ESTIMATION OF BROOD AND NEST SURVIVAL: COMPARATIVE METHODS IN THE PRESENCE OF HETEROGENEITY

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Abstract: The Mayfield method has been widely used for estimating survival of nests and young animals, especially when data are collected at irregular observation intervals. However, this method assumes survival is constant throughout the study period, which often ignores biologically relevant variation and may lead to biased survival estimates. We examined the bias and accuracy of 1 modification to the Mayfield method that allows for temporal variation in survival, and we developed and similarly tested 2 additional methods. One of these 2 new methods is simply an iterative extension of Klett and Johnson's method, which we refer to as the Iterative Mayfield method and bears similarity to Kaplan-Meier methods. The other method uses maximum likelihood techniques for estimation and is best applied to survival of animals in groups or families, rather than as independent individuals. We also examined how robust these estimators are to heterogeneity in the data, which can arise from such sources as dependent survival probabilities among siblings, inherent differences among families, and adoption. Testing of estimator performance with respect to bias, accuracy, and heterogeneity was done using simulations that mimicked a study of survival of emperor goose (*Chen canagica*) goslings. Assuming constant survival for inappropriately long periods of time or use of Klett and Johnson's methods resulted in large bias or poor accuracy (often >5% bias or root mean square error) compared to our Iterative Mayfield or maximum likelihood methods. Overall, estimator performance was slightly better with our Iterative Mayfield than our maximum likelihood method, but the maximum likelihood method provides a more rigorous framework for testing covariates and explicitly models a heterogeneity factor. We demonstrated use of all estimators with data from emperor goose goslings. We advocate that future studies use the new methods outlined here rather than the traditional Mayfield method or its previous modifications.

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Many studies of the survival of nests or young birds prior to fledging assume that survival is constant over time (Schmidt and Whelan 1998). However, constant survival may often be an unrealistic assumption, and modeling time or age-specific survival can reveal biologically meaningful patterns (Grand 1995).

Independence of fates among study animals is one of the basic assumptions of mark–recapture studies for estimating survival rates in natural populations (Burnham et al. 1987). Given an appropriate model, violation of this assumption causes little bias in survival estimates but results in underestimation of variances (Nichols et al. 1982, McCullagh and Nelder 1989:124–128). Lack of independence can also result in the selection of inappropriate models and thus incorrect inference about what factors are associated with variation in survival (Anderson et al. 1994). Methods for detecting lack of independence in survival among family members have been developed (Winterstein 1992, Schmutz et al. 1995), but these fail to provide a clear means for how to then use data that contain dependencies in survival.

Loss and gain of young in families due to adoption is common, particularly for precocial waterfowl (Afton and Paulus 1992). Further, a heterogenous pattern of loss of young among families is expected, as variation in lifetime reproductive success can be large (Clutton-Brock 1988, Newton 1989). This heterogeneity among ages (time), families, adoptive events, and the predisposition for siblings to die from the same mortality events all induce additional variation in data beyond the expectation of a binomially distributed survival probability. A robust method must account for this extra-binomial variation, or overdispersion (Anderson et al. 1994), which commonly occurs in survival data.

The Mayfield method (Mayfield 1961, 1975) has long been used to estimate survival of nests and young birds. The impetus for this method arises from the common situation where individuals are detected at irregular intervals of time, and consequently, mortality rates are calculated as the number

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of mortalities divided by the sum of time all individuals were at risk of mortality—the concept of exposure days. A constraint of this method has been that survival is assumed constant for whatever interval of days (or other time unit) is used for the summation of numbers at risk. Klett and Johnson (1982) modified the Mayfield method to allow for temporal variation in survival and demonstrated the utility of this modification to nesting studies. This modification has also been favored for studies of young broods, where the magnitude of age- or time-related variation in survival is often large (Grand and Flint 1996). We demonstrate in this paper that the Klett and Johnson (1982) modification can sometimes be biased, and provide an additional, iterative modification which removes this bias. This new, iterative Mayfield method is quite flexible in modeling temporal (or age) variation in survival and makes minimal assumptions about the nature of the data. In the absence of temporal variation in survival, the iterative and previous Mayfield methods provide similar results.

We also demonstrate a maximum likelihood method. Like other similar maximum likelihood methods (Johnson 1979, Bart and Robson 1982, Heisey and Fuller 1985), this method requires more assumptions about variation in data (e.g., random distribution of error) than the various modifications of the Mayfield method. However, our ML method allows for increases in family size, explicitly models a heterogeneity factor, allows for incorporation of covariates, and provides a theoretically robust framework for comparison of multiple candidate models that may potentially fit the data (Burnham and Anderson 1998).

We first describe our 2 new methods (iterative Mayfield and ML), and then present a simulation study of these methods and their precursors to assess bias and accuracy. We demonstrate use of these methods with 1 year of data from a 4-year study of emperor geese during brood rearing (Schmutz et al. 2001). We conclude with a discussion of the merits of these methods and recommendations for their use.

THE ITERATIVE MAYFIELD METHOD

The Mayfield method (Mayfield 1961, 1975) defines a daily mortality rate (DMR) as the total number of mortalities divided by the total number of exposure days, where an exposure day is obtained whenever an individual animal is known to be alive at the start of a day and the fate of the individual at the end of the day is certain. The daily survival rate is then DSR = 1 – DMR.

A complication occurs when observations are made several days apart and an individual dies between 2 successive observation times, because then the exact number of exposure days becomes uncertain. Johnson (1979) and Klett and Johnson (1982) discussed Mayfield's original method and several modifications to allow for this uncertainty. In particular, Klett and Johnson (1982) proposed a modification that allows for temporal variation in the DSR. Our iterative method is a simple extension of this modification, but in terms of age-specific variation in the DSR because we assume that the ages of individuals are known when they are first observed.

