Slade et al. -- Simplified calculations of growth rates

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Alternatives to Robinson and Redford's Method of Assessing Overharvest from

Incomplete Demographic Data

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Abstract: Conservation biologists often must make decisions regarding sustainability of harvest rates based on minimal demographic information. To assist them, Robinson and Redford (1991) formulated a method to estimate maximum rates of production which could be used to detect overharvesting based on knowing only age at first reproduction, fecundity, and maximum longevity. By assuming constant adult survival, we reduce the Euler equation to a simple form that allows calculation of population growth from the same minimal demographic data, but that can incorporate empirical prereproductive and adult survival rates if available. With this formula, we compute growth rates using various explicit survival schedules and compare these rates, and those from Robinson and Redford's (1991) method, to rates calculated from 19 relatively complete mammalian life tables gleaned from the literature. When we applied our method (assuming 1% survival to maximum longevity) and that of Robinson and Redford (1991) to the same minimal demographic data, we found that our growth rates were closer to those from complete life tables. We therefore reexamined the data of Fa et al. (1995) and Fitzgibbon et al. (1995) who analyzed overharvesting of several populations of commercially exploited African mammals based on Robinson and Redford's (1991) methods. Our reanalysis indicates that several additional populations may be overharvested. Our analysis also suggests that data on survival to age at first reproduction improves estimates of population growth rates more than data on age-specific adult survival. Regardless of the method, one can use approximate growth rates based on incomplete life tables to detect when populations are overharvested, but one should not conclude that harvest rates are sustainable when they are less than approximate production rates, because simplifying assumptions often lead to overestimates.

Introduction

Conservation biologists are often faced with trying to make decisions with incomplete information. Specifically two recent papers in Conservation Biology used only litter size and reproductive lifespan to document commercial overharvest of several species of African mammals (Fa et al. 1995; Fitzgibbon et al. 1995). Both papers compared estimates of current rates of harvest to maximal production rates (the excess of growth over replacement rate) of exploited populations based on the method of Robinson and Redford (1991). Central to Robinson and Redford's method is estimation of the maximum finite rate of population growth, denoted herein as λ_C, using the formula of Cole (1954):

$$1 = \lambda_C^{-1} + b\lambda_C^{-\alpha} - b\lambda_C^{-(\omega+1)}, \qquad\qquad (1)$$

where α is the age at first reproduction, ω is the age at last reproduction, and b is the number of female offspring per adult female per time unit (assumed constant for all ages between α and ω). Cole's formula has two advantages for estimating a maximum finite growth rate—it 1) requires minimal demographic information and 2) involves relatively simple calculations. However, Cole's (1954) formula was intended only to explore the adaptive consequences of varying reproductive strategies. Because it uses the unrealistic assumption of no mortality of juveniles or adults prior to age ω, this formula does not provide realizable growth rates (Hayssen 1984). To allow for prereproductive and adult mortality, Robinson and Redford (1991) multiplied maximal production, defined as λ_C - 1, by a factor, f_{RR}, of 0.6, 0.4, or 0.2, depending on maximum length of life being < 5 years, $\geq$ 5 but < 10 years, or $\geq$ 10 years, respectively. If harvestable surplus is the increment in growth rate in excess of replacement, Robinson and Redford's modification of Cole's rate implies an effective rate of population growth, λ_{RR}, of

$$\lambda_{RR} = 1 + (\lambda_C - 1)f_{RR} . \qquad\qquad\qquad (2)$$

Robinson and Redford (1991) emphasized that their method was intended to estimate the <u>maximal</u> rate of production of harvestable animals. They argued that if the harvest rate exceeds the maximal production rate (λ_{RR} -1), the population is in grave danger of extinction by harvesting and immediate measures should be taken to limit harvest. However, to the extent that λ_{RR} overestimates realized rates of growth, overexploitation can occur at harvest rates below the rates indicated by their equation. It is also possible that production rates from Robinson and Redford's (1991) method might be less than production estimates from complete life tables. Their multiplicative factors, f_{RR}, represent implicit survivorship schedules but it is unclear how these schedules relate to actual mortality patterns in natural populations.

