

Bet-hedging applications for conservation

MARK S BOYCE*, EILEEN M KIRSCH[†] and CHRISTOPHER SERVHEEN[‡]

Department of Biological Sciences, University of Alberta, Edmonton, Alberta T6G 2E9, Canada

[†]*US Geological Survey, Division of Biological Resources, Upper Midwest Environmental Sciences Center,
2630 Fanta Reed Road, La Crosse, WI 54603, USA*

[‡]*US Fish and Wildlife Service, University of Montana, Missoula, MT 59812, USA*

**Corresponding author (Fax, 780-492-9234; Email, boyce@ualberta.ca)*

One of the early tenets of conservation biology is that population viability is enhanced by maintaining multiple populations of a species. The strength of this tenet is justified by principles of bet-hedging. Management strategies that reduce variance in population size will also reduce risk of extinction. Asynchrony in population fluctuations in independent populations reduces variance in the aggregate of populations whereas environmental correlation among areas increases the risk that all populations will go extinct. We review the theoretical rationale of bet-hedging and suggest applications for conservation management of least terns in Nebraska and grizzly bears in the northern Rocky Mountains of the United States. The risk of extinction for least terns will be reduced if we can sustain the small central Platte River population in addition to the larger population on the lower Platte. Similarly, by restoring grizzly bears to the Bitterroot wilderness of Idaho and Montana can reduce the probability of extinction for grizzly bears in the Rocky Mountains of the United States by as much as 69–93%.

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1. Introduction

Bet-hedging has its conceptual roots in economics (Samuelson 1969; Diamond and Rothschild 1978) and has applications in the evolution of life histories (Slatkin 1974; Boyce 1988; Philippi and Seger 1989). Bet-hedging also has important applications in conservation involving strategies to minimize risk of extinction of populations. We suggest relevant theory and provide applications to two case studies: conservation of least terns (*Sterna antillarum*) along the Platte River in Nebraska and grizzly bears (*Ursus arctos horribilis*) in the Rocky Mountains of the United States.

Bet-hedging involves betting so as to offset a bet already made (Diamond and Rothschild 1978). In commerce, hedging may refer to sales of securities against previous purchases of other securities to avert possible loss or, conversely, to buy against previous sales. Hedg-

ing is common in the futures market. For example, a farmer can contract a grain in advance of crop harvest. The contract price ensures against loss if the market should fall. Yet, if markets improve, the farmer is obligated to sell his crop at the contracted price. In an uncertain market, a hedging investor can reduce the risk of devastating losses during bad times, but of course, gains during a favourable period would not be as great as if he had taken the risk. By hedging, one may reduce or eliminate risk, in this case risk associated with market fluctuations (Boyce 1988).

There are several forms of bet-hedging (Boyce 1988) but all involve some sort of investment that may be advantageous because it reduces future risks. At least two types of bet-hedging have applications in conservation: (i) conservative strategies that avoid extremes, and (ii) diversified strategies that offer insurance against risks (Philippi and Seger 1989).

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Conservative strategies follow the adage that “a bird in the hand is worth two in the bush.” The idea is to minimize fluctuations in population size, largely because losses are recovered slowly. Population management to minimize overall population fluctuations are bet-hedging strategies.

Diversified strategies for conservation, on the other hand, are aligned with the adage that “one should not put all of one’s eggs in one basket.” Their consequences can be essentially be the same as conservative bet-hedging because diversifying reduces variance in growth rate. Applications in conservation might involve securing multiple populations so that fluctuations among areas cancel each other resulting in lower variance among years. Such diversification of portfolios of conservation areas is a justification for Soulé’s (1987) recommendation that population viability be secured by maintaining multiple populations.

Natural environments always vary temporally and spatially, so designing conservation schemes to minimize risks is always advantageous. Our discussion focuses primarily on the risk of extinction in a situation with multiple populations, such as the non-equilibrium population paradigm of Harrison (1994, p. 114). Although considerable recent interest has focused on models of metapopulations, we question how frequently conservation is focused on species with dynamics governed by a balance between local extinction and recolonization (see Harrison 1994; Hanski 1999, p. 182). Modern conservation problems are often about trying to minimize risk of extinction. We will first consider the consequences of variability to the appropriate measure of population growth, and then address hedging extinction risks.