Klett and Johnson's (1982) modification is based on estimating for each day the number of individuals at risk, and the number of survivors from those at risk the previous day. Following their example, if an individual is known to be alive at time 0 and known to be dead 7 days later, then this individual may have died at any time in the 7 days. Klett and Johnson (1982) suggest allocating the single mortality to days in such a case using probabilities conditional on mortality by day 7, based on an assumed value for the DSR. For example, the mortality occurs during day 2 with probability

$$\begin{aligned}&\Pr\{\text{death on day 2}|\text{death by day 7}\}\\ &= \Pr\{\text{death on day 2}\}/\Pr\{\text{death by day 7}\}\\ &= \mathrm{DSR}(1-\mathrm{DSR})/(1-\mathrm{DSR}^7).\end{aligned}$$

This fraction of the death is therefore allocated to day 2.

Numerical calculations show that the allocation of mortality to days using this method is insensitive to the actual value used for the DSR. However, as we demonstrate in a subsequent section, if the true DSR varies rather than being constant, then the allocation of mortalities by this method leads to biased estimation of survival rates. This bias is much reduced by using a generalization of Klett and Johnson's method, which allows the DSR to vary when calculating the probabilities of mortality for different days. As an illustration with the above example, let DSR_i be the daily survival rate for day i. Then the probability of the mortality occurring during day 2 would be calculated as

$$\mathrm{DSR}_1 \times (1-\mathrm{DSR}_2)/(1-\mathrm{DSR}_1 \times \mathrm{DSR}_2 \times \mathrm{DSR}_3 \times \mathrm{DSR}_4 \times \mathrm{DSR}_5 \times \mathrm{DSR}_6 \times \mathrm{DSR}_7).$$

To use this generalization, an iterative approach is needed. It proceeds by starting with a constant initial value (say, 0.95) for all the DSR. All mortalities are then allocated to days according to the probabilities of death on those days. This first allocation is the same as used in Klett and Johnson's

method of allocation because the assumed DSR is the same on each day.

Having allocated the mortalities, it is possible to calculate for each study day the number at risk to mortality at the start of the day, and the number surviving until the end of the day. This then allows daily survival rates $DSR_{1(1)}$, $DSR_{2(1)}$, $DSR_{3(1)}$, etc., to be estimated for day 1, day 2, day 3, etc. These are the estimated values that are obtained by Klett and Johnson's method.

The calculations are then repeated. Using the daily survival rates $DSR_{i(1)}$, the mortalities in the original data are allocated again to the possible days where they could have occurred using the probability of death on a given day, conditional on the probability of death by the end of the observation interval being considered. Once this is done, new daily survival rates $DSR_{1(2)}$, $DSR_{2(2)}$, $DSR_{3(2)}$, etc. are calculated for day 1, day 2, day 3, etc. These will differ to some extent from the estimates obtained from Klett and Johnson's method. Using these new estimates, the mortalities can be allocated again to the possible days when they could have occurred, and the daily survival rates are estimated again. After several iterations the estimated daily survival rates change little with each recalculation, and 20 iterations are usually sufficient for convergence to fixed values.

A further modification involves averaging DSR, or, more precisely, assuming that the DSR is constant for blocks of *d* days. This is motivated by the principle of parsimony (Burnham and Anderson 1992) because estimating a separate DSR for each day can be expected to reduce the precision of estimates if the true DSR changes little from day to day. The calculations are done as follows, assuming that after allocating mortalities to days for the first time in the iterative procedure there are estimated to be R_i individuals at risk at the start of day i, and S_i survivors at the end of that day. An estimate of the daily survival rate for days 1 to *d* is then the sum of the survival days divided by the sum of the exposure days, which is

$$DSR_{1\to d} = (S_1 + S_2 + \ldots + S_d)/(R_1 + R_2 + \ldots + R_d).$$

Similarly, the daily survival rate for days d+1 to 2d is estimated by

$$DSR_{d+1\to 2d} = (S_{d+1} + S_{d+2} + \ldots + S_{2d})/(R_{d+1} + R_{d+2} + \ldots + R_{2d}),$$

and so on for the later blocks of *d* days. These survival rates that are constant for blocks of *d* days can then be used for allocating mortalities to days for the second step of the iterative process. This will give new estimates for the numbers at risk and the numbers surviving each day, which can in turn be used to determine new values for the *d* day survival rates, for the next iteration, and so on.

Once stable values for the exposure numbers R_i and the survivors S_i are obtained from the iterations, they can be used in 2 alternative ways. First, the estimates $DSR_{1\to d}$, $DSR_{d+1\to 2d}$, $DSR_{2d+1\to 3d}$, etc. can be used for the days that they relate to. We refer to these as the smoothed iterative estimates. Second, DSR_i can just be estimated by S_i/R_i using the values from the final iteration. We refer to this as the unsmoothed iterative estimate. We demonstrate later how consistent differences between the smoothed and unsmoothed estimates are an indication that the number of days used for averaging is too large.

The smoothed and unsmoothed estimates may both differ substantially from the estimates obtained by Klett and Johnson's (1982) method, which amounts to a single iteration of the above process with no averaging of survival rates over days. However, it is interesting to note that if the iterative method is applied assuming a single constant DSR rate for all days, then this should produce estimates that are rather similar to those of Klett and Johnson. The only difference is that the DSR used is determined from the data instead of being an arbitrary assumed value.

MAXIMUM LIKELIHOOD ESTIMATION

An alternative method to estimate the DSR uses an approximate maximum likelihood approach. We assume a piecewise survival function such that the survival rate from age *t* to age *t + 1* is

$$\phi_t = \exp(-\alpha_i), \qquad (1)$$

$\alpha_i \geq 0$, for $t_{i-1} \leq t < t_i$, with $t_0 = 0$, and $i = 1, 2, \ldots, p$. That is to say, the DSR for ages 0 to t_1 days is assumed to be $\exp(-\alpha_1)$, the DSR for ages t_1 to t_2 days is assumed to be $\exp(-\alpha_2)$, and so on, with p such intervals.

With no complications from heterogeneity, if N_a goslings are observed in a brood at age *a* then the number of observable survivors at age $b > a$, N_b, would have a binomial distribution with mean

$$E(N_b|N_a) = N_a\phi_a\phi_{a+1}\ldots\phi_{b-1}, \qquad (2)$$

and variance

$$V(N_b|N_a) = N_a\phi_a\phi_{a+1}\ldots\phi_{b-1}(1 - \phi_a\phi_{a+1}\ldots\phi_{b-1}). \qquad (3)$$

Estimating the unknown parameters $\alpha_1, \alpha_2, \ldots, \alpha_p$ is then a straightforward application of gener-

alized linear modeling using GLIM or equivalent software (McCullagh and Nelder 1989, Francis et al. 1993), with a log link and a binomial distribution for errors.