We present a more general, but still simplified, method of calculating population growth rates that can incorporate several explicit assumptions or empirical values of age-specific survivorship depending on what data are available. Detailed survivorship data are rarely available for species in danger of overexploitation, thus conservation biologists have two options for making educated guesses about survivorship. First, one can examine the literature for survival rates of related species and base an estimate on this information. Second, one can postulate various survival schedules using the lifespan data required for Robinson and Redford's (1991) original model. We focus on the latter approach and offer alternatives to the procedure of Robinson and Redford (1991). We compare estimates of population growth from Robinson and Redford's (1991) approach and our modifications using several data sets for mammals. For most mammalian species, demographic data are sparse, but we compute growth rates from nearly complete demographic data from the literature for

several rodents, a lagomorph, two carnivores, and a pinniped, all from North America, and for ungulates from three continents. We then apply our approaches to the data from Fa et al. (1995) and Fitzgibbon et al. (1995) and identify several additional mammalian species in their papers that may be overharvested.

Methods

The finite growth rate, λ, of a discrete-aged breeding population in stable age distribution can be estimated as the positive root of Euler's equation (Birch, 1948):

$$1 = \sum_{x=\alpha}^{\omega} l_x m_x \lambda^{-x}, \qquad (3)$$

where l_x is the probability of surviving from birth to age x, m_x is the number of female offspring born to a female in the age interval x to x+1, and α and ω are as defined previously. We used equation 3 to calculate potential rates of population growth, λ_{COM}, from complete life tables.

A fixed fecundity for all reproductives, b, any value of prereproductive survival, l_α, and a constant yearly probability of survival of adults, p, will lead to the terms in equation 3 from ages α to ω forming a geometric series. The right hand side of the equation then can be replaced by a closed-form solution for a geometric series yielding,

$$1 = p\lambda^{-1} + l_\alpha b\lambda^{-\alpha} - l_\alpha b p^{(\omega-\alpha+1)}\lambda^{-(\omega+1)} \ . \qquad (4)$$

Cole's equation (our equation 1) is a special case of equation 4 with l_α and p both equal 1, but the more general form can incorporate independent values of l_α and $p \leq 1$, if appropriate. We calculated potential rates of population growth under five sets of explicit assumptions regarding survival (Table 1) in addition to those of Cole (1954) and Robinson and Redford (1991) and compared those values to λ_{COM}.

Most of the complete life tables include age-specific fecundities; all other calculations assume fixed values of b, therefore differences among estimated growth rates are due to variation in survival schedules. If l_α and p both equal 1, we have Cole's (1954) result, λ_C. Adjusting via Robinson and Redford's (1991) multiplier (equation 2) gives λ_{RR}. We used the same demographic information as λ_{RR}, and a single value for yearly survival of all age groups, $p = 0.01^{1/\omega}$, in equation 4 to define λ_L. This definition assumes that maximum longevity is synonymous with age at last reproduction, ω, (as is consistent with the demographic studies in Table 2) and that 1% of a cohort survives to that age (Table 1). The latter assumption was made because survival schedules in Table 2 were typically estimated from samples of >100 animals. Growth rates λ_P, λ_{PL}, and λ_{PM} (Table 1) combine empirical estimates of prereproductive survival, l_α, with various assumptions about p in equation 4: λ_P is derived under the assumption that p is 1, an extreme case (parallel to Cole's) in which every adult survives to age ω then dies; λ_{PL} is derived by assuming a value of adult survival that is consistent with a 1% probability of surviving to maximum longevity; and λ_{PM} is derived using an empirical estimate of mean adult survival through age ω. Finally, λ_{PA} uses the complete age-specific survival schedule but average rather than age-specific values for fecundities. λ_{PA} still may exceed λ_{COM} when primiparous females have lower m_x values than do experienced breeders. Note that our use of subscripts for the new λ's emphasizes the similarity among the equations: all λ's with L in the subscripts share the same assumed survival to maximum longevity, all λ's with P in the subscripts have empirically based prereproductive survival values, while M and A, respectively, refer to use of mean or age-specific adult survival data.

To compare the λ's to λ_{COM}, we calculated product-moment correlation coefficients between λ's, reasoning that whereas high correlations do not ensure

agreement (for example, λ consistently might be twice λ_{COM}), low correlations indicate lack of concordance.   We also calculated mean absolute deviations of λ from λ_{COM}.

