

MODELING APPROACHES TO BALD EAGLE POPULATION DYNAMICS

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Abstract: Combinations of hypothetically low to high rates of reproduction and survival were substituted for missing real data in models of bald eagle (*Haliaeetus leucocephalus*) population dynamics. A deterministic life table model and a stochastic Monte Carlo model were used. The outcomes of these simulations suggested that differences in survival rates may be relatively more important to the status of eagle populations than similar differences in reproduction. The exercise also emphasized the need for real data on survival and the percentage of adults that are attempting to breed.

The data needed to calculate bald eagle life equations are insufficient at present. Survival information is almost nonexistent. Gerrard et al. (1978) obtained estimates of survival for bald eagles through the first 3 years from returning wing-marked birds. Their data suggested rates might be higher than formerly believed. Banding data are still inadequate to estimate survival rates because of small sample sizes and lack of adult banding (Brownie et al. 1978). Certain aspects of reproduction are fairly well documented (Grier 1974, Mathisen 1973, McEwan and Hirth 1979, Sherrod et al. 1976, Sprunt et al. 1973, Whitfield et al. 1974), but those data are only for birds that breed or attempt to breed; we do not know what percentage of the adult population is attempting to breed or at what age they normally begin breeding in the wild.

Reproduction of bald eagles appears to be increasing throughout much of the species' range, following a period of reduced productivity during the late 1960s and 1970s. Sprunt et al. (1973) compared reproduction among several bald eagle populations believed to be having different rates of growth or decline. But it is not safe to infer population dynamics based on productivity data alone or only with rough, subjective in-

formation on whether the actual size of the population is stationary or declining. Grier (1979) illustrated the problems that can arise from using insufficient data.

Bald eagle population dynamics can be modeled, however, using a range of reasonable hypothetical values. Such techniques can provide insight and suggest direction for management even when real data are missing. This approach emphasizes those data that are missing and most critically needed from further field research.

Young (1968) used a simple population model that suggested that relative to insects and robins, eagle populations are more sensitive to changes in survival rates than in reproduction. I used 2 different models, 1 deterministic and 1 stochastic, and a range of hypothetical values to obtain a series of population outcomes for bald eagles. Both models led to similar inferences and inclusion of both might seem redundant. I included both, however, for 2 reasons. First, they span the range of population sizes: the stochastic model is more realistic and preferred for small populations whereas the deterministic is adequate and most practical for use with large populations. The similarity of inferences only confirms that the principles apply regardless of population size or model

Table 1. Hypothetical reproduction and survival rates used for bald eagle population modeling.

	Low	Moderate	A stationary combination	High
Reproduction				
Age begin breeding	5	5	5	5
% of adult ♀ producing 0 young	70	40	20	20
% of adult ♀ producing 1 young	24	26	57	20
% of adult ♀ producing 2 young	6	32	21	56
% of adult ♀ producing 3 young	0	2	2	4
No. young (total) per ♀ with young	1.20	1.60	1.31	1.80
No. ♀ young per ♀ with young	0.60	0.80	0.66 ^a	0.90
No. young (total) per adult ♀	0.36	0.96	1.06	1.44
No. ♀ young per adult ♀ (mx)	0.18	0.48	0.53	0.72
Survival				
Annual finite survival rate (%) of first-year birds	30	60	60	70
Annual finite survival rate (%) of older eagles	70	80	85	90

^a 0.6563.

Table 2. Calculated bald eagle life table characteristics under different rates^a of reproduction and survival.

	Reproduction			
	Low	Moderate	Stationary schedule	High
Survival				
Low				
<i>r</i>	-0.41	-0.30	—	-0.25
% population change ^b	-33	-26	—	-22
% year 0 ^c	12	22	—	27
% year 0-4 ^d	34	54	—	62
Moderate				
<i>r</i>	-0.15	-0.06	—	-0.02
% population change	-14	-6	—	-2
% year 0	11	19	—	24
% year 0-4	40	59	—	67
Stationary schedule				
<i>r</i>	—	—	0.00	—
% population change	—	—	0	—
% year 0	—	—	21	—
% year 0-4	—	—	60	—
High				
<i>r</i>	-0.02	0.065	—	0.11
% population change	-2	6.7	—	11
% year 0	11	19	—	24
% year 0-4	38	48	—	68

^a See Table 1.

