

A PARADIGM FOR POPULATION ANALYSIS OF LONG-LIVED VERTEBRATES

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Abstract. A sequence of changes in vital rates observed as populations approach maximal levels has been used as the basis for a “paradigm” for population analysis. Previous work indicates that early survival decreases first, followed by lower reproductive rates; ultimately, adult female survival may decrease. “Sensitivity” of population growth rates, as measured by partial derivatives of an approximation to the Lotka-Leslie model, appears to follow the same sequence, suggesting that population regulation may follow that sequence. This may imply some evolutionary significance in the sequence.

Thus, it may be possible to assess population status by measuring the vital rates, as shown in a number of examples reported here. Measuring vital rates in the field is subject to a variety of biases; hence, an analysis should include direct estimates of population trend. In the absence of complete data, suitable trend data might be used to estimate missing rates. Bootstrapping provides a simple way to obtain confidence intervals, and the delta method can be used to obtain components of variance and thus improve sampling. Various methods for studying trend are given, with examples and simple statistical tests.

Key words: bootstrapping; lambda; long-lived vertebrates; Lotka-Leslie model; population regulation; sensitivity; survival; trend regressions.

INTRODUCTION

It appears to be a generally accepted principle that adult female survival is the key to the well-being of populations of the long-lived vertebrates, at least, and quite possibly to other sexually reproducing species. Sæther and Bakke (2000) reported that “elasticity” of the adult survival rate was significantly larger than that of the fecundity rate for 49 avian species. However, it should be noted that this generalization may not hold for many smaller, short-lived species (e.g., small mammals, passerine birds).

Over 20 yr ago, it was proposed that there is an apparent sequence of changes in vital rates as population density increases toward maximal levels (Eberhardt 1977). Later studies (Fowler 1981, 1987, Gaillard et al. 1998) support this sequence, which is:

Increase in mortality rate of immatures

- increase in age of first reproduction
- reduction in reproductive rate of adult females
- increase in mortality rate of adults.

With the advent of effective mark-recapture methods, particularly those employing radiotelemetry, it has become possible to obtain data on this sequence for a number of large-mammal populations, and to estimate the rate of change (λ) from such data. Often the resulting estimate of λ can be checked by direct estimates

of population density over time, or through measures of relative abundance (indices of abundance). Inasmuch as most estimates from field data are subject to a variety of potential biases, it is very important to have estimates from both reproductive and survival data and from independent direct measures (census or index).

A paradigm is defined by the Oxford Dictionary as referring to a pattern or example (Webster’s Dictionary adds “model”). The purpose of the present paper is to argue that the previously proposed sequence should serve as a paradigm for analysis of data on population dynamics of the larger vertebrate species. The paradigm can now be tested with the much better data and methods that have become available in the 25 yr since it was originally developed.

MATERIAL AND METHODS

The data used here are largely from published sources, with a few cases from as yet unpublished studies in which the author has participated. In many cases, relatively small samples of reproductive and survival data are available and the widely used Lotka-Leslie model must be replaced by an approximation. Because closed solutions of the Lotka-Leslie model are not available, variance estimates have been difficult to obtain. This problem is now readily managed by using the bootstrapping technique (Efron and Tibshirani 1993). For practical applications, it is important to determine the relative contribution of individual components of reproductive and survival rates to variance estimates of λ in order to consider possible improvements in the field sampling. The bootstrap approach

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thus needs to be supplemented by use of the delta method (Seber 1982), which utilizes these individual components. Field data have been used here to check that the two methods give similar results.

Approximation to the Lotka-Leslie model

Analysis of limited data sets is facilitated by an approximation suggested by Eberhardt (1985). The approximation was tested on curves fitted to various data sets (Eberhardt 1985) and it appears to fit survivorship (l_x) and reproductive (m_x) data quite satisfactorily. The basic Lotka-Leslie equation is

$$1 = \sum_{x=a}^w \lambda^{-x} l_x m_x \quad (1)$$

where λ is the rate of change of the population ($\lambda = e^r$ or $\lambda = 1 + r$; cf. Eberhardt [1985]); l_x is survival to age x ; m_x is reproductive rate at age x , expressed as female births per female; a , is age of first reproduction; and w is the maximum age considered. The approximation used here serves when individual age-specific rates cannot be obtained for all age classes, as frequently is the case. It represents survivorship by $l_x = l_a s^{(x-a)}$, when $x \geq a$, and reproductive rate by $m_x = m$, where l_a denotes survival to the age of first parturition and s denotes adult survival rate. Senescence is approximated by truncating the net maternity curve, i.e., w in Eq. 1 is reduced to approximate the effect of senescence on survival. Lotka's equation (Eq. 1) then has the solution used by Eberhardt (1985: Eq. 9), expressed here as a polynomial in λ :

$$\lambda^a - s\lambda^{a-1} - l_a m \left[1 - \left(\frac{s}{\lambda} \right)^{w-a+1} \right] = 0. \quad (2)$$

In those few cases in which much more survival and reproductive data are available, the "structured accounting" approach of Brown et al. (1993) and "λ contribution analysis" of Sibly and Smith (1998) should be considered as alternative approaches.

Bootstrapping and the delta method

Bootstrapping and the delta method have been used with Eq. 2 in six published examples. Eberhardt et al. (1994) gave the partial differential equations and a bootstrap frequency distribution for the grizzly bear (*Ursus arctos horribilis*) population in Yellowstone National Park; Hovey and McLellan (1996) and Mace and Waller (1998) gave results for two other grizzly populations. Gilmartin and Eberhardt (1995) applied the technique to Hawaiian monk seals (*Monachus schauinslandi*), Eberhardt and O'Shea (1995) gave results for manatees (*Trichechus manatus latirostris*), and Eberhardt (1995a) presented results for the sea otter (*Enhydra lutris*). Alvarez-Bulla and Slatkin (1993) provided another method for estimating confidence intervals.

Basis for assessment of trend data

Usually trend data are analyzed by regression methods, with the dependent variable being the natural logarithm of the trend index, and time in years being the independent variable. The basic underlying model is assumed to be $N_t = N_0 \lambda^t$ where N_t is population size at time t and N_0 is the initial population size. Log-linear regression then is calculated from

$$\log_e N_t = \log_e N_0 + t \log_e \lambda.$$

Eberhardt (1987) reported on 16 examples of the use of this equation. Data studied here were assessed by the error mean square in this log-linear regression, along with R^2 , which was defined (Draper and Smith 1998) as

$$R^2 = \frac{\sum (\hat{y}_i - \bar{y})^2}{\sum (y_i - \bar{y})^2} = 1 - \frac{\text{RSS (full)}}{\text{RSS (reduced)}} \quad (3)$$

where \bar{y} is the mean of the independent variable and \hat{y}_i is the value predicted by the regression equation. The right-hand side of Eq. 3 is expressed in terms of regression sums of squares: RSS(full) is the regression sum of squares for the fitted regression line and RSS (reduced) is the sum of squares when only the overall mean of the dependent variable is considered. Because the error mean square (variance about regression) is calculated as $s^2 = \text{RSS (full)} / (n - p)$, it is clear that R^2 and s^2 are correlated. Anderson-Sprecher (1994) discussed R^2 in more detail.