2. Minimizing variance in population growth rates

A standard measure of population growth is simply the ratio of sequential population sizes, $I(t) = N(t+1)/N(t)$. When a population varies over time, the appropriate measure of growth rate is the geometric mean I rather than the arithmetic mean or expected value of I (Lewontin and Cohen 1969). The geometric mean is the n th root of the product of a series of n annual I values:

$$I^* = \left(\prod_{i=1}^n I_i \right)^{1/n}. \quad (1)$$

In general, the geometric mean declines as the variance increases placing emphasis on conservative management strategies that seek to reduce variance.

Alternatively, one can use the logarithmic form,

$$r = \ln I = \ln[N(t+1)] - \ln[N(t)], \quad (2)$$

in which case the arithmetic mean of r , \bar{r} , gives an analogous value because $I^* = \exp(\bar{r})$. The geometric mean is especially relevant in the context of population persistence as illustrated by the following argument.

First, we rearrange eq. 2 to

$$\ln[N(t)] = r(t-1) + \ln[N(t-1)]. \quad (3)$$

We can expand the right-hand side to $r(t-1) + [r(t-2) + \ln N(t-2)]$. Following this pattern recursively we find

$$\ln N(t) = \sum r(i) + \ln N(0). \quad (4)$$

Next, following the convention of defining the arithmetic mean r to be \bar{r} ,

$$\bar{r} = \frac{\sum r(i)}{t}. \quad (5)$$

If \bar{r} is not vanishingly close to 0 for large t , then note that by substituting $t\bar{r}$ for $\sum r(i)$ into eq. 4 we get

$$\ln[N(t)] = t \cdot \bar{r} + \ln[N(0)], \quad (6)$$

so that inevitably, $|\ln[N(t)] - \ln[N(0)]| \rightarrow \infty$ as $t \rightarrow \infty$.

The fact that \bar{r} does not converge to 0 for $t \rightarrow \infty$ means that the population has an unchecked trend. Thus for persistence, it is necessary that \bar{r} averages at least 0 in the limit, i.e.,

$$\lim_{t \rightarrow \infty} \bar{r} = 0. \quad (7)$$

This leads to the conclusion that for persistence, gains and losses in the context of r must cancel each other in the long run (Royama 1992). One can make a parallel mathematical argument for bounded populations (see Botkin and Sobel 1975).

These calculations identify I^* (or \bar{r}) as the appropriate measure for characterizing population growth in random environments. Analogous models for structured populations have been developed with similar results (Nations and Boyce 1997). Again, the important message for conservation applications is that, generally, the greater the variance in vital rates, the lower the long-term population growth trajectory (Boyce 1977; Tuljapurkar 1990). A related caveat for conservation applications is that estimates of $E I$ are invariably overestimates of the true long-term growth rate for a population.

3. Hedging extinction risks

Diversification by managing multiple populations can affect variance in growth rates directly simply because fluctuations in one population are likely to cancel independent fluctuations in other populations. Thereby, the variance in growth rate for the aggregate population is reduced. Diversification strategies also can reduce the

joint probability of extinction. If populations in two areas are completely independent, the joint probability that both will go extinct during a given time interval, say 100 years, is the product of their independent probabilities. More generally for $i = 1, 2, \dots, q$ populations,

$$P_{\text{ext(all)}}(100) = \prod_{i=1}^q P_{\text{ext}}(100)_i, \quad (8)$$

where $P_{\text{ext}}(100)_i$ is the probability of extinction over a 100-yr interval for the i th population, and $P_{\text{ext(all)}}$ is the joint probability that all of q populations go to extinction over the 100-yr period.

