Population Viability Analysis for the Puritan Tiger Beetle in the Chesapeake Bay Region: An Update

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Introduction

This report presents an updated population viability analysis (PVA) for Puritan tiger beetle (*Cicindela puritana*) populations in the Chesapeake Bay region. An initial report was prepared in January 2005 (Gowan and Knisley 2005) based on data available at that time. This update revises certain model parameters with new data, and also examines relevant management scenarios not included in the first report. Otherwise, the overall techniques and modeling approaches are the same in both reports.

The beetle is currently listed under the Endangered Species Act (ESA), and a recovery plan has been prepared (USFWS 1993). For the purposes of the recovery effort, the sub-populations are grouped into two distinct geographic areas, both in Maryland (Calvert County and the Sassafras River; Figure 1). The recovery plan calls for protection of at least six, large (>500 adults) sub-populations in each area. However, there is still uncertainty about how best to protect beetle habitat in order to promote recovery. In particular, because the beetle exists as a series of distinct sub-populations within each area, better information is needed regarding how many and which particular sub-populations merit strongest protection. The goal of this PVA analysis is to provide a more reliable basis for deciding on numbers and locations of sites to protect in each area.

Methods

Study Area

The beetles currently exist as 17 sub-populations distributed along the eastern and western shores of Maryland, with an individual population consisting of a few to >1,500 beetles (Figure 1; Table 1). The PVA was designed to examine population viability for each geographic area.

General Modeling Approach

The individual tiger beetle sub-populations within each geographic area were assumed to operate together as a metapopulation. To conduct the PVA, a metapopulation model was developed that accounted for population growth within sub-populations, dispersal between sub-populations, and the degree to which inter-annual variations in population growth rates were correlated. The model was used to predict the probability that the beetle population would decline to zero, or other specified thresholds, within the next 100 cohorts under a series of management strategies that involved protection of different sets of sub-populations. The goal was to determine which particular set of sub-populations, if protected, would give an acceptably-low risk of extinction.

It must be cautioned that the main purpose of the analysis was to compare management strategies, not to estimate extinction probability per se. Accurate estimates of extinction probability require reliable estimates for each of the parameters in the metapopulation model, including population growth rates, interannual variation in growth rates, carrying capacities, dispersal rates, and correlation among sub-populations. Although estimates based on our current knowledge of the species were generated for each of these parameters, they are not dependable enough to provide trustworthy estimates of true extinction probability. However, the estimates are reliable enough to compare the effectiveness of different management strategies. The goal was to determine which strategy reduced extinction risk the most, even if the exact extinction risk could not be quantified with certainty. In order to evaluate the influence of alternative parameter estimates on the relative rankings of the different management strategies, a sensitivity

analysis was conducted. This analysis (described later) examined the effects on predicted extinction risk of changing several of the model parameters.

Estimating Model Parameters

Before the model could be used to examine different management strategies, parameter values had to be developed. Three items were of particular importance. First, a population growth model had to be developed in order to predict annual increases or decreases in abundance within each sub-population. Next, the correlation among sub-populations in their population growth rate had to be estimated. Finally, the dispersal rate among sub-populations had to be quantified. Each of these issues was examined using empirical data collected during previous monitoring and other studies funded by the U.S. Fish and Wildlife Service.

Table 1. Information on 18 Puritan tiger beetle sub-populations located in the Chesapeake Bay region. Protected status refers to the current regulatory status of each location (P = protected as a state, federal or private preserve, NP = not protected). UTM = Universal Transverse Mercator location, WGS84, Zone 18. Starting population size was the population size used in Year 1 of the metapopulation model. WMA=Wildlife Management Area. NRMA= Natural Resource Management Area.

Site	UTM Northing	UTM Easting	Area	Length (m)	Protected status	Starting Population	Carrying Capacity
Randle	4281769	366773	Calvert	889	NP	43	62
Bayside Forest	4270906	367892	Calvert	1535	NP	11	28
Scientists Cliffs	4263883	368427	Calvert	3853	NP	319	436
Parker Marsh South*	4265725	367864	Calvert	812	P	1430	2732
W. Shore/Calvert Beach	4259574	370512	Calvert	627	NP	950	1772
Calvert Cliffs State Park	4252110	376774	Calvert	1335	P	1259	3218
Calvert Cliffs Nuclear Plant	4254195	375090	Calvert	1471	NP	372	552
Little Cove Point	4246787	378123	Calvert	2894	NP	1238	2232
Cliffs of Calvert	4244680	377291	Calvert	1512	NP	544	1658
Grove Point	4361196	410927	Sassafras	1995	NP	1016	1972
Grove Point WMA	4359580	414467	Sassafras	150	P	0	20
Ordinary Point	4359580	414767	