RISKMAN: Risk Analysis for Harvested Populations of Age Structured, Birth-Pulse Species

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Abstract

Management recommendations, particularly harvest policies, are often based on life table models of population dynamics. Estimates of population number, sex and age distribution, survival, recruitment, and harvest (if any) may be used in age-structured, birth-pulse simulation models to estimate: population trend or status, number at some future time, and to explore the demographic consequences of a range of management options. Birth pulse models include both standard life table models that mimic the reproductive biology of species that reproduce annually (e.g. ungulates, wolves, and seals) and multi-annual models for species that reproduce in 2 or 3 year intervals (e.g. bears, elephants, and walrus).

Models may allow both exponential growth and density dependent feedback mechanisms. Harvest can be modeled in a variety of ways ranging from detailed simulations that include the age specific vulnerability and selectivity of the kill to simple apportionment of the kill according to the relative abundance of the population sex and age types. A WINDOWS© compatible program named RISKMAN (RISK MANagement) was developed for the full range of options described above.

Deterministic simulations are difficult to interpret because all results are based on very uncertain estimates of input parameters, and cannot be objectively distinguished from results based on relatively precise estimates of input parameters. Similarly, simulation results from small populations are less certain than simulations for large populations. RISKMAN provides a stochastic option that uses the variance of input parameters and the structure identified by the simulation options that are selected. Monte Carlo techniques are applied to generate a distribution of results, and that distribution is used to estimate the variance of summary parameters (e.g. number at time, population growth rate, and proportion of runs that result in a decline to a user set value). RISKMAN utilizes the correct distributions of the population and rate variance estimates to provide accurate estimates of the uncertainty of simulation results. Input parameters may co-vary or be independent; RISKMAN allows the user to set the correlation to one or zero to bound the possibilities.

Key Words: bear, elephant, harvest, life table, management, modelling, population, risk assessment, simulation, stochastic, sustainable, vertebrate, walrus

A Management Context for RISKMAN

Wildlife management is considered to be not so much a matter of managing wildlife as it is managing human activities. Human activities can place wildlife populations at risk by reducing numbers and by reducing rates of survival and recruitment. Often the activity of wildlife management is simply identifying and mitigating a negative impact on a given population. On other occasions wildlife management is identifying limits to human activities that will keep the impacts to acceptable levels. This paper describes a tool for researchers and managers to assist in quantifying the risk that human activities pose to wildlife populations. The tool is a generalized simulation model that is structured to employ population parameters that can be readily measured in the field. The simulation model is called RISKMAN (RISK MANagement).

Unique Features of RISKMAN

o   RISKMAN differs from other simulation models in several ways.

o   First it provides an option to accurately model the population dynamics of species with multi-year reproduction schedules. RISKMAN was initially developed to model bear populations, and annual reproduction schedules were included simply because it was easy to do so, and in recognition that most managed species have annual reproduction schedules.

o   Second, RISKMAN allows sex and age specific harvests to occur that take into account differential sex and age class vulnerability to harvest and differential hunter sex and age class selectivity.

o   Third, RISKMAN has a Monte Carlo option which estimates the variance of output parameters based on the population size, and the variance of the input parameters.

o   Fourth, RISKMAN allows the user to include and state explicitly the mechanism of density dependent reductions to survival and recruitment that act to regulate a population. Both linear and non-linear density effects are possible, and unique relationships are possible for each parameter based on any combination of sex and age classes. This flexibility also emphasizes the information requirements for mechanistic simulations of density effects.

o   Fifth, and perhaps most important, RISKMAN is designed as a tool for managers making real world decisions rather than as an exploratory model for teaching or exploring theory. All the parameters can be estimated in the field, and the model is designed to provide a Monte Carlo (Rubinstein 1981, Gilchrist 1984) estimate of the variance of output parameters, not just provide an example of what such a program might do. Restated, RISKMAN uses the actual underlying probability distributions of the input parameters rather than make unsupported simplifying assumptions about those distributions.

RISKMAN is a single species model, and does not include any consideration of spatial dynamics. RISKMAN also does not consider the depressive effects of inbreeding like the Vortex model (Lacy, 1993, Lindenmayer et al., 1995). The only ecological feedback that the model is currently capable of including is density dependent reductions in survival and recruitment.

Like all models based on empirical parameter estimates, the accuracy of the results depend on meeting the assumptions. However, if the assumptions are met, RISKMAN will allow objective risk management for harvested and unharvested, birth-pulse populations.

Management and Uncertainty

Management prescriptions based on uncertain information should also consider uncertainty in the projected outcome. Application of any precautionary principle is simply arbitrary without an objective estimate of the uncertainty. In the deterministic mode, RISKMAN allows the user to identify a model structure that is appropriate for the level of information that is available. The input requirements also identify what information is needed to estimate future population parameters. Once the model structure is established, and estimates for the input parameters (mean and variance) are obtained, the uncertainty of the simulated population dynamics can be estimated. Management policy based on the likelihood of a decline to a certain limit, or the likelihood of persistence to a future date can be developed. RISKMAN can also guide research by identifying how precise the estimates of input parameters must be to meet the precision requirements for Monte Carlo estimates of population dynamics for a set period.

The Life Table Modelling Approach

Most managed populations are age-structured, birth-pulse populations (Caughley, 1977). Two approaches to modelling the population dynamics of species that reproduce in a discrete rather than continuous fashion have been developed: the Leslie (1945) matrix and the life table (Birch 1948 Cole 1957, Caughley 1977). The main difference between the two is the recruitment term (Taylor and Carley 1988).

The difference is noteworthy because the Leslie matrix recruitment term includes both recruitment and survival information, and cannot be estimated directly from the standing age distribution, while the classical life table recruitment term is simply the number of female offspring produced by females of age x divided by the number of females of age x. Individuals simultaneously survive and reproduce with the Leslie matrix approach, whereas the life table approach has the females survive first, then they reproduce.

The mathematical relationship between the Leslie matrix recruitment rate and the life table recruitment rate also depends on the time chosen for the census (Taylor and Carley 1988). Both approaches identify a single time of census that defines both survival and recruitment values (Taylor and Carley 1988).

A discussion of the historical development and relationships between various definitions of Leslie matrix recruitment and life table recruitment is given in Taylor and Carley (1988).

RISKMAN uses the life table approach expanded to include males.