Only λ_C, λ_{RR}, and λ_L could be calculated from the data in Fa et al. (1995) and Fitzgibbon et al. (1995) because their tables do not include survival probabilities.   To evaluate the effect of using λ_L rather than λ_{RR}, we calculated observed harvest rates as the number of animals harvested per year divided by the estimated population size (i.e. the product of density per square km^2, area in km^2, and 0.6). The value 0.6 was introduced by Robinson and Redford (1991) under the assumption that maximum production would occur at intermediate population densities.   A population growing at a rate λ is stabilized by an additional mortality factor or per capita harvest rate, h, equal to $(\lambda - 1)/\lambda$ if the harvest is applied uniformly to all age groups [Usher 1972; see Williamson (1967) for an alternative harvest regime].   We calculated this allowable harvest using both λ_L and λ_{RR} and compared it to the observed harvest rate. Overharvested populations were defined as cases where the observed harvest rate exceeded the allowable harvest. Note that estimated production ($\lambda - 1$), as in Robinson and Redford (1991), is a reasonable estimate of allowable harvest rate when λ is near one. Because of its potential demographic importance, we also calculated the minimum value of l_α ($l_{\alpha,sus}$) necessary to support the observed harvest in Fa et al. (1995) and Fitzgibbon et al. (1995) if there were no natural adult mortality . That is, we found the l_α such that $\lambda_P = 1/(1-h)$, using h calculated from their data (see Appendix for computational details).

Results

Values of λ_{RR} exceeded λ_{COM} in 14 of 19 data sets (Table 2), consistent with the intent of Robinson and Redford (1991) to overestimate rates of population growth or production. However, λ_{RR} was not correlated with λ_{COM} in the overall data set (Table 2, Fig. 1a). Strength of this correlation varied with maximum longevity, being weak for

shorter-lived species (Fig. 1a, r = 0.22) and high for longer-lived species (r = 0.945).

Deviations from λ_{COM} were large and negative for several shorter-lived species, whereas

some longer-lived species had large positive deviations (i.e., "maximal rates of increase"

underestimated predicted rates from complete life tables). Growth rates calculated

assuming a constant mortality rate consistent with 1% of the population reaching

maximum longevity, λ_L, also generally exceeded λ_{COM}, but λ_L was sometimes greater

than and sometimes less than λ_{RR} (Table 2). Further, λ_L was positively correlated with

λ_{COM} and showed smaller deviations from λ_{COM} than did λ_{RR} (Table 2, Fig. 1b). As with

λ_{RR}, the relationship of λ_L with λ_{COM} varied with longevity, but correlations were

appreciable for both shorter-lived (Fig. 1b, open symbols, r = 0.585) and longer-lived

species (filled symbols, r = 0.918); the only large deviations from λ_{COM} occurred in the

shorter-lived species and were negative. We recognize that phylogenetic dependence

exists in several data sets in Table 2, but the relationships between λ's does not seem to

be phylogenetically determined (Fig. 1).

We found survival to age at first reproduction, l_α, to be a critical piece of

information for further refining estimates of population growth or production. Values of

λ_P, incorporating observed values of l_α from complete life tables and ignoring any adult

mortality, did not reduce deviation from, but were more highly correlated with λ_{COM}

than was λ_L. When we combined observed l_α with the assumption of adult mortality

consistent with 1% survival to age ω (λ_{PL}), we further reduced deviations from, and

increased correlations with, λ_{COM} (Table 2). Not surprisingly, additional refinements

involving empirical estimates of mean or age-specific adult survival (λ_{PM}, λ_{PA}) further

improved fits to λ_{COM} as measured by correlations or mean absolute deviations (Table

2).

Using λ_L to estimate harvestable surplus was more conservative than the

Robinson and Redford (1991) procedure (λ_{RR}, Table 3) with regard to potential

overharvesting. All species indicated as overharvested using λ_{RR} were also identified with λ_L, and an additional seven species from Fa et al. (1995) and two species from Fitzgibbon et al. (1995) had harvest rates exceeding (λ_L - 1)/ λ_L or should never be harvested because $\lambda_L < 1$ (Table 3).