Unfortunately, this approach cannot be used in situations where it sometimes occurs that $N_b > N_a$, because the binomial likelihood becomes undefined. Such situations arise with emperor geese, many additional waterfowl species (Afton and Paulus 1992), and other taxa (Riedman 1982) due to brood mixing and adoption. Furthermore, the common approaches of using quasi-likelihood (McCullagh and Nelder 1989), or introducing random effects (Breslow and Clayton 1993) to account for heterogeneity cannot be used either for the same reason.

We have therefore allowed for heterogeneity by assuming that the observable number of survivors at time *b* from a brood of size N_a at time *a* is approximately normally distributed with a mean given by equation 2 and a variance given by

$$V_1(N_b|N_a) = D \times V(N_b|N_a), \qquad (4)$$

where $V(N_b|N_a)$ is the binomial variance from equation (3) and D is a constant. Thus, we assume that the binomial variance is inflated by D because of adoptions and other heterogeneity in survival probabilities. We are also assuming that most extra-binomial variation is induced by heterogeneity among families, which seems reasonable for waterfowl (Rotella and Ratti 1992, Flint et al. 1995), and likely many other taxa as well.

Given our assumptions, the log-likelihood function for the observed number n_b at the end of a survival period is derived from the normal density function and takes the form

$$L(\alpha_1,\alpha_2,\ldots,\alpha_p,D) = \sum [-\tfrac{1}{2}\log_e\{2\pi V_1(N_b|N_a)\} - \tfrac{1}{2}\{n_b - E(N_b|N_a)\}^2/V_1(N_b|N_a)], \qquad (5)$$

where the summation is over all the instances in the data set where a brood size is observed at a time *a* and then observed next at time *b*. Maximum likelihood estimates of the unknown parameters are obtained by numerically maximizing the function using Newton-Raphson iteration (Manly 1985:406) after finding good initial approximations using the algorithm AMOEBA from Press et al. (1992).

An advantage of this approach is that the model for survival as given by equation 1 can be extended easily to include covariates such as birth date of goslings. Another advantage is that the relative fits of different models can be compared using Akaike's Information Criterion (AIC), which is defined as the deviance plus twice the number of estimated parameters, where the deviance is minus twice the maximized log-likelihood (Burnham and Anderson 1998). The best model of those considered is the 1 with the smallest AIC. This criterion accounts for the fact that as the number of parameters increases, the deviance of models is expected to decrease (fit better), but the precision of estimated parameters also decreases.

Some caution is called for in using AIC for model selection because of the approximate nature of the normal distribution model being used, particularly when there are many instances of small numbers at risk and small numbers surviving.

COMPARISON OF METHODS OF ESTIMATION

We conducted a simulation experiment to compare various methods for estimating cumulative survival. To ensure that our simulations closely mimicked real data, we used the actual sample size and observation schedule used in 1993 by Schmutz et al. (2001) in their study of gosling survival in emperor geese. In that year, there were 344 sighting records of 83 individual broods, resulting in 261 time intervals for which the number in a brood was known at the start and the end. Hence there were 261 terms in the log-likelihood function of equation (5). Broods were observed at 1 to 38 days old.

We simulated 5 scenarios of temporal variation in survival. In the first 2 scenarios, the expected DSR was constant for all ages at 0.95 and 0.98, respectively. For the third scenario, the expected DSR increased with time from 0.92 for ages 1–10 days, to 0.96 for ages 11–20, and to 0.99 for ages of 21 days or more. This pattern is similar to that observed in emperor geese (Schmutz et al. 2001) and other waterfowl populations (Williams et al. 1993, Grand and Flint 1996, Flint and Grand 1997). For the fourth scenario, expected DSR decreased with age from 0.99 for ages 1–10 days, to 0.96 for ages 11–20 days, and to 0.92 for ages of 21 days or more. The fifth scenario contained both increasing and decreasing survival as expected DSR was 0.90 for ages 1–10 days, 0.99 for ages 11–20 days, and 0.95 for ages of 21 days or more. The last 2 scenarios do not seem plausible for geese, but may be relevant to other taxa and allow us to examine the performance of these methods with other patterns of survival.

We generated data with no heterogeneity, moderate heterogeneity, and high heterogeneity, corresponding to D equal to 1, 2, or 4 in equation 4.

With no heterogeneity (D = 1) each individual gosling at age i was given a survival probability equal to the expected survival rate for that age and survived or died independently of the fate of any other gosling. The number surviving any particular interval of time was therefore a random value from a binomial distribution with a mean and variance given by equations (2) and (3). With moderate heterogeneity (D = 2), the mean of the number surviving an interval was still given by equation (2) but the variance was set at twice the binomial variance. With high heterogeneity (D = 4) the mean was again given by equation (2) but the variance was set at 4 times the binomial variance. With D = 2 and D = 4, the number surviving any particular interval of time was a random value from a normal distribution with the appropriate mean and variance, rounded to the nearest integer, or set to 0 if the generated value was less than 0.5. We generated 100 sets of data for each survival scenario and each level of heterogeneity.

Estimates were obtained by 9 different methods. These were: K&J, Klett and Johnson's (1982) modified Mayfield method; IT(1), our iterative method with no averaging of survival probabilities; ITSM(5), the iterative method with averaging over 5 days and smoothed DSR; ITUSM(5), the iterative method with averaging over 5 days using unsmoothed DSR; ITSM(10), ITUSM(10), ITSM(20), and ITUSM(20) being the smoothed and unsmoothed estimates with 10- or 20-day averaging; and ML, maximum likelihood estimation with different estimated daily survival rates for ages 1 to 10 days, ages 11 to 20 days, and 21 or more days. Note that the intervals chosen for constant survival rates for maximum likelihood estimation match those used for scenarios 3 to 5. The maximum likelihood model was therefore correct except for rounding and truncation for all simulations.

