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APPROXIMATING VARIANCE OF DEMOGRAPHIC PARAMETERS USING THE DELTA METHOD: A REFERENCE FOR AVIAN BIOLOGISTS

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Abstract. Avian biologists routinely estimate sampling variance for parameter estimates such as daily nest survival, fecundity, annual survival, and density. However, many biologists are not certain of methods to derive sampling variance for parameters when survival rates change temporal scales. Similar methods are needed to obtain sampling variance when biologists combine parameter estimates to calculate an indirect demographic parameter, such as population growth rate. The delta method is a useful technique for approximating sampling variance when the desired demographic parameter is a function of at least one other demographic parameter. However, the delta method is rarely taught in most graduate-level biology or ecology courses, and application of this method may be discouraged by seemingly daunting formulas in reference books. Here, I provide five examples of sampling variance approximations for common situations encountered by avian ecologists, with step-by-step explanations of the equations involved.

Key words: delta method, demographic analyses, sampling variance approximation.

Aproximación de la Varianza para Parámetros Demográficos Utilizando el Método Delta: una Referencia para Biólogos de Aves

Resumen. Los biólogos que estudian aves estiman la varianza muestral para los estimados de parámetros como la supervivencia diaria, la fecundidad, la supervivencia anual o la densidad. Sin embargo, muchos biólogos no tienen la certeza sobre los métodos adecuados para derivar la varianza muestral para los parámetros cuando las tasas de supervivencia cambian de escala temporal. Métodos similares son requeridos para obtener la varianza muestral cuando se combinan estimados de parámetros para calcular un parámetro demográfico indirecto como la tasa de crecimiento poblacional. El método delta es una técnica útil para aproximar la varianza muestral cuando el parámetro demográfico deseado es función de por lo menos un otro parámetro demográfico. Sin embrago, el método delta es enseñado en raras ocasiones en cursos de biología o ecología de nivel de post-grado, y la aplicación de este método en muchos casos es desincentivada debido a las formulas aparentemente complicadas que aparecen en libros de referencia. Aquí brindo cinco ejemplos para la aproximación de la varianza muestral en situaciones a las cuales se pueden enfrentar comúnmente los ecólogos de aves con explicaciones paso a paso de las ecuaciones involucradas.

Avian biologists routinely need to estimate standard deviation, standard error, confidence intervals, or other measures of sampling variance for parameter estimates such as daily nest survival, fecundity, annual survival, and density. Software packages, such as program MARK (White and Burnham 1999) and program DISTANCE (Buckland et al. 2001), provide estimates of standard error (SE; $S\hat{E}\left(\hat{\theta}\right) = \sqrt{\hat{\mathrm{var}}\left(\hat{\theta}\right)}$). Traditional statistical software packages also provide direct estimates of sampling variance. Thus, when a parameter is estimated directly from raw data and can be reported in the temporal scale in which the parameter was estimated, it is straightforward to report estimates of sampling variance.

Variance estimates become problematic when biologists are required to: (1) change temporal scales (e.g., extrapolate daily nest survival estimates to 24-day nest success estimates), (2) combine demographic parameter estimates to indirectly calculate a demographic parameter (e.g., multiply nest success and clutch size to calculate fecundity), or (3) average demographic parameters across years (e.g., mean of three years of density estimates). In all of these cases, the new demographic parameter is a function of at least one other demographic parameter; thus, the sampling variance of the new parameter is also a function of the sampling variance of the former parameters (Williams et al. 2002).

The delta method is a useful technique for approximating sampling variance in situations such as those described above (Seber 1982). Although the delta method is not new, few ecologists are exposed to this method, and few use it to approximate sampling variances. The delta method is not lacking in proponents; recently, Hilborn and Mangel (1997:58–59), Williams et al. (2002:736), Skalski et

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TABLE 1. General rules for calculating sampling variances using the delta method. Examples are provided for each set of simple relationships. In the functions provided, c is a constant, and θ is a parameter (e.g., survival rate or density estimate).

