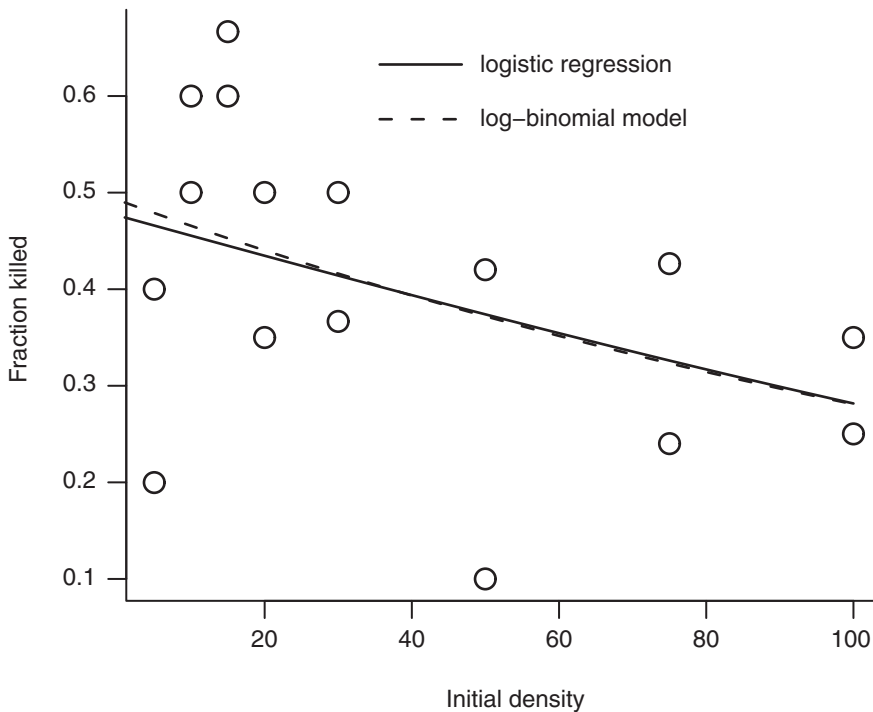


Figure 9.5 Logistic (binomial) regression and log-binomial regression of fraction of tadpoles killed as a function of tadpole density. Logistic regression:

```
glm(cbind(Killed, Initial-Killed) ~ Initial, family="binomial",
data=ReedfrogFuncresp)
```

Log-binomial regression: `glm(..., family=binomial(link="log"), ...)`

moth caterpillars as a decreasing function of density (and as a function of the presence or absence of entomopathogenic nematodes); Tiwari et al. (2006) modeled the probability that nesting sea turtles would *not* dig up an existing nest as a decreasing function of nest density. You can fit such a model this way:

```
> glm3 = glm(cbind(y, N - y) ~ x, family = binomial(link =
+ "log"))
```

Use `family=binomial(link="log")` instead of `family="binomial"` to specify the log instead of the logit link function. The equivalent negative log-likelihood function is

```
> logregfun = function(a, b) {
+   p.pred = exp(a + b * x)
+   -sum(dbinom(y, size = N, prob = p.pred, log = TRUE))
+ }
```

You can use either a logistic or a log-binomial model to fit Vonesh's tadpole mortality data (Figure 9.5), but the fact that expected survival decreases exponentially at high densities in both models causes problems of interpretation. If the probability

of survival declines exponentially with density—which is true for the log-binomial model and approximately true at high densities for the logistic—then the expected *number* surviving is $p(x) \cdot x = e^{-(a+bx)}x = cxe^{-bx}$. This is a Ricker function, which decreases to zero at high density rather than reaching an asymptote. In predator-prey systems for example, rather than this *overcompensation* response to density, we usually expect *compensatory* behavior—predation rate reaching an asymptote—the standard type II functional response model uses $p(x) = A/(1 + Abx)$, which has a weaker dependence on x , and which makes the limit of $p(x)x$ as x becomes large equal to $1/b$. The GLM, while convenient, may not be ecologically appropriate in this case.

After you fit a GLM, you can use the same generic set of modeling functions—`summary`, `coef`, `confint`, `anova`, and `plot`—to examine the parameters, test hypotheses, and plot residuals. `anova(glm1, glm2, ...)` does an *analysis of deviance* (Likelihood Ratio tests) on a nested sequence of models. As with `lm`, the default parameters represent (1) the intercept (the baseline value of the first treatment), (2) differences in the intercept between the first and subsequent treatments, (3) the slope(s) with respect to the covariate(s) for the first group, or (4) differences in the slope between the first and subsequent treatments. However, all of the parameters are given on the scale of the link function (e.g., log scale for Poisson models, logit scale for binomial models). To interpret them, you need to transform them with the inverse link function (exponential for Poisson, logistic (`=plogis`) for binomial). For example, the coefficients of the logistic regression shown in Figure 9.5 are intercept = -0.095 , slope = -0.0084 . To find the probability of mortality at a tadpole density of 60, calculate $\exp(-0.095 + -0.0084 \cdot 60)/(1 + \exp(-0.095 + -0.0084 \cdot 60)) = 0.355$.