Modelling Multi-Annual Birth-Pulse Species

Not all birth-pulse species reproduce each year. Examples of multi-annual reproducing species include bears, elephants, and walrus. Taylor et al. (1987a) noted that for simulations of populations at stable age distribution, models which mimic the actual reproduction schedules give the same results as annual models that use averaged recruitment rates. However, when the averaged recruitment estimates are taken from populations not at stable age distribution, or when the population deviates from stable age distribution, simulations using averaged recruitment rates are incorrect. Testa (1996) supported these results, but pointed out that simplified birthing schedules (i.e. annual averages) often gave simulations results that were qualitatively identical to the more detailed models. RISKMAN provides options for annual, bi-annual, and tri-annual reproduction schedules.

The Closed Population Assumption

The distribution and abundance of wildlife populations are not separate issues. RISKMAN is a closed population model. The input parameters are assumed to be estimated from and to apply to a discrete geographic unit (i.e. the population). In many areas, habitat fragmentation makes the boundaries of the population apparent (e.g. parks, reserves, watersheds). However, when individuals are free-ranging across large areas, the first step is to determine if the area is best regarded as one or several populations. In this context, a population is not necessarily genetically isolated, nor are the boundaries necessarily absolute barriers to movements (Lincoln et al. 1982:199, Ricklefs 1986:507).

Identifying Population Boundaries

For demographic simulations, the best method of identifying population boundaries is to study the movements of individuals. Population boundaries may result from discontinuities to movements caused by natural or man-made barriers. RISKMAN simulations assume that the delineated population is a biological unit whose population dynamics are wholly determined by birth and death factors within the population, and that emigration and immigration is negligible. Bethke et al. (1995) describes an objective approach to identifying population boundaries from animal movements.

The "Time of Census" Requirement

An essential step in estimating recruitment and survival rates for the purpose of calculating sustainable yield is identification of the time of census. Life table projections are intended for, and accurate to, the time of census only. Additionally, the time of census for estimating recruitment rates must be the same as that for estimating survival rates (Caughley 1977, Taylor and Carley 1988). For example, one may call recruitment the per female number of ova produced, the number of implanted embryos, the number of offspring born, or the number of offspring counted with the mother some time after leaving the den. Each measure is an acceptable definition of recruitment so long as cub (and adult) survival is also determined from the same temporal reference point. The terminology of ecological or physiological studies of reproduction is often different than the terminology in demographic studies. In demographic studies, the value of recruitment is determined by the time of census.

Recruitment for Multi-Annual Reproduction

For annual reproduction models, the age specific recruitment term mx is simply the number of female offspring produced by females of age x divided by the number of females of age x (Birch 1948 Cole 1957, Caughley 1977). RISKMAN expands that definition to include male as well as female offspring to allow simulations of harvest that include both sexes.

For multi-annual reproduction models the recruitment terminology must be expanded. As mentioned previously, errors are incurred in life table simulations of non-stable age populations with extended parental

care that use averaged rates in order to use annual models. These errors occur because extended parental care results in a variable fraction of the females of a given age class being available to mate and reproduce the following year. For non-stable (e.g. selectively harvested, experiencing density effects, or stochastic) population dynamics, accurate simulations require that the fraction of females available to mate in a given age class be determined as part of the model dynamics (Taylor et al. 1987b).

For the example of bears, female bears with cubs-of-the-year (COYs), and female polar and grizzly bears with yearlings, are not available to mate, and therefore will not produce offspring the following year. (Fig.1). Mature grizzly and polar bear females with two-year-old cubs, and those with no cubs are available for mating (Craighead et al. 1974, Bunnell and Tait 1980, 1982, Knight and Eberhardt 1985, Ramsay and Stirling 1988). Female black bears with yearlings and no cubs are also available for mating (Erikson 1964, Rogers 1977, Bunnell and Tait 1980, 1981). Unbiased simulation models must mimic, not summarize, the reproduction biology of bears for non-stable-age simulations. The same is true for all species with multi-year reproduction cycles.

Figure 1: Availability of Females to Mate

Female bears are not available to mate when they are encumbered with cubs. Females with cubs become available to mate by losing litters (either whole litter loss or by individual cub mortality) and by weaning cubs (typically 2 years old for grizzly and polar bears, and as yearlings for black bears).

Polar Bear Potential Encumbrance Status and Availability to Mate
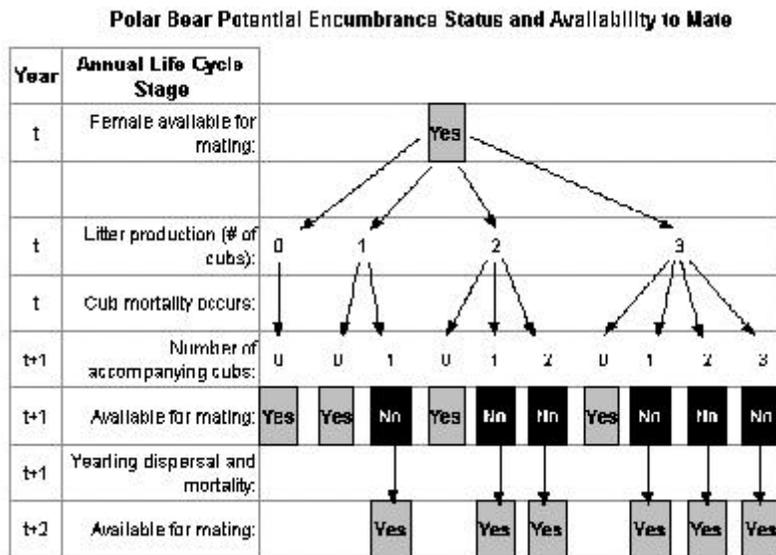
Recruitment Rate Definition

The terminology for multi-year reproduction schedules must be expanded from the conventional life table terms (Taylor et al. 1987b). Age-specific recruitment rate (m_x) has 3 components: availability to mate and produce offspring the following year (A_x), litter production rate of mating females (B_x), and litter size of recruits (L_x) at time of census (t). Age specific recruitment rate (m_x) can be expressed as:

$$m_x \;=\; A_{x-1} \cdot B_{x-1} \cdot L_x$$

m_x can also be expressed as:

$$m_x = \frac{N_{x-1,t-1} \cdot A_{x-1} \cdot B_{x-1} \cdot P_{x-1} \cdot L_x}{N_{x,t}}$$

where:

0 = initial age class,

w = final age class,

x = discrete age class,

t = discrete time interval (i.e. 1 year),

$N_{x,t}$ = number of females of age x at time t,

p_{x-1} = fraction of $N_{x-1,t-1}$ that survive to be $N_{x,t}$ (i.e. annual survival rate),

m_x = age specific recruitment rate of $N_{x,t}$ (i.e. the number of $N_{0,t}/N_{x,t}$ at the time of census),

A_{x-1} = proportion of $N_{x-1,t-1}$ available for mating,

B_{x-1} = proportion of $A_{x-1,t-1}$ available for reproduction at time t-1 that would produce recruits at time t if all $N_{x-1,t-1}$ survived to be $N_{x,t}$ (i.e. litter production rates), and

L_x = litter size of female recruits produced by those $N_{x,t}$ that produce recruits.