We used 2 metrics to compare the 9 methods of estimation: the average absolute bias (AAB) and root mean square error (RMSE). We present

Table 1. Values of the average absolute bias for 9 methods of estimation with 5 survival scenarios and 3 levels of heterogeneity (D = 1, 2, or 4) within each scenario. ML refers to maximum likelihood estimation. Average absolute bias definitions provided in text.

	Survival probability for days				Average absolute biases								
							IT(5)		IT(10)		IT(20)		
Scenario	1–10	11–20	21+	D	K&J	IT(1)	SM	USM	SM	USM	SM	USM	ML
1	0.95	0.95	0.95	1	1.6	0.4	0.3	0.2	0.3	0.3	0.3	0.3	0.3
				2	1.6	1.5	0.6	0.5	0.4	0.4	0.3	0.4	1
				4	1.4	2.7	1.2	1.1	0.8	0.9	0.6	0.9	2
				Avg	1.5	1.5	0.7	0.6	0.5	0.5	0.4	0.5	1.1
2	0.98	0.98	0.98	1	0.7	0.7	0.7	0.6	0.5	0.5	0.3	0.4	0.7
				2	0.3	1.3	0.5	0.6	0.2	0.3	0.3	0.3	0.4
				4	0.6	2.8	0.7	0.3	0.4	0.3	0.1	0.3	0.8
				Avg	0.5	1.6	0.6	0.5	0.4	0.4	0.2	0.3	0.6
3	0.92	0.96	0.99	1	5	1.7	1.7	1.6	1.6	1.6	4.3	3	1.7
				2	5.7	1.7	2.4	2.2	1.9	2	4.3	3.6	1.5
				4	5	0.9	1.2	1.6	1.1	1.3	4.2	2.9	0.6
				Avg	5.2	1.5	1.8	1.8	1.5	1.6	4.3	3.2	1.3
4	0.99	0.96	0.92	1	4.2	1.7	1.4	1.6	1.5	1.5	5.3	2.7	1.7
				2	4.2	2.9	1.7	1.7	1.6	1.7	5.4	3.2	2.7
				4	5.7	4.4	2.5	2.3	2.5	2.5	5.8	3.8	3.7
				Avg	4.7	3	1.9	1.9	1.9	1.9	5.5	3.2	2.7
5	0.9	0.99	0.95	1	6.5	1.7	1.8	2	1.9	2	8.8	4.8	2
				2	7	1.8	2	2.4	2	2.1	8.9	4.6	2.5
				4	6.5	2	1.3	1.6	1.7	1.6	8.9	4.5	1.8
				Avg	6.7	1.9	1.7	2	1.9	1.9	8.8	4.6	2.1
	Avg of all scenarios				3.7	1.9	1.3	1.4	1.2	1.3	3.8	2.4	1.6

averages for these metrics calculated from estimated survival to 5, 10, 20, and 35 days of age.

AAB is the average difference between the mean of the estimates of survival to 5, 10, 20, and 35 days rates and the true values for those survival rates. RMSE is calculated as $\{(\text{Bias})^2 + \text{Variance}\}^{1/2}$ and is summarized similarly to AAB. High values of RMSE indicate an estimator is either strongly biased, has a large variance, or both.

When DSR was constant (scenarios 1 and 2), all methods performed reasonably well with regard to both AAB (Table 1) and RMSE (Table 2). However, when DSR varied with time (scenarios 3–5), the K&J method exhibited severe biases, as did ITSM(20) and, to a lesser extent ITUSM(20). The biases with the K&J and ITSM(20) methods (when DSR varied) led to overall poor performance in terms of RMSE. The best methods were ITSM(10) and ITUSM(10); however, this result was not surprising because true survival rates were constant for ages in 10-day blocks (1–10 days, 11–20 days, and 21 days or more). Averaging over 5 days or not averaging at all with the iterative method generally gave estimates with little bias, but SD of estimates were substantially higher.

The much reduced AAB and RMSE for ITUSM(20) compared to ITSM(20) suggests that unsmoothed estimates are more robust than smoothed estimates when an averaging period is too long for daily survival estimates.

We conclude from this simulation experiment that the K&J method of estimation is biased by changing DSR, and that the iterative method with averaging over an appropriate number of days for survival estimates can remove this bias almost entirely. Furthermore, the iterative method with appropriate averaging can outperform maximum likelihood, again providing that an appropriate averaging interval is used.

ACCURACY OF ESTIMATES

We used bootstrapping to assess accuracy of survival estimates generated from the various

Table 2. Root mean square errors for 9 methods of estimation with 5 survival scenarios and 3 levels of heterogeneity (D = 1, 2, or 4) within each scenario. Root mean square error definitions provided in text.

	Survival probability for days				Root mean square errors								
							IT(5)		IT(10)		IT(20)		
Scenario	1–10	11–20	21+	D	K&J	IT(1)	SM	USM	SM	USM	SM	USM	ML
1	0.95	0.95	0.95	1	2.9	3.8	3.5	3.5	2.7	2.8	2.3	2.4	3.1
				2	3.9	5.6	5.4	5.6	4.1	4.3	3.6	3.9	4.6
				4	4.7	7.3	7.1	7.2	5.5	5.6	4.7	5	6.8
				Avg	3.8	5.6	5.3	5.4	4.1	4.2	3.5	3.8	4.8
2	0.98	0.98	0.98	1	2.7	3.5	3.3	3.3	2.9	3	2.5	2.7	3.4
				2	3.7	4.8	4.8	5.1	4.2	4.4	3.8	4.1	3.8
				4	5	6.8	6.4	6.7	5.6	5.9	4.9	5.3	5.5
				Avg	3.8	5	4.8	5.1	4.3	4.4	3.7	4.1	4.2
3	0.92	0.96	0.99	1	6.5	4.2	4	3.9	3.2	3.3	6	4.4	3.7
				2	6.9	5.5	5.6	5.6	4.1	4.3	6.3	4.9	5
				4	7.2	7.2	7.4	7.7	5.2	5.5	6.8	5.7	7
				Avg	6.9	5.6	5.7	5.7	4.2	4.3	6.4	5	5.2
4	0.99	0.96	0.92	1	5.3	4	3.4	3.6	3.1	3.2	6.9	4.5	3.6
				2	5.7	5.4	4.7	4.8	4.2	4.3	7.2	5.2	4.8
				4	7.3	7.5	6.6	6.7	5.8	5.9	8.2	6.5	8.1
				Avg	6.1	5.6	4.9	5.1	4.4	4.5	7.4	5.4	5.5
5	0.9	0.99	0.95	1	9.2	4.1	4	4.1	3.4	3.5	10.7	6.8	3.6
				2	9.8	5.4	5.4	5.6	4.1	4.3	11.2	7.3	5.1
				4	9.7	7.9	7.5	7.7	5.9	6.1	11.7	8	9.6
				Avg	9.5	5.8	5.6	5.8	4.5	4.6	11.2	7.4	6.1
	Avg of all scenarios				6	5.5	5.3	5.4	4.3	4.4	6.4	5.1	5.2

