

A Birth-Interval Model for Estimating Cetacean Reproductive Rates from Resighting Data

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ABSTRACT

Three approaches are examined for estimating reproductive rates from data on multiple resighting of distinctly marked animals. The three approaches correspond to parameter estimation for three population growth models. Two of the approaches, parameter estimation for the Leslie matrix and geometric series models, are based only on known-aged individuals. A third approach, the birth-interval model, is developed making fuller use of available information. The birth-interval approach uses only known-aged individuals to estimate the first-birth ogive and uses all females with previous births to estimate the probabilities associated with various birth intervals. A Monte Carlo simulation is used to examine the bias and precision of the three methods given the quantity of data that is usually available in a multiple resighting study. All three approaches appear capable of giving unbiased estimates of population growth rate. The variance associated with such estimates is greatest for the Leslie model, less for the geometric series model and least for the birth-interval model.

INTRODUCTION

The number of repeated sightings of individually-identified cetaceans continues to increase. Many examples, including both large whales and delphinids, are discussed in this volume. Some studies will soon have 20 years of continuous data including records of thousands of sightings of identified individuals from particular populations. In many cases, the presence or absence of a calf is noted when observations are made. Thus, these sighting records include potentially valuable information on cetacean reproduction. In this paper, I examine methods for calculating reproductive rates from repeated sightings of known individuals.

The more obvious approaches used to estimate reproductive rate from resighting data tend to be biased. For example, one approach is to calculate the average number of mature females that give birth in a given year. Typically, the only measure of maturity is the presence of a calf in close proximity to the female. If the first observation of a particular cow with a calf were included in calculating an average birth rate for the population, that rate would be biased upwards. If the first observation were excluded, average birth rate would be biased downwards. A second approach is to calculate an average calving interval. Typically, these estimates are also biased. Mean calving interval is affected by a downward bias because one cannot expect to observe calving intervals that terminate after the study period. Mean calving interval is affected by an upward bias because some birth events will be missed (assuming some cows are not seen every year). The intent of this paper is to develop methods for estimating reproductive rates that are robust and unbiased.

I examine three methods for estimating reproductive rates from resighting data. (For this work, resighting data is defined as records of repeated sightings of distinctly marked individuals for which the presence or absence of a calf is unambiguously noted.) The first method is based on estimating the reproductive parameters of a Leslie matrix model. The second is based on estimating parameters for a geometric series model. Both use information collected

only from known-aged individuals. Because most individuals in a resighting study will not be of known age, these methods do not utilise all sources of information and might, therefore, be expected to be relatively imprecise. If parameters are correctly estimated, both are unbiased. I also present a third method which more fully utilises available information. This new approach (termed the birth-interval model) is compared to the other two approaches with respect to bias and precision.

METHODS

Reproductive rates have no clear meaning outside of the specific model to which they apply. There is no single definition of *the* reproductive rate of a population. Although one can invent statistics that are measures of reproductive output, it is difficult to judge bias or precision in the estimation of reproductive rate except in the context of a particular model. Methods for estimating reproductive parameters of three population growth models are presented below. The accurate estimation of population growth rate is the basis of measuring bias and precision. Bias and precision are evaluated using Monte Carlo simulations.

For all three models, it is assumed that mean survival rates of mature and immature individuals can be estimated from the same resighting data (Buckland, 1990).

Leslie matrix model

The Leslie matrix model is commonly used to model growth in age-structured populations. Details of the model are presented by Leslie (1945) and in most texts on population biology (e.g. Keyfitz, 1977; Pielou, 1977). In brief, the model is based on an age-structured projection matrix. When a vector of age specific population size is multiplied by this matrix, the result is the predicted vector of age-specific abundances one time unit later. Typically only females are modelled; however, because sex may not be known for the majority of individuals in a resighting study, I model males and females combined.

Table 1

Parameters used to construct the three population growth models considered here. Parameters subscripted with x or t are vectors.