The number of age 0 at time t, produced by x-year-old females is $m_x \times N_x$, and the total number of age 0 produced is the sum:

$$\sum_{x=1}^{w} m_x \cdot N_x$$

The above notation is useful to indicate briefly and explicitly how recruitment for species with extended parental care is modelled. One can also understand how recruitment is modelled by revisiting the sex, age, and family structure. For the example of bears, the population is described by an array that has columns for males, females with no cubs, females with 1 cub, females with 2 cubs, females with 1 yearling, females with 2 yearlings, and females with two-year-olds; and one row for each age, beginning with age zero (cubs) (Table 1). As males are born, and age, they simply move down the age structure as a gradually diminishing cohort due to harvest and natural mortality. Females are similar until they reach reproductive maturity. Once females have cubs, they are removed from the pool of available females (i.e. available to mate). These females cycle back into the available pool when their cubs reach weaning age, or when their cubs are lost due to mortality (Fig. 1).

Thus offspring survival can affect realized recruitment rates for species with extended parental care. For the example of bears, if cub survival is low, more females will lose their litters, and be available for mating. Similarly, if mating success is high, fewer females will fail to produce cubs, and the pool of females available to mate will be reduced. For species with extended parental care, these interactions make effects on sustainable harvest caused by increases or declines in population parameters (e.g. cub survival and mating success) difficult to anticipate. Simplistic annual models of species with extended parental care are structurally incapable of correctly modelling the actual life history. The list of life history parameters for bears (Table 2 and Table 3) is necessarily longer than that for the annual life table because of the requirements imposed by extended parental care.

Table 1: Age-Sex and Family Classes for Grizzly, Polar, and Black Bear Populations

Grizzly and polar bears typically have a three year reproduction cycle while black bears have a two year cycle. Subadult and adult male bears are solitary except for the mating season, but adult female grizzly and polar bears may be encumbered with cubs-of-the-year (COYs), yearlings, or 2-year-olds (2-YR). Litter size is not recorded with 2-YR because females with 2-YR will accept a mate. Adult female black bears may be encumbered with up to six cubs-of-the-year. Litter size is not recorded for female black bears with yearlings because females with yearlings will accept a mate.

Table 1a: Grizzly and Polar Bears

AGE	MALES	FEMALES encumbered by:							
		NO. CUBS	COYs			YEARLINGS			2-YEAR OLDS
			1	2	3	1	2	3	
0									
1									
2									
3									
4									
5									
6									
7									
8									
9									
. . .									
Oldest									

Table 1b: Black Bears

AGE	MALES	FEMALES								
		NO CUBS	CUBS-OF-THE-YEAR						YEARLINGS	
			1	2	3	4	5	6		
0										
1										
2										
3										
4										
5										
6										
7										
8										
9										
. . .										
(oldest)										

Table 2: Life History Parameters of Grizzly, Polar, and Black Bears Use for Simulation Modelling of Sustainable Harvests

PARAMETER	GRIZZLY BEAR	POLAR BEAR
Individual COY Survival	0.65	0.85
Individual Yearling Survival	0.80	0.85
Litter COY Survival	1.00	0.90
Litter Yearling Survival	1.00	0.90
Subadult Survival (Male)	0.93	0.94
Subadult Survival (Female)	0.93	0.94
Adult Survival (Male)	0.96	0.96
Adult Survival (F)	0.96	0.96
Litter Production Rate (Subadult)	0.15	0.15
Litter Production Rate (Adult)	0.67	0.70
Probability of COY Litter = 1	0.10	0.20
Probability of COY Litter = 2	0.60	0.80
Probability of COY Litter = 3	0.30	0.00
Age of First Litter Production	6.00	5.00

PARAMETER	BLACK BEARS
Individual COY Survival	0.70
Litter COY Survival	1.00
Subadult (1-3) Survival (Male)	0.75
Subadult (1-3) Survival (Female)	0.75
Adult (4+) Survival (Male)	0.96
Adult (4+) Survival (F)	0.96
Litter Production Rate (4-year-old)	0.50
Litter Production Rate (Adult)	0.85
Probability of COY Litter = 1	0.10
Probability of COY Litter = 2	0.40
Probability of COY Litter = 3	0.50
Probability of COY Litter = 4	0.00
Probability of COY Litter = 5	0.00
Probability of COY Litter = 6	0.00
Mean Litter Size of Yearlings	2.1083

Table 3: Population Growth Rates and Sustainable Harvest Rates for a Range of Population Parameters Reported for North American Species of Bears

Population growth rates and sustainable harvest rates are given for a range of population parameters reported for North American species of bears (Taylor 1994).   The harvests were selective for males, protected females with cubs and yearlings, and reduced vulnerability of females with 2-year-olds (grizzly and polar bears) and yearlings (black bears) by 30 percent. Subadult (first two age classes post weaning) males were twice as vulnerable as adult males. The harvest was typically two males per female from the stable age distribution (i.e. starting conditions).