Discussion

Our study was motivated by skepticism as to the practical utility of demographic analyses based on Cole's (1954) equation with its unrealistic assumption regarding survival. Clearly, solving Cole's equation (equation 1) gives a "maximum rate of increase", but such a growth rate would never be realized. Robinson and Redford's (1991) use of multipliers as implicit survival rates to adjust λ_C brings such extreme overestimates of population growth rates into the realm of reality, but λ_{RR} is no longer necessarily an overestimate of the actual growth rate. Values of λ_{RR} were less than λ_{COM} in 5 of 19 data sets in Table 2 -- all from species with maximum life spans of 10 or more years (Fig. 1a). Following Robinson and Redford's (1991) reasoning, conservatism (i.e. underestimating actual rates of population growth) might be desirable because young animals with high reproductive value are often overrepresented in harvested samples.

However, λ_{RR} is not universally conservative. The minimum value of λ_C is one, and then only if fecundity, b, is zero. Any b > 0 results in both λ_C and λ_{RR} being > 1, hence there always appears to be some allowable harvest if λ_{RR} is interpreted as an estimate of growth rate. Perhaps constraining maximal growth rates to be > 1 is reasonable because species with growth rates < 1 will become extinct without harvest, but natural populations can exist, at least temporarily, with realized growth rates < 1. We prefer an analysis that allows for the possibility of $\lambda < 1$ as an indicator of species needing protection for persistence. Several populations in Table 2 have $\lambda_{COM} < 1$ and should not be harvested under extant conditions. For example, λ_{COM} for <u>Dipodomys</u> <u>spectabilis</u> (banner-tail kangaroo rats) is 0.83 and λ_L is 0.95, but λ_{RR} is 1.42 which

would not indicate overharvest unless harvest rates exceeded 30%. Like λ_{RR}, λ_L generally, but not universally, is an overestimate of rate of population growth, and is less than λ_{COM} in 6 of 19 data sets (again most are long-lived species; Fig. 1b). However, λ_L can be < 1, we think desirably. Because neither λ_{RR} nor λ_L always exceeds λ_{COM}, the criteria of closeness-of-fit between the simplified and complete model or correlation between estimates from the models may aid the resource manager in selecting an approach. By those criteria, λ_L is preferable to λ_{RR} (Fig. 1) for the data sets in Table 2. Both approaches (as well as λ_P, λ_{PL}, λ_{PM}, and λ_{PA}) should be compared using additional complete data sets.

Cole's (1954) paper illustrated sensitivity of population growth rate to the age at first reproduction in populations that are growing or have the potential to grow. Our analysis clearly shows that incorporating additional life history information, particularly survival to age at first reproduction, l_α, more closely approximates the results of complete life tables. Caughley (1966) noted that a common pattern in survival curves of mammals was high mortality early in life, followed by low mortality of young adults with increases through adult life. Promislow (1991) and Slade (1995) confirmed the generality of high prereproductive mortality in a variety of mammals, although senescent increases in mortality were not obvious in data from small rodents (Slade 1995). Caughley's general pattern seems most consistent with λ_P, which incorporates observed prereproductive survival, no or very low mortality of reproductive adults, and catastrophic senescence just after age ω. It appears that assuming a constant adult mortality rate, derived by setting l_ω equal to 0.01, further improves the fit to complete life tables (λ_{PL}, Table 2) and requires no more data than does λ_P. Further refinements to age-specific survival (λ_{PM} and λ_{PA}) do not increase the match to λ_{COM} appreciably, supporting our contention that l_α is the most critical additional information that might be added to a basic demographic data set. Unfortunately, l_α is quite difficult to estimate in

the field; in fact, several of the studies cited in Table 2 assumed stationary populations to estimate all survival rates.