Model	Parameters	Definition
Leslie Matrix	p_x	Survival rate of age-class x
	f_x	Fecundity rate of age-class x
Geometric Series	α	First sexually mature age class
	l_α	Survival from birth to age class
	\bar{p}	Mean survival rate of mature age classes
	\bar{m}	Mean fecundity rate of mature age classes
Birth-Interval	p_x	Survival rate of age-class x
	β_x	Fecundity rate of age-class x for females without prior births
	δ_t	Mean fecundity at t time periods after a previous birth

The non-zero elements of the Leslie matrix include age-specific survival rates (in the first sub-diagonal) and age-specific fecundity rates (in the first row) (Table 1). The survival rates represent the probability of surviving from the beginning of one age class to the beginning of the next. The fecundity rate represents the expected number of offspring produced per individual of a given age at time t and which survive until one time unit later, at time $t+1$. The components of fecundity thus include reproductive rates and survival rates (the mother must survive from some arbitrary census time to parturition time and the offspring must survive from birth to the next census time).

I use here a formulation of the Leslie model that assumes census immediately after parturition. Thus, the only significant component of survival in the fecundity term is the survival of the mother from census to parturition. Let the first age class be called age class 1 and include individuals which are essentially newborns (remembering that births occurred immediately before census). This convention conforms to a formulation recommended by Goodman (1982).

Fecundity rates can be estimated from resighting data using known-aged individuals. I assume that cows and calves are observed together shortly after parturition. A crude birth rate, b_x , at age x is calculated as the number of calves observed with presumed mothers of age x , divided by all individuals (males and females) of age x . The fecundity rate, f_x , is then estimated as the product of the survival rate of females at a given age and the crude birth rate of the next age class:

$$f_x = p_x b_{x+1} \tag{1}$$

The population growth rate, e^r , is estimated as the one real-number solution to the discrete-time formulation of Lotka's equation

$$\sum_{x=1}^{\infty} (e^r)^{-x} l_x f_x = 1 \tag{2}$$

where $l_x = \prod_{i=1}^{x-1} p_i$ = survivorship from birth to age x

(Goodman, 1982). This rate is equivalent to the dominant Eigen value of the Leslie matrix.

Geometric series model

The geometric series model can be thought of as a collapsed form of the Leslie model. The model is named after an arithmetic identity that allows considerable

Age class	Age class	Age class	Age class	Age class
α	$\alpha+1$	$\alpha+2$	$\alpha+3$	$\alpha+4$

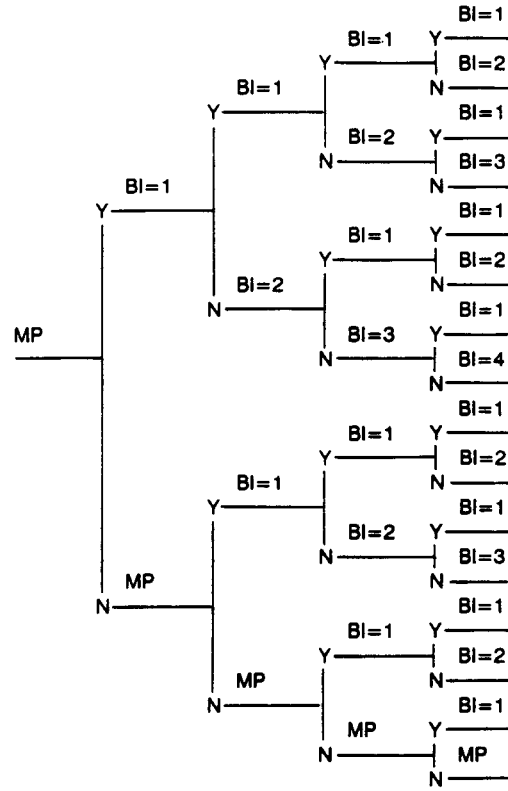


Fig. 1. Illustration of the Markovian method used to estimate Leslie matrix fecundity parameters from first-birth and birth-interval probabilities. Each node represents a decision point. At each node, the probability of having a calf, Y, or not having a calf, N, is given by either the first-birth probability, MP, for that age class (if no prior birth) or the birth-interval probability corresponding to the time, t , since the previous birth ($BI=t$). The probability of reaching each node is the product of all probabilities leading up to that node. The probability of giving birth for each age class is the sum of the probabilities of all nodes which result in a birth in that age class.