Table 3a:

POPULATION PARAMETER	BLACK BEAR			GRIZZLY BEAR		
	min	mid	max	min	mid	max
Single Cub Survival Rate	0.50	0.70	0.85	0.56	0.65	0.75
Litter Cub Survival Rate	1.0	1.0	1.0	1.0	1.0	1.0
Single Yearling Survival Rate	-	-	-	0.80	0.80	0.85
Litter Yearling Survival Rate	-	-	-	1.0	1.0	1.0
Subadult Male Survival Rate	0.75	0.75	0.90	0.93	0.93	0.95
Subadult Female Survival Rate	0.75	0.75	0.90	0.93	0.93	0.95
Adult Male Survival Rate	0.94	0.96	0.96	0.96	0.96	0.96
Adult Female Survival Rate	0.94	0.96	0.96	0.96	0.96	0.96
Subadult Litter Production Rate	0.50	0.70	0.60	0.15	0.15	0.15
Adult Litter Production Rate	0.85	0.85	0.85	0.60	0.67	0.75
Mean Litter Size of Cubs	1.60	2.4	2.65	2.0	2.2	2.5
Age of Adult Reproduction Rates[1]	5	5	4	8	7	6
Population Growth Rate (l)	1.0	1.09	1.253	1.0	1.031	1.085
Rate of Sustainable Harvest[2]	0	0.091	0.252	0	0.032	0.084

Table 3b:

POPULATION PARAMETER	POLAR BEAR		
	min	mid	max
Single Cub Survival Rate	0.98	0.85	0.85
Litter Cub Survival Rate	0.72	0.85	0.85
Single Yearling Survival Rate	0.62	0.85	0.90
Litter Yearling Survival Rate	0.74	0.75	0.90
Subadult Male Survival Rate	0.94	0.93	0.94
Subadult Female Survival Rate	0.94	0.93	0.94
Adult Male Survival Rate	0.96	0.96	0.96
Adult Female Survival Rate	0.96	0.96	0.96
Subadult Litter Production Rate	0.0	0.15	0.15
Adult Litter Production Rate	1.0	0.70	0.70
Mean Litter Size of Cubs	1.72	1.71	1.80
Age of Adult Reproduction Rates[1]	6	6	6
Population Growth Rate (l)	1.006	1.014	1.041
Rate of Sustainable Harvest[2]	0.007	0.015	0.044

1   Subadult Litter Production Rate applies to the next younger age class only.

2   The harvest is selective for males and the initial age distribution is the stable age distribution with no harvest defined by the population parameters.

Estimating Recruitment Parameters

The simulation model determines the fraction of females available for mating. However, the time of census determines what mating success actually measures. Mating success is the fraction of the available females that are encumbered with cubs the following year. If the time of census is in spring after emergence from the den, a female that mated, produced cubs, but lost the cubs prior to census would be counted as an unsuccessful mating. If the census was during the denning period, the same female would be counted as successfully mating, however the cub survival estimate would be lower. Taylor et al. (1987a) provides a procedure for calculating mating success of polar bears for both age-specific and age-constant strata from the standing age distribution. This method applies without modification to both black and grizzly bears. Typically, there is an age at which adult mating success rates are age-constant. This is the age of reproductive maturity. There is also a tendency of limited mating success for bears one year younger than the age of reproductive maturity. The semantics of what is mating success, age of first reproduction, or cub survival are unimportant in estimating sustainable rates of harvest. What is important is that the population parameter rate measures all have a common time of census.

The estimate of litter size is simply the mean litter size at the time of census. The sex ratio of litters determines the relative contribution to the male and female population vectors.

These are the essential recruitment parameters for species with extended parental care. For species with extended parental care, average age of first reproduction, reproduction interval, and mating interval, are summary parameters of interest for comparisons between populations. They are functions of mating success, cub survival, and litter size (Taylor et al. 1987a). They will not allow accurate determination of non-stable age population dynamics, and may mislead the naive researcher into using biassed annual models. Recruitment parameters for both annual and multi-annual reproducing species may be estimated directly from unstable standing age distributions without regard for the underlying population growth rate (Caughley 1977).

An alternative to analysis of the standing age distribution for recruitment rates is to follow individuals through their reproduction cycles using telemetry. The analysis procedure is the same as described above, with the exception that the observations are restricted to surviving individuals, and are not corrected for the decline in number with age (Taylor et al. 1987a). A significant constraint to this approach is the requirement for long-term telemetry studies involving many individuals. For example, for some bear populations, the interval between cub production may be 5 or more years.

Survival: Natural and Harvest Mortality

For harvest simulations, mortality is divided into two components: harvest and natural mortality. The actual number of a particular sex/age strata that are lost to natural mortality is determined by multiplying the annual per capita mortality rate by the number of individuals in the strata. Harvest mortality is different because the number killed is only partly a function of the number present. The number lost also depends on the selectivity of the hunters, the vulnerability of the sex/age strata, and limits to the number harvested (e.g. a quota). Therefore, we simply subtract from the strata the number of individuals in a particular strata lost to harvest mortality.

The time of census and actual circumstances of the harvest determine the order of harvest and natural mortality. Typically, both harvest and natural mortality are not spread equally throughout the annual cycle. The circumstances are not critical so long as they are incorporated into the model in the correct order. RISKMAN assumes that natural mortality occurs before harvest mortality. The rationale is that most recruitment occurs after winter, and most natural mortality occurs during winter. The time of census can be

anything, but RISKMAN assumes the order of events is survival then recruitment, then harvest. Two harvests are possible in a given year to allow harvest selectivi ty (and intensity) to differ. The first harvest is termed "spring" and the second "fall", however they are calculated sequentially with no demographic changes in between. All harvest is additive for a given year, and unless the density effects function is in effect, all harvest mortality is additive.

Natural Mortality

Natural mortality rates can be specific for every sex and age class in the model. However, in practice strata of age-constant rates can be identified for both males and females. These strata typically include age zero (i.e. recruits), subadults (i.e. pre-reproductive), adults (i.e. reproductively mature), and senescent. For species with extended parental care, each age class that the young are with the mother is usually identified as an age strata. When species with extended parental care it is also useful to distinguish between per capita mortality of offspring and whole litter mortality because when a female loses her entire litter she become available to mate. Failing to correctly calculate the fraction of females that lose their dependent offspring and become available to mate results in underestimation of population recruitment and population growth rate.

There are several possible methods for estimating annual survival rate. These include analysis of the standing age distribution and cohort analysis. Cohort analysis can include analysis of radio telemetry data or studies of the survival of marked animals. Both standing age distribution and telemetry analysis could produce accurate estimates, but difficulties in meeting the underlying assumptions of these techniques are insurmountable in most bear studies. Analysis of the capture history of marked animals appears to be the strongest option, provided an appropriate model is used.

Estimating Survival From the Standing Age Distribution

Caughley (1977) provides a clear explanation of the difficulties in determining survival rates from the standing age distribution. Essentially, it cannot be done unless the population growth rate is already known and the population is at stable age distribution (except see Udevitz and Ballachey 1998 when the age at death is also known). In some circumstances, however, analysis of the standing age distribution can be useful. These circumstances are characterized by: having a series of precise and accurate population estimates to allow an estimate of population growth rate that is independent of the age distribution; and harvest rates that have not fluctuated so that the age distribution is at least approximately stable.