Further reading: McCullagh and Nelder (1989); Dobson (1990); Hastie and Pregibon (1991); Lindsay (1997). R-specific: Crawley (2002); Faraway (2006).

9.4.1 Models for Overdispersion

To go beyond the exponential family of distributions (normal, binomial, Poisson, Gamma) you may well need to roll your own ML estimator. R has two built-in possibilities for the very common case of discrete data with *overdispersion*, i.e., more variance than would be expected from the standard (Poisson and binomial) models for discrete data.

9.4.1.1 QUASI LIKELIHOOD

Quasi-likelihood models “inflate” the expected variance of models to account for overdispersion (McCullagh and Nelder, 1989). For example, the expected variance of a binomial distribution with N samples and probability p is $Np(1 - p)$. The *quasi-binomial* model adds another parameter, ϕ , which inflates the variance to $\phi Np(1 - p)$. The *overdispersion parameter* ϕ (Burnham and Anderson (2004) call it \hat{c}) is generally greater than 1—we usually find more variance than expected, rather than less. Quasi-Poisson models are defined similarly, with variance equal to $\phi\lambda$. This approach is called *quasi* likelihood because we don’t specify a real likelihood model

with a probability distribution for the data. We just specify the relationship between the mean and the variance. Nevertheless, the quasi-likelihood approach works well in practice. R uses the `family` function to specify quasi-likelihood models.

Because the quasi likelihood is not a true likelihood, we cannot use Likelihood Ratio tests or other likelihood-based methods for inference, but the parameter estimates and t statistics generated by `summary` should still work. However, various researchers have suggested that using an F test based on the ratio of deviances is appropriate: use `anova(..., test="F")` (Crawley, 2002; Venables and Ripley, 2002). Burnham and Anderson (2004) suggest using differences in “quasi-AIC” (qAIC) in this case, where the $\Delta qAIC$ uses the difference in deviance divided by the estimate of ϕ .

Since the log is the default link function for the `quasipoisson` family, you can fit a quasi-Poisson log-log model for fecundity as follows:

```
> glm(TOTCONES ~ log(DBH), data = firdata, family =
+      "quasipoisson")
```

9.4.1.2 NEGATIVE BINOMIAL MODELS

Although the exponential family does not strictly include the negative binomial distribution, negative binomial models can be fit by a small extension of the GLM approach, iteratively fitting the k (overdispersion) parameter and then fitting the rest of the model with a fixed k parameter. The `glm.nb` function in the MASS package fits linear negative binomial models, although they restrict the model to a single k parameter for all groups. (Use `$theta` to extract the estimate of the negative binomial k parameter from a negative binomial model.)

Because we can use a log link (which is `glm.nb`'s default link), we can exactly replicate our original log-likelihood model (`cones ~ NegBin($a \cdot DBH^b, k$)`) with the following command:

```
> glm.nb(TOTCONES ~ log(DBH), data = firdata)
```

The only difference from our earlier model is that the estimated intercept parameter is $\log(a)$ rather than a .

9.5 R Supplement

Here's how to fit various linear models to the log-transformed fir data. Since the data (TOTCONES) contain some zero values, taking logarithms would give us negative infinite values. We need either to drop these values (`subset=TOTCONES>0`) or to add an offset of 1, in order to avoid infinities. However, since there are few zeros in the data (`sum(firdata$TOTCONES==0)` is 10 out of a total of 242 data points) and the mean number of cones is large, this adjustment shouldn't affect the results much. If zeros are frequent so that such an adjustment would affect your results significantly, or if the results vary depending on how large an offset you add, consider a different model (Section 9.4).


```

> logcones = log(firdata$TOTCONES + 1)
> lm.0 = lm(logcones ~ 1, data = firdata)
> lm.d = lm(logcones ~ log(DBH), data = firdata)
> lm.w = lm(logcones ~ WAVE_NON, data = firdata)
> lm.dw = lm(logcones ~ log(DBH) + WAVE_NON, data = firdata)
> lm.dwi = lm(logcones ~ log(DBH) * WAVE_NON,
+           data = firdata)

```

Since $\log(\text{DBH})$ is a covariate and WAVE_NON is a factor, lm.d is a regression; lm.w is a one-way ANOVA; and lm.dw and lm.dwi are ANCOVA models with parallel and nonparallel slopes, respectively.

