CAUTION ON USING PRODUCTIVITY OR AGE RATIOS ALONE FOR POPULATION INFERENCES

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One frequently sees published statements or hears that a population is declining because reproduction is decreasing or because age ratios are changing. Examples are easy to find; I deliberately have not singled out any specific instances here. The conclusion "declining population" might be true, but it also might not be. Such a conclusion does not necessarily follow from the observed reproductive or age-ratio changes unless other characteristics of the population, such as time-specific mortality rates, remain constant. The assumption that other population characteristics remain constant is rarely stated and may be very dangerous to the interpretation.

The points I wish to make are already known to population biologists (see, e.g., C. J. Krebs, *Ecology*, Harper and Row, 1978, ch. 9–11; and D. B. Mertz, in: J. H. Connell et al. (eds.), *Readings in Ecology and Ecological Genetics*, Harper and Row, 1970, pp. 4–17). Caughley (*J. Wildl. Manage.* 38:557-562, 1974) described the problem well: "Age ratios unsupported by other information seem to be statistics in search of an application." But the principles are not intuitive or obvious. Enough researchers, including raptor workers, are routinely trapped by them that they need to be emphasized.

To illustrate these principles I have chosen hypothetical but realistic examples using standard life-table or life-equation calculations (see Krebs, 1978, ch. 10). The computations were facilitated with a BASIC computer program (which can be used on most computers, including many small office or home models). The program is of general utility and is provided in the Appendix. Any potential users are cautioned, however, that life tables themselves can be misleading; they involve several assumptions, such as age stability and constant population characteristics. Life tables are useful for modeling, as I have done here, but they should not be used for estimating survival rates from band recoveries, a common practice in the past (see note in the program listing). The program given in the Appendix additionally assumes a constant age-specific mortality rate for all birds over one year of age and death before they reach their physiological "old-age" under normal ecological conditions.

For example proving that reproductive information alone can be misleading, consider the hypothetical situation in table 1. In population B the rate of reproduction is only one-half that of population A, but population B is *growing* at a rate of 14 percent per year while population A is decreasing at a rate of 12 percent per year! If you find that hard to believe, study the table and perhaps perform the calculations youself. The reason for the seeming paradox is that higher survival (lower mortality) more than compensated for the lower reproduction in population B.

Table 2 illustrates the problem with age ratios. Again, one of the hypothetical populations is declining while the other is increasing, but the age ratios are identical! A researcher watching these two populations, perhaps Peregrine Falcons, passing on migration could not distinguish between them on the basis of age ratios. The increasing

 Raptor Research 13(1):20–24

population does so because higher reproduction is producing more first-year birds *and* because lowered mortality is resulting in more older birds. But the *ratio* of first-year to older birds has remained the same. The point is that age ratios are difficult, if not often impossible, to interpret. It is like, in a case of simple division, trying to determine the dividend and the divisor when only the quotient is known. Caughley (1974) provides more examples.

Age ratios in the form of "catch curves" are occasionally useful in fisheries, but even they are beset with problems. They often have the advantage of strong age-classes to help serve as markers in the population. Usually when age ratios are reliable, one does not know it unless other data are also available for comparison. But then those other data are sufficient for what one wants to know, and the age ratios are unnecessary.

Population trends can be estimated by comparing age-specific reproduction and mortality (i.e., the life-table approach) but only when both reproduction and mortality information are available or if a constant time-specific mortality rate can be assumed. The only good, clear data that I have seen in an example where reproductive changes are in fact reflected in population changes involves Paul Spitzer's Osprey data for the northeastern United States (personal communication and presentation at the 1978 RRF Annual Meeting). In addition to the presence of good data on both reproduction and the actual total size of the breeding population over a period of years, the Osprey example involves a relatively unique (for raptors) situation: a small but fairly rapidly growing population where intraspecific competition and related mortality probably have not resumed significantly. Hence the mortality rate is probably at a relatively low, constant "background" level.