^b Change in population size from 1 year to next; $(R-1.00) (100)$.

^c Stable age ratio; percentage of first-year birds (year 0) in the population.

^d Percentage of subadults in the theoretical stable age ratio. If they molt into adult plumage the fourth summer and are surveyed the following winter, then only 0-3 year olds should be considered, and the ratio (percentage) would be lower.

Table 3. Numbers of bald eagles alive^a for 15 years of simulation with high rates^b of reproduction and survival.

Year	First-year males	First-year females	Subad. males	Subad. females	Adult males	Adult females	Total alive
0	4	4	0	0	0	0	8
	2	3	0	0	0	0	5
1	0	0	2	3	0	0	5
	0	0	2	3	0	0	5
2	0	0	2	3	0	0	5
	0	0	1	3	0	0	4
3	0	0	1	3	0	0	4
	0	0	1	3	0	0	4
4	0	0	1	3	0	0	4
	0	0	0	2	0	0	2
5	0	0	0	0	0	2	2
	0	0	0	0	0	2	2
6	0	0	0	0	0	2	2
	0	0	0	0	0	1	1
7	0	0	0	0	0	1	1
	0	0	0	0	0	1	1
8	0	0	0	0	0	1	1
	0	0	0	0	0	1	1
9	0	0	0	0	0	1	1
	0	0	0	0	0	1	1
10	0	0	0	0	0	1	1
	0	0	0	0	0	1	1
11	0	0	0	0	0	1	1
	0	0	0	0	0	1	1
12	0	0	0	0	0	1	1
	0	0	0	0	0	1	1
13	0	0	0	0	0	1	1
	0	0	0	0	0	1	1
14	0	0	0	0	0	1	1
	0	0	0	0	0	1	1
15	0	0	0	0	0	1	1
	0	0	0	0	0	1	1

^a The first line for each year represents the number alive in each category at the end of the breeding season. The second line is for numbers alive at the end of the year, prior to the next breeding season. The simulation was initiated with 8 artificially reintroduced young birds.

^b See Table 1.

being used. Secondly, different readers may prefer to see 1, the other, or both. The deterministic is probably more familiar to most persons whereas others prefer stochastic models because they are more realistic.

I thank J. Gerrard for discussions on hypothetical rates for stationary eagle populations. Computer facilities and

time were provided by the North Dakota Higher Education computing system.

THE MODELS

The deterministic model used was the standard life table (Grier 1979, Krebs 1978:150-172). The stochastic model was a Monte Carlo rather than probability-theory type (cf. Krebs 1978:199-

Table 4. Another simulation of the numbers of bald eagles alive under the same conditions as in Table 3. Differences in outcome resulted solely from chance.

Year	First-year males	First-year females	Subad. males	Subad. females	Adult males	Adult females	Total alive
0	4	4	0	0	0	0	8
	3	3	0	0	0	0	6
1	0	0	3	3	0	0	6
	0	0	3	3	0	0	6
2	0	0	3	3	0	0	6
	0	0	2	3	0	0	5
3	0	0	2	3	0	0	5
	0	0	2	3	0	0	5
4	0	0	2	3	0	0	5
	0	0	2	2	0	0	4
5	3	1	0	0	2	2	8
	0	1	0	0	2	2	5
6	3	0	0	1	2	2	8
	2	0	0	1	2	2	7
7	1	1	2	1	2	2	9
	1	1	2	1	2	2	9
8	3	0	3	2	2	2	12
	3	0	3	2	2	2	12
9	3	1	6	2	2	2	16
	2	0	5	2	2	2	13
10	1	3	7	1	2	3	17
	1	3	6	1	2	3	16
11	2	3	6	4	3	3	21
	1	2	6	4	3	3	19
12	2	2	6	5	4	4	23
	2	2	6	4	4	4	22
13	3	3	5	6	7	4	28
	2	2	5	6	7	4	26
14	2	2	6	8	8	4	30
	2	0	5	7	8	4	26
15	2	5	6	6	9	5	33
	1	2	5	6	8	5	27

204). It incorporated the effects of chance for mortality, reproduction, and sex of offspring through the use of random numbers (Grier 1980). For sex of each offspring, for example, a 0 or 1 was generated at random and the individual was assigned to either male or female. For mortality during each year of simulation, a random number was generated between 0 and 99 for each individual and, pending the stated mortality rate and the outcome, the individual was either kept or subtracted from the population. If I provided a mortality rate of 25%, for example, a randomly generated number of 0-24 would lead to an individual being dropped from the population whereas 25-99 caused it to be retained for that year. An analogous but more complex, multinomial subroutine generated

the number of young at random for each potential pair for each year of simulation, at reproductive rates that I provided.