Even though l_α may be difficult to estimate, one can calculate the lowest prereproductive survival required to maintain a population under a specified harvest rate if adult mortality is negligible ($l_{\alpha,sus}$, see Appendix). We know of no universal standard for what survival rates are attainable, but conservation biologists may judge whether a minimum prereproductive survival is tenable using their knowledge of the species in question. In the data of Fa et al. (1995) and Fitzgibbon et al. (1995), the current harvest rates for several of the species would require l_α greater than 0.6 which seems high relative to observed survival rates (Table 2). In our sample of complete life tables, only the ungulates consistently show l_α values as large as 0.6. If reasonable values of adult mortality are available the required l_α will be increased accordingly. Even so, several populations that seem to be overexploited using λ_L as a criterion (and Mandrillus leucophaeus which is overexploited using λ_{RR}) have minimum values of l_α less than 0.30, a figure that is exceeded by many species in Table 2. Thus, while it may be worthwhile to consider $l_{\alpha,sus}$ as a criterion for assessing overharvest, it should not be the sole measure.

Robinson and Redford (1991) accurately characterized their method as a "first assessment" to determine when a population was clearly being overharvested. However populations can be overharvested at levels below the maximal production rate from their method (λ_{RR} - 1). Researchers with empirical data must be careful when forming conclusions regarding populations exploited at such levels. Thus Table 3 indicates species with harvest rates exceeding "maximal production rates" based on λ_{RR}, but the remaining species (15 of 17 species studied by Fa et al. 1995 and 1 of 5 in Fitzgibbon et al. 1995) may or may not be overharvested. Although Fa et al. (1995) and Fitzgibbon et al. (1995) were careful to use the term "maximal sustainable rate" in several places in

their papers, Fitzgibbon et al. (1995: 1116) also stated "current offtake rates of elephant shrews, squirrels, and duikers (Cephalophus spp.) are sustainable". Our concern is that readers (particularly policy makers) who are not familiar with Cole (1954) and the somewhat ad hoc nature of Robinson and Redford's (1991) correction factors will erroneously conclude that if harvest rates do not exceed maximal production rates, these situations truly represent "sustainable" harvests. Although other estimated population growth rates, e.g. λ_L, are somewhat more conservative, similar cautions apply. Moreover, because we have assumed a deterministic model of population growth at a stable age distribution and have ignored the stochastic nature of real reproduction and survival, even our more conservative assessment of harvest rates may not detect overexploitation. Allowable harvest rates under stochastic models generally will be lower (Bayliss 1989). Given these uncertainties and the errors in estimating growth from incomplete life tables, one should avoid concluding that species are being sustainably harvested unless the harvest rate is well below maximum production rates that are not only possible, but are actually realizable under natural conditions.

Acknowledgments

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APPENDIX

Our form of Euler's equation (4) can be re-written as

$$(1-x) - \frac{x^\alpha b l_\alpha}{p^\alpha}\left(1 - x^{\omega-\alpha+1}\right) = 0, \tag{A1}$$

where $x = p/\lambda$ and the other parameters are defined in the text. Because $1 - x^{\omega-\alpha+1} = (1-x)\sum_{i=0}^{\omega-\alpha} x^i$, equation (A1) becomes

$$(1-x)\left[1 - \frac{x^\alpha b l_\alpha}{p^\alpha}\sum_{i=0}^{\omega-\alpha} x^i\right] = 0 \quad . \tag{A2}$$

This implies that the equation (4) has one root $x = p/\lambda = 1$ and a second root that satisfies the equation

$$1 = \frac{x^\alpha b l_\alpha}{p^\alpha}\sum_{i=0}^{\omega-\alpha} x^i = \frac{b l_\alpha}{p^\alpha}\sum_{i=\alpha}^{\omega}\left(\frac{p}{\lambda}\right)^i \quad . \tag{A3}$$

A rearrangement of (A3) shows how prereproductive survival, l_α, is related to the other demographic parameters at a stable age distribution:

$$l_\alpha(\alpha,\omega,b,p,\lambda) = \frac{p^\alpha}{b\sum_{i=\alpha}^{\omega}(p/\lambda)^i} = \begin{cases} \dfrac{\lambda^\omega(\lambda-p)}{b\left(\lambda^{\omega-\alpha+1} - p^{\omega-\alpha+1}\right)} & \text{if } p \neq \lambda \\[2ex] \dfrac{p^\alpha}{b(\omega-\alpha+1)} & \text{if } p = \lambda \end{cases} \quad . \tag{A4}$$

This equation is used in Table 3 to determine $l_{\alpha,\text{sus}}$, the lowest prereproductive survivorship that would allow a population to be sustained when the harvest rate is h, by setting λ equal to the growth rate that would occur without harvesting, $1/(1 - h)$, and $p = 1$ (this assumes negligible adult mortality in the absence of harvesting).