In the case of Peregrine Falcons in the eastern United States (see J. J. Hickey, ed.), *Peregrine Falcon Populations,* Univ. of Wisconsin Press), reproduction dropped and the falcons disappeared. But the specific relationships betwen reproduction, mortality, time, and actual population changes are far from clear, and we are left with only a rough picture based on hindsight. Reproductive changes might be serious, as they apparently were for Peregrines, and we could lose a population by waiting. Or changes in reproduction might not be significant and we can make fools of ourselves and stretch credibility by rushing in and sounding alarms that are not needed. Hindsight can be painful either way. To avoid the problem of not knowing whether estimated reproductive changes are serious and having to wait for hindsight, the solution is to invest more time and effort (and money) to obtain better data for both reproduction *and* mortality. Trying to make inferences when you have only half the picture can be tricky. As a further safeguard for one's inferences, it helps to have, if possible, other measures of the population, such as proper sampling surveys and/or mark-recapture programs with adequate proportions of recaptures.

In summary, although age ratios and reproductive information occasionally might be useful if used alone, it is risky unless one has additional information (as in P. Spitzer's Osprey case) for a backup. Perhaps in the future after more clear examples consistently show that assumptions like constant time-specific mortality are reasonable, we can use age ratios and reproductive data alone with more confidence. But until then I urge that we proceed with caution.

Acknowledgments

I thank D. H. Johnson and H. Postovit for comments on earlier drafts of this article and P. Spitzer for discussions on his Osprey data.

Table 1. Hypothetical example of lowered reproduction in an increasing population.

	Population 1	Population 2
Average number young per successful nest	6	2
Average number young per adult	1.5	0.5
Age begin breeding	2	2
Proportion of adult females successfully breeding	50%	50%
Average number of daughters per successful female	3	1
First-year mortality	70%	35%
Annual mortality for older birds	50%	10%
ANNUAL RATE OF POPULATION CHANGE	–24%	+14%

Table 2. Age ratios in two hypothetical Peregrine Falcon populations.

Life Table Characteristics	Declining Population	Increasing Population
GIVEN		
First-year mortality	70%	50%
Annual mortality for older birds	25%	20%
Age begin breeding	3	3
Breeding success rate for adult females	60%	60%
Average number of daughters per successful female	1.15	1.25
CALCULATED		
Average number of young per adult	0.69	0.75
Maximum age (for an initial cohort of 1,000)	18	24
Annual rate of population change	–12%	+2%
Age ratios:		
first year (immature plumage)	32%	31%
over first year ("adult" plumage)	68%	69%

APPENDIX

```
10 PRINT
20 PRINT "        *** AVIAN LIFE TABLE ANALYSIS ***"
30 PRINT
40 PRINT "              BY JAMES W. GRIER"
50 PRINT "        ZOOLOGY DEPT., NDSU, FARGO 58105"
60 PRINT

70 PRINT
80 PRINT "DO YOU WANT INTRODUCTORY INFORMATION (1=YES, 2=NO)";
90 INPUT A0
100 IF A0=2 THEN 310
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CORRECTION: Table 1, page 22, Vol. 13 (1) 1979
Grier — Caution on Population Inferences

Table 1. Hypothetical example of lowered reproduction in an increasing population

	Population A	Population B
Average number young per successful nest	4	2
Average number young per adult	1.0	0.5
Age begin breeding	2	2
Proportion of adult females successfully breeding	50%	50%
Average number of daughters per successful female	2	1
First year motality	65%	35%
Annual mortality for older birds	35%	10%
ANNUAL RATE OF POPULATION CHANGE	-12%	+14%

Table 2. Age ratios in two hypothetical Peregrine Falcon populations.

Life Table Characteristics	Declining Population	Increasing Population
GIVEN		
First-year mortality	70%	50%
Annual mortality for older birds	25%	20%
Age of first breeding	3	3
Breeding success rate for adult females	60%	60%
Average number of daughters per successful female	1.15	1.35
CALCULATED		
Average number of young per adult	0.69	0.81
Annual rate of population change	-12%	+3.5%
Age ratios:		
first year (immature plumage)	32%	32%
over first year ("adult" plumage)	68%	68%