When the standing age distribution is analysed, researchers should first stratify the age distribution into strata of constant survival rates. Chapman and Robson (1960) and Robson and Chapman (1961), provide a minimum variance unbiased estimator (p) for age-constant survival rates from stratified data, a variance estimate for (p), and a full discussion of the considerations in estimating age-constant survival. Chapman and Robson (1960) suggest truncating the age distribution when the number of individuals in each age class is less than five.

A commonly used alternative to the Chapman-Robson method for standing age distributions is linear regression of the log transformed exponential decay model given by:

$$\ln (N_x) = \ln (N_0) + p \cdot x$$

This method is unduly affected by sampling error in the older, less abundant age classes because large numbers are reduced more by log transformation than small numbers. This difficulty can be eliminated by using non-linear regression on the untransformed exponential decay model:

$$N_x = (N_0) \cdot p^x$$

Non-linear regression may also be used to explore models where survival is not age-constant such as the Siler (1979) model. The final choice of models is guided by both goodness-of-fit statistics and examination of the residuals. None of these approaches will provide accurate estimates of survival rates from standing age distributions that are not stable, and where the population growth rate is not already known. The correction when the population growth rate (l) is known is: $p_{corrected} = p_{estimated}/l$ (Caughley 1977). Thus, estimates of survival rates may be taken directly from the standing age distribution only when the population is stationary (i.e. l = 1.0).
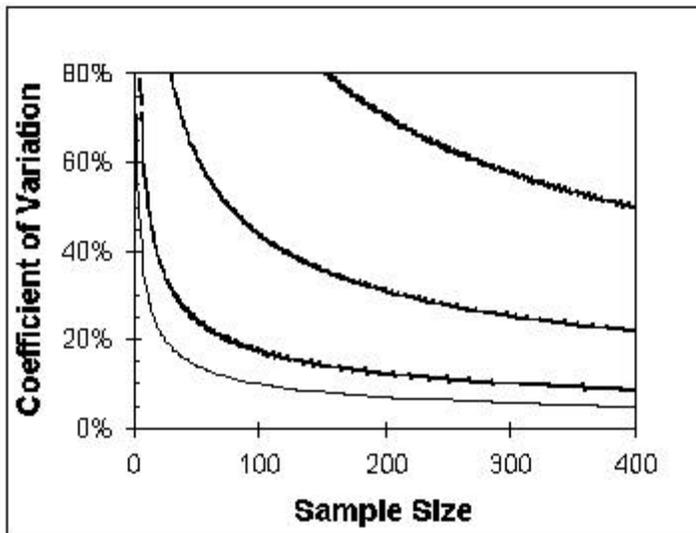
Estimating Cohort Survival Using Telemetry

Cohort estimates of survival may be obtained in two main ways. The first is by following individuals through time, typically by using radio telemetry. Several models have been used to analyze mortality schedules obtained from following individuals with radio collars (Trent and Rongstad 1974, Heisley and Fuller 1985, Pollock et al. 1989, Amstrup 1995). These methods have two major drawbacks, particularly for estimating adult survival rates when adult survival is high. The population dynamics of species with high adult survival rates is sensitive to and typically dominated by the adult survival rate. This is a life history adaptation which minimizes the impact of fluctuations in recruitment rates caused by environmental variability (Stearns, S.C. 1977). Because estimates of population growth rate and sustained yield are very sensitive to the estimate of adult survival rate for long lived species (Taylor et al. 1987c), accurate estimates of adult survival rate are essential for meaningful risk analysis. Reasonably precise estimates of rates of sustainable harvest require estimates of adult survival rate (a binomial parameter) that has a coefficient of variation less than 5 percent. It is instructive to examine the relationship between sample size and coefficient of variation for binomial parameters (Fig. 2). Even assuming annual survival rates do not vary between years, acceptable precision requires 60100 bear years of monitoring. This is expensive, invasive, and may be impractical for small populations.

The second difficulty with telemetry studies of mortality rates is that dead individuals may have a higher probability of being undetected than live individuals. Starving individuals may disperse from the study area, may burrow into dens which retard or eliminate radio signals, or may die in a rivers lakes, oceans, or ice, and sink. The radio may be carried away from the carcass by a scavenger, or picked up by a hunter or hiker and removed. All telemetry studies have a certain fraction of radios that simply disappear. If a larger fraction of these missing radios are dead bears than the active radios, mortality rates are underestimated by procedures that censor silent radio beacons as missing data. For long-lived species, regarding lost radios as missing data is equivalent to assuming essentially all of them survived. The validity of this assumption can be examined by comparing telemetry estimates of mortality with estimates from the standing age distribution and from open mark-recapture survival estimates.

Telemetry estimates of the survival of dependent young are not as vulnerable to lost radio transmitter bias. A radio-collar is typically on the mother, so the estimates of cub survival are for surviving females only. However, simulation model estimates of rates of sustainable harvest include adult female mortality as a part of cub mortality because the cubs are dependent on their mothers. Telemetry estimates of cub mortality are unbiased, and do not affect estimates of population growth rate and sustainable harvest to the same extent as errors in estimates of adult survival rates.

Figure 2: Sample Size Effects on Variation of Estimates of a Proportion

Estimating Cohort Survival Using Mark-Recapture

The second cohort method of estimating survival is mark-recapture studies. There are several excellent reviews of the considerations for mark-recapture estimates of population numbers and survival (Cormack et al. 1979, Nichols et al. 1981, Pollock 1981, White et al. 1982, Seber 1982, Pollock et al. 1990, Skalski and Robson 1992, and Lancia et al. 1994). One of the most practical discussions of options for field applications is Begon (1979), and the reader is referred to these references for a general treatment of mark-recapture population estimates. We begin by restating the importance of identifying a spatial unit that has barriers to movements or is sufficiently large so that immigration and emigration can be neglected. Then, loss of marked animals occurs by harvest and natural mortality only. Harvest mortality is usually recorded and natural mortality for most bears older than cubs appears to be constant. A constant survival mark-recapture model that does not include cubs can provide unbiased and reasonably precise estimates of natural survival provided that sampling assumptions are met, and the model is sufficiently flexible to allow harvest mortality to be incorporated separately from natural mortality. Alternatively, harvest and natural mortality can be pooled when the harvest rates have remained approximately constant throughout the sampling period. When male and female survival rates are believed to differ, separate estimates can be calculated for each sex.

