

Review of Probability Theory

- ❖ Measurements of random events may be made in either continuous or discrete time.
- ❖ Examples are, height, number of heads when a coin is tossed 10 times.
- ❖ Random variables are characterized by a probability density function (probability mass function for discrete random variables), $g(x)$, which have the property that $\int_{-\infty}^{\infty} g(x)dx = 1$, or $\sum_{i=a}^{i=b} g(x_i) = 1$, where x_i takes on values, x_a, \dots, x_b .
- ❖ Examples: uniform distribution on $(0,2)$, $g(x)=0.5$,
$$\int_0^2 0.5dx = 0.5x \Big|_0^2 = 0.5(2 - 0) = 1$$

Review of Probability Theory (cont.)

- ❖ Binomial distribution, $g(x) = \binom{n}{x} p^x (1-p)^{n-x}$, where

$$\binom{n}{x} = \frac{n!}{x! (n-x)!}$$

- ❖ mean = np and variance = $np(1-p)$
- ❖ Example, with $n=2$, $p=0.6$,

$$\begin{aligned} \sum_{x=0}^{x=2} \binom{2}{x} 0.6^x (1-0.6)^{2-x} &= 1 \cdot 0.6^0 \cdot 0.4^2 + 2 \cdot 0.6^1 \cdot 0.4^1 + 1 \cdot 0.6^2 \cdot 0.4^0 \\ &= 0.16 + 0.48 + 0.36 = 1 \end{aligned}$$

Expectation

- ❖ The expected value of a function, $f(x)$, of a random variable is,
 $E[f(x)] = \int_{-\infty}^{\infty} f(x)g(x)dx$ or $E[f(x)] = \sum_{i=a}^b f(x_i)g(x_i)$
- ❖ Example, let $f(x)=x$, then using the previous examples,
Uniform: $\int_0^2 0.5x dx = 0.5 \cdot 0.5x^2 \Big|_0^2 = 0.25(4 - 0) = 1$
Binomial: $0.16 \cdot 0 + 0.48 \cdot 1 + 0.36 \cdot 2 = 0 + 0.48 + 0.72 = 1.2$
- ❖ The mean of a random variable can be defined as, $E[x]$, and the variance, $E[(x-E(x))^2]$.
- ❖ $\text{Cov}(xy) = E\{[x-E(x)][y-E(y)]\}$

Expectation and Variance

- ❖ $E[cx] = cE[x]$, where c is a constant
- ❖ $E[k+cx] = k + cE[x]$, where k and c are constants
- ❖ $\text{Var}(c) = 0$
- ❖ $\text{Var}(cx) = c^2\text{Var}(x)$ -> prove this by using the definition of variance, $E[(x - E(x))^2]$
- ❖ Show that, $\text{Var}(x) = E(x^2) - E(x)^2$ and $\text{Cov}(xy) = E(xy) - E(x)E(y)$
- ❖ $\text{Var}(x+y) = \text{Var}(x) + \text{Var}(y) + 2\text{Cov}(xy)$ -> prove by using the definition of variance

Conditional Expectation and Probability

- ❖ For discrete random variable
- ❖ $E[Y] = \sum_{\text{over } x} E[Y|X = x]g(x) = E[E[Y|X = x]]$
- ❖ If X and Y are independent, $E[Y|X=x] = E[Y]$
- ❖ $E[f(X, Y)|X = x] = E[f(x, Y)|X = x]$
- ❖ $\text{Var}[Y] = E[\text{Var}(Y|X)] + \text{Var}[E(Y|X)]$

Conditional Mean and Variance: Example

- ❖ Example: Suppose we have many vials with fruit flies. The number of females in a vial (N) is a random variable with a binomial distribution, $\sim B(\tilde{N}, p)$, where \tilde{N} is the total number (constant) of flies placed in a vial. Suppose the number of eggs laid by each female (X) has a Poisson distribution, with parameter λ (mean and variance $=\lambda$). Then the total number of eggs laid in a vial is,
 $Y = X_1 + X_2 + \dots + X_N$.
- ❖ $E[Y|N=n] = nE[X] \rightarrow E[Y] = E[X] \sum_{j=0}^{\tilde{N}} j \binom{\tilde{N}}{j} p^j (1-p)^{\tilde{N}-j} = E[X] \tilde{N} p = \lambda \tilde{N} p$

Conditional Mean and Variance: Example (cont.)