Evaluating the pattern in deviations from regression can be aided by the Durbin-Watson test (Draper and Smith 1998). This simple test depends on the fact that the squared difference between successive deviations can be used to approximate the variance of the deviations if the pattern of deviations is random. The test is

$$d = \frac{\sum (e_u - e_{u-1})^2}{\sum d_u^2} \quad (4)$$

where the summation in the numerator runs from $u = 2$ to n , and that in the denominator runs from 1 to n . It can be shown that the ratio, d , has an expected value of 2 under a random pattern. Draper and Smith (1998) note that $0 \leq d \leq 4$, and give tables of significant deviations from the expected value of 2 for different sample sizes. A simple test for curvilinearity may also be useful, when one independent variable (time) is used. It depends on fitting a straight line and a quadratic to the data and conducting an F test of the ratio of the two variances about regression to determine whether the quadratic gives a better fit (Snedecor and Cochran 1967:455).

Multiple regressions for trend data

The use of multiple regressions with trend data has been attempted with Cox's (1972) "proportional haz-

ards model" (Eberhardt et al. 1999). When there are a number of potential auxiliary variables to consider, Draper and Smith (1998) recommend evaluating all possible regressions and selecting the "best" equation. Mallow's C_p is often used in multiple regression studies (Draper and Smith 1998). The equation is

$$C_p = \frac{RSS_p}{\hat{\sigma}^2} + 2p - n \quad (5)$$

where RSS_p is the regression sum of squares, p is the number of parameters considered (including the intercept), n is the number of observations, and $\hat{\sigma}^2$ is an estimate of the "true" variance about the regression.

Estimation of $\hat{\sigma}^2$ is an important issue in applying Mallow's C_p to ecological data. Draper and Smith (1998) suggest using the variance about regression estimated from the "largest" regression equation considered (the equation with the largest number of parameters). They then suggest plotting the resulting values of C_p against p , and selecting a regression line based on the plot. The expected value of C_p is p , the number of parameters used in the equation from which C_p is computed. Hence, selection of a "best" equation is limited to those cases in which C_p lies in the general neighborhood of p , excepting the largest equation used, in which $C_p = p$ (from Eq. 5).

As Draper and Smith (1998) note, no single approach can be shown to be truly "best" for selecting a regression model. Generally speaking, it is desirable to select only those parameters that contribute information about the underlying "true" relationship. Hence, it is useful to review various aspects of the regression fit. R^2 , s^2 , and Mallow's C_p are thus used here in combination with the standard regression assessment of significance levels for individual coefficients. Eberhardt et al. (1999) reported data showing that the logarithmic transformation tends to normalize deviations from regressions fit to trend data.

A useful further tool in selecting a regression equation is to fit a minimal equation and plot the deviations from the fitted regression against a variable being considered as a candidate for improving the fit. Because the present study is concerned with population trends, all of the equations considered include time (year) as the first independent variable in the equation. An initial step may then be to regress $\log_e N_t$ on year (t) and to obtain deviations from this regression.

In a general search for the "best" multiple regression equation, all possible regressions are calculated, so that r independent variables require calculation of 2^r regression equations. However, as noted above, the main goal of the present study is to estimate trend over time, so time (in years) is included in the candidate regressions. Cox's (1972) proportional hazards model incorporates auxiliary variables to give (after \log_e transformation)

$$\log_e N_t = \log_e N_0 + t \log_e \lambda + b_2 x_2 + \cdots + b_k x_k \quad (6)$$

or, $y = b_0 + b_1 x_1 + b_2 x_2 + \cdots + b_k x_k$ with $x_1 =$ time in years and b_1 estimating $\log_e \lambda$. The remaining x_i will often be environmental variables. Inasmuch as no more than four auxiliary variables other than time were considered in the present examples, all (16) possible regressions were calculated. If larger numbers of candidate variables are used, it may be desirable to use one of the elimination procedures suggested in references on regression techniques, or a stepwise approach.

Akaike's Information Criterion (AIC) has been used in a number of recent analyses of survival data (Gaillard et al. 1993, Jorgenson et al. 1997, and Toigo et al. 1997). The equation is (Burnham and Anderson 1998):

$$AIC = n \log[L(\hat{\theta} | x)] + 2K$$

where $L(\hat{\theta} | x)$ is the maximized likelihood function of the model parameters, given the data x , and K is the number of parameters. For use in multiple regression situations, the equation is:

$$AIC = n \log(\hat{\sigma}^2) + 2K \quad (7)$$

where $K = p + 1$, p is the number of regression coefficients (including the intercept), n is sample size, and $\hat{\sigma}^2 = RSS_p/n$, with RSS_p being the usual residual sum of squares based on p parameters.

In their recent book, Burnham and Anderson (1998) recommend using AIC and limiting the number of models evaluated to a relatively small number chosen on the basis of prior information and careful consideration of the circumstances of the study. When $n/K < 40$, they recommend a "small sample" adjustment:

$$AIC_c = AIC + \frac{2K(K+1)}{N-K+1} \quad (8)$$

They note that Mallow's C_p and AIC will generally provide essentially the same rankings in linear regression studies. Because sample sizes in the examples studied here were < 40 , AIC_c was used in calculations.

Nine examples using multiple regressions on trend data were used in the present study. Data on the Florida manatee, Yellowstone grizzly bear, and Hawaiian monk seal were taken from the study by Eberhardt et al. (1999). Data on moose (*Alces alces*) were obtained by R. O. Peterson and were described in the study of Post et al. (1999). Data on gray whales (*Eschrichtius robustus*) were furnished by R. C. Hobbs and were collected as described by Buckland et al. (1993). Counts of harbor seals (*Phoca vitulina richardsi*) were provided by K. J. Frost and were collected by aerial survey in the study reported by Frost et al. (1999). Data from an aerial survey of Steller sea lions (*Eumetopias jubatus*) were supplied by D. G. Calkins and assessed in the study of Calkins et al. (1999). Kit fox (*Vulpes macrotis mutica*) numbers were assessed by roadside surveys reported by Ralls and Eberhardt (1997). Results of aerial surveys for harbor porpoise (*Phocoena phocoena*) were provided by K. A. Forney and reported by

Forney et al. (1991). Several different methods were used to assess the data in the original studies, and are described in the references just cited.