```
110 PRINT "THIS PROGRAM CALCULATES POPULATION GROWTH RATES AND"
120 PRINT "A NUMBER OF OTHER POPULATION CHARACTERISTICS FOR"
130 PRINT "BIRDS -- ASSUMING A CONSTANT MORTALITY RATE FOR "
140 PRINT "INDIVIDUALS OVER ONE YEAR OF AGE AND THAT THE BIRDS"
150 PRINT "DIE BEFORE REACHING THEIR PHYSIOLOGICAL LIMITS,"
160 PRINT 'THAT IS, FEW BIRDS DIE IN THE WILD FROM "OLD AGE."'
170 PRINT
180 PRINT "FOR A REFERENCE FOR SOME OF THE OTHER ASSUMPTIONS,"
190 PRINT "SYMBOLS AND MATHEMATICS, SEE: C. J. KREBS."
200 PRINT "1978. ECOLOGY. HARPER AND ROW, PUBL. N.Y. CHAPTER 10."
210 PRINT
220 PRINT "CAUTION: LIFE TABLES ARE USEFUL FOR MODELING BUT THEIR"
230 PRINT "         INTERPRETATION CAN BE TRICKY AND THEY SHOULD"
240 PRINT "         NOT BE USED FOR ESTIMATING SURVIVAL RATES --"
250 PRINT "         SEE: BROWNIE, ANDERSON, BURNHAM, AND ROBSON,"
260 PRINT "         1978. U.S. DEPT. OF INTERIOR, FISH & WILDLIFE"
270 PRINT "         SERVICE, RESOURCE PUBL. NO. 131."
280 REM   NOTE TO PERSONS READING THE PROGRAM: SOME OF THE VARIABLES
290 REM   USED INTERNALLY (NOT PRINTED) MAY NOT BE THE SAME AS IN THE
300 REM   TEXT. E.G., R1="R(0)" AND R2="LITTLE R".
310 PRINT
320 PRINT "WHAT SPECIES ARE YOU WORKING WITH";
330 INPUT S$
340 PRINT "NOTE: INDICATE ALL RATES OR PERCENTAGES AS PERCENTAGES."
350 PRINT "WHAT IS YOUR ESTIMATE OF THE FIRST YEAR MORTALITY"
360 PRINT "RATE FOR ";S$;"S";
370 INPUT I
380 PRINT "WHAT IS YOUR GUESS FOR THE ANNUAL MORTALITY"
390 PRINT "RATE OF OLDER BIRDS";
400 INPUT O
410 PRINT "AT WHAT AGE DO YOU BELIEVE ";S$;"S NORMALLY"
420 PRINT "BEGIN BREEDING";
430 INPUT B
440 PRINT ;"WHAT IS YOUR ESTIMATE OF THE PERCENTAGE OF ADULT"
450 PRINT "FEMALES THAT PRODUCE FLEDGLINGS EACH YEAR";
460 INPUT F
470 PRINT "WHAT IS THE ANNUAL AVERAGE NUMBER OF FEMALE YOUNG"
480 PRINT "RAISED BY SUCCESSFUL FEMALES (CAUTION: THINK"
490 PRINT "CAREFULLY  THIS IS USUALLY OBTAINED BY DIVIDING THE"
500 PRINT "AVERAGE TOTAL NUMBER OF YOUNG PER FEMALE BY 2)";
510 INPUT Y
520 PRINT
530 DIM X(75),L(75),D(75),Q(75),S(75),M(75),W(75),A(75)
540 MAT X=ZER(75)
550 MAT L=ZER(75)
560 MAT D=ZER(75)
570 MAT Q=ZER(75)
580 MAT S=ZER(75)
590 MAT W=ZER(75)
600 MAT M=ZER(75)
610 FOR P=1 TO 75
620 LET X(P)= P-1
630 NEXT P
640 LET L(1)=1000
650 LET L(2)=INT(1000*(1-(I/100)))
660 FOR P=2 TO 75
670 LET L(P+1)=INT(L(P)*(1-(O/100)))
680 IFL(P+1)=0THEN700
690 NEXT P
700 FOR P=1 TO 75
710 LET D(P)=L(P)-L(P+1)
720 IFD(P)=0THEN740
730 NEXT P
740 FOR P=1 TO 75
750 IFL(P)=0THEN780
760 LET Q(P)=D(P)/L(P)