For populations that are nearby to each other, or that share the same management administration, independence is unlikely. Generally, environmental correlation increases extinction probability. If the correlation is 1.0, then populations will fluctuate together and the probability of extinction for the entire collection of populations will be equivalent to the extinction probability for the population with the lowest extinction risk. Assuming that increasing correlation is linearly related to extinction risk, a model for estimating extinction probability with environmental correlation $P_{\text{ext-corr}}$ is:

$$P_{\text{ext-corr}} = P_{\text{ext(all)}} + (P_{\text{ext-min}} - P_{\text{ext(all)}})R^2, \quad (9)$$

where $P_{\text{ext(all)}}$ is the joint extinction probability of all the populations from 1 to q if they were independent, $P_{\text{ext-min}}$ is the extinction probability of the most persistent population, and R^2 is the coefficient of determination between/among populations. Eq. 9 yields a function where $P_{\text{ext-corr}}$ decreases as number of populations increases but quickly reaches an asymptote that is determined by the degree of correlation (figure 1). From these observations we see that bet-hedging schemes are most effective when environmental correlation among populations is low.

4. Case study: Least terns on the Platte River

Least terns are the smallest of the North American terns and are piscivorous. The interior least tern, which nests on bare sandy areas such as sandbars, spoil piles at sand and gravel pits, reservoir shorelines, and saltflats along inland river systems in the United States, was listed as endangered in 1985 because of perceived low numbers and threats to its breeding habitat (Federal Register 1985). Least terns are migratory; interior least terns return to nesting areas late April to late May, and depart mid-late August. Least terns are long-lived [longevity reports of 20–24 years (Thompson *et al* 1997)], do not breed until their 2nd or usually their 3rd year, and typically lay clutches of 2–3 eggs. Incubation lasts 19–25 days, and chicks fledge at about 20 days of age. Chicks are semi-precocial but are unable to forage for themselves until

after they have fledged. Least terns reneest after egg or chick loss, but there are no reliable reports of least terns raising more than one clutch to fledging (Thompson *et al* 1997).

A recent examination of interior least tern status (Kirsch and Sidle 1999) revealed local areas where population sizes were typically small, population trends were negative or not discernable from zero, and fledging success was marginal, at best. Managers often ask whether conservation efforts are warranted in areas where terns typically have low productivity or where there are few birds. An example of such an area is the central Platte River in Nebraska, where riverine sandbar habitat has degraded to the point that few terns now nest on sandbars (Ziewitz *et al* 1992) and those that do typically have zero productivity due to flooding mortality of eggs and chicks (Lingle 1993a). Terns use several sand pits in the area, many of which are managed intensively to benefit terns, bolstering productivity and numbers of terns (Kirsch and Lingle 1992; Sidle and Kirsch 1993).

A stochastic density-dependent model derived using diffusion theory (Foley 1994, 1997) was used to estimate the time to extinction for both the central and lower Platte terns:

$$T_e = \frac{2n_0 \left[k - \frac{n_0}{2} \right]}{V_r}, \quad (10)$$

where r is the per capita rate of population change; n_0 is the ln of initial population size; k is the ln of carrying

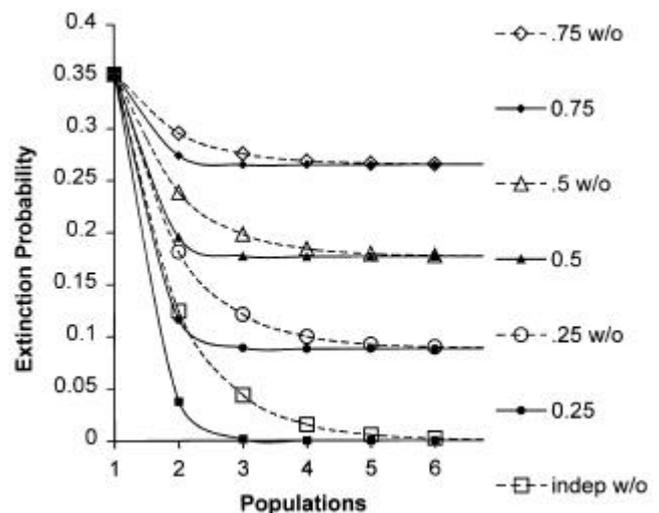


Figure 1. Risk of extinction as a function of the number of populations based on eq. 9. Calculations are presented for populations with and without (w/o) dispersal and with coefficients of determination (R^2) at 0 (independent), 0.25, 0.5, and 0.75. The bottom curve is the risk of extinction with dispersal and with independence amongst populations, i.e., $R^2 = 0$.

capacity; and V_r , the variance in r . We estimated these parameters using data from Platte River least terns provided by the Nebraska Game and Parks Commission, for the period 1986–1996 (table 1).