RESULTS

Adult female survival

For populations with little impact of human activities, adult female survival appears likely to be at least 0.95 (Table 1). Many of the examples used here (Table 1) were subjected to impacts that probably reduced survival below a feasible maximum. For kudu (*Tragelaphus strepsiceros*), Owen-Smith (1990) reported that "Predation was probably responsible for a background mortality level of 5–10% per annum even among prime-age animals," whereas bighorn sheep (*Ovis canadensis*) may well have suffered some losses from predation and accidents (Jorgenson et al. 1997). The moose (*Alces alces*) population (Ballard et al. 1991) was subjected to hunting, ostensibly for males alone, but accidental and illegal killing can be expected in a hunted population. The Atlantic Coast manatees were probably subjected to more accidental kills than the other two populations (Eberhardt and O'Shea 1995), and the California sea otter population was affected by fishing-net mortality that probably stabilized the population during the interval when the telemetry data were collected (Eberhardt 1995a). Most grizzly bears are killed by humans, and few die natural deaths. Consequently, it seems very likely that adult female survival will be at least 0.95 and may be 0.99 or higher in the prime age classes under truly undisturbed conditions. Such a high annual survival is necessarily accompanied by reductions in survival due to senescence, which may not always be taken into account in reported estimates of adult female survival. Eleven of the survival estimates of Table 1 were identified in the valuable review of Gaillard et al. (1998).

Bootstrapping results

The bootstrapping technique (Efron and Tibshirani 1993) provides a convenient way to obtain confidence limits on an estimate of λ obtained from survival and reproductive data. Seven examples were used in the present study, six of which have been published (references cited under *Materials and Methods: Bootstrapping and the delta method*), and the seventh was based on the data of Garrott and Taylor (1990) for feral horses (*Equus caballus*). Results (Table 2) are based on estimates of the parameters of Eq. 2. Bootstrapping and the delta method gave very much the same estimates of λ and variability. Variability was calculated as a coefficient of variation, estimated from standard errors from bootstrapping or the delta method divided by the estimate of λ obtained by the respective methods. In five cases, λ could be estimated independently from data on trend over time, and was close to the value estimated from survival and reproductive data.

Components of variability were estimated by the delta method as the fraction of total variability due to the three major parameters (survival to age of first reproduction, reproductive rate, and adult female survival rate). Proportions of total variability due to these sources varied substantially in the several examples (Fig. 1), due largely to different sample sizes. With the exception of the feral horse example, reproduction accounted for only a small fraction of the total variability. For feral horses, both early survival and adult survival were very high, yielding a relatively small variance (assumed to be binomial in nature), so that the lower foaling rate appeared to contribute a large fraction of the total variance. In the case of grizzly bears, relatively few subadult females were monitored; hence, that source accounted for much of the total variance. In practice, it should be possible to increase sample sizes to reduce the major contributions to variability (some calculations along those lines were made by Eberhardt (1995a) for sea otters). In the case of monk seals, nearly all weaned pups are tagged so that the sample of adults is only increased by the passage of time. Due to late maturation of monk seals, not enough data have yet been accumulated to reduce the variance of adult survival. In other species (e.g., elk), vestigial teeth can be removed for aging purposes.

Data from the delta method

The delta method can be applied to additional data from the literature (see Table 3). In most of these examples, a direct estimate of λ was available from either census or trend data, making it possible to compare estimates based on the reproductive and survival data with direct estimates (Fig. 2). Data from Table 2 are also used in Fig. 2, in which the line is a 1:1 line. The major discrepancy in the comparison is with the caribou (*Rangifer tarandus granti*) data, in that the estimate of λ from reproductive and survival data is appreciably lower ($\lambda = 1.01$ vs. 1.05 from trend data). Walsh et al. (1995) devised a stochastic model for the same data set and found that the resulting mean rate of change also suggested a virtually stationary population. The trend data were obtained from presumably complete counts of a herd ranging from 135 000 to 178 000, so sampling variation in that estimate is unlikely to be consequential. Hence, the two estimates appear to be significantly different. The survival rate for adult female caribou was estimated to be 0.842, whereas the rates for female yearlings and 2-yr-olds were substantially higher (0.93 and 0.95, respectively; Fancy et al. 1994: Table 4). The available data from other ungulates make it seem unlikely that these rates should be higher than those for prime-age adult females. Using the same average survival rate for adult females as observed for subadults (0.94) gives $\lambda = 1.07$. Inasmuch as the adult females in the study were not aged beyond a determination, based on tooth wear and body size, that they were ≥ 3 yr old, it seems possible that the presumed

TABLE 1. Annual adult female survival rates for various populations of long-lived vertebrates.