Implementation of this method requires handling a significant (>15%) fraction of the population. The capture and recapture effort must allow for every animal in the population to have an equal chance to be captured. This assumption can be difficult to meet when the vulnerability to trapping or aerial capture differs for some sex and age classes. Furthermore, all individuals of all species appear to have home ranges. Therefore, the entire area of the population must be given equal capture effort to avoid geographic anomalies in the marked to unmarked fraction and sampling that can bias estimates of both annual survival and population numbers.

The most powerful method for analyzing mark-recapture data from open populations is the Jolly-Seber method (Jolly 1965, Seber 1965) because it considers open population models and provides robust survival rate estimates between sampling occasions (Lancia et al. 1994). A significant problem with the Jolly-Seber model is that the data are interrelated between years. If non-representative sampling occurs in a given year,

the impact not only affects the current estimate but also cascades throughout all subsequent estimates. The Jolly-Seber method also provides no estimates for the first or last sampling interval. Excluding all marks deployed in years when the sampling was non-representative, and the initial and final year are significant limitations when the cost of marking animals is high.

More recent work on mark-recapture has focused on model development that accommodates capture heterogeneity. Which mark-recapture method is used to calculate survival is unimportant, as long as the estimate is accurate, precise, and also estimates the variance. Accurate and precise mark-recapture estimates of survival and population numbers require multi-year sampling of the entire population area.

Estimating Cub Survival

For species with multi-annual reproduction schedules the survival rate of cubs may be estimated from changes in litter size, and the frequency of litters of a given age (Taylor et al. 1987a). This procedure divides cub mortality into individual survival, and whole litter survival. Individual mortality causes litter size to decline between cubs of the year and yearlings, and between yearlings and two year olds. Whole litter mortality does not affect litter size, but does reduce the number of litters that survive to the next age class. Individual survival is estimated by the change in litter size. Given individual survival, the rate of loss of entire litters from individual mortality can be calculated. If more litters are lost than can be accounted for from individual mortality, these litters must have been lost as units. The expected number of litters must take into account both adult female (mother) survival rate, population growth rate, and the possibility that the age distribution is not stable (Taylor et al. 1987a). Fortunately the correction term (f_x) is: N_x/N_{x+1}, which is taken directly from the standing age distribution (stable or unstable). If f_x is age constant, the Chapman-Robson technique can be used for the age-constant strata.

Harvest

The sustained yield from a harvested population depends partly on the sex and age distribution of the kill. The yield of age zero is higher than mature. Additionally most harvests are selective for particular sex and age strata, and for most species particular sex and age strata are more vulnerable than others. The sex and age structure of the harvest are partly determined by hunter selectivity, but also depends on relative availability of the various sex, age, and family status classes. For instance, if the males in a population became depleted, even a harvest that was selective for males might result in mainly females being taken. When selectivity/vulnerability is constant, relative availability changes in a dynamic fashion. The sex and age distribution changes through time as a result of changes in relative availability caused by selective harvest. If the harvest is exactly sustainable, the population standing sex/age distribution will eventually become constant. However, if selectivity, vulnerability, or numbers harvested change; the sex and age distribution will also change.

The sex/age distribution of a selective harvest affects the sex/age distribution of the population each year. Additionally, the sex/age distribution of the population affects the sex and age of the harvest in a dynamic fashion. The dynamics of both interactions are partly determined by the overall population numbers, which are affected directly by harvest, and indirectly (i.e. recruitment) by the standing age distribution.

Estimating Harvest Parameters

The data requirements are the sex, age, and in the case of species with extended parental care, the family status distribution of the harvest and the population standing age distribution. These may be tabulated as counts or fractions of the total. The two distributions are normalized by dividing each cell by the total of all cells. If the harvest was non-selective, the two distributions would be the same. The difference between the two results from differential selection/vulnerability for certain categories.

The RISKMAN approach to modelling selectivity/vulnerability is to divide the number or fraction harvested in a given sex/age/family status category by the number/fraction in the same category of the standing age distribution. The resulting selectivity/vulnerability distribution may also be normalized by dividing by the total number from both categories. Calculation of the sex/age/family status of a harvest is accomplished by multiplying the number (or proportion) of each sex/age/family status category in the standing age distribution by the corresponding category in the selectivity/vulnerability distribution. The resulting distribution is normalized by dividing each sex/age/family status category by the sum of the categories to get a harvest distribution that sums to one. The fraction of the total harvest is then indicated. This apportionment of harvested animals into sex/age/family status categories is done at each time iterate, and the harvest is then subtracted from the population.

In practice, the full sex/age/family status structure is seldom used. Strata of like types can be identified, and when data are limited, categories may be pooled. When strata are identified, another step is required. The kill per strata is apportioned according to the relative availability of the pooled sex/age/family status categories. This is accomplished by dividing the cell counts of each category by the sum of pooled cell counts. The result is the fraction of the strata kill that each cell should receive, assuming the pooled types are equally vulnerable to harvest.

Modelling Harvest

Models which subtract a constant harvest structure implicitly assume that the availability of the various sex/age/family status categories does not influence the distribution of the harvest. Models which subtract a constant fraction of each sex/age/family status type assume all animals are equally vulnerable and hunters are not selective. Neither of these assumptions is consistent with the existing information on harvesting (Kolenosky 1986, Reynolds et al. 1990, Miller and Chihuly 1987, Lee and Taylor 1994).

We recognize that many harvested populations are managed by controlling season length, and that the number of individuals taken varies from year to year, even in a quota system. Our comments are within the context of calculating a sustained yield given a particular standing age distribution, and assumes that the vulnerability of various sex/age/and family status groups and given hunter selectivity does not change, although the availability of the various strata will change in a dynamic fashion as the simulation proceeds.

Estimating Population

The number of individuals in the population may be estimated in many ways (see Lancia et al. 1994 for a recent review). The methods used to estimate population numbers are beyond the scope of this description of RISKMAN. The population estimate should be accurate, and the precision of the estimate will greatly influence the variance of in simulation results. In stochastic mode, RISKMAN obtains a random normal

deviate based on the mean and variance of the population estimate to determine the initial population number. The initial number is then randomly sorted into the starting sex and age structure as described above. Only the initial number and initial distribution is calculated from a random deviate. The simulation proceeds based on the contingencies described by model selection for each individual for the remainder of the simulation. When Monte Carlo (i.e. many) simulations are run, the initial population number is randomized for each run.