methods (Manly 1997). We used broods as the sample unit, similar to Flint et al. (1995), and suspect that most heterogeneity is among families in real populations. The likely sampling error in the estimate of the probability of survival to a particular age is then determined by generating many bootstrap sets of data with the same number of broods as for the real data, but with the data for each of these broods chosen by resampling real broods with replacement.

The standard 95% bootstrap confidence interval for the true survival probability to age *t* days is

$$\hat{\theta}_t \pm 1.96\mathrm{SD}(\hat{\theta}_t) \qquad (6)$$

where $\hat{\theta}_t$ is the estimate of this probability from the real data and SD $(\hat{\theta}_t)$ is the standard deviation of the estimates of the same probability as found from the bootstrap resamples (Manly 1997). A modification of this procedure that might work better if the standard deviations of estimates are approximately proportional to their means is to use $\log_e(\hat{\theta}_t)$ instead of $\hat{\theta}_t$ (Zar 1984).

With the maximum likelihood model, an approximate covariance matrix is available for all of the estimated parameters (Manly 1985:406). To calculate $\mathrm{SD}(\hat{\theta}_t)$ from likelihood theory, note that from equation (1) the survival rate to age t can be written as

$$\theta_t = \exp(-\alpha_1 h_1 - \alpha_2 h_2 - \ldots - \alpha_p h_p), \qquad (7)$$

where h_i is the number of days for which the daily survival rate $\exp(-\alpha_i)$ applies up to age *t* (which may be 0). The estimated survival to age *t* is then

$$\hat{\theta}_t = \exp(-\hat{\alpha}_1 h_1 - \hat{\alpha}_2 h_2 - \ldots - \hat{\alpha}_p h_p), \qquad (8)$$

where $\hat{\alpha}_i$ is the maximum likelihood estimate of α_i. The variance of $\log_e(\hat{\theta}_t)$ is then given by

$$\mathrm{Var}\{\log_e(\hat{\theta}_t)\} = \sum_{i=1}^{p} \sum_{j=1}^{p} h_i h_j \mathrm{Cov}(\hat{\alpha}_i, \hat{\alpha}_j), \qquad (9)$$

where $\mathrm{Cov}(\hat{\alpha}_i, \hat{\alpha}_j)$ can be approximated using the covariance matrix obtained while fitting the model. To obtain an approximate standard deviation for $\hat{\theta}_t$, the standard result

$$\mathrm{SD}(\hat{\theta}_t) \approx \hat{\theta}_t\, \mathrm{SD}\{\log_e(\hat{\theta}_t)\} = \hat{\theta}_t[\mathrm{Var}\{\log_e(\hat{\theta}_t)\}]^{1/2} \qquad (10)$$

can be used (Kendall and Stuart 1977).

Alternatively, the SD with the maximum likelihood method can be obtained by bootstrapping, in the same way as for the other methods of estimation.

We investigated the validity of these confidence limits for the simulated data in Tables 1 and 2. For each of the 100 sets of data generated for the 15 situations considered (5 survival rate scenarios × 3 levels of heterogeneity), we generated 50 bootstrap samples to estimate standard deviations, which suffice for a good estimate (Efron and Tibshirani 1993:52). For each generated set of data, bootstrap standard deviations and confidence limits were calculated for the 9 methods of estimation considered before. For maximum likelihood estimation, theory-derived standard deviations and confidence limits were also obtained using equation (9). As before, we summarized results in terms of mean estimated survival rates to 5, 10, 20, and 35 days.

We calculated average values for the mean of the estimated standard deviations of estimates as a percentage of the observed standard deviation. The desired value is then 100, indicating that on average estimated standard deviations equal the correct values. We also calculated the coverage (percentage of times that a nominal 95% confidence interval actually included the true value of the survival rate) of confidence limits based on equation (6).

Bootstrap estimates of standard deviations were usually approximately correct on average, but standard deviations for maximum likelihood estimates using equation (9) were consistently too low (Table 3). When the DSR was constant, so that all methods of estimation had little bias, coverage of bootstrap confidence limits was usually less than the nominal 95%, varying from 81% to 94% for scenario averages (Table 4, scenarios 1 and 2). With ML estimation, bootstrap confidence limits were clearly better than those based on equation (9). Also, limits based on $\log_e(\hat{\theta}_t)$ were slightly better than those based on equation (6), either using the bootstrap or equation (9).

When daily survival rates varied, biases in the K&J, ITSM(20), and ITUSM(20) resulted in poor coverage for some or all of the scenarios considered (Table 4, scenarios 3–5). The coverage for the other methods of estimation tended to be slightly low, except for the limits based on equation (9), which were sometimes very low. Overall, bootstrap standard deviations for estimates other than ITSM(20) and ITUSM (20) are accurate, and nominal 95% confidence limits for survival estimates based on bootstrapping and a log transformation are reasonable except that the actual confidence level may be more like 90% than 95%.

The tendency for standard deviations to be too low and the poor coverage of confidence intervals for maximum likelihood estimation when equations (9) and (10) are used appears to be mainly due to the fact that the approximate covariance matrix calculated using likelihood

theory tends to give values that are too low. At least, an inspection of the simulation results shows that in almost all cases the average of the likelihood theory variances for the estimates of α parameters are lower than the actual observed variances for these parameters.