simplification in estimating population growth rates. The number of parameters is reduced to 4 (Table 1): the age at sexual maturation, α ; the survivorship from birth to that age, l_α ; the mean survival rate of mature animals, \bar{p} ; and the mean fecundity rate of mature animals, \bar{m} . Goodman (1984) provides a more detailed description of this model. Given the parameters for a Leslie model, it is possible to derive the parameters for the geometric series model. Typically, however, parameters are estimated independently of the Leslie model, and, because fewer parameters are needed, the geometric series model may perform better when sample size is limited. The population growth rate, e^r , is estimated as the solution to the equation

$$e^{r\alpha} - p \cdot e^{r(\alpha-1)} - m \cdot l_\alpha = 0 \tag{3}$$

(Goodman, 1984).

Again, the reproductive parameters of this model can be estimated from resighting data using known-aged individuals. The age at sexual maturation is simply one less than the age class of the youngest individual known to have given birth. The mean crude birth rate is the total number of calves born to known-aged individuals divided by the total number of known-aged individuals in age classes greater than or equal to the age of sexual maturation. The mean fecundity rate is estimated as this mean crude birth rate multiplied by the mean survival rate of mature females.

Birth-interval model

A third model, the birth-interval model, is developed here specifically to deal with the problems encountered using resighting data to estimate birth rates. The reproductive terms include two vectors (Table 1). The first vector, β_x , gives the probability that an individual of age x which has not given birth previously will give birth at age $x+1$. The second vector, γ_t , gives the probability of giving birth t years following the preceding birth. The first-birth probabilities, β_x , are estimated only from known-aged individuals. The birth-interval probabilities, γ_t , are estimated from all individuals which have given birth previously. Given estimates for these two sets of probabilities, the fecundity terms of a Leslie matrix can be estimated using Markov probability chains (Fig. 1). At this stage, population growth rates can be estimated as described above for the Leslie matrix.

First-birth and birth-interval probability vectors are estimated using iterative maximum-likelihood procedures. Birth-interval probabilities are estimated first. Calves are defined as young-of-the-year. An individual which is seen with a calf in one year can be classified in subsequent years as being in one of three states: (1) seen with a different calf; (2) seen without a calf; or (3) not seen at all. This information can be tabulated as given in Table 2. The probability, $\text{Pr}(t,j)$, of being in state j (of the three states given above) at time t after the birth of a calf can be calculated given estimates of the birth-interval probabilities (described above), the probability of being seen in a given year, and the mean survival rate. The likelihood of obtaining the aggregate sample is the product of the likelihoods of each individual observation. The likelihood function is thus

$$L = \prod_{t=1}^{\infty} \prod_{j=1}^3 (\text{Pr}(t,j))^{n(t,j)} \quad (4)$$

where

t = time since previously seen with calf,

j = observation state at time t and

$n(t,j)$ = number of individuals observed in state j at time t .

Table 2

Examples of the data used to estimate birth-interval probabilities. Values represent the number of individuals seen with a calf, seen without a calf, or not seen, as a function of time since a previous calf.

	Time since previous birth						
	0	1	2	3	4	5	6
No. with calf	195	76	70	70	68	60	61
No. without calf	23	30	25	22	34	24	
Not seen	96	95	100	105	101	110	

The probability of being seen in a subsequent year is assumed to decrease each year at a rate equal to one minus the mean survival rate. Furthermore, it is assumed that the mean survival rate and the probability of being seen have been estimated using standard mark-recapture techniques. The iterative approach to maximum likelihood proceeds as follows. First, a 'guess' is made for the birth-interval probabilities and the likelihood of the observed aggregate sample is calculated. Next, small changes are made to the estimates of birth-interval probabilities and the likelihood function is re-evaluated. This procedure is repeated until the values are found for birth-interval probabilities that maximise the likelihood function. In practice, I used the simplex algorithm to maximise the natural logarithm of the likelihood function. To reduce the number of parameters estimated, $\text{Pr}(t,j)$ was assumed to be constant for all t greater than three.