- ❖ $\text{Var}(Y) = E[\text{Var}(Y)|N=n] + \text{Var}(E[Y|N=n]) = E[n\text{Var}(X)] + \text{Var}(nE(X))$,
since $\text{Var}(Y)|N=n = \text{Var}[X_1 + X_2 + \dots + X_n] = n\text{Var}(X)$ and
 $E[Y|N=n] = E[X_1 + X_2 + \dots + X_n] = nE(X)$

$$\text{Var}(Y) = E(N)\text{Var}(X) + E(X)^2\text{Var}(N),$$

since $\text{Var}(X)$ and $E(X)$ are constants

$$\text{Var}(Y) = \tilde{N}p\lambda + \lambda^2p(1-p)\tilde{N}$$

- ❖ If $\tilde{N} = 100$, $p = 0.5$, $\lambda = 10$, then $E[Y] = 500$, and $\text{Var}(Y) = 3,000$
an approximate 95% confidence interval is $2 \cdot \sqrt{3000} = 110$

Taylor Series

- ❖ The value of a function near a point x^* can be approximated with the Taylor Series.
- ❖ For the function $f(x)$ let $f^{(n)}(x^*)$ be the n th derivative evaluated at the point x^* , then

$$f(x) = f(x^*) + \frac{(x - x^*)}{1!} f^{(1)}(x^*) + \dots + \frac{(x - x^*)^n}{n!} f^{(n)}(x^*)$$

- ❖ Example: exponential function at $x^*=0$,

$$e^x \cong 1 + x + \frac{x^2}{2!} + \frac{x^3}{3!} + \dots + \frac{x^n}{n!}$$

- ❖ If we just use the first two terms, $e^{0.1} \cong 1.1$, while the true answer is 1.105.
- ❖ If x is far from x^* then the approximation will be poor. So $e^5 \cong 6$, while the true value is 148.

Delta Method

- ❖ The delta method is a way of approximating the variance of complicated functions.
- ❖ M , which is a complicated function of k parameters, c_1, c_2, \dots, c_k , e. g. $M = F(c_1, c_2, \dots, c_k)$.
- ❖ The parameters are estimated as, $\hat{c}_1, \hat{c}_2, \dots, \hat{c}_k$. Then, $\hat{M} \cong F(\hat{c}_1, \hat{c}_2, \dots, \hat{c}_k)$.
- ❖ The delta method uses a Taylor series expansion around $E(c_i)$ which in practice will be estimated by \hat{c}_i .

$$\hat{M} \cong F[E(c_1), E(c_2), \dots, E(c_k)] + (c_1 - E(c_1)) \frac{dF}{dc_1} \Big|_{c_1=E(c_1)} + \dots + (c_k - E(c_k)) \frac{dF}{dc_k} \Big|_{c_k=E(c_k)}$$

- ❖ Then noting that $Var(\hat{M}) = E\left[\left(\hat{M} - F[E(c_1), \dots, E(c_k)]\right)^2\right]$

- ❖
$$\sum_i Var(\hat{c}_i) \left(\frac{dF}{dc_i}\right)^2 + \sum_i \sum_{j \neq i} Cov(\hat{c}_i, \hat{c}_j) \frac{dF}{dc_i} \frac{dF}{dc_j}$$