Source	Adult female survival	Species	Human influence†
Houston (1982)	0.995	Yellowstone elk (<i>Cervus elaphus</i>)	0
Amstrup and Durner (1995)	0.996	polar bears (<i>Ursus maritimus</i>)	0
Olesiuk et al. (1990)	0.995	killer whale (<i>Orcinus orca</i>)	0
Eberhardt et al. (1996)	0.990	ALE elk	0
D. B. Siniff (<i>personal communication</i>)	0.990	Weddell seals (<i>Leptonychotes weddelli</i>)	0
Gilmartin and Eberhardt (1995)	0.980	monk seals, Kure Atoll	0
R. A. Garrott (<i>personal communication</i>)	0.980	Yellowstone elk	0
Zhou and Pan (1997)	0.977	giant panda (<i>Ailuropoda melanoleuca</i>)	0
Garrott and Taylor (1990)	0.974	Pryor Mountain feral horses	0
Toigo et al. (1997)	0.970	ibex (<i>Capra ibex ibex</i>)	0
Smith (1975: Table 62)	0.970	ringed seals (<i>Pusa hispida</i>)	0
Gaillard et al. (1993)	0.967	roe deer	1
Eberhardt and O'Shea (1995)	0.965	Crystal River manatees	0
Eberhardt and O'Shea (1995)	0.961	Blue Spring manatees	0
Loison et al. (1994)	0.960	chamois (<i>Rupicapra rupicapra</i>)	0
Marcot and Holthausen (1987)	0.960	Spotted Owl (<i>Strix occidentalis caurina</i>)	?
Sibly and Smith (1998)	0.952	red deer on Rhum (<i>Cervus elaphus</i>)	0
Hovey and McLellan (1996)	0.950	British Columbia grizzly bears	1
Ballard et al. (1991)	0.949	moose	1
Fisher (1975)	0.946	Laysan Albatross (<i>Diomedea immutabilis</i>)	0
Jorgenson et al. (1997)	0.945	bighorn sheep	1
Skogland (1985)	0.944	reindeer (<i>Rangifera tarandus</i>)	1
Eberhardt (1995b)	0.943	Yellowstone grizzly bears	1
Noon and Biles (1990)	0.942	Spotted Owl (<i>Strix occidentalis caurina</i>)	?
Gilmartin and Eberhardt (1995)	0.940	monk seals, Pearl and Hermes Reef	?
Jorgenson et al. (1997)	0.939	bighorn sheep	1
Eberhardt et al. (1982)	0.935	Jackie's Butte feral horses	0
Owen-Smith (1990)	0.933	kudu	1
Gilmartin and Eberhardt (1995)	0.930	monk seals, French Frigate Shoals	?
Gaillard et al. (1993)	0.927	roe deer (<i>Capreolus capreolus</i>)	1
Eberhardt et al. (1982)	0.926	Beaty's Butte feral horses	0
Eberhardt (1995a)	0.910	California sea otters	1
Eberhardt et al. (1999)	0.910	Laysan monk seals	?
Eberhardt (1990)	0.910	fur seals	1
Eberhardt and O'Shea (1995)	0.907	Atlantic Coast manatees	1
Smith (1975: Table 61)	0.900	ringed seals	1
Mace and Waller (1998)	0.900	Swan Mtn. grizzly bears	1
Owen-Smith (1990)	0.889	kudu	0
Gilmartin and Eberhardt (1995)	0.870	Lisianski monk seals	?
Fancy et al. (1994)	0.842	caribou	1
Eberhardt (1969)	0.700	whitetailed deer	1

† Likely human influences on survival are indicated by 0 (none), 1 (present), or ? (uncertain).

adult female survival may have been biased by the inclusion of too many senescent animals in the radio-telemetry sample.

A particularly interesting feature of the numerical values of partial derivatives from Tables 2 and 3 is the relative magnitudes of the partials for the three parameters (Fig. 3). It is widely accepted that changes in adult female survival have the greatest relative impact on λ , and this is borne out by the relative size of the numerical values of the partial derivatives (Tables 2 and 3, Fig. 3). Reproductive rate appears to be the next most influential parameter, with survival to reproductive age the least influential. These results support the earlier assessment of Eberhardt and Siniff (1977) that depended on what now is generally designated as a "perturbation analysis" (Caswell 2000).

Analysis of trend data

Trend data for a number of species (Table 4) provide the basis for an empirical relationship (Fig. 4) between

$1 - R^2$ (Eq. 3) and the variance (s^2) about the fitted log-linear regression line. It is proposed here that the solid points of Fig. 4 may represent a useful relationship (the curve is included to suggest the general form of the relationship). A number of the data sets deviated substantially from this supposed relationship. Four sets (open boxes in Fig. 4) show evidence of significant curvature, using the simple test of curvilinearity from Snedecor and Cochran (1967), described in *Methods*. Four other pairs of points (open circles in Fig. 4) show lower R^2 values than suggested by the empirical relationship. One such data set (gray whales) appears to be much more variable than would be anticipated from the magnitude of the counts. Breiwick (1994) gave estimates of sampling error of the individual counts that indicate a significantly larger variability (F test) than estimated by the regression mean square. Two other such points (red deer and fur seals) show highly significant values of the Durbin-Watson test and are characterized by marked oscillations when plotted, as are

TABLE 2. Data from populations of long-lived vertebrates for which bootstrapping and the delta method were used to estimate various parameters.

Parameter	Grizzly bears						
	Laysan monk seals	Yellowstone	British Columbia	Swan Mountain	Blue Spring manatees	Feral horses	California sea otters
Survival to age a , $l(a)$	0.44	0.44	0.61	0.33	0.82	0.92	0.63
Reproductive rate, m	0.28	0.35	0.42	0.26	0.15	0.29	0.23
Adult survival, s	0.90	0.94	0.95	0.9	0.96	0.97	0.91
Age of first reproduction, a	6	4	6.4	6	4	3	3.5
Maximum age, w	20	20	20	25	50	20	15
Lambda							
Lotka method	1.02	1.05	1.08	0.98	1.06	1.16	1.01
Trend data	1.00	1.03			1.08	1.18	1.00
Coefficients of variation	0.03	0.04	0.04	0.04	0.01	0.01	0.08
Components of variation							
Survival	0.94	0.19	0.24	0.37	0.82	0.21	0.83
Reproduction	0.01	0.04	0.16	0.03	0.11	0.76	0.08
Early survival	0.05	0.77	0.6	0.6	0.07	0.03	0.09
Partial derivatives							
Survival	1.02	0.65	0.47	0.58	1.02	1.03	0.97
Reproduction	0.25	0.32	0.23	0.29	0.51	0.55	0.56
Early survival	0.14	0.25	0.17	0.23	0.09	0.16	0.16

Note: Monk seal data are from Laysan Island (Gilmartin and Eberhardt 1995), Swan Mountain grizzly bear data are from Mace and Waller (1998), and the remaining sources are as in Table 1.

the Soay sheep (*Ovis* sp.) data, although the Durbin-Watson test is not significant for Soay sheep.

Some of the solid points of Fig. 4 also show significance under the test for curvilinearity or the Durbin-Watson test (Table 4). Muskox (*Ovibos moschatus*) show significant oscillations about the regression line, but the deviations are small and may well be indicative of the oscillations known from theory to occur while

the age distribution approaches the stable state. Similarly, the deviations from linearity for bison (*Bison bison*), although statistically significant, are very small. Many of the species with high R^2 (>0.95) and low s^2 (<0.02) appear to show significant F ratios in the test for curvilinearity, but the very high R^2 makes it clear that these deviations are of minor consequence.