Table 3

Examples of data used to estimate first-birth probabilities. Values represent the number of known-aged individuals seen with or without a calf as a function of their age. The first reproductive age class is denoted as α .

	Age class					
	1	2	...	α	$\alpha+1$	$\alpha+2$
No. with calf	0	0	...	11	50	28
No. without calf	517	424	...	112	48	42

A similar approach was used to estimate first-birth probabilities. For each year they are observed, known-aged individuals can be classified in one of two states: (1) seen with a calf; or (2) seen without a calf. This information can be tabulated as given in Table 3. The probability of an individual of age x being with a calf, $\text{Pr}(x,1)$, is given by the crude birth rate, b_x . The probability of being without a calf, $\text{Pr}(x,2)$, is given as the complement of this rate, $1 - b_x$. The likelihood of observing an aggregate sample is the product of likelihoods of each individual observation. The likelihood function is thus

$$L = \prod_{x=1}^{\infty} \prod_{j=1}^2 (\text{Pr}(x,j))^{n(x,j)} \quad (5)$$

where

x = age of individual

j = observation state at age x

$n(x,j)$ = number of individuals observed in state j at age x .

Again, an iterative approach was used to find the maximum likelihood values for first-birth probabilities. First, a 'guess' is made for the probabilities of having a first calf at each age. These first-birth probabilities and the birth-interval probabilities estimated earlier are used to calculate the expected crude birth rates. The likelihood of the observed aggregate sample is calculated. Next, small changes are made to the estimates of first-birth probabilities and the likelihood function is re-evaluated. This procedure is repeated until the values are found for first-birth probabilities that maximise the likelihood function. Again the simplex algorithm was used to maximise the natural logarithm of the likelihood function. To reduce the number of parameters estimated for this study, $\text{Pr}(x,j)$ was assumed to be constant for all x greater than $\alpha+2$.

Monte Carlo simulations

Computer simulations were used to test the bias and precision of the birth-interval model relative to the more familiar Leslie and geometric series models. Simulations used full demographic stochasticity in which transition probabilities (birth or death) were applied to individuals. Initially a sample of *n* individuals was drawn from a population with known first-birth and birth-interval probabilities and known survival rates. The age distribution of the sample was drawn randomly with respect to the stable age distribution of that population. For each individual, the simulation program had variables to indicate age and sex and, for females, time since the previous birth. This initial population was then projected *t* time units into the future. At each time step, the probability of dying was evaluated for each individual. At each time step, the probability of having an offspring survive until the next time step was evaluated for each female. New births were distributed randomly among males and females.

A simulation of the process of sighting individuals was superimposed on this stochastic population projection. All individuals were assumed to have the same probability of being seen. At each time step, each individual was randomly assigned as being seen or not being seen based on this probability. A new calf was classified as being seen if its mother was seen. Individuals were classified as known-aged only if they were seen as calves.

Population growth rates were estimated using simulated sightings data collected over *t* years and using the Leslie, geometric series and birth-interval models. This process was repeated for 40 iterations, and the mean and variance in the resulting population growth rates were calculated for each of the three models.

Conditions for the simulations were designed to cover a feasible range of study conditions. The length of the simulated studies, *t*, ranged from 10 to 20 years. Values for the simulated population size, *n*, ranged from 100 to 200 individuals. Values for the probability of being seen ranged

Table 4

Survival rates, birth-interval probabilities, first-birth probabilities, and Leslie matrix fecundities used in simulations to yield a growth rate of 0.998. Fecundities were calculated from the other three vectors using Markovian probability chains.