Delta method: example

- ❖ Let X and Y be independent random variable with means, μ_x and μ_y and variances σ_x^2 , and σ_y^2 .
- ❖ Find $\text{Var}(X/Y)$
- ❖ $\frac{\partial(X/Y)}{\partial X} = \frac{1}{Y}$, evaluated at μ_y yields $1/\mu_y$
- ❖ $\frac{\partial(X/Y)}{\partial Y} = -X/Y^2$, evaluated at μ_x and μ_y yields, $\frac{-\mu_x}{\mu_y^2}$
- ❖
$$\text{Var}\left(\frac{X}{Y}\right) = \frac{\sigma_x^2}{\mu_y^2} + \sigma_y^2 \frac{\mu_x^2}{\mu_y^4} = \frac{\mu_x^2}{\mu_y^2} \left[\frac{\sigma_x^2}{\mu_x^2} + \frac{\sigma_y^2}{\mu_y^2} \right]$$

Euphydryas editha: example



- ❖ 1985, Genetics 110: 495
- ❖ Estimates of effective population size require an estimate of the variance in reproductive success
$$N_e = \frac{2(2N-1)}{(V_m/2+3)}$$
(assuming equal sex ratio, no pop growth, male variance = mean)
- ❖ X_i number of eggs laid in the i th egg mass, with mean μ_{X_i} and variance $\sigma_{X_i}^2$.
- ❖ Host plant desiccation $\rightarrow Y \begin{cases} 0 \text{ w.p. } \delta \\ 1 \text{ w.p. } 1 - \delta \end{cases}$
- ❖ Z_j is a Bernoulli random variable that represent the chance that the j th individual that did not dry out survives to become an adult w.p. λ .
- ❖ The number of surviving larvae that become adults from egg mass- i is W_i .
- ❖ Find the mean and variance of W_i .

Conditional mean

- ❖ Lower case variables are realizations of the random variable.
- ❖ Given, $Y=y$ and $X_i=x_i$, then the number of adults is $\sum_{j=1}^{yx_i} z_j = E[W_i | x_i, y, \sum z_j]$.
- ❖ $E \left[\sum_{j=1}^{yx_i} Z_j | x_i, y \right] = yx_i\lambda$, since $\sum Z_j \sim B(x_i y, \lambda(1 - \lambda)x_i y)$
- ❖ $E[x_i Y \lambda | x_i] = x_i \cdot 0 \cdot \lambda \cdot \delta + x_i \cdot 1 \cdot \lambda \cdot (1 - \delta) = x_i \lambda (1 - \delta)$
- ❖ $E[W_i] = E[X_i \lambda (1 - \delta)] = \mu_{X_i} \lambda (1 - \delta)$

Conditional Variance

- ❖ Let $E[W_i] = \mu_{x_i}\lambda(1 - \delta) = \widehat{W}$
- ❖
$$\begin{aligned} Var(\sum_{j=1}^{y_{x_i}} z_j | x_i, y) &= E[yx_i\lambda(1 - \lambda)] + Var(yx_i\lambda) \\ &= yx_i\lambda(1 - \lambda) + E\{[yx_i\lambda - \widehat{W}]^2\} \\ &= E(Yx_i\lambda(1 - \lambda) | x_i) + E[(Yx_i\lambda - \widehat{W})^2 | x_i] \\ &= x_i \lambda(1 - \lambda)(1 - \delta) + \widehat{W}^2\delta + (1 - \delta)E[(x_i\lambda - \widehat{W})^2] \\ &= x_i \lambda(1 - \lambda)(1 - \delta) + \widehat{W}^2\delta + (1 - \delta)E[\lambda^2 x_i^2 - 2\lambda x_i \widehat{W} + \widehat{W}^2] \\ &= \mu_x \lambda(1 - \lambda)(1 - \delta) + \widehat{W}^2\delta + (1 - \delta)[\lambda^2(\mu_{x_i}^2 + \sigma_{x_i}^2) - 2\lambda\mu_{x_i}\widehat{W} + \widehat{W}^2] \\ &= \dots algebra = \widehat{W} \left(1 - \lambda - \widehat{W} + \lambda \frac{\sigma_{x_i}^2}{\mu_{x_i}} + \lambda\mu_{x_i} \right) \end{aligned}$$
- ❖ Since this is for one clutch if the clutches are independent then we sum this quantity over all 1-4 clutches.
- ❖ The total variance could then range from 2.9 to 31. For the standard Wright-Fisher model this would be assumed to be 2.