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In general, the minimum value of l_α consistent with growth, $l_{\alpha,min}$, occurs when

$\lambda = 1$. Substituting $\lambda = 1$ into (A4) gives

$$l_{\alpha,min} = \frac{1}{b\left(1 - p^{\omega - \alpha + 1}\right)/(1 - p)},$$ \hfill (A5)

assuming $p < 1$. Finally, if $p = 1$, as is assumed in Cole's approach, equation (A4) with

$\lambda = 1$ becomes

$$l_{\alpha,min} = \frac{1}{b(\omega - \alpha + 1)}.$$ \hfill (A6)

Note that the minimum prereproductive survival consistent with population growth is

simply the reciprocal of lifetime reproductive success (A5, A6).

Figure 1. Relationship between λ_{COM} and λ_{RR} (a) and λ_L (b) using 19 mammalian data sets. The 45° line indicates equal values of λ_{COM} and the estimated λ. Filled symbols indicate maximum longevities $\geq$ 10 years; open symbols, < 10 years. The "2" next to the filled up triangle signifies two long-lived ungulate species.

Table 1. Parameter values and corresponding growth rates for alternative simplifications of the Euler equation.

Growth rate	Prereproductive survival(l_α)	Adult survival(p)	Survival to maximum longevity (l_ω)
λ_C	1.0	1.0	1.0
λ_{RR}[a]	indefinite	indefinite	<1.0
λ_L	p^α	$0.01^{(1/\omega)}$	0.01
λ_P	observed	1.0	l_α
λ_{PL}	observed	$(0.01/l_\alpha)^{1/(\omega-\alpha)}$	0.01
λ_{PM}	observed	average for adults	$l_\alpha p^{(\omega-\alpha)}$
λ_{PA}	observed	age-specific	$l_\alpha \prod\limits_{x=\alpha+1}^{\omega} p_x$ [b]

[a] The λ_{RR} is based on the same parameters as λ_C but includes the multiplication factors of Robinson and Redford (1991) to account for mortality. Thus, assumptions regarding juvenile and adult survival are not explicit, but survival rates are < 1.

[b] The p_x is the probability of surviving from age x-1 to age x; hence, λ_{PA} uses the observed age-specific survival schedule.

Table 2. Alternative simple estimates of finite population growth rates for mammal species with complete life tables in the literature.

Species and source[a]	Parameters[b]						Growth rates[c]							
	α	ω	b	l_α	p	p'	λ_C	λ_{RR}	λ_L	λ_P	λ_{PL}	λ_{PM}	λ_{PA}	λ_{COM}
Ochotona princeps Smith (1974)	1	6	3.25	0.11	0.70	0.62	4.25	2.30	1.97	1.27	0.95	1.02	--[f]	0.98
Sciurus carolinensis Barkalow et al. (1970)	1	7	2.28	0.25	0.70	0.58	3.28	1.91	1.70	1.54	1.15	1.26	1.14	1.06
Spermophilus armatus H)[d] 	0.75	4.75	2.08	0.33	0.43	0.42	3.92	2.75	1.49	1.74	1.12	1.13	1.14	0.96
Spermophilus armatus (L)[d] Slade and Balph (1974)	0.75	6.75	2.24	0.40	0.53	0.54	4.21	2.28	2.13	2.07	1.54	1.53	1.53	1.36
Spermophilus beldingi Sherman and Morton (1984)	1	9	2.00	0.39	0.50	0.63	3.00	1.80	1.80	1.78	1.41	1.28	1.29	1.14
Spermophilus columbianus[e]	1	5	1.94	0.25	0.60	0.45	2.93	1.77	1.17	1.39	0.92	1.06	1.05	1.00
Spermophilus columbianus Zammuto (1987)	2	7	1.47	0.38	0.62	0.48	1.79	1.32	0.93	1.35	1.02	1.10	1.08	1.00
Spermophilus lateralis Bronson (1979)	1	7	2.00	0.21	0.70	0.60	3.00	1.80	1.55	1.37	1.01	1.10	1.10	1.00
Tamias striatus Tryon and Snyder (1973)	1	11	2.10	0.63	0.65	0.66	3.10	1.42	2.04	2.32	1.98	1.97	--[f]	1.94
Dipodomys spectabilis Waser and Jones (1991)	1	6	1.06	0.40	0.40	0.48	2.05	1.42	0.95	1.36	0.89	0.82	0.82	0.83

Table 2 (Con.)