The instantaneous rate of change r and V_r were estimated by calculating $\ln I$ s between years. Carrying capacities for each river reach were estimated as the intercept of a regression of annual r as a function of the numbers of terns. A regression of r on years for both the central and lower Platte was not different from zero so we used the Foley (1994, 1997) equation for the $r = 0$ condition to estimate time to extinction T_e . Because the distribution of T_e is skewed, the persistence probability to some arbitrary time horizon is a better representation (Ludwig 1996). Then we estimated persistence probability to a 100 years:

$$P(100) = e^{(-100/T_e)} \quad (11)$$

For the central Platte $P(100) = 0.805$, for the lower Platte $P(100) = 0.917$, and the probability of extinction, $P_{\text{ext}}(100) = 1 - P(100)$. The joint extinction probability for a population composed of more than one independent population is the product of the independent extinction probabilities for each population. That is, if the central and lower Platte terns can be considered separate populations, the extinction probability for Platte River terns is $P_{\text{ext}}(100) = [P_{\text{ext}}(100) \text{ central Platte}][P_{\text{ext}}(100) \text{ lower Platte}] = 0.016$, and the joint persistence probability is $P(100) = (1 - 0.016) = 0.984$.

Table 1. Least tern numbers and estimates for model parameters of the central and lower reaches of the Platte River.

Year	Parameter estimate	Number of terns	
		Central	Lower
1986		114	324
1987		171	420
1988		123	497
1989		157	409
1990		149	361
1991		197	487
1992		191	427
1993		178	451
1994		169	426
1995		119	190 [†]
1996		134	290
	I^*	1.050	1.035
	k	5.0625	6.073
	r	0.016	0.034
	V_r	0.0556	0.0316

[†]This estimate was excluded from analyses because Nebraska Game and Parks Commission was unable to survey least terns nesting on sandbars in 1995 before the river flooded.

We would expect some degree of correlation between numbers of terns on the central and lower Platte simply because they are along different stretches of the same river, and sand pits suitable for nesting are distributed about evenly between the central and lower Platte (Sidle and Kirsch 1993). However, the coefficient of determination between yearly r 's for central and lower Platte terns was only 0.066. Nevertheless, applying eq. 9 to the Platte River tern data we estimate $P(100)_{\text{corr}} = 0.979$.

Long and short-range dispersal among breeding areas has been documented for least terns (Boyd and Thompson 1982; Boyd 1993; Lingle 1993b; Renken and Smith 1995). Dispersal, to a point, lowers extinction probabilities. Kuno (1981) found that random migration between 2 populations over a wide range of environmental fluctuations had the effect of lowering the variance in rate of population change V_r by $1/(\text{number of populations})$. Because we assume that migration has started occurring and is already contributing to the calculated joint extinction probability, we applied Kuno's basic conclusion to the Foley (1994, 1997) analytical model by multiplying V_r by the number of sites (2), which yields a joint probability of persistence for the Platte River terns of 0.944. Further, if there was no migration between the central and lower Platte, each population would have lower persistence probabilities, and applying Kuno's (1981) model results to the central and lower Platte, yields the probability of persisting 100 years of 0.648, and 0.842, respectively. Finally, we adjust the above estimate of persistence probability with correlation, which includes dispersal, to estimate the effect of no dispersal, $P(100)_{\text{corr w/out dispersal}} = 0.937$.

Although the probability of persistence of the central Platte terns is far less than that on the lower Platte, the central Platte still contributes to increasing the probability of persistence of the entire population of Platte River least terns. Given the relatively high V_r estimated for central Platte terns, would increasing carrying capacity or number of populations be a better strategy for increasing persistence of central Platte terns? Preliminarily, we examined the simultaneous effects of carrying capacity and numbers of subpopulations on $P(100)$ using the estimate of V_r from the central Platte. With only one population, increases in persistence probability level off, once K of 25 is reached. With increasing numbers of populations (without dispersal or correlation), persistence time increases more quickly than increasing K . However, the effect seems to reach an asymptote (near 1) at four subpopulations (figure 2). This indicates that with the current estimate of a carrying capacity on the central Platte River of 158, the only way to increase persistence would be to lower V_r , or to ensure that other populations with the same or lower V_r are present.