A few different ways to analyze the data:

```

> anova(lm.0, lm.d, lm.dw, lm.dwi)

```

Analysis of Variance Table

```

Model 1: logcones ~ 1
Model 2: logcones ~ log(DBH)
Model 3: logcones ~ log(DBH) + WAVE_NON
Model 4: logcones ~ log(DBH) * WAVE_NON

```

	Res.Df	RSS	Df	Sum of Sq	F	Pr(>F)
1	241	384.53				
2	240	250.33	1	134.20	127.7512	<2e-16 ***
3	239	250.29	1	0.04	0.0393	0.8431
4	238	250.02	1	0.27	0.2535	0.6151

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

```

> AIC(lm.0, lm.d, lm.w, lm.dw, lm.dwi)

```

	df	AIC
lm.0	2	802.8349
lm.d	3	700.9556
lm.w	3	786.5281
lm.dw	4	702.9157
lm.dwi	5	704.6580

(I left lm.w out of the `anova` statement because it and lm.d cannot be nested.) `anova` compares the models sequentially, while `AIC` compares them simultaneously. `AICtab` in the `emdbook` package offers several more options such as sorting the table in order of increasing AIC or computing AIC weights. Try `coef`, `summary`, and `confint` on these models as well.

The full ANCOVA model fit via `mle2`:

```

> ancovafun = function(i1, i2, slope1, slope2, sigma) {
+   int = c(i1, i2)[WAVE_NON]
+   slope = c(slope1, slope2)[WAVE_NON]
+   Y.pred = int + slope * log(DBH)
+   -sum(dnorm(logcones, mean = Y.pred, sd = sigma,

```

```
+      log = TRUE))
+ }
> m1 = mle2(ancovafun, start = list(i1 = -2, i2 = -2,
+      slope1 = 2.5, slope2 = 2.5, sigma = 1),
+      data = firdata)
> AIC(m1)
[1] 704.658
```

The maximum likelihood fit gives the same AIC as the `lm` fit. You can't always take this equality for granted, since different models that are formally equivalent may include different constants in the likelihood, and different functions may count the number of parameters differently. This is especially true when comparing results from different statistics packages.

As pointed out in the text, the models are parameterized differently:

```
> coef(lm.dwi)

(Intercept)      log(DBH)      WAVE_NONw      log(DBH):WAVE_NONw
-2.3871702      2.7303449      0.5162954      -0.2630837

> coef(m1)

      i1      i2      slope1      slope2      sigma
-2.387134 -1.870762  2.730329  2.467205  1.016441
```

You can check that the answers are equivalent; for example, the slope of the wave population is $\text{slope2} = 2.467 = \log(\text{DBH}) + \log(\text{DBH}): \text{WAVE_NONw}$.

To do the full model comparison with `mle2`, you have to construct a series of nested models (analogous to `lm.dw`, `lm.d`, `lm.w`, `lm.0`). This is a bit tedious—one reason for using built-in functions where possible. You may want to read about the `model.matrix` function, which can simplify model construction. `model.matrix` uses a user-specified formula to construct a *design matrix* that, when multiplied by a vector of parameters, gives the expected value of each data point. By default the design matrix uses parameters that represent baseline levels and differences among groups, as in `lm` and `glm`. `mle2`'s formula interface uses `model.matrix` internally, so that (e.g.) you can easily fit the full ANCOVA model by specifying

```
> mle2(log(TOTCONES + 1) ~ dnorm(i + slope*log(DBH), sd),
> parameters = list(i ~ WAVE_NON, slope ~ WAVE_NON),
+      data = firdata, start = ...)
```

Congratulations

You have now finished the first part of the book, which covers all the important basic tools. You know everything you need to know to fit reasonably complex, realistic ecological models to your data.



Models with multiple levels of variability and dynamical models, the subjects of the last two chapters, are much harder to create and fit from scratch. Powerful and specialized statistical methods that have been developed to handle these problems are beginning to make their way into ecology. The second part of the book will give a brief overview of these topics, but to use them in any serious way you will have to go to a specialized reference such as Gelman and Hill (2006) or Clark (2007) to learn more. The good news is that the concepts and terminology you have now learned should speed up the learning process considerably.

If your brain is full after the first part of the book, stop here. If you are eager for more, read on. If you are already swamped but desperately need to incorporate multiple levels of variability in your analysis, see Section 10.4.3 for ways of avoiding multilevel models. If you are swamped but must do something to estimate parameters for a dynamic model, see Section 11.4.