Species and source[a]	Parameters[b]						Growth rates[c]							
	α	ω	b	l_α	p	p'	λ_C	λ_{RR}	λ_L	λ_P	λ_{PL}	λ_{PM}	λ_{PA}	λ_{COM}
Ursus americanus Powell et al. (1996)	2	15	0.70	0.52	0.73	0.74	1.47	1.09	1.08	1.28	1.08	1.07	1.06	0.99
Lynx rufus Crowe (1975)	1	10	1.40	0.64	0.60	0.63	2.40	1.28	1.51	1.89	1.53	1.50	--[f]	1.46
Mirounga angustirostris Clinton and Le Boeuf (1993)	5	14	2.40	0.26	0.60	0.70	1.48	1.10	1.07	1.24	1.11	1.07	1.07	0.93
Equus burchellii Spinage (1972)	4	20	0.50	0.66	0.80	0.77	1.25	1.05	0.99	1.19	1.05	1.07	--[f]	1.13
Phacochoerus aethiopicus Spinage (1972)	2	16	2.40	0.39	0.75	0.77	2.13	1.22	1.60	1.59	1.43	1.41	--[f]	1.33
Odocoileus hemionus Taber and Dasmann (1957)	1	9	0.39	0.63	0.86	0.60	1.37	1.14	0.82	1.20	0.83	1.07	1.09	1.07
Aepyceros melampus Spinage (1972)	2	11	0.50	0.75	0.65	0.62	1.35	1.07	0.89	1.27	0.99	1.02	--[f]	1.16
Hemitragus jemlahicus Caughley (1966)	2	15	0.42	0.46	0.75	0.74	1.31	1.06	0.97	1.14	0.94	0.95	1.02	1.00
Syncerus caffer Spinage (1972)	4	18+	0.50	0.39	0.80	0.77	1.25	1.05	0.97	1.12	0.98	0.99	--[f]	0.99
Mean deviation from λ_{COM}							0.50	0.31	0.36	0.10	0.08	0.08		

Correlations (r) with λ_{COM} -0.06 0.55 0.79 0.90 0.94 0.95

Table 2 (Con.; footnotes)

[a] Species are arranged in orders and families following Nowak and Paradiso (1984), then alphabetically within families.

[b] α, age of first reproduction; ω, maximum longevity; b, number of female offspring per mother; l_α, survival to age α; p, observed average probability of surviving one age interval for ages α to ω; p', probability of surviving one age interval calculated from observed l_α so that survival to age ω (l_ω) = 0.01.

[c] Growth rates are subscripted as in the text. All except λ_{COM} use fixed fecundity of b. See Table 1 for definition of parameters.

[d] Data are from complete life tables determined at high (H) and low (L) population densities.

[e] Data are from populations 1 and 3 in Zammuto (1987).

[f] Fecundities are not age specific, hence $\lambda_{PA} = \lambda_{COM}$. Fecundities are from Millar and Zammuto (1983) except for Ochotona princeps and Lynx rufus.

Table 3. Estimated rates of population growth from λ_c, λ_{RR}, and λ_L and minimum survival to first reproduction applying λ_p to the data of Fa et al. (1995) and Fitzgibbon et al. (1995).