Estimating and Modelling Variation

The stochastic functions in RISKMAN are strictly demographic, that is not genetic, as in the Vortex model (Lacy, 1993, Lindenmayer et al., 1995). The survival and recruitment mean values are assumed to vary between years due to environmental uncertainty. Additionally the standard error of the demographic rate estimates is partly due to sampling error. Both sources of uncertainty are pooled and assumed to be normally distributed in the variance estimates of all demographic rates. If there was no year-to-year variability, the variance would be due to sampling error only. In that instance, because most of the parameters are binomial, a normal approximation for the variance in a given year would be incorrect. However, as the sample size, for parameter estimates increases, the relative contribution of sampling error decreases. In any event, the inter-annual mean is a mean of means, and that distribution would be expected to be normal regardless of the underlying distribution of the variance of the individual year mean. The standard error requested by RISKMAN for stochastic simulations is the standard deviation of the mean of inter-year means, not the standard deviation from a single sample. If only a single sample mean is available, the standard deviation is the best approximation of the standard error of the mean of means.

The Stochastic Mechanism

RISKMAN obtains a random normal deviate for each survival and recruitment rate based on the mean and standard error for the particular sex/age strata. Each individual is then exposed in a series of Bernoulli trials to the probability described by the annual random deviate. For example if 100 individuals of the adult age strata were exposed to a mean survival rate of 0.90, one might find the annual random deviate to be 0.9133472, or 0.8922378; and one could find that any number between 0 and 100 survived, but usually the number survived would be around 90. This process incorporates annual variability and sampling error (normal distribution), and also the uncertainty associated with applying the random mean to individual trials where the result is either a success of a failure (e.g. survival or death, or produce a litter or fail to produce a litter). Most of the steps in a stochastic demographic simulation can be represented as a binomial process. Each individual experiences survival, recruitment, and harvest contingencies as a Bernoulli trial. In stochastic mode individuals are assigned to the initial sex/age distribution as whole numbers; and birth and death occur as integer events for all subsequent simulation events.

Modelling Litter Size

Litter sizes of up to two can be treated as binomial because an individual either has a litter or not (binomial). If an individual has a litter it will be two offspring or one offspring (binomial). If more than two offspring are possible, the process is multinomial, but can be modeled in the same way using the proportion of litters that are 1, 2, 3, ...n as the probability of a litter of that size. Any random number between 0 and 1 will fall into

one of the categories identified in the cumulative sum of the probabilities of litter count. RISKMAN assigns each individual that does produce a litter a litter size based on this process.

Modelling the Initial Age Distribution

Similarly the initial age distribution can be modeled as a multinomial assignment based on the proportions determined from the age/sex category count divided by the sample size that the age/sex distribution was based on. The random assignment of the same sample size based on those proportions gives a starting distribution that is then used to assign, in multinomial fashion, the initial population number to the starting age/sex array. The resulting starting sex/age distribution array takes into account both the sample size that the estimate of the initial distribution is based on, and the number of individuals in the initial population.

Modelling Harvest Variation

The harvest sex/age vulnerability-selectivity array is calculated based on a random deviate standing age distribution, and a random deviate harvest distribution. The mechanism of selecting which individuals are taken as harvested is a multinomial process based on the actual (simulation) sex age distribution and the annual random vulnerability-selectivity array. For clarity, a random deviate of the standing age distribution is obtained only for the initial assignment of the starting population to sex age categories. However, a random harvest sex/age selectivity-vulnerability array is obtained every iteration (year) if the stochastic harvest options are selected.

Parameter Covariance

This approach implicitly assumes there is no covariance between population parameters. However, it is possible and perhaps likely that population parameters are correlated. Environmental fluctuations that would improve survival would probably also improve recruitment. The difficulty in incorporating parameter covariance, as well as the difficulty in measuring it in the field were the reasons that the default RISKMAN structure assumes annual random deviates of parameter values are independent (r=0.0). However, RISKMAN does allow the user to specify the other extreme (r=1.0) as well. This option uses the same uniform random seed for all normal random deviates in a given year. This allows the user to bound the effects of co-variance, although the current version of RISKMAN does not incorporate covariance directly.

## Monte Carlo Risk Analysis of Harvest Policy

A Monte Carlo simulation is many stochastic simulations providing a distribution of outcomes for each time of census for any chosen simulation period. Managers can use this information to manage the risk from harvest. For example, a policy could be set that the harvest rate must not cause the population to decline

more than 20% in more than 30% of the cases.   A second (or alternative) condition could be that the harvest rate selected could not result in a decline of 50% or more, more than 5% of the time (Fig. 3). The user is required to define the level of reduction that will be termed "extinction". In this context extinction means only that the run has resulted in a decline that is sufficient to discontinue the run. The extinction criterion should always be 5% of the initial population or larger to avoid error conditions resulting from a harvest that exceed the total number remaining. By the time the population has been reduced to 5% of the original number, the outcome of the simulation is clear in any case.

Similarly researchers can use the requirements of management policy to determine the precision required for parameter estimates. This is a two edged sword, because one very possible outcome of a risk analysis is that there is no risk from current activities under even worst case scenarios. Alternatively simulations can identify precision requirements that exceed the resources available for such estimates, requiring a more conservative management policy. The value of a quantitative approach to the precautionary principle is that it requires an explicit statement of how much risk is acceptable, and how much certainty the current information can provide.