SURVIVAL OF EMPEROR GOOSE GOSLINGS

We demonstrate in this section a detailed use of these methods with data from a 1993 study of emperor geese during brood rearing (Schmutz et al. 2001). As noted before, there were 344 sighting records of 83 individual broods, resulting in 261 time intervals for which the number in a brood was observed at both the start and end of the interval.

We estimated survival to 5, 10, 20, and 35 days with each method. The variation among estimates of cumulative survival to different ages indicates that choice of method is important (Table 5). Estimates with and without smoothing were very close for both 5- and 10-day averaging; however, differences between smoothed and unsmoothed estimates with 20-day averaging are a clear indication that the assumption of a constant DSR for ages 1–20, and then another constant rate for ages 21–35 was not correct. We conclude that averaging over 10 days is reasonable and more parsimonious than averaging over 5 days.

We also analyzed these data with the ML method. We fitted the model with expected numbers in a brood at the end of a survival period given by equation (2) and the variance given by equation (4). We initially modeled 4 survival parameters corresponding to ages 1–5, 6–10, 11–20, and >20 days, and constructed 2 models pertaining to whether D = 1 or D was estimated. We also constructed models with less temporal variation in survival, i.e., models with 3, 2, or only 1 DSR.

Table 3. Observed standard deviations as a percentage of the true standard deviations for 9 methods of estimation with 5 survival scenarios and 3 levels of heterogeneity (D = 1, 2, or 4) within each scenario. With maximum likelihood estimation (ML), standard deviations were estimated using equation 10 (Approx) or by bootstrapping (BS). Estimated standard deviation definitions provided in text.

	Survival probability for days				Estimated standard deviation as a precent of the observed (true) standard deviation									
							IT(5)		IT(10)		IT(20)		ML	
Scenario	1–10	11–20	21+	D	K&J	IT(1)	SM	USM	SM	USM	SM	USM	Approx	BS
1	0.95	0.95	0.95	1	105	95	98	98	103	103	102	104	84	96
				2	92	91	95	97	99	99	93	96	84	94
				4	94	88	92	95	99	102	94	96	68	89
				Avg	97	91	95	97	101	101	96	99	79	93
2	0.98	0.98	0.98	1	95	95	95	95	93	95	98	95	73	93
				2	97	95	94	95	98	98	102	98	95	97
				4	94	90	92	95	95	98	98	96	88	98
				Avg	95	93	94	95	95	97	100	97	85	96
3	0.92	0.96	0.99	1	103	95	99	99	98	97	95	98	75	92
				2	113	100	107	107	108	110	117	113	75	95
				4	98	93	95	97	100	100	99	99	61	90
				Avg	105	96	100	101	102	102	103	103	71	93
4	0.99	0.96	0.92	1	107	97	98	98	102	100	102	101	66	91
				2	101	90	98	100	102	104	99	101	73	92
				4	99	86	91	94	102	103	95	100	53	78
				Avg	102	91	95	97	102	102	99	101	64	87
5	0.9	0.99	0.95	1	106	95	96	96	95	96	98	98	81	96
				2	111	101	103	105	106	107	108	109	74	96
				4	94	86	90	92	88	91	90	92	45	76
				Avg	104	94	96	97	97	98	98	100	67	90
	Avg of all scenarios				101	93	96	97	99	100	99	100	73	92

Table 4. Percentage coverage of nominal 95% confidence limits for 9 methods of estimation with 5 survival scenarios and 3 levels of heterogeneity (D = 1, 2, or 4). The coverage of confidence limits were calculated using equation 10 (Approx) or by bootstrapping. Lower and upper ends of confidence limits are denoted by CL1 and CL2, respectively.

					Percent coverage of nominal 95% confidence limits																			
									IT(5)				IT(10)				IT(20)				ML			
	Survival probability for days				K&J		IT(1)		SM		USM		SM		USM		SM		USM		Approx		BS	
Scenario	1–10	11–20	21+	D	CL1	CL2	CL1	CL2	CL1	CL2	CL1	CL2	CL1	CL2	CL1	CL2	CL1	CL2	CL1	CL2	CL1	CL2	CL1	CL2
1	0.95	0.95	1	1	80	82	92	92	92	92	92	92	94	96	94	95	94	93	93	95	87	87	94	93
				2	87	90	87	91	92	94	93	94	91	94	92	95	91	92	90	94	82	84	88	92
				4	89	93	84	92	89	92	90	94	90	93	90	94	91	93	90	93	75	78	82	89
				Avg	85	88	88	92	91	93	92	93	92	94	92	94	92	92	91	94	81	83	88	91
2	0.98	0.98	1	1	92	92	93	93	93	92	92	92	92	92	93	92	94	94	92	91	82	81	93	92
				2	92	92	89	91	90	91	91	92	92	92	93	93	94	95	93	93	91	92	91	92
				4	92	92	84	87	89	90	89	90	90	92	92	93	93	94	92	93	89	91	91	91
				Avg	92	92	89	90	90	91	91	91	91	92	92	93	94	94	92	92	87	88	92	92
3	0.92	0.96	1	1	43	41	89	88	90	89	89	89	91	90	90	89	49	50	68	65	83	80	90	88
				2	49	48	94	93	93	92	94	92	95	93	94	93	56	54	83	81	84	83	96	93
				4	63	61	90	91	91	91	92	90	93	92	93	92	75	74	90	87	77	78	84	91
				Avg	52	50	91	91	91	90	92	90	93	92	93	91	60	59	80	78	81	80	90	90
4	0.99	0.96	0.9	1	36	38	86	89	88	89	88	89	87	90	88	90	45	45	52	53	71	73	87	89
				2	54	58	79	84	87	90	88	91	88	92	90	93	46	48	64	68	75	78	83	85
				4	54	62	74	85	83	89	84	90	86	92	86	93	49	54	65	73	57	61	73	81
				Avg	48	53	79	86	86	89	86	90	87	91	88	92	47	49	60	65	68	71	81	85
5	0.90	0.99	1	1	47	46	87	84	88	85	88	85	86	83	84	82	36	36	49	49	75	73	83	80
				2	46	48	93	93	93	92	92	92	94	94	94	93	39	44	53	53	80	79	92	91
				4	47	48	87	90	90	90	91	90	90	91	91	91	41	43	74	72	61	64	83	89
				Avg	47	47	89	89	90	89	90	89	90	89	90	89	37	41	59	58	72	72	86	86
	Avg of all scenarios				65	66	87	89	90	90	90	91	91	92	91	92	66	67	76	77	78	79	87	89

Table 5. Estimates of the cumulative survival rate of emperor goose goslings to 5, 10, 20, and 35 days in 1993, with standard deviations (SD) calculated by bootstrapping.