Time/Age	Birth-interval probabilities	First-birth probabilities	Survival rates	Fecundity rates
1	0.75	0.00	0.66	0.00
2	0.90	0.00	0.74	0.00
3	0.90	0.00	0.80	0.00
4	0.90	0.00	0.84	0.04
5	0.90	0.10	0.88	0.23
6	0.90	0.50	0.91	0.37
7	0.90	0.90	0.93	0.36
8	0.90	0.95	0.94	0.37
9	0.90	1.00	0.95	0.37
10	0.90	1.00	0.95	0.37
11	0.90	1.00	0.95	0.37
12	0.90	1.00	0.94	0.37
13	0.90	1.00	0.92	0.36
14	0.90	1.00	0.89	0.35
15	0.90	1.00	0.86	0.34
16	0.90	1.00	0.80	0.31
17	0.90	1.00	0.73	0.29
18	0.90	1.00	0.63	0.25
19	0.90	1.00	0.51	0.20
20	0.90	1.00	0.00	0.00

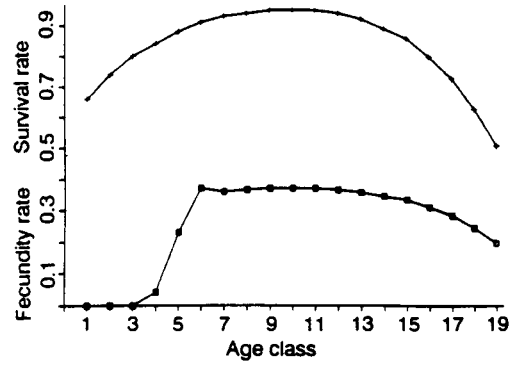


Fig. 2. Fecundity rates and survival rates used in simulation studies. Fecundity rates are as defined by first-birth and birth-interval probabilities (Table 4) and result in a population growth rate of 0.998. It is assumed that the survival rate of age-class 20 is zero.

Table 5

Survival rates, birth-interval probabilities, first-birth probabilities, and Leslie matrix fecundities used in simulations to yield a growth rate of 1.025. Fecundities were calculated from the other three vectors using Markovian probability chains.

Time/Age	Birth-interval probabilities	First-birth probabilities	Survival rates	Fecundity rates
1	0.90	0.00	0.66	0.00
2	1.00	0.00	0.74	0.00
3	1.00	0.00	0.80	0.04
4	1.00	0.10	0.84	0.23
5	1.00	0.50	0.88	0.40
6	1.00	0.90	0.91	0.41
7	1.00	0.95	0.93	0.42
8	1.00	1.00	0.94	0.43
9	1.00	1.00	0.95	0.43
10	1.00	1.00	0.95	0.43
11	1.00	1.00	0.95	0.43
12	1.00	1.00	0.94	0.43
13	1.00	1.00	0.92	0.42
14	1.00	1.00	0.89	0.40
15	1.00	1.00	0.86	0.39
16	1.00	1.00	0.80	0.36
17	1.00	1.00	0.73	0.33
18	1.00	1.00	0.63	0.29
19	1.00	1.00	0.51	0.23
20	1.00	1.00	0.00	0.00

from 0.5 to 1.0. Birth-interval and first-birth probabilities and survival rates were chosen to be representative of a stable population of a marine mammal with a lifespan of approximately 20 years (Table 4, Fig. 2). Variations on this life table included increasing birth rates to yield a population growth rate, *r*, of 1.025 (Table 5), and increasing birth and survival rates to yield a population growth rate of 1.062 (Table 6).

RESULTS

The mean population growth rates estimated from simulations are given in Table 7 for each of the three models. The expected population growth rate (based on the underlying survival and fecundity schedules) and the realised mean growth rates of the populations are also given. Standard errors in the estimation of population growth rates are given in Table 8 for each of the three models.

Table 6

Survival rates, birth-interval probabilities, first-birth probabilities, and Leslie matrix fecundities used in simulations to yield a growth rate of 1.062. Fecundities were calculated from the other three vectors using Markovian probability chains.