Figure 3: Allowable Harvest Rate Analysis

This example of a harvest policy specifies that a decline of 50 percent or more may occur only 5 percent of the time. The uncertainty of outcomes would expand with time, so the harvest could be maximized by more frequent population inventory as well as more precise studies.
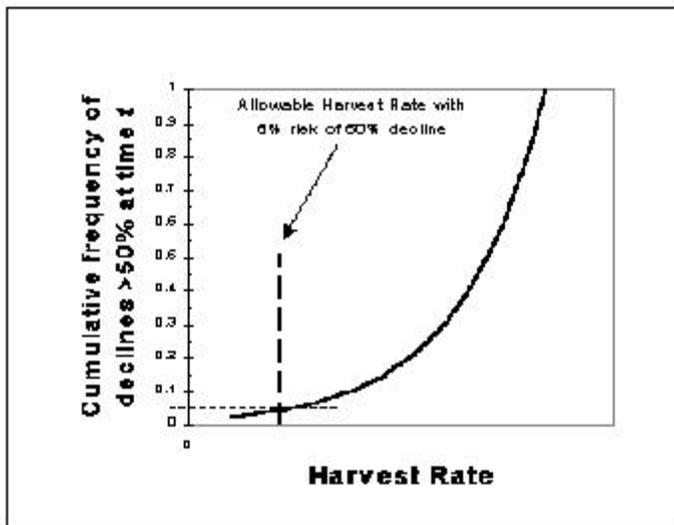
Density Effects

All populations are ultimately regulated by density dependent feedback mechanisms that progressively reduce survival, recruitment, or both. A population at carrying capacity has, by definition, a population growth rate of 1.0 and a sustainable yield of 0, because the population produces only enough recruits to sustain itself. However, a quantitative understanding of the mechanism of density effects is seldom available. Typically density effects are modeled by looking at the relationship of numbers to population growth rate. However, density does not affect population growth rate directly, density affects survival and/or recruitment. RISKMAN and all age/sex structured models make it apparent that the possible mechanisms for density effects are very large in number. Density dependent feedback may occur between only certain

strata (e.g. large male bears killing cubs of the year), or density dependent feed back may be more general (e.g. total numbers reducing survival rates of all individuals equally). Or perhaps there are dozens of density feedback relationships, each involving different sex and age strata, each with their own unique relationship (e.g. linear and non-linear, threshold of response, magnitude of reduction with per capita increase in strata density), and these may not be constant each year because of inter-annual ecological differences.

Modelling Density Effects

RISKMAN allows the user to model all but inter-annual density effects, but does not allow the user to summarily affect population growth rate with a density function involving all or some strata of the population. The point of an age/sex structured model is that the age and sex structure is a determining factor in the population dynamics. It is inconsistent to apply a general density function to population growth rate in an age/sex structured model. The density function in RISKMAN will allow appropriate modelling, but hopefully it will also serve to make the point that the density issues are potentially complex (perhaps insurmountably complex) for most age and sex structured populations. Long term, detailed (i.e. stratified) demographic studies of populations over a range of densities would have to be conducted to develop a mechanistic understanding of how populations are regulated.

A number of linear and non-linear equations have been proposed to model density effects (e.g. Eberhardt and Siniff 1977, Fowler 1981 a,b). RISKMAN employs a transposed, threshold-corrected, Mechalis-Menton function (Taylor 1994) (Fig. 4). This is not based on any idea that density effects derive somehow from enzyme kinetics, but was chosen because the equation is fitted with only two parameters, one that describes shape, and one that describes the density required to zero the affected rate. Provided both estimates of rate and density are available, the equation can be fitted using non-linear regression methods to provide estimates of both the mean and the variance of the two fitted constants. The current version of RISKMAN employs only the mean value of the constants in all simulations, including stochastic simulations. This limitation was accepted because it was anticipated this feature would be mainly used in an exploratory fashion. A full stochastic implementation of density effects is planned for a later version.

Figure 4: Mechalis-Menton Function for Density Effects
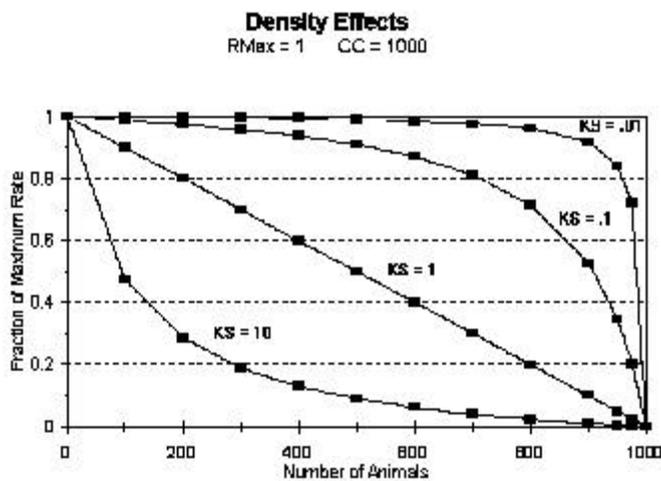
Model Outputs

The mean and variance of the population number, number of males, number of females, total harvest, number of males harvested, number of females harvested, mean age of the harvest, mean age of the population, population growth rate, and reproductive value of a selected age class of females is recorded. The means are output as graphs, and the mean, variance, and standard error are recorded in a results table that can be viewed on screen, printed, or saved as a file. The starting, final, and stable age/sex/family status distribution is recorded.

In stochastic mode, the number of runs that went "extinct" as defined by the user is also recorded. The number of runs (n) are known, and so the variance of the cumulative proportion of runs that went extinct over a given time (c_t) as well as the number of runs that went extinct in a given year are calculated as the binomial variance. This variance approaches zero as the number of runs approach infinity, and the number of runs are set by the user. This allows the user to reduce the variance of the cumulative proportion of runs that went extinct or the proportion of runs that went extinct in a given year to a negligible value. The number of runs required will vary depending on the range of years over which extinctions occur. When the range is large, the number of runs required to interpret the cumulative proportion of runs that went extinct or the proportion in a given year that went extinct as the probability of extinction is correspondingly large. An analytical solution for the number of runs required for negligible variance is not possible because the distribution of outcomes depends on the parameter values, variances, and model structure. Fleiss (1981) provides a discussion and a formula for calculating the standard error of a proportion from the occurrence per observation data.

Concluding Discussion

RISKMAN was developed primarily as a decision support tool for harvested populations. In deterministic mode, RISKMAN identifies the required demographic information for a quantitative (i.e.objective) estimate of the maximum sustainable yield or current population growth rate of a given population. When estimates of the uncertainty of the demographic information are also known, a quantitative assessment of the risk of a given management policy can be determined. When data based estimates are unavailable for a given population literature values for similar populations and minimum-maximum range estimates can be employed to explore the uncertainty of management strategies.

RISKMAN simulations do not allow for ecological interactions not captured by the variance estimates. Systematic declines in rates due to contaminant accumulation, global warming or other uni-directional perturbations cannot be simulated by the current version. Similarly, ecological interactions that depend on the population dynamics of other species such as competitors, prey, and predators cannot be modeled. The results from long term simulations must be evaluated with these limitations in mind. However, for situations where conditions may be expected to remain approximately constant through the time course of the simulation, RISKMAN provides a powerful tool for looking into the future to see the likely result of management policies.

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