When several subpopulations are studied, it may not

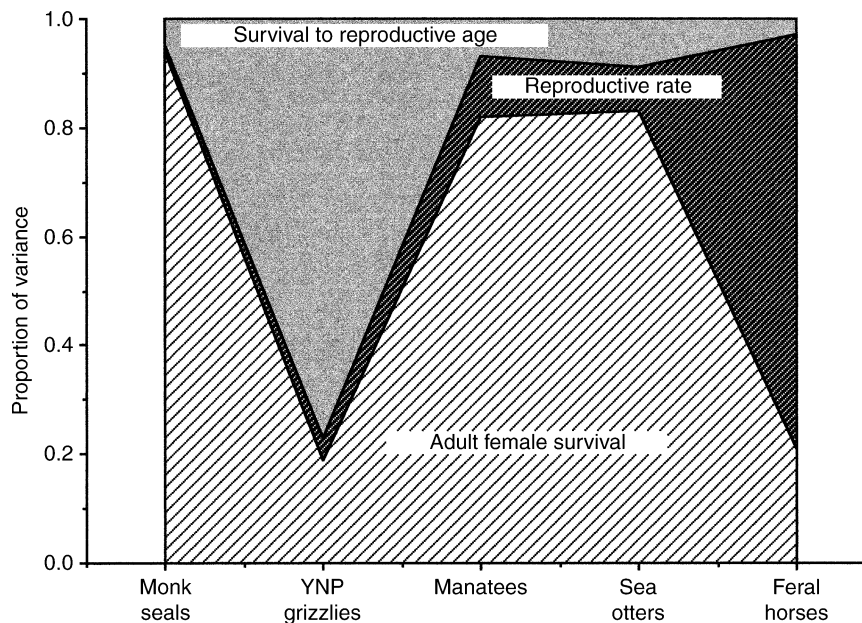


FIG. 1. Estimates of the proportion of overall variance in estimating λ (rate of population change) associated with the main components of sampling error. Sources and details are given in Table 2. YNP = Yellowstone National Park.

TABLE 3. Estimates of various parameters and values of partial derivatives for different species of long-lived vertebrates.

Parameter	Yellow-stone elk ¹	Weddell seals ²	Moose ³	Caribou ⁴	Red deer ⁵	White-tailed deer ⁶	Fur seals ⁷	Giant panda ⁸	Spotted Owl ⁹	Killer whale ¹⁰
Survival to age a , $l(a)$	0.66	0.27	0.31	0.51	0.53	0.41	0.33	0.42	0.08	0.78
Reproductive rate, m	0.48	0.30	0.56	0.4	0.37	0.71	0.45	0.2	0.24	0.11
Adult survival, s	0.99	0.99	0.95	0.84	0.95	0.7	0.91	0.98	0.94	0.99
Age of first reproduction, a	3	6	3	3	4	2	5	4	2	15
Maximum age, w	18	20	25	16	16	16	18	18	25	50
Lambda										
Lotka method	1.20	1.01	1.09	1.01	1.08	0.99	1.02	1.00	0.9	1.03
Trend data	1.22	1.00	1.06	1.05	1.09	0.97	1.00			1.03
Partial derivatives										
Survival	0.69	0.54	0.76	0.67	0.59	0.76	0.54	0.64	0.83	0.49
Reproduction	0.36	0.27	0.22	0.37	0.35	0.32	0.23	0.48	0.24	0.34
Early survival	0.26	0.29	0.40	0.32	0.24	0.56	0.32	0.23	0.73	0.04

Note: Sources for species data are: (1) Houston (1982); (2) D. B. Siniff (*personal communication*); (3) Ballard et al. (1991); (4) Fancy et al. (1994); (5) Sibly and Smith (1998); (6) Eberhardt (1969); (7) Eberhardt (1990); (8) Zhou and Pan (1997); (9) Noon and Biles (1990); and (10) Olesiuk et al. (1990).

be feasible to obtain estimates of all of the reproductive and survival parameters for each area, and a parameter estimate from another area may need to be used. Given a reliable method for estimating trend, it is possible to check the validity of the substitution by comparing the resulting λ with that calculated from trend data. Such a substitution was used for monk seals by Gilmartin and Eberhardt (1995) and for manatees by Eberhardt and O'Shea (1995). A trend estimate for the Gulf Coast manatee population was obtained in a later study by Eberhardt et al. (1999). The major discrepancy for monk seals appeared to be an appreciably lower estimate of λ from the trend data at Kure Atoll, and was associated with highly erratic trend counts at that site. In some instances, as with the caribou data discussed in the section *Results: Data from the delta method*, it is helpful to use the trend data estimate to calculate a likely value for a parameter that seems to be aberrant.

Estimates of trend from multiple regression equations

Results from the nine sets of data assessed by multiple regressions are summarized in Table 5. Both Mallows's C_p and AIC were computed for the nine sets of data, and the two methods selected the same independent variables as having significant effects on the counts. Values of R^2 (Eq. 3) for multiple regressions on all variables, for the selected sets, and for time variables alone as the independent variable appear in Table 5, along with correlation coefficients calculated separately for each variable and the counts. Eq. 6 was used for six of the examples, whereas regressions on average counts were used for gray whales, harbor seals, and Steller sea lions because of the way the data were collected. Initial analyses included the square of the year (or day) of collection as an independent variable, but this term was removed in the final analyses due to the high correlations ($r > 0.95$) induced between the time

of observation and its square. These high correlations induced collinearity (Draper and Smith 1998), making interpretation of the results uncertain. Very likely an independent test for curvilinearity, such as that of Snedecor and Cochran (1967:455), should be used to determine whether a squared term might be incorporated.

DISCUSSION

Assessment of trend data

The trend data of Tables 4 and 5 exhibit a wide range of behaviors. The wide range of values of R^2 (plotted as $1 - R^2$ in Fig. 4) may be due to a variety of sources, some of which are identified in Fig. 4 and Table 4. However, in a sizable number of cases, R^2 is very large, indicating that simple log-linear regression provides an adequate description of the data. Bringing in auxiliary variables complicates matters, but substantial reductions in variability are possible, as evidenced by the appreciable increases in R^2 from multiple regression as compared to calculations in which only time is used as an auxiliary variable (Table 5). Subsets of the auxiliary variables were selected by Mallows's C_p (Eq. 5) and AIC (Eqs. 7 and 8). In all of the nine cases examined, the two methods selected the same subsets of auxiliary variables. Both methods utilize the regression sum of squares, number of parameters, and sample sizes, but in different arrangements. However, Mallows's C_p was designed for regression studies, whereas AIC, as Burnham and Anderson (1998) argued, is useful with a wide range of models and may thus be preferred, being readily computed and not requiring a plot of the data, as does selection with C_p . Burnham and Anderson (1998) recommend a correction (AIC_c of Eq. 8) for "small" samples ($n/K < 40$). AIC_c was used here, but AIC and AIC_c selected the same subsets in all nine examples. In nearly all of the examples, R^2 for the selected set of variables was negligibly smaller than that for all of the variables considered (Table 5). Some other methods for