Species	α	ω	b	$l_{\alpha,sus}$ [a]	p	λ_c	λ_{RR}	λ_L	h[a]	Overharvested? λ_{RR}	Overharvested? λ_L
From Fa et al. (1995)											
Cercopithecus cephus	4.0	30.8	0.17	0.30	0.86	1.12	1.02	0.96	0.02		yes
Cercopithecus erythrotis	3.0	30.8	0.25	--	0.86	1.18	1.04	1.01	--		
Cercopithecus mona	4.0	30.8	0.17	0.21	0.86	1.12	1.02	0.96	0.00		yes
Cercopithecus nictitans	5.0	30.8	0.17	0.43 0.31	0.86	1.11	1.02	0.95	0.04 0.02	yes	yes
Cercopithecus pogonias	5.0	28.0	0.17	0.62	0.85	1.10[b]	1.02	0.94	0.06	yes	yes
Cercopithecus preussi	4.0	30.8	0.17	1.0+	0.86	1.12	1.02	0.96	0.11	yes	yes
Procolabus pennanti	4.1	30.0	0.24	0.18	0.86	1.15	1.03	0.99	0.01		yes
Colobus satanas	4.8	30.5	0.48	0.13 0.11	0.86	1.22	1.04	1.05	0.02 0.01		
Gorilla gorilla	10.0	50.0	0.13	0.19	0.91	1.07	1.01	0.97	0.00		yes
Mandrillus leucophaeus	5.0	28.6	0.41	0.29	0.85	1.20	1.04	1.02	0.07	yes	yes
Mandrillus sphinx	4.0	46.3	0.35	0.13	0.91	1.20	1.04	1.09	0.03		
Atheurus africanus	2.0	22.9	1.50	0.04 0.04	0.82	1.82	1.16	1.49	0.02 0.03		
Cricetomys emini	0.4	7.8	20.2	0.01 0.01	0.55	1836.4[b]	735.2	1018.	0.02 0.00		
Cephalophus dorsalis	1.7	8.0	0.50	0.47	0.56	1.36[b]	1.14	0.77	0.11		yes
Cephalophus leucogaster	0.8	8.0	0.50	0.24	0.56	1.53	1.21	0.86	0.00		yes

Table 3 (Con.)

Species	α	ω	b	$l_{\alpha,sus}$[a]		p	λ_C	λ_{RR}	λ_L	h[a]		Overharvested? λ_{RR}	λ_L
Cephalophus monticola	1.1	7.0	0.69	0.24	0.29	0.52	1.63	1.25	0.85	0.03	0.08		yes
Cephalophus ogilbyi	1.7	8.0	0.38	0.96		0.56	1.26	1.10	0.71		0.20	yes	yes
Cephalophus sylvicultor	1.7	10.3	1.00	0.11		0.64	1.69[b]	1.14	1.08		0.01		
Potamochoerus porcus	1.5	10.0	7.80	0.02		0.63	4.63[b]	1.73	2.92		0.03		
Manis triscuspis	1.0	13.1	1.32	0.06	0.06	0.70	2.32[b]	1.26	1.63	0.01	0.01		
Civecttictis civetta	2.0	13.0	2.00	0.04		0.70	2.00	1.20	1.40		0.00		
Genetta servalina	2.0	12.5	1.80	0.06		0.69	1.93	1.19	1.34		0.03		
Nandinia binotata	2.0	13.0	1.80	0.05		0.70	1.93	1.19	1.36		0.02		
From Fitzgibbon et al. (1995)													
Petrodomus tetradactlus	1.0	<5.0	2.00	0.12		0.40	2.99	2.19	1.19		0.07		
Rhynchocyon chrysopygus	1.0	>5.0	2.00	0.21		0.40	3.00[b]	1.80	1.19		0.24		yes
Cercopithecus mitis	5.0	25.0	0.25	0.67		0.83	1.14	1.03	0.95		0.09	yes	yes
Papio cynocephalus	5.0	25.0	0.25	1.0+		0.83	1.14	1.03	0.95		0.19	yes	yes
Duikers (Cephalophus spp.)	1.0	10.0	0.50	0.21		0.63	1.49	1.10	0.94		0.01		yes

[a] The $l_{\alpha,sus}$ are values of prereproductive survival necessary to generate $\lambda_P = 1/(1-h)$ (see Appendix). Fa et al. (1995) analyzed data from two sites; values in the right column of h are from Bioka and in the left from Rio

Muni. We used areas of 2000 km^2 for populations at Rio Muni and nonprimates at Bioko. Area for each species

of primate at Bioko was estimated by dividing reported harvest by harvest per km^2 (Fa et al. 1995). The value

of h obtained for Cercopithecus erythrotis was unreasonably high and was omitted.

[b]Population growth rates that differ from those in the original papers by more than 0.01.