Rule		Example	
Function	Variance approximation	Function	Variance approximation
$c\theta$	$c^2\mathrm{var}(\theta)$	$\mathrm{N}\theta$	$\mathrm{N}^2\mathrm{var}(\theta)$
$\frac{\theta}{c}$	$\left(\frac{1}{c}\right)^2 \mathrm{var}(\theta)$	$\frac{1}{5}\theta$	$\frac{1}{25}\mathrm{var}(\theta)$
$c + \theta$	$\mathrm{var}(\theta)$	$\theta + 0.10$	$\mathrm{var}(\theta)$
θ^c	$c^2\theta^{(c-1)2}\mathrm{var}(\theta)$	θ^7	$49\theta^{12}\mathrm{var}(\theta)$
$\theta^{\frac{1}{c}}$	$\frac{1}{c^2}\theta^{\left[\frac{2(1-c)}{c}\right]}\ \mathrm{var}(\theta)$	$\theta^{\frac{1}{7}}$	$\frac{1}{49}\sqrt[7]{\theta^{12}} \cdot \mathrm{var}(\theta)$

al. (2005:570–571), Cooch and White (2006:B1–B23), and MacKenzie et al. (2006:66, 73–75) have referred biologists to the delta method. However, these references provide a set of potentially daunting source equations that include partial derivatives, and biologists are left with few step-by-step examples to follow to apply the delta method. Thus, despite recent suggestions to use the delta method to approximate sampling variance, avian biologists continue to publish critical comparisons without estimates of sampling variance to guide decision-making or hypothesis evaluation.

The goal of this paper is to provide a sample of variance approximations for common parameters calculated by avian ecologists. I provide several case examples to serve as guides for potential applications of the delta method to avian data. Here, I focus specifically on sampling variance, resulting from estimating demographic parameters from a sample of an avian population. White et al. (1982) and Franklin et al. (2000) provide valuable overviews of the difference between sampling and process variation.

THE DELTA METHOD

The "delta method" (Seber 1982) approximates the variance of any parameter (e.g., G) that is a function of one or more random variables (X_1, X_2, ..., X_n), each with its own estimate of variance. The delta method is based on a first-order Taylor series transformation (Snedecor and Cochran 1989:286–287). When random variables are independent, the following generalized formula can be used (Seber 1982:7–9):

$$\mathrm{var}(G) = \mathrm{var}[f(X_1, X_2, ..., X_n)] = \sum_{i=1}^{n} \mathrm{var}(X_i)\left[\frac{\partial f}{\partial X_i}\right]^2, \quad (1)$$

where $\frac{\partial f}{\partial X_i}$ is the partial derivative of G, with respect to X_i. When random variables are not independent, covariance of the random variables must be incorporated into the variance approximation:

$$\begin{aligned}\mathrm{var}(G) &= \mathrm{var}[f(X_1, X_2, ..., X_n)] \\ &= \sum_{i=1}^{n} \mathrm{var}(X_i)\left[\frac{\partial f}{\partial X_i}\right]^2 \\ &+ 2\sum_{i=1}^{n}\sum_{j=1}^{n} \mathrm{cov}(X_i, X_j)\left[\frac{\partial f}{\partial X_i}\right]\left[\frac{\partial f}{\partial X_j}\right].\end{aligned} \quad (2)$$

CASE EXAMPLES

SINGLE VARIABLE TRANSFORMATIONS

Simple transformation. The simplest application of the delta method is when we manipulate a single variable (Table 1). For example, we might have a known number of nesting female birds (N), with a subsample of nests from which we obtain an average clutch size ($\hat{\mu}_c$) and its sampling variance, $\hat{\mathrm{var}}(\hat{\mu}_c)$. From this sample of nests, a biologist might need to predict the number of eggs produced by the population, as well as the sampling variance for this prediction. To apply the delta method, we must start by describing the relationship between the demographic rates in question. The estimate of total egg production ($\hat{p}$) by the nesting population would be: $\hat{p} = N \cdot \hat{\mu}_c$. But, we also need to derive the variance for $\hat{p}$.