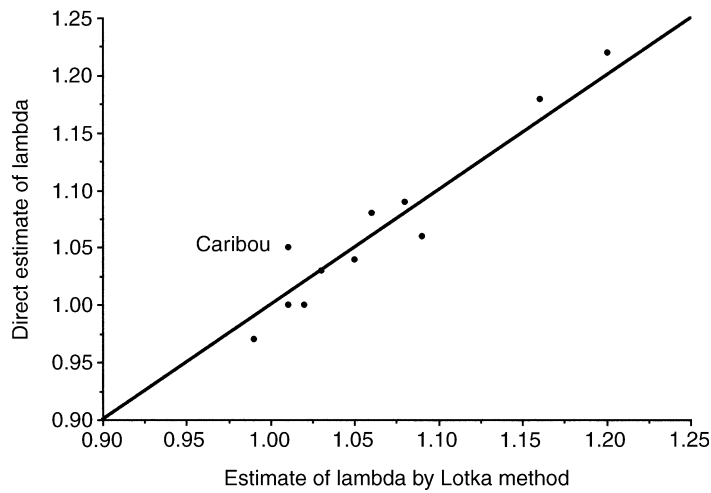


FIG. 2. Estimates of λ (rate of population change) from direct measures of trend (censuses or indices) compared with estimates based on reproductive and survival data (Lotka method). Sources and details are given in Tables 2 and 3.

TABLE 4. Tests for curvature, Durbin-Watson test, and log-linear regressions of abundance.

Species	n	Slope <i>b</i>	MS _{reg} [†]	R ²	Test for curvature		Durbin-Watson test		Source
					<i>F</i> ratio	<i>P</i>	<i>d</i>	<i>P</i>	
Grizzly bears (Yellowstone)	18	0.039	0.068	0.409	2.07	0.17	2.59	NS	Knight et al. (1995)
Soay sheep	20	0.026	0.062	0.295	0.26	0.62	2.35	NS	Boyd (1974)
George Reserve deer	7	0.488	0.061	0.956	11.16	0.03	—	—	McCullough (1983)
Pearl and Hermes monk seals	16	0.050	0.052	0.606	0.10	0.76	2.69	NS	Gilmartin and Eberhardt (1995)
FFS monk seals	22	0.062	0.048	0.882	56.97	0.00	0.44	<0.02	Gilmartin and Eberhardt (1995)
Crystal River manatees	21	0.097	0.043	0.912	6.17	0.02	1.12	NS	Ackerman (1995)
Lisianski monk seals	35	-0.029	0.036	0.714	35.48	0.00	0.68	<0.02	Gilmartin and Eberhardt (1995)
Laysan monk seals	34	-0.034	0.028	0.812	0.04	0.85	1.42	NS	Gilmartin and Eberhardt (1995)
Wood Buffalo N.P. bison	19	-0.052	0.021	0.849	5.80	0.03	0.92	<0.02	Carbyn et al. (1993)
Blue Springs manatees	19	0.079	0.021	0.920	0.47	0.50	1.54	NS	Ackerman (1995)
Beatty horses	8	0.245	0.018	0.959	13.10	0.02	—	—	Eberhardt et al. (1982)
Gray whales	18	0.026	0.018	0.718	0.63	0.44	1.98	NS	Breiwick (1994)
Seneca deer	11	0.411	0.017	0.992	4.59	0.06	—	—	Hesselton et al. (1965)
ALE elk	11	0.165	0.015	0.956	0.17	0.69	—	—	Eberhardt et al. (1996)
Fur seals (decreasing)	38	-0.027	0.013	0.871	1.54	0.22	0.794	<0.01	Trites (1989)
Longhorn cattle	7	0.302	0.010	0.981	19.18	0.01	—	—	Fredin (1984)
Yellowstone elk	8	0.191	0.009	0.964	33.23	0.00	—	—	Houston (1982)
Red deer	22	-0.010	0.008	0.385	0.33	0.58	0.88	<0.02	Clutton-Brock et al. (1982)
Bison	14	0.207	0.008	0.989	65.92	0.00	0.70	<0.02	Fredin (1984)
Muskox	15	0.146	0.004	0.991	19.07	0.00	0.84	<0.05	Spencer and Lensink (1970)
Serengeti buffalo	11	0.064	0.003	0.969	1.81	0.21	—	—	Sinclair (1977)
California sea otters	13	0.052	0.003	0.940	0.68	0.43	—	—	R. J. Jameson (<i>personal communication</i>)
Gray seals	16	0.069	0.003	0.977	3.45	0.09	1.61	NS	Bonner (1975)
Cusino deer	5	0.370	0.002	0.995	0.02	0.89	—	—	Ozaga and Verme (1982)
Fur seals (increasing)	12	0.082	0.002	0.984	8.17	0.02	—	—	Kenyon et al. (1954)
Pryor horses	5	0.185	0.000	0.999	1.00	0.42	—	—	Garrott and Taylor (1990)

Note: For the Durbin-Watson test, dashes indicate that sample sizes were too small for the test; NS indicates nonsignificance.

[†] Regression mean square.

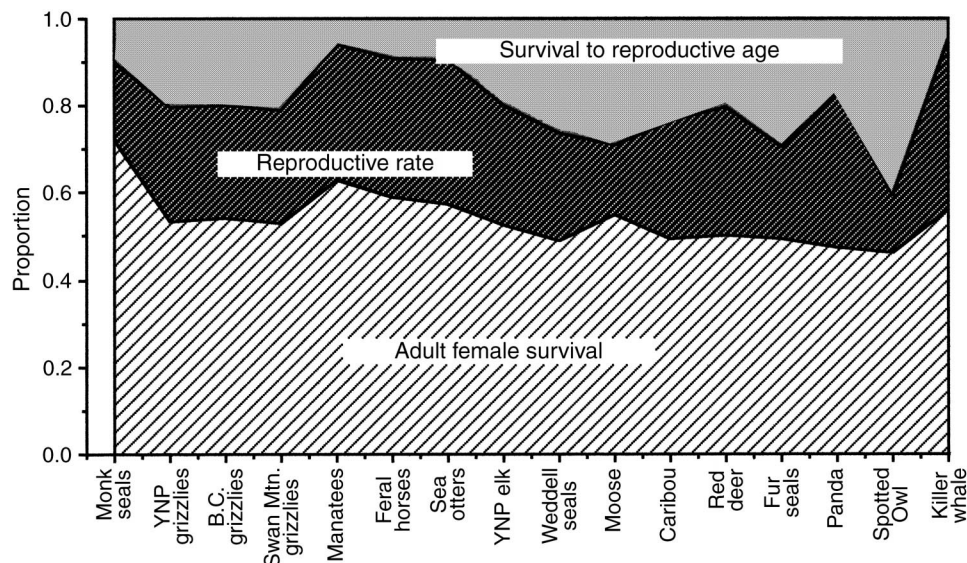


FIG. 3. Relative proportions of the numerical magnitude of partial derivatives of the three components of an approximation to Lotka's equation. Sources and values are given in Tables 3 and 4. YNP = Yellowstone National Park; B.C. = British Columbia.

evaluating models are described by Wei Pan (2001) and Hansen and Yu (2001).