Time/Age	Birth-interval probabilities	First-birth probabilities	Survival rates	Fecundity rates
1	0.90	0.00	0.75	0.00
2	1.00	0.00	0.80	0.00
3	1.00	0.00	0.85	0.04
4	1.00	0.10	0.87	0.23
5	1.00	0.50	0.89	0.40
6	1.00	0.90	0.91	0.41
7	1.00	0.95	0.93	0.42
8	1.00	1.00	0.94	0.43
9	1.00	1.00	0.95	0.43
10	1.00	1.00	0.95	0.43
11	1.00	1.00	0.95	0.43
12	1.00	1.00	0.94	0.43
13	1.00	1.00	0.92	0.42
14	1.00	1.00	0.89	0.40
15	1.00	1.00	0.86	0.39
16	1.00	1.00	0.80	0.36
17	1.00	1.00	0.73	0.33
18	1.00	1.00	0.63	0.29
19	1.00	1.00	0.51	0.23
20	1.00	1.00	0.00	0.00

Table 7

Population growth rates estimated from Monte Carlo simulations based on three methods for estimating birth rates. Expected growth rates were determined by the underlying survival and birth rates.

Expected growth rate	Prob. being seen	Study period	Sample size	Realized growth rate	Birth-interval model	Leslie matrix model	Geometric series model
0.998	0.5	10	100	1.003	0.992	1.009	0.997
		20	200	0.995	0.994	0.989	0.993
	1.0	10	100	0.997	0.993	0.984	0.979
20		200	0.997	0.997	0.993	0.995	
1.025	0.5	20	200	1.024	1.023	1.024	1.030
	1.0	20	200	1.023	1.025	1.028	1.032
1.062	0.5	20	200	1.054	1.059	1.061	1.062
	1.0	20	200	1.054	1.060	1.063	1.063

In general, biases in the estimation of population growth rates are small for all three models. Mean growth rates from each of the three models (Table 7) differ from the mean realised growth rates by less than the standard error of the estimates (Table 8).

The precision of the three models in estimating population growth rates shows a consistent order. The standard errors for the birth-interval model are consistently lower than those for the geometric series model, which are lower than those of the Leslie matrix model (Table 8). All methods perform better with higher population growth rates. This improved performance is probably a result of greater sample size (although all simulations started with the same population size, a growing population would have more simulated sightings over the course of the study).

Because the simulation study was stochastic, the realised growth rates did not exactly equal the growth rate characteristic of the underlying life table (Table 7). Deviations from the expected growth rates were small, however, indicating no systematic biases in the

Table 8

Standard errors of population growth rates estimated from Monte Carlo simulations based on three methods for estimating birth rates. Expected growth rates were determined by the underlying survival and birth rates.

Expected growth rate	Prob. being seen	Study period	Sample size	Realized growth rate	Birth-interval model	Leslie matrix model	Geometric series model
0.998	0.5	10	100	0.017	0.024	0.034	0.027
		20	200	0.010	0.009	0.020	0.015
	1.0	10	100	0.017	0.019	0.039	0.024
20		200	0.009	0.004	0.015	0.010	
1.025	0.5	20	200	0.008	0.004	0.017	0.015
	1.0	20	200	0.010	0.002	0.010	0.008
1.062	0.5	20	200	0.008	0.006	0.014	0.013
	1.0	20	200	0.008	0.003	0.008	0.007

construction of the simulation model. It is interesting to note that the standard error of estimated growth rates from the birth-interval model is, in most cases, smaller than the standard error of the realised population growth rate.

DISCUSSION

The purpose of this paper was to test the relative bias and precision of three methods for estimating reproductive rates from individual resighting data. The simulation study was not intended to estimate accurately the precision that should be expected in the application of these methods to data collected in the field. Survival rates were assumed to be known in the simulation and would have to be estimated if these methods were applied to field data. Simulations did, however, cover a range of sample sizes and study durations that are attainable or have been attained in field studies.

Leslie matrix model

The assumptions of the Leslie matrix model are the least restrictive of the three models considered here. The primary assumption (common to all three models) is that the sample of individuals that are sighted is representative of the population being studied. Estimation of reproductive rates for the Leslie model does not require any implicit assumptions about the age distribution of the population. This advantage may be outweighed by the restrictive numbers of known-aged individuals available for the estimation of reproductive rates. Ages that are greater than the study period will not be represented at all. Given the longevity of cetaceans, very long-term studies may be necessary in order to estimate accurately fecundities for all age classes using the Leslie model.