5. Case study: Grizzly bears in the Rocky Mountains

Only four populations of grizzly bears persist in the conterminous United States: about 420 bears in the Yellowstone ecosystem (Boyce *et al* 2001a), 400 in the Northern Continental Divide Ecosystem (NCDE), 40 in the Selkirk Mountains, and 35 in the Cabinet/Yaak Mountains. Although a few grizzly bears are known also to exist in the Cascades of Washington, these animals appear to have dispersed from south Canada and we do not have evidence as yet that this is a reproducing population. A proposal to restore a grizzly bear population to the Selway–Bitterroot wilderness of Idaho and Montana could potentially add another population of 308–321 grizzly bears (Boyce and Waller 2000). Here we use stochastic population models to estimate the reduced extinction risk afforded by the addition of the proposed fifth population in the Bitterroots.

Underlying our calculations is the same stochastic model from diffusion theory that we used for least terns, which we now use to estimate the probability of extinction during the next 100 years, $P_{\text{ext}}(100)$, for each of four populations of grizzly bears, and a hypothetical population in the Bitterroots (Foley 1994, 1997):

$$P_{\text{ext}}(100) = 1 - \exp\left\{-\frac{100/2n_0[k - (n_0/2)]}{V_r}\right\}. \quad (12)$$

Again, we require three parameters to estimate extinction risk: n_0 , ln of initial population size; k , ln carrying capacity; and V_r , variance in the per capita population growth rate, r . With this model we make the conservative assumption that the long-term average growth rate will be approximately 0. Using a larger value of r would usually

reduce extinction risk by strengthening density dependence (Foley 1997).

The per capita growth rate, $r(t)$, was estimated from a series of population estimates, $N(t)$, for $t = 1, 2, \dots$ by taking the sequential differences in \log_e population sizes between years, i.e. $r(t) = \ln[N(t+1)] - \ln[N(t)]$. We then took the variance of these $r(t)$ values to estimate V_r . Our best series of population estimates is from the Yellowstone population (Boyce *et al* 2001a), so these were used as the basis for estimating V_r for each population in two ways to provide reasonable estimates of high and low V_r . First, we used the variance in $r(t)$ from a series of 12 population estimates based on cumulative counts of the number of females with cubs of the year (Boyce *et al* 2001a). Second, we reconstructed a series of population estimates for 1961–1985 by adding 11.5 to the counts of the number of females with cubs, based on the difference between cumulative-count estimates and actual counts for 1986–1997 (Boyce *et al* 2001b). Then we used Lowess regression (tension = 0.7) to remove trend in the time series, and calculated V_r from the residuals of this regression. Both methods may overestimate the variance in per capita growth rates because the cumulative counts also reflect variation in reproductive output over time. The first method yields a relatively “high” estimate of V_r because it includes a population increase over the period 1983–1997 (Boyce *et al* 2001a). The second method is a relatively conservative estimate because we have removed all trend in population size; we call this our “low” estimate of V_r .

For the Yellowstone ecosystem, estimates of density-dependent survival suggest that the current population of 420 is nearing a carrying capacity of about 450 grizzly bears (Boyce *et al* 2001b). Carrying capacity for the Bitterroot population was estimated to be 308–321 using projected populations from an analysis of resource selection functions for the projected recovery zone (Boyce and Waller 2000). Carrying capacities for each of the other populations were approximated by three methods: (i) assuming that carrying capacity was equal to the official recovery goal in the Grizzly Bear Recovery Plan (US Fish and Wildlife Service 1993) for each population, (ii) assuming that the current population size reflects the long-term carrying capacity for each area except the Bitterroots, or (iii) assuming that the US populations are merely the southern extension of much larger contiguous Canadian bear populations that were all part of the carrying capacity and thereby contributed to the long-term viability of populations in the United States (table 2).