770 NEXT P
780 FOR P=1 TO 75
790 LET S(P)=1-Q(P)
800 IFL(P)=0THEN820
810 NEXT P
820 FOR P=1 TO 75
830 IFX(P)<BTHEN850
840 LET M(P)=(F*Y/100)*L(P)/1000
850 NEXT P
860 FOR P=1 TO 75
870 LET W(P)=X(P)*M(P)
880 IFL(P)=0THEN900
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 890 NEXT P
 900 LET R1=0
 910 LET T=0
 920 FOR P=1 TO 75
 930 LET R1=R1+M(P)
 940 LET T=T+W(P)
 950 NEXT P
 960 LET G=T/R1
 970 LET R2=(LOG(R1))/G
 980 PRINT "M(X) FOR BREEDING ADULTS IS";F*Y/100;". "
 990 PRINT "L(X) WILL START AT 1,000 BUT IT WILL BE CONSIDERED"
1000 PRINT "AS STARTING AT 1.00 FOR L(X)M(X) PURPOSES."
1010 PRINT
1020 :  ###     ####     ####     ####     ####     ########
1030 :  ###     ####     ####     #.##     #.##      ##.###
1040 PRINT "TABLE 1. LIFE TABLE FOR ";S$;"S."
1050 PRINT
1060 PRINTUSING1020,"X","L(X)","D(X)","Q(X)","S(X)","L(X)M(X)"
1070 PRINT "----------------------------------------------------------"
1080 FOR P=1 TO 75
1090 PRINTUSING1030,X(P),L(P),D(P),Q(P),S(P),M(P)
1100 IFL(P)=0THEN1120
1110 NEXT P
1120 PRINT "----------------------------------------------------------"
1130 LET T=0
1140 MAT A=ZER(75)
1150 FOR P=1 TO 75
1160 LET A(P)=(EXP((-R2)*X(P)))*M(P)
1170 LET T=T+A(P)
1180 NEXT P
1190 PRINT
1200 PRINT "TABLE 2. ESTIMATE OF INNATE CAPACITY FOR INCREASE."
1210 PRINT
1220 PRINT "X","E**(-LITTLE R*X)L(X)M(X)"
1230 PRINT
1240 FOR P=1 TO 75
1250 PRINT X(P), A(P)
1260 IFL(P)=0THEN1280
1270 NEXT P
1280 PRINT
1290 PRINT " ","---------------"
1300 PRINT "TOTAL", T
1310 PRINT
1320 PRINT "THE ESTIMATE OF THE INSTANTANEOUS RATE OF INCREASE"
1330 PRINT '("LITTLE R") IS';R2;', OR A FINITE ANNUAL RATE'
1340 PRINT '("BIG R") OF';EXP(R2);'.'
1350 PRINT
1360 PRINT "ARE YOU SATISFIED WITH THIS ESTIMATE (1=YES, 2=NO)";
1370 INPUT A
1380 IF A=2 THEN 1640
1390 MAT W=ZER(75)
1400 FOR P=1 TO 75
1410 LET W(P)=((EXP(R2))**(-(P-1)))*(L(P)/1000)
1420 IFL(P)=0THEN1440
1430 NEXT P
1440 LET T=0
1450 FOR P=1 TO 75
1460 LET T=T+W(P)
1470 NEXT P
1480 PRINT
1490 PRINT "TABLE 3. PERCENTAGE OF POPULATION IN EACH AGE CLASS."
1500 PRINT "            (THE STABLE AGE DISTRIBUTION)"
1510 PRINT
1520 PRINT "X","PERCENTAGE IN CLASS"
1530 PRINT
1540 FOR P=1 TO 75
1550 PRINT X(P), 100*(W(P)/T)
1560 IFL(P)=0THEN1610
1570 NEXT P
1580 PRINT "DO YOU WANT TO RUN ANOTHER LIFE TABLE ANALYSIS (1=YES, 2=NO)";
1590 INPUT A9
1600 IF A9=1 THEN 310
1610 PRINT
1620 PRINT "SEE YA"
1630 STOP
1640 PRINT "WHAT INSTANTANEOUS RATE DO YOU WANT TO TRY THIS TIME";
1650 INPUT R2
1660 GOTO1130
1670 END
```