Geometric series model

The geometric series model shares a common weakness with the Leslie model; birth rates for both are based on small samples of known-aged individuals. Furthermore, when estimating mean birth rate for the geometric series model there is an explicit assumption that the population has a stable age distribution. If, after maturation, birth rates change appreciably with age and if the age distribution is not stable, the estimation of asymptotic population growth rate will be biased. This bias may be small, however, and the lower variance of the geometric series model would make it preferable to the Leslie model in most applications.

Birth-interval model

In estimating birth-interval probabilities, it is assumed that the sample has a stable age distribution. If not, and if birth-interval probabilities change with age, the resulting estimate of population growth rate will be biased. In addition to this assumption (which was the same for the geometric series model) there is the additional assumption that the probability of being seen is the same for all individuals. Based on previous field studies, this is almost certainly not true. Although the mean probability of being seen may be estimated very accurately, individual heterogeneity in sighting probability can lead to serious biases. (This is separate from the assumption that the probability of being seen is independent of the presence of a calf, an assumption that was common to all methods.) Additional work is needed to determine whether sighting heterogeneity would bias the estimation of birth-interval probabilities. If this bias is present, it is probably small. The birth-interval model is still likely to be the best approach for estimating reproductive rates from resighting data.

Simulation studies

The simulation studies here do not account for all sources of error and imprecision that are likely to be encountered in estimating growth rates from field data. First (and probably most importantly), I assumed that survival rates were known. Because I wanted to measure the accuracy in estimating reproductive rates, I did not want to add this additional source of random error. Methods for estimating age-specific survival rates from resighting data have not been examined in depth. It is likely that some method of estimating an aggregate survival rate for all age classes (Buckland, 1990) may have to be incorporated into the models presented here. If age-specific rates are not available, estimates of population growth rates may be sensitive to departures from a stable age distribution.

These simulation studies may also have overestimated the number of known-aged individuals that could be obtained in any field study. I assumed that any individual seen as a calf could later be identified as a known-aged individual. It is likely that many young animals have no distinguishing marks and thus would not be recognised as adults. This would affect all three models, but would affect the Leslie and geometric series models more because they are entirely dependent on known-aged individuals.

No attempt was made to analyse the effect of deviations from a stable age distribution on the estimation of population growth rate. Such deviations would affect each model differently. Also, changes in reproductive rates with age were not explicitly modelled. The number of permutations needed to simulate these effects is overwhelming and beyond the scope of this work. Because the Leslie model has fewer assumptions, it would be less affected than would the other models. Whether this advantage would outweigh the disadvantages of this method would depend on the specific application.

Future research

Methods for estimating reproductive rates for each of the three models could benefit from additional studies. For the Leslie model, it is likely that precision can be increased if

age groups are lumped into larger age categories. This is especially true for the older age classes for which the sample of known-aged individuals is very small. As age classes are combined, however, the assumption of a stable age distribution becomes important. Simulation studies could be used to examine the trade-offs between greater precision and violations of this assumption.

For the geometric series model, it may be possible to use individuals of known-minimum-age to augment the sample of known-aged individuals in calculating the mean crude birth rates and mean survival rates. This approach could, however, lead to biases. By adding individuals whose minimum age is greater than the age at sexual maturation, the sample may be weighted towards older mature animals. This would introduce a bias if birth rates or survival rates change appreciably with age. [Mean birth rates and survival rates should be estimated as an average of age-specific rates that are weighted by the actual number of individuals in each age class (Goodman, 1984)]. This latter source of bias should be balanced, however, against the likelihood that older individuals would not be represented in the sample at all unless known-minimum-aged individuals are included. This approach deserves further consideration.

For the birth-interval model, the largest problem (alluded to above) is likely to be heterogeneity in the probability of resighting individuals. This problem should be examined using simulation studies.

For all three approaches, simulation studies should be extended to include the estimation of survival rates. Only then could a realistic appraisal be made of the standard error of estimating population growth rates from resighting data. Based on the results presented here, the component of error due to the estimation of reproductive rates is small. The possibilities of estimating population growth rates from resighting data should be viewed with considerable optimism.

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