To use the delta method to arrive at this approximation, using equation 1 with a single variable transformation, we simply have:

$$\hat{\mathrm{var}}(\hat{p}) = \hat{\mathrm{var}}(\hat{\mu}_c)\left[\frac{\partial \hat{p}}{\partial \hat{\mu}_c}\right]^2. \quad (3)$$

Next, we take the derivative of the function, p, which we can express as $(N \cdot \hat{\mu}_c)'$. Because $\hat{\mu}_c$ is our parameter of interest (generically, x) for the partial derivative, N becomes a constant (generically, c). So we use the cx rule in Table 2 to find that our derivative equals N. By substituting N for the derivative in equation 3 and squaring, we arrive at our variance approximation (Table 1):

$$\hat{\mathrm{var}}(\hat{p}) = N^2 \cdot \hat{\mathrm{var}}(\hat{\mu}_c). \quad (4)$$

Changing temporal scale. Let's evaluate a second example with a single variable. Consider that we want to take a daily nest survival rate estimate ($\hat{S}_d$), and extrapolate it to a weekly nest survival estimate ($\hat{S}_w$). Following the process outlined in our first example, above, we first need to establish the relationship as: $\hat{S}_w = (\hat{S}_d)^7$.

Next, substitute values in equation 1:

$$\hat{\mathrm{var}}\left(\hat{S}_w\right) = \hat{\mathrm{var}}\left(\hat{S}_d\right)\left[\frac{\partial \hat{S}_w}{\partial \hat{S}_d}\right]^2. \quad (5)$$

We have an estimate of $\mathrm{var}(\hat{S}_d)$ from our daily nest survival analysis, so we only need the derivative of $\hat{S}_d{}^7$. In this case, our parameter of interest (x) for the derivative is $\hat{S}_d$, and it is raised to the power of 7. We use the x^c rule in Table 2, to find:

$$\left[\frac{\partial \hat{S}_w}{\partial \hat{S}_d}\right] = \left(\hat{S}_d^7\right)' = 7\hat{S}_d^6.$$

After substituting for the derivative in equation 5, the resulting approximation of $\mathrm{var}(\hat{S}_w)$ is (Table 1):

$$\hat{\mathrm{var}}\left(\hat{S}_w\right) = 49 \cdot \hat{\mathrm{var}}\left(\hat{S}_d\right) \cdot \hat{S}_d^{12}. \quad (6)$$

More examples of changes in temporal scale for survival rate estimates of interest to avian ecologists are provided in Table 3 (an on-line variance calculator for these examples can be found at <http://snr.unl.edu/powell/research/research.htm>).

TABLE 2. Simple rules for calculating derivatives for use in the approximation of variance using the delta method. In the functions provided, c is a constant, and x is a parameter (e.g., survival rate or density estimate). Derivative rules after Larson and Hostetler (1982).

Function	Derivative
c	0
x	1
cx	c
$x + c$	x
x^c	$cx^{(c-1)}$
$\frac{x}{c}$	$\frac{1}{c}$
$\frac{c}{x}$	$-\frac{c}{x^2}$

TABLE 3. Approximations for sampling variance of survival estimates, by the delta method, when changing the scale of temporal units.