As for the least tern example, we assumed that dispersal was possible, but only between the four northern sites, NCDE, Selkirks, Cabinet/Yaak Mountains, and the Bitterroots. We presumed that Yellowstone would remain

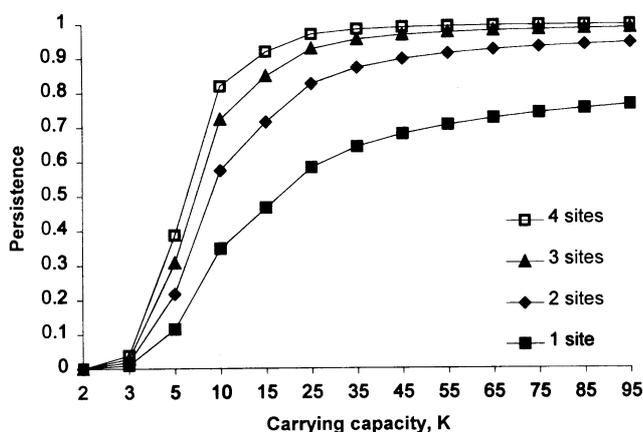


Figure 2. Effects of carrying capacity (K) and the number of populations (sites) on the probability of persistence for interior least terns.

independent. Thus for the northern four populations we multiplied the variance by 1/4 to account for the fact that we have four populations amongst which dispersal might occur. For the second option where we assumed that populations would not increase to management objectives, we allowed for dispersal among 3 populations: Selkirks, Cabinet/Yaaks, and the Bitterroots. For the calculations presented in table 2 we ignored the possible consequence of correlation among areas because we have no basis to suspect such a correlation. If such a correlation is identified, application of eq. 9 is straight forward.

The results of our calculations predict that the addition of the Bitterroot population will reduce the probability of extinction by 88–99% depending on the variance in r . We were somewhat surprised that the relative change in extinction probability was about the same whether we assumed a baseline K equal to the projected recovery targets, or estimated number of bears in the entire ecosystem including bears from Canada. We recall from the central Platte River least tern example that K is relatively weaker than the number of populations in increasing $P(100)$.

Table 2. Extinction probability for Rocky Mountain grizzly bear populations in the United States as influenced by the addition of a population in the Bitterroot wilderness of Idaho and Montana. The model assumes dispersal among the Northern Continental Divide Ecosystem (NCDE), Selkirk Mountain, and Cabinet-Yaak Mountain populations. Carrying capacities for the first three areas are set first at the recovery goals, then at current population sizes, and finally at levels that include Canadian extensions of the three northern populations.

Variable	NCDE	Selkirks	Cabinet/ Yaak	Yellowstone	Bitterroot
(1) Assuming k = recovery targets for each population					
N	400	40	35	420	25
$n(0)$	5.992	3.689	3.555	6.04	3.219
K	500	106	106	450	308
k	6.215	4.663	4.663	6.109	5.73
V_r (high)	0.0243	0.0243	0.0243	0.097	0.0243
$P_{\text{ext}}(100)$ (high V_r)	0.061	0.110	0.112	0.229	0.087
V_r (low)	0.0025	0.0025	0.0025	0.01	0.0025
$P_{\text{ext}}(100)$ (low V_r)	0.0065	0.012	0.012	0.026	0.009
		<u>Low V_r</u>		<u>High V_r</u>	
$P_{\text{ext}}(\text{all})$		2.318×10^{-10}		0.000015	
$P_{\text{ext}}(\text{all})$ w/o Bitterroots		2.472×10^{-8}		0.000171	
Improvement in P_{ext} w/Bitterroots		99.1%		91.3%	
(2) Assuming $k = n(0)$ and no dispersal with NCDE					
$P_{\text{ext}}(100)$ (high V_r)	0.237	0.212	0.226	0.234	0.115
$P_{\text{ext}}(100)$ (low V_r)	0.028	0.024	0.026	0.027	0.013
		<u>Low V_r</u>		<u>High V_r</u>	
$P_{\text{ext}}(\text{all})$		5.841×10^{-9}		0.000303	
$P_{\text{ext}}(\text{all})$ w/o Bitterroots		4.677×10^{-7}		0.00264	
Improvement in P_{ext} w/Bitterroots		98.8%		88.5%	
(3) Assuming K includes Canadian populations					
K	2000	1000	1000	450	308
$P_{\text{ext}}(100)$ (high V_r)	0.0411	0.0496	0.0496	0.2289	0.0874
$P_{\text{ext}}(100)$ (low V_r)	0.0043	0.0052	0.0052	0.0264	0.0094
		<u>Low V_r</u>		<u>High V_r</u>	
$P_{\text{ext}}(\text{all})$		2.924×10^{-11}		2.018×10^{-6}	
$P_{\text{ext}}(\text{all})$ w/o Bitterroots		3.117×10^{-9}		0.000023	
Improvement in P_{ext} w/Bitterroots		99.1%		91.3%	