Burnham and Anderson (1998) used the term "data-dredging" to describe procedures such as those employed here for the multiple regression analyses, in which all possible regressions are calculated. They recommended that a relatively small number of models should be used, based on prior experience and consideration of the circumstances of the survey. In many respects, the assessments considered here (Table 5)

may be regarded as an initial step in assembling some prior experience. Several recent examples of the application of AIC (Gaillard et al. 1993, Jorgenson et al. 1997, and Toigo et al. 1997) have evaluated survival data. In such studies it may be feasible to consider a logical sequence based on prior experience showing, for example, that male and female survival rates often differ, as do adult and juvenile rates. Such differences may supply the basis for a "structural" model, and it seems likely that the results from the studies referenced

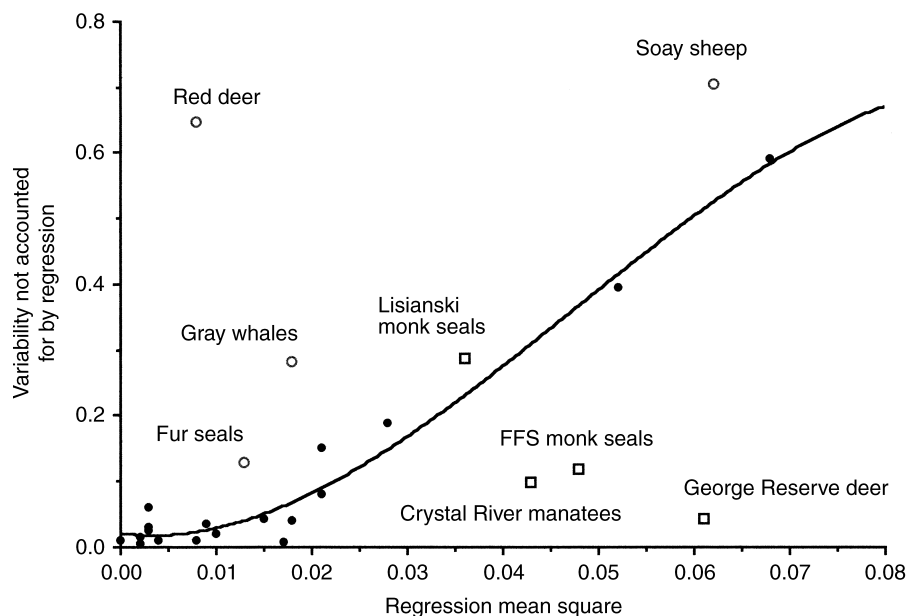


FIG. 4. Relationship between $1 - R^2$ (variability not accounted for by R^2) and the regression mean square. See *Results: Analysis of trend data* for details.

TABLE 5. Estimates of trend data from multiple regressions.

Species	Sample size	Variables selected		Other variables		R^2 values†			Reference
		Variable	Correlation	Variable	Correlation	All	Selected	Time	
Grizzly bears	20	year sight freq. snowpack	0.73 0.63 0.32	precipitation	-0.09	0.805	0.804	0.529	Eberhardt et al. (1999)
Monk seals	10	year median count pop. estimate	0.58 -0.57 0.48	slope	0.02	0.838	0.834	0.337	Eberhardt et al. (1999)
Manatees	52	year DD10 DD30	0.42 0.57 0.31	DX30 DX30 ²	0.08 -0.05	0.689	0.641	0.176	Eberhardt et al. (1999)
Moose	31	year fir-west	0.57 -0.66	wolves calves NAO	-0.20 -0.19 0.37	0.560	0.503	0.326	Post et al. (1999)
Gray whales	38	day distance size Beaufort	0.76 0.71 0.61 -0.32	visibility	-0.31	0.780	0.776	0.598	Buckland et al. (1993)
Harbor seals	58	year sunrise date	-0.72 0.16 -0.30	tide tide height	0.14 -0.13	0.737	0.733	0.525	Frost et al. (1999)
Sea lions	15	time of day	-0.43	year tide date	-0.30 -0.12 0.29	0.273	0.179	0.090	Calkins et al. (1999)
Kit foxes	20	precipitation	0.64	year biomass	0.40 -0.10	0.440	0.30	0.009	Ralls and Eberhardt (1997)
Harbor porpoise	48	Beaufort cloud cover	-0.35 0.71	year	-0.05	0.632	0.630	0.002	Forney et al. (1991)

† R^2 values are given for all variables pooled, for selected variables pooled, and for time variables only.

in Table 5 might be used to begin construction of some “structural” models for trend counts. Several of the references cited in Table 5 do provide much more sophisticated analyses than have been attempted here. The goal of the present study has been mainly one of demonstrating that including auxiliary variables can reduce variability in measuring trend.

It should be emphasized that only two models for trend were considered here: the “proportional hazards” model (Eq. 6) and multiple regressions on the means of trend data. AIC and C_p were used to select a subset of independent variables that appear to contribute significant information when a particular model is used. Hence, the search for a “best” model may also include the form of the model among a range of mathematical formulations. From the point of view of the paradigm proposed here, we need to determine if there is a trend (i.e., if λ is essentially unity) and, if there is a trend, whether it is linear (on a log scale). Thus, the process can be much more complex than the approaches presented here.

Paradigm

The purpose of the present effort has been to emphasize a pattern in the demography of populations of large vertebrates: the paradigm. Under conditions with limited human interference, it appears that annual adult female survival will be at least 0.95, and quite likely 0.99 or better (Table 1). When resources are abundant, rates of survival to reproductive age are also high, and may approach adult rates. As the population increases, reduction in resource abundance leads to a reduction in early survival, which may be accompanied by slower physical growth of the youngest age classes and a delay in the age of first reproduction. In some cases, reduction in reproductive rates of adult females will also ensue and the ultimate change in the sequence is that of lower adult survival rates (Eberhardt 1977). This sequence has been described as a paradigm because I believe that encountering a deviation from the pattern should lead investigators to focus on causes for the anomaly.

Because often only small samples are available, and

biases in estimating demographic parameters may be difficult to detect, an effort should be made to obtain an independent measure of population trend from censuses or an index of relative abundance. If estimates of λ from reproductive and survival data and from trend data are in accord, as in Fig. 2, the agreement provides strong support for the validity of the estimates of demographic parameters. An obvious difficulty in applying the proposed paradigm is that it is likely to require five years or more to obtain the needed data. Beissinger and Westphal (1998) have described some of the problems in endangered species management when inadequate demographic data are used in "population viability analyses."