The chores of performing the steps and bookkeeping were accomplished with a digital computer. The program (Grier 1980) kept track of age for all individuals and added them to the potential breeding population at maturity at whatever age I provided. The program contains an option to permit either monogamous or polygamous breeding patterns; monogamous breeding was assumed and chosen for bald eagles.

Because of the stochastic nature of the model, different simulations lead to different outcomes, unlike the single, fixed, deterministic outcome of the life table. The computer program for the stochastic model permits the simulation to be repeated any number of times and calculates the mean and standard deviation of final outcomes. It also records the number of simulations that lead to extinctions.

I chose arbitrary, hypothetical values for low to high rates of reproduction and survival. Although hypothetical, these rates were based on my subjective understanding from several years' experience with the species as to what might constitute a reasonable range of rates. Preliminary guesses about rates for a stationary population came from discussions between J. Gerrard and myself in 1978 on our respective Saskatchewan and Ontario data. Those guesses were then modified in subsequent modeling. The rates used in the modeling are shown in Table 1.

RESULTS AND CONCLUSIONS

The life table modeling (Table 2) illustrates the importance of both reproduction and survival, but shows that survival

is far more critical to the existence of the population. This confirms the results of Young (1968). It also demonstrates the uselessness of age ratio information (Caughley 1977:118-123). A population with high reproduction and high survival *increases* at a rate of 11% per year while another population with only 10% lower survival rates *decreases* at a rate of 2% per year. They both have the same rate of reproduction and *essentially identical age ratios!* Another population with both lowered reproduction and survival decreases at a rate of 6% annually but has an age ratio structure that is very similar to a stationary population. Comparisons of extremes in either reproduction or survival, while holding the other (survival or reproduction) constant, show that a 75% cut in reproduction only leads to a drop of about 12 percentage points in annual population change whereas smaller cuts into survival (decreases of about 57% for first-year birds and 33% for older birds) lead to a much larger difference of about 32 percentage points in annual population change (Table 2).

The results with chance yield similar conclusions even more strikingly. Tables 3 and 4 illustrate 2 of the many possible outcomes for stochastic modeling. These tables were deliberately chosen to illustrate extreme cases. Note that the 2 simulations are similar through year 4, but then differences resulting only from *chance* accumulate and cause the 2 simulations to diverge markedly; the underlying annual rates of reproduction and survival are the same! These 2 cases were taken from a set of 100 repeated simulations. For the entire 100, the mean final population of bald eagles (for successful cases) was 10.9 with a standard deviation of 8.4. There were 11 simulated populations that went to extinction. The results of similar, repeated simulations under

Table 5. Monte Carlo simulations of bald eagle reintroductions under different rates^a of reproduction and survival.

No. of birds initially released ^b	Reproduction	Survival	No. of extinctions in 100 simulations	Average no. alive ^c after 15 years of simulation	Standard deviation of final no. alive ^c	Coefficient of variation ^d
8	low	low	97	1.0	0.0	0
8	low	high	13	2.6	1.9	73
8	high	low	99	1.0	0.0	0
8	high	high	11	10.9	8.4	77
40	low	low	93	1.0	0.0	0
40	low	high	0	15.1	5.8	38
40	high	low	91	1.0	0.0	0
40	high	high	0	62.1	20.0	32

^a See Table 1.

^b Fledglings artificially reintroduced, e.g., transplanted or from captive breeding (initial sex ratio 50:50).

^c Among those not going to extinction.