K , Carrying capacity where $dN/dt = 0$; k , ln carrying capacity; I , finite growth factor [= $N(t+1)/N(t)$]; I^* , geometric mean of I ; N , population size; n , ln population size; $P(100)$, probability of persistence over a 100-yr time interval; P_{ext} , probability of extinction; $P_{\text{ext}}(100)$, probability of extinction within 100 years; $P_{\text{ext(all)}}(100)$, joint probability that all populations go extinct within 100 years; r , per capita growth rate; t , time; T_e , time to extinction; V_r , variance in r .

6. Discussion

These examples illustrate how bet-hedging can be a powerful force in setting conservation priorities. Clearly, having multiple populations strongly decreases the probability of extinction, because in all cases except perfect correlation of populations, additional populations cause a geometric decline in extinction risk.

The results of this exercise also support the tenets of metapopulation theory, that many populations (with dispersal) help to maintain the viability of the overall population. A caveat to this prevailing result is that dispersal into “sinks” in a metapopulation can act to decrease the overall population size and thereby increase the risk of extinction (Doak 1995). Clearly, the assumptions and specific constructs of models have much to do with this apparent discrepancy. Model results depend heavily on the assumptions and parameterization of the proportion and spatial distribution of suitable and unsuitable habitat as well as the demographic characteristics of populations in these habitats (Akçakaya 1994; Boyce 1996). The Foley (1994, 1997) models and our modifications are population based, not habitat-based models. Situations in which metapopulation models can give the result of dispersal into sink areas lowering overall population size include (i) dispersers “searching” for suitable habitat in a “sea” of unsuitable habitat, (ii) high cost of dispersing, or (iii) sink habitat is so bad that source habitat is not good enough to counterbalance the losses to the sink. We did not consider dispersal into unoccupied patches, nor whether any population is a “sink”.

One might ask how our models differ from a metapopulation approach. Technically, the original formulation of a metapopulation involved a model of the interaction between local extinction and recolonization (Levins 1969; Hanski 1997, 1999). In contrast, we do not consider explicitly a role for recolonization or rescue effect (Brown and Kodric-Brown 1977) and the only effect that we attribute to dispersal is as a process that reduces the variance in population size. A variety of model structures can be envisaged for spatially structured populations, e.g. core-satellite, patchy populations, non-equilibrium populations, and metapopulations (Harrison 1994). We agree with Hanski and Simberloff (1997) that there is danger in widespread application of the metapopulation approach for species that may not be structured as assumed by the models. Our deliberate focus is to consider the minimization of extinction risk.

A variety of approaches have been used to model the effect of dispersal (see review in Hanski 1999). For our application, Kuno's (1981) method provides an analytical result that can be used to account for the effect of dispersal on the variance in population size. We realize that the assumption of random dispersal may be un-

realistic in most real world conservation applications. This is an area in need of further theoretical development. Also, we assume that dispersal has a negligible cost to the dispersers. For least terns, which migrate thousands of miles twice a year, this assumption roughly may hold. Dispersing bears, on the other hand, are likely to incur high risks whilst moving through developed landscapes. Management programs are underway to relax barriers to dispersal, and dispersal by a grizzly bear between the NCDE and Cabinet/Yaak population was recorded recently. An alternative to natural dispersal is the possible relocation of bears among populations (Servheen *et al* 1995).

As a final caveat, we agree with Ludwig (1999) that estimates of the risk of extinction are burdened with enormous uncertainty. For example, our calculations of the risk of extinction for grizzly bears appear disturbingly low, and may not be realistic. Yet we believe that population viability analysis is useful only in comparative context (Lindenmayer and Possingham 1996). By comparing the consequences of management alternatives to relative values of extinction risk, PVA can be a useful tool in resource planning.

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