Survival temporal rescaling			
From	To	Relationship	Variance approximation
Daily	Weekly	$\hat{S}_w = (\hat{S}_D)^7$	$\hat{\mathrm{var}}(\hat{S}_w) = 49 \cdot \hat{\mathrm{var}}(\hat{S}_D) \cdot \hat{S}_D{}^{12}$
Daily	Monthly (30 days)	$\hat{S}_M = (\hat{S}_D)^{30}$	$\hat{\mathrm{var}}(\hat{S}_M) = 900 \cdot \hat{\mathrm{var}}(\hat{S}_D) \cdot \hat{S}_D{}^{58}$
Daily	Annual	$\hat{S}_A = (\hat{S}_D)^{365}$	$\hat{\mathrm{var}}(\hat{S}_A) = 133225 \cdot \hat{\mathrm{var}}(S_D) \cdot \hat{S}_D{}^{728}$
Weekly	Daily	$\hat{S}_D = \sqrt[7]{\hat{S}_W}$	$\hat{\mathrm{var}}\left(\hat{S}_D\right) = \frac{1}{49} \cdot \hat{\mathrm{var}}\left(\hat{S}_W\right) \cdot \sqrt[7]{\hat{S}_W^{12}}$
Weekly	Monthly (4 weeks)	$\hat{S}_M = (\hat{S}_W)^4$	$\hat{\mathrm{var}}(\hat{S}_M) = 16 \cdot \hat{\mathrm{var}}(\hat{S}_W) \cdot \hat{S}_W{}^6$
Weekly	Annual (52 weeks)	$\hat{S}_A = (\hat{S}_W)^{52}$	$\hat{\mathrm{var}}(\hat{S}_A) = 2704 \cdot \hat{\mathrm{var}}(\hat{S}_W) \cdot \hat{S}_W{}^{102}$
Monthly (30 days)	Daily	$\hat{S}_D = \sqrt[30]{\hat{S}_M}$	$\hat{\mathrm{var}}\left(\hat{S}_D\right) = \frac{1}{900} \cdot \hat{\mathrm{var}}\left(\hat{S}_M\right) \cdot \sqrt[30]{\hat{S}_M^{58}}$
Monthly (4 weeks)	Weekly	$\hat{S}_W = \sqrt[4]{\hat{S}_M}$	$\hat{\mathrm{var}}\left(\hat{S}_W\right) = \frac{1}{16} \cdot \hat{\mathrm{var}}\left(\hat{S}_M\right) \cdot \sqrt[4]{\hat{S}_M^{6}}$
Monthly	Annual	$\hat{S}_A = (\hat{S}_M)^{12}$	$\hat{\mathrm{var}}(\hat{S}_A) = 144 \cdot \hat{\mathrm{var}}(\hat{S}_M) \cdot \hat{S}_M{}^{132}$
Annual	Daily	$\hat{S}_D = \sqrt[365]{\hat{S}_A}$	$\hat{\mathrm{var}}\left(\hat{S}_D\right) = \frac{1}{133225} \cdot \hat{\mathrm{var}}\left(\hat{S}_A\right) \cdot \sqrt[365]{\hat{S}_A^{728}}$
Annual (52 weeks)	Weekly	$\hat{S}_W = \sqrt[52]{\hat{S}_A}$	$\hat{\mathrm{var}}\left(\hat{S}_W\right) = \frac{1}{2704} \cdot \hat{\mathrm{var}}\left(\hat{S}_A\right) \cdot \sqrt[52]{\hat{S}_A^{102}}$
Annual	Monthly	$\hat{S}_M = \sqrt[12]{\hat{S}_A}$	$\hat{\mathrm{var}}\left(\hat{S}_M\right) = \frac{1}{144} \cdot \hat{\mathrm{var}}\left(\hat{S}_A\right) \cdot \sqrt[12]{\hat{S}_A^{22}}$

MORE THAN ONE VARIABLE

Annual population growth. Annual, discrete population growth (λ) can be defined for avian populations as: $\lambda = S_A + B \cdot S_J$ (Pulliam 1988). Avian biologists commonly use this relationship to analyze source-sink dynamics. If $\lambda_i < 1$ then populations are classified as sinks during year i (mortality exceeds reproduction); similarly, if $\lambda_i > 1$ then populations are classified as sources (reproduction exceeds mortality). Thus, it becomes necessary to derive $\hat{\text{var}}(\hat{\lambda})$ to rigorously determine if the population is increasing or decreasing; indeed, confidence intervals for each quantity could be used to reject H_o: $\lambda = 1$. However, I am not aware of a published method for deriving var(λ) when $\lambda = S_A + B \cdot S_J$.