^d (s.d./ \bar{x}) 100.

different combinations of reproduction and survival are shown in Table 5. The short-term chances of extinction (e.g., during 15 years of simulation) depended largely on survival rate, partially on the initial size of the population, and almost not at all on reproductive rate. Higher reproduction simply led to larger populations among those that survived. The standard deviations increased proportionately with the average final outcome (i.e., coefficients of variation, CV, did not vary markedly) for populations of similar starting size, but final outcomes were more variable (larger CVs) for smaller initial populations (8 vs 40), as expected for stochastic considerations.

Thus the population dynamics of bald eagles appear to hinge more on survival than on reproduction. And, somewhat contrary to intuition, rates of reproduction may be relatively inconsequential to this long-lived, slow-breeding species. Our knowledge, on the other hand, is concentrated on reproduction with almost no information on survival. Age ratio information is of little value and should be treated very carefully, if at all.

This modeling has assumed constant time-specific rates, even when subjected

to chance fluctuations. In addition to needing real, objective data, the models need to be modified to consider more realistic, variable, time-specific rates of reproduction and survival.

Modeling based on partially hypothetical values accentuates the need for estimates of survival rates. The most critical missing value for reproduction involves the percentage of adults producing *no* young each year. Our most complete estimates are for reproductive rates among birds that either are producing young (successful) or at least are attempting to produce (active or occupied nests). Although rates of reproduction are relatively less important than rates of survival, that does not mean that reproduction can be discounted wholly (Tables 2 and 5). Furthermore, rates of reproduction may vary over time and our understanding of the reproductive component is still far from complete. Thus we need to seek the whole life equation picture and keep abreast of future changes, at least until the picture is better understood. While we attempt to obtain the missing links for survival and the percentage of adults that are breeding, we cannot afford to drop or lose data on reproduction. Current sur-

veys must be maintained, if not expanded, and modeling should be corroborated with changes based on accurate and precise estimates of actual numbers of eagles. Management, while continuing to maintain or bolster reproduction, should be directed toward increased survival of the individuals already in the population.

LITERATURE CITED

- BROWNIE, C., D. R. ANDERSON, K. P. BURNHAM, AND D. S. ROBSON. 1978. Statistical inference from band recovery data—a handbook. U.S. Fish Wildl. Serv. Resour. Publ. 131. 221pp.
- CAUGHLEY, G. 1977. Analysis of vertebrate populations. John Wiley & Sons, New York, NY. 234pp.
- GERRARD, J. M., D. W. A. WHITFIELD, P. GERRARD, P. N. GERRARD, AND W. J. MAHER. 1978. Migratory movements and plumage of subadult Saskatchewan bald eagles. *Can. Field-Nat.* 92:375-382.
- GRIER, J. W. 1974. Reproduction, organochlorines, and mercury in northwestern Ontario bald eagles. *Can. Field-Nat.* 88:469-475.
- . 1979. Caution on using productivity or age ratios alone for population inferences. *Raptor Res.* 13:20-24.
- . 1980. Ecology: a simulation model for small populations of animals. *Creative Computing* 6(7):116-121.
- KREBS, J. 1978. Ecology. Harper and Row, New York, NY. 678pp.
- MATHISEN, J. E. 1973. Bald eagle-osprey status report, 1972. *Loon* 45:15-16.
- MCEWAN, L. C. AND D. H. HIRTH. 1979. Southern bald eagle productivity and nest site selection. *J. Wildl. Manage.* 43:585-594.
- SHERROD, S. K., C. M. WHITE, AND F. S. L. WILLIAMSON. 1976. Biology of the bald eagle on Amchitka Island, Alaska. *Living Bird* 15:143-182.
- SPRUNT, A. IV., W. G. ROBERTSON, JR., S. POSTUPALSKY, R. J. HENSEL, AND C. E. KNODER. 1973. Comparative productivity of six bald eagle populations. *Trans. North Am. Wildl. Natur. Resour. Conf.* 38:96-106.
- WHITFIELD, D. W. A., J. M. GERRARD, W. J. MAHER, AND E. W. DAVIS. 1974. Bald eagle nesting habitat, density, and reproduction in central Saskatchewan and Manitoba. *Can. Field-Nat.* 88:399-407.
- YOUNG, H. 1968. A consideration of insecticide effects on hypothetical avian populations. *Ecology* 49:991-994.

Received 13 June 1980.

Accepted 15 July 1980.



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