Method of estimation	Survival to age 5		Survival to age 10		Survival to age 20		Survival to age 35	
	Estimate	SD	Estimate	SD	Estimate	SD	Estimate	SD
K&J	0.818	0.027	0.704	0.042	0.588	0.042	0.419	0.068
IT(1)	0.727	0.053	0.638	0.055	0.604	0.045	0.412	0.078
ITUSM(5)	0.725	0.060	0.653	0.051	0.604	0.044	0.419	0.065
ITSM(5)	0.725	0.060	0.652	0.051	0.605	0.044	0.420	0.063
ITUSM(10)	0.786	0.034	0.651	0.050	0.600	0.046	0.423	0.065
ITSM(10)	0.804	0.032	0.646	0.051	0.596	0.047	0.424	0.061
ITUSM(20)	0.814	0.030	0.699	0.041	0.584	0.046	0.420	0.063
ITSM(20)	0.864	0.020	0.746	0.035	0.556	0.051	0.408	0.057
ML	0.759	0.064	0.610	0.059	0.544	0.052	0.459	0.078

The best model, as judged by AIC, estimated D and 2 survival parameters (Table 6). However, this model was only slightly better than the corresponding model with 3 survival parameters (ΔAIC = 1.16) or the corresponding model with 4 survival parameters (ΔAIC = 2.28). Estimates for the minimum AIC model were as follows, with the approximate standard deviations obtained from 200 bootstrap samples shown in parentheses: $\hat{\alpha}_1 = 0.0474$ (0.0085), $\hat{\alpha}_2 = 0.0121$ (0.0035) and $\hat{D} = 3.22$ (0.49). ML estimates were quite similar to estimates from ITUSM(10) for 5 days, but lower for 10 and 20 days and higher for 35 days.

We show the standardized residuals for the fitted model, which are the differences between the observed number of survivors and the expected number from the fitted model, divided by the standard deviation for the expected number of survivors as given by the square root of the variance from equation (4) (Fig. 1). Large positive residuals arise from increases in brood size, and large negative residuals result from an unusually large loss of goslings. The residuals appear to be reasonably random as required for our model to be acceptable.

The maximum likelihood estimate of D (3.22) implies that the variance in the numbers surviving over observation periods was about 3 times as large as expected from purely binomial variation. The amount of heterogeneity displayed by the data is therefore considerable. Our simulations indicated that estimates of D values are usually slightly biased upwards, a result similar to that obtained by Anderson et al. (1994). Nevertheless, it is clear that the heterogeneity in the data is substantial.

DISCUSSION

Many studies that address major ecological issues continue to use methods of survival estimation that assume constant survival, without testing this assumption, and do not account for the heterogeneity likely to be present in such data (Martin 1998). Use of biased methods facilitates a bias in our ecological understanding. Because our iterative method outperformed

Table 6. Deviances and AIC values for maximum likelihood models fitted to 1993 data concerning survival rates of emperor goose goslings.

Model	Number of parameters	Degrees of freedom	Deviance	AIC	ΔAIC
4 survival parameters, D=1	4	258	804.14	812.14	145.90
4 survival parameters, D estimated	5	257	658.52	668.52	2.28
3 survival parameters, D=1	3	259	804.68	810.68	144.44
3 survival parameters, D estimated	4	258	659.4	667.4	1.16
2 survival parameters, D=1	2	260	805.74	809.74	143.50
2 survival parameters, D estimated	3	259	660.24	666.24	0
1 survival parameters, D=1	1	261	841.74	843.74	177.50
1 survival parameters, D estimated	2	260	707.22	711.22	44.98