Because λ is a function of more than one random variable, each of which has an associated sampling variance estimate, it follows that λ will have a variance that is a function of the sampling variance of the individual parameters. Further complicating matters, fecundity (B) is defined as the number of female fledglings per year, and B is a function of three random variables, $B = \pi \bullet \phi \bullet \psi$, where π equals mean number of female fledglings per successful nest, ϕ equals nest survival probability, and ψ equals the average number of nests built per female per year. Thus, var(B) is a function of the variances of π, ϕ, and ψ.

To derive $\hat{\text{var}}(\hat{B})$, where $\hat{B} = \hat{\pi} \cdot \hat{\phi} \cdot \hat{\psi}$ (assuming independence of π, ϕ, and ψ), we use equation 1:

$$\hat{\text{var}}\left(\hat{B}\right) = \hat{\text{var}}(\hat{\pi})\left[\frac{\partial \hat{B}}{\partial \hat{\pi}}\right]^2 + \hat{\text{var}}\left(\hat{\phi}\right)\left[\frac{\partial \hat{B}}{\partial \hat{\phi}}\right]^2 + \hat{\text{var}}\left(\hat{\psi}\right)\left[\frac{\partial \hat{B}}{\partial \hat{\psi}}\right]^2. \tag{7}$$

After finding the three partial derivatives (use the cx rule in Table 2) in equation 7, we arrive at:

$$\hat{\text{var}}\left(\hat{B}\right) = \left(\hat{\text{var}}(\hat{\pi}) \cdot \left(\hat{\phi}\hat{\psi}\right)^2\right) + \left(\hat{\text{var}}\left(\hat{\phi}\right) \cdot \left(\hat{\pi}\hat{\psi}\right)^2\right) + \left(\hat{\text{var}}\left(\hat{\psi}\right) \cdot \left(\hat{\pi}\hat{\phi}\right)^2\right). \tag{8}$$

We now have a derived variance for $\hat{B}$, which could be useful on its own merits. But, to obtain $\hat{\text{var}}(\hat{\lambda})$, the next step is to use $\hat{\text{var}}(\hat{B})$ with direct estimates (potentially from mark-recapture survival analyses) of $\hat{\text{var}}(\hat{S}_A)$ and $\hat{\text{var}}(\hat{S}_J)$ to approximate the variance of λ.

To derive $\hat{\text{var}}(\hat{\lambda})$, where $\hat{\lambda} = \hat{S}_A + \hat{S}_J \cdot \hat{B}$,

$$\hat{\text{var}}\left(\hat{\lambda}\right) = \hat{\text{var}}\left(\hat{S}_A\right)\left[\frac{\partial \hat{\lambda}}{\partial \hat{S}_A}\right]^2 + \hat{\text{var}}\left(\hat{B}\right)\left[\frac{\partial \hat{\lambda}}{\partial \hat{B}}\right]^2 + \hat{\text{var}}\left(\hat{S}_J\right)\left[\frac{\partial \hat{\lambda}}{\partial \hat{S}_J}\right]^2. \tag{9}$$

After taking the three partial derivatives (use rules in Table 2) in equation 9, we arrive at:

$$\hat{\text{var}}\left(\hat{\lambda}\right) = \hat{\text{var}}\left(\hat{S}_A\right) + \left(\hat{\text{var}}\left(\hat{B}\right) \cdot \hat{S}_J^2\right) + \left(\hat{\text{var}}\left(\hat{S}_J\right) \cdot \hat{B}^2\right). \tag{10}$$

Mean annual density. Let's consider a second example of the transformation of multiple variables. Biologists often obtain annual estimates of density for a bird species over multiple years. Consider a situation in which a biologist is interested in the effects of prescribed burning on grassland bird densities. To compare densities in different treatment types (burned, b, and control, c) across years (i), it is necessary to calculate the mean density ($\bar{D}^b{}_i$, $\bar{D}^c{}_i$) in each treatment. The sampling variance of the mean density for the burned treatment, $\hat{\text{vr}}(\bar{D}^b)$, is not simply the average sampling variance of the annual estimates of $\hat{D}^b{}_i$ used to calculate $\bar{D}^b$. But, as expected, $\hat{\text{var}}\ \bar{D}^b$ is certainly a function of the annual sampling variances of $\hat{D}^b{}_i$.