The evidence for reduced juvenile survival as the first parameter to change with increasing population density is now quite substantial. Gaillard et al. (1998: Table 1) reported that juvenile survival was implicated in seven of eight species for which there was evidence of density dependence. They noted that Fowler's (1987) review showed juvenile survival to be involved in 15 of 21 species for which density dependence was reported. A major problem in assessing data from the literature is that the chronological sequence in which various parameters change often cannot be determined from the reports, but it does seem clear that changes in the age of first reproduction largely follow as a consequence of the reduced resource availability leading to reduced early survival. A logical, but not inevitable, further consequence is a reduction in reproductive rate.

Gaillard et al. (1998: Tables 2 and 3) presented data that showed much greater relative variability (coefficient of variation) in juvenile survival than in adult female survival. (Unfortunately, Table 3 of Gaillard et al. [1998] was left out of the paper and appeared as an Erratum in *Trends in Ecology and Evolution* 13:170.) The likely cause of the higher variability in juvenile survival was illustrated by Gaillard et al. (1998: Fig. 1) as the sequence in time of adult female and juvenile survival rates. As density increased, juvenile survival decreased sharply, thus substantially increasing the coefficient of variation. Gaillard et al. (1998) noted that "only two island populations (Soay sheep and red deer) exhibited density dependence in adult survival" and that "Even for these two species, survival of adult females varies much less than juvenile survival." Discussing red deer, Sæther (1997) pointed out that "the major density dependent mortality losses occur among calves during their first winter," and that "This pattern was found in three different studies of the species in both Europe and North America." Gaillard et al. (2000) reviewed a substantially larger set of data that confirmed the results of Gaillard et al. (1998) and ranked variability from highest in juvenile survival to lowest for adult survival.

Clutton-Brock et al. (1987) reported that the survival of red deer calves through their first year of life was related to both birth mass (survival decreased with low-

ered birth mass) and birth date (late-born calves were less likely to survive the winter) and that increasing population density was accompanied by a delay in average birth date. At high densities, the influence of birth mass on calf survival over winter intensified. Albon et al. (1987) reported that early growth and development of red deer appear to have a permanent effect on reproductive success "presumably because the prevailing environmental conditions in the first summer of life influence adult size." They showed that annual survival of 2–8 yr olds increased with mean daily temperature in April and May in the year of birth of cohorts of female red deer. The range of their fitted regression line was from ~0.93 to 0.99 annual survival.

Clutton-Brock et al. (1991) reported that "The persistent instability of the St. Kilda [Soay] sheep population is probably caused by their consistently high fecundity associated with a super-abundance of food in summer. In conjunction these may permit the population to pass through winter at a level close to carrying capacity; to increase as much as 50% during the subsequent summer; and to enter the next winter at a level substantially higher than the island can support."

Population regulation

A major problem in assessing the paradigm proposed here is the uncertainty as to the forces that regulated undisturbed populations before human interference became all pervasive. The relative magnitudes of the numerical values of the essential parameters (Fig. 3) indicate that "sensitivity" of λ to parameter changes is least in early survival and greatest in adult survival, with reproductive rate in an intermediate position. It might thus be supposed that this sequence may have some significance in an evolutionary sense. The notion of "*r* and *K* selection" has lost some of its earlier preeminence, but nonetheless provides a convenient shorthand classification of species, with *r*-selected groups able to recoup losses in a very short period and *K*-selected species requiring many years to recover from reductions in numbers. Consequently, it seems logical that selection might favor a regulatory process that tends to maintain equilibrium numbers by small, rather than large, changes in λ ; hence, by modifying early survival. This argument is supported by the results of Gaillard et al. (2000), who evaluated temporal variation in "fitness components" of large herbivores. These authors found that the coefficient of variation for early survival was highest (0.64) in large herbivores and lowest for prime-age adult survival ($cv = 0.09$). They suggested that "the immature stage . . . may be the critical component of population dynamics of large herbivores," indicating that "our review support's Eberhardt's hypothesis and generalizes it to all sources of temporal variation."

Three major forces can be proposed as influencing the large vertebrates under "natural" conditions: weather, resources, and predation. The preponderance

of evidence from demographic studies indicates that early survival responds first to both severe weather and to resource limitations. As a population begins to outstrip its resources, inclement weather may have a much more pronounced effect, and may result in rather sharp fluctuations.

Weather and resources clearly can and do tend to limit populations. A key question is the possible regulatory role of predation. In most natural systems, human interference severely limits opportunities to evaluate the role of predation. Wolf (*Canis lupus*) predation on ungulates has been observed to dominantly affect early survival and survival of senescent individuals (Peterson 1977, Peterson et al. 1984:Fig. 5, Ballard et al. 1987:Fig. 16, Mech et al. 1998). To serve a regulatory function, predation should exhibit a reciprocal relationship with prey density, increasing at high prey densities and decreasing at lower prey numbers. The notion of ratio dependence (Matson and Berryman 1992) may fulfill this requirement. Evidence has accumulated to favor the ratio dependence model in wolf-ungulate interactions (Eberhardt 1997, 1998). The crucial question may then be whether predation tends to hold ungulate populations below levels at which weather and resource limitations become important. If so, then an evolutionary pattern may be implicated. Eberhardt and Peterson (1999) summarized data that provide an estimate of a prey-predator equilibrium of 122 "deer equivalents" per wolf. Deer equivalents (Keith 1983) were used to combine data from different prey species, with one moose being assumed equal to six deer (*Odocoileus virginianus*) in biomass. The best prey utilization data appear to be those for moose, and Eberhardt (1997) summarized data that indicate as many as seven moose per year per wolf may be utilized. This gives a very high fraction utilized at the assumed equilibrium ratio, suggesting that wolf predation might very well utilize a high, sustainable yield from a prey population.

Application of the paradigm

A simple prescription for application of the paradigm is as follows:

- 1) Determine adult female survival rate. If it is below ~0.95–0.97, assess the cause.
- 2) Determine early survival (here, mainly considered to be survival from birth to full maturity or age of first reproduction).
- 3) Determine reproductive rates (usually the least difficult element).
- 4) Compute λ from Eqs. 1 or 2. Compare with estimates from trend data and compare the various individual rates with those of Tables 2 and 3. A notion of the factors with the greatest influence on the population should emerge. Information about past abundance will be helpful if available, but it should be appreciated that various environmental factors may

change and that human influence is not always easy to detect and assess.

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