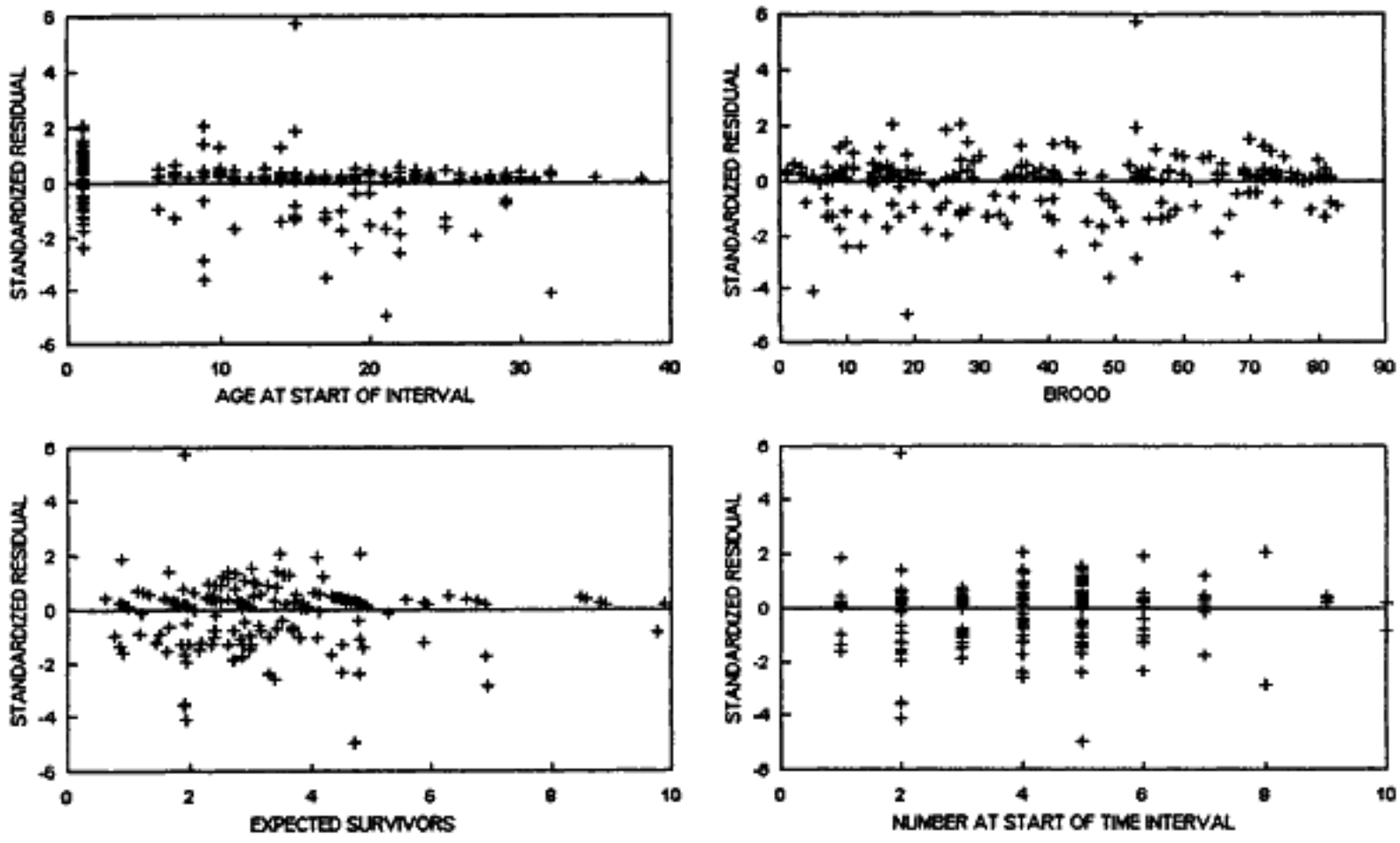

Fig. 1. Standardized residuals plotted against the age of the brood at the start of the survival interval, the brood number, the expected number surviving at the end of the survival period, and the number at the start of the survival period. The residuals are from the maximum likelihood model fitted to 1993 data concerning survival of emperor goose goslings.

existing methods and is readily programmed on a computer, we see no reason for continued use of the Mayfield method or its previous modifications. Results from our iterative method will differ from those of prior Mayfield methods only when survival is not constant, and the iterative method will accurately model such nonconstancy in survival. The iterative Mayfield method is applicable to data concerning survival of eggs, nests, or identifiable families of individuals. Numbers of individuals can be assessed at either regular (structured) or irregular periods of time and knowing unique identities of individuals within clutches or families is not required.

Our simulation study demonstrated that the estimator with the most bias was 1 where true survival varied, but we modeled survival as constant for 20-day periods. With this variation in true survival, a traditional Mayfield approach, which assumes constant survival for the whole study period (here 38 days), would likely have performed even more poorly. In such cases, Klett and Johnson's (1982) modified Mayfield method performed only slightly better with respect to bias and had the poorest coverage. Our iterative modification to Klett and Johnson's methods clearly resulted in improved estimates. The least biased and most parsimonious model can be found by allowing for time-varying survival but averaging survival over an appropriate number of days. A protocol for finding an appropriate number of days for averaging begins with a general model that averages for as short a period of time, say 1 to 5 days, as one deems biologically plausible. Then, one can construct additional models with averaging over progressively longer periods. When smoothed and unsmoothed estimates start to diverge from each other, then averaging periods are too long.

We point out that our iterative Mayfield method is essentially a Kaplan-Meier model (Pollock et al. 1989) in that it is a measure of binomial survival being calculated as the number of survivors divided by the numbers at risk. Mayfield methods have most frequently been applied to data collected with unstructured designs so that individuals within a study are observed on different days and with differing amounts of time elapsing since their prior observation. In contrast, Kaplan-Meier methods rely on a structured design wherein the status of all individuals are assessed in each observation period (Pollock et al. 1989). Flint et al. (1995) demonstrated that with a structured set of data, Mayfield and Kaplan-

Meier methods provide identical point estimates and similar confidence interval coverage. Our iterative Mayfield method with no averaging computes numbers of mortalities and exposure days for each day of study, and thus can be thought of as a structured sampling approach with daily intervals of observation. Given the S_i and R_i values for each day, point estimates for Mayfield and Kaplan-Meier methods are identical (Flint et al. 1995). The difference between methods is simply that for Kaplan-Meier models, the real data would have to actually reflect daily observation of all individuals, whereas with our iterative Mayfield method we compute these daily quantities from an unstructured design.

Our ML method was slightly more biased and had poorer coverage than our iterative method. Use of a normal rather than binomial approximation was necessitated by frequent increases in brood sizes, but the finite set of small brood sizes and associated rounding and truncation contributed to this approximation sometimes being poor and contributing to the underperformance of the ML model. If one wishes to study survival of individuals where increases in number do not happen (as in nest survival studies), then other ML methods based on a binomial distribution would be more appropriate (Bart and Robson 1982). Nonetheless, for estimating survival of broods, the ML approach (with bootstrapping) is useful as it outperforms previous methods, can incorporate covariates, and covariates can be evaluated via model selection in a likelihood context. Additionally, our ML method is robust in the presence of heterogeneity (as is the iterative method) and it estimates a heterogeneity factor. This heterogeneity parameter may sometimes be of biological interest, particularly if there is only 1 suspected source of heterogeneity.

For our empirical data on emperor geese, we suspected there to be 3 significant sources of heterogeneity other than time (age) variation–adoption events, correlated survival among siblings, and inherent differences among broods. The structure of our data was inadequate to distinguish among these sources. The latter 2 sources could be distinguished if broods experienced multiple events of large losses (or gains), rather than 1 or no such large events per brood as with our data.

We have introduced 2 methods for estimating survival of nests and young animals. These methods are superior to previous methods, and we suggest that future investigators employ them. Computer programs for these iterative Mayfield and maximum likelihood methods can be downloaded from www.west-inc.com. We point out that similar simulation studies could be carried out to mimic each researcher's particular study and thus identify the extent of biases to be expected when using these and the prior methods for estimation.

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