For our example, let's consider the data from only the burned portion of the above experiment and assume we have five years of density estimates, $\bar{D}^b{}_1$, $\bar{D}^b{}_2$, $\bar{D}^b{}_3$, $\bar{D}^b{}_4$, and $\bar{D}^b{}_5$. Again, our goal is to obtain $\bar{D}^b$ and $\hat{\text{var}}(\bar{D}^b)$. For simplicity, we'll assume that the densities are estimated from separate datasets, and the annual estimates are independent. The relationship of the parameters is:

$$\bar{D}^b = \frac{\hat{D}_1^b + \hat{D}_2^b + \hat{D}_3^b + \hat{D}_4^b + \hat{D}_5^b}{5} = \frac{1}{5}\hat{D}_1^b + \frac{1}{5}\hat{D}_2^b + \frac{1}{5}\hat{D}_3^b + \frac{1}{5}\hat{D}_4^b + \frac{1}{5}\hat{D}_5^b. \tag{11}$$

To apply equation 1 (assuming independence), we have:

$$\hat{\text{var}}\left(\bar{D}^b\right) = \hat{\text{var}}\left(\hat{D}_1^b\right)\left[\frac{\partial \bar{D}^b}{\partial \hat{D}_1^b}\right]^2 + \hat{\text{var}}\left(\hat{D}_2^b\right)\left[\frac{\partial \bar{D}^b}{\partial \hat{D}_2^b}\right]^2 + \hat{\text{var}}\left(\hat{D}_3^b\right)\left[\frac{\partial \bar{D}^b}{\partial \hat{D}_3^b}\right]^2 + \hat{\text{var}}\left(\hat{D}_4^b\right)\left[\frac{\partial \bar{D}^b}{\partial \hat{D}_4^b}\right]^2 + \hat{\text{var}}\left(\hat{D}_5^b\right)\left[\frac{\partial \bar{D}^b}{\partial \hat{D}_5^b}\right]^2. \tag{12}$$

To calculate the partial derivatives, each $\hat{D}^b{}_i$ becomes the parameter of interest (x) and all other terms in equation 11 are constants (c). We use the cx and c rules in Table 2. By the c rule, the derivative of the string of constants is 0 (Table 2). Thus, with respect to each $\hat{D}^b{}_i$ in equation 12, the partial derivative is:

$$\frac{\partial \bar{D}^b}{\partial \hat{D}_i^b} = left(\frac{1}{5}\hat{D}_1^b + \frac{1}{5}\hat{D}_2^b + \frac{1}{5}\hat{D}_3^b + \frac{1}{5}\hat{D}_4^b + \frac{1}{5}\hat{D}_5^b)' = \frac{1}{5}. \tag{13}$$

After substituting for the partial derivatives in equation 12, we arrive at our solution:

$$\hat{\text{var}}(\bar{D}^b) = \frac{1}{25}\hat{\text{var}}(\hat{D}_1^b) + \frac{1}{25}\hat{\text{var}}(\hat{D}_2^b) + \frac{1}{25}\hat{\text{var}}(\hat{D}_3^b) + \frac{1}{25}\hat{\text{var}}(\hat{D}_4^b) + \frac{1}{25}\hat{\text{var}}|(\hat{D}_5^b). \quad (14)$$

Effect size (correlated variables). The use of the delta method is most straightforward when dealing with single variable transformations. When working with multiple variables, it is possible (probable in many cases) that variables $X_1, X_2, \ldots, X_n$ (equation 1) will not be independent. In this case, the covariance between variables must be considered when approximating the sampling variance (equation 2).

Doherty et al. (2002) incorporated covariance into an approximation of the sampling variance of effect size. Although a useful example of the use of the delta method for multiple variables that are not independent, Doherty et al. (2002) do not provide instructions to guide similar applications. To understand how Doherty et al. (2002) used the delta method to arrive at the formula in their manuscript, we begin with the function in question. Doherty et al. (2002) estimated effect size ($\hat{\theta}$) as the ratio of male and female fidelity rates (F^m and F^f, respectively), where $\hat{\theta} = \frac{\hat{F}^m}{\hat{F}^f}$. Sampling variance for the individual fidelity rates is available, but we now need $\hat{\text{var}}(\hat{\theta})$.

To use the delta method (equation 2) to approximate $\hat{\text{var}}(\hat{\theta})$, incorporating covariance between F^m and F^f, we have:

$$\hat{\text{var}}(\hat{\theta}) = \hat{\text{var}}(\hat{F}^m)\left[\frac{\partial\hat{\theta}}{\partial\hat{F}^m}\right]^2 + \hat{\text{var}}(\hat{F}^f)\left[\frac{\partial\hat{\theta}}{\partial\hat{F}^f}\right]^2 + 2\cdot\hat{\text{cov}}(\hat{F}^m, \hat{F}^f)\left[\frac{\partial\hat{\theta}}{\partial\hat{F}^m}\right]\left[\frac{\partial\hat{\theta}}{\partial\hat{F}^f}\right]. \quad (15)$$

We use two rules to find the partial derivatives in equation 15. For the partial derivative when F^m is our parameter of interest (x), our constant (c) is $1/F^f$, and we use the x/c rule (Table 2). When, F^f is our parameter of interest (x), our constant (c) is F^m, and we use the c/x rule (Table 2). Thus, the partial derivatives are: $\frac{\partial\hat{\theta}}{\partial\hat{F}^m} = \frac{1}{\hat{F}^f}$ and $\frac{\partial\hat{\theta}}{\partial\hat{F}^f} = -\frac{\hat{F}^m}{(\hat{F}^f)^2}$.

Substituting the partial derivatives into equation 15 and simplifying, we have:

$$\hat{\text{var}}(\hat{\theta}) = \left[\frac{1}{(F^f)^2}\right]\cdot\left[\hat{\text{var}}(\hat{F}^m) + \frac{\hat{\text{var}}(\hat{F}^f)(\hat{F}^m)^2}{(\hat{F}^f)^2} - \frac{2\cdot\hat{\text{cov}}(\hat{F}^m, \hat{F}^f)\cdot\hat{F}^m}{\hat{F}^f}\right]. \quad (16)$$

By further simplifying, we arrive at the formula provided by Doherty et al. (2002):

$$\hat{\text{var}}(\hat{\theta}) = \hat{\theta}^2\cdot\left[\frac{\hat{\text{var}}(\hat{F}^m)}{(\hat{F}^m)^2} + \frac{\hat{\text{var}}(\hat{F}^f)}{(\hat{F}^f)^2} - \frac{2\cdot\hat{\text{cov}}(\hat{F}^m, \hat{F}^f)}{\hat{F}^m\hat{F}^f}\right]. \quad (17)$$

The estimate for covariance can be obtained from software packages that provide variance-covariance matrices. But, in other cases, covariance matrices must be derived. MacKenzie et al. (2006) and Cooch and White (2006) provide additional examples of how to incorporate covariance matrices into the delta method.

DISCUSSION

Some reflection on the appropriateness of the delta method may be useful for avian biologists considering the application of the delta method to data. Cooch and White (2006) note that when transformation of variables is highly nonlinear over the range of values being examined, the delta method may not approximate variance well. Of the case examples provided, the approximation of $\hat{\text{var}}(\hat{\lambda})$ has the most potential to be problematic. Powell et al. (2000) used simulation modeling as an alternative to the delta method for estimating the uncertainty surrounding estimates of population growth rates.

The delta method is not the only method that is useful for deriving variance approximations and confidence intervals for transformed variables. Williams et al. (2002) provide additional methods, including the use of bootstrapping methods. Indeed, when relationships are complex (nonlinear) or when estimates of covariance are not available to judge the independence of variables, the delta method should not be used. However, the examples presented here suggest that there are many circumstances in which the delta method can be applied in a straightforward and rigorous fashion. I encourage avian biologists to explore the delta method as a tool for providing useful approximations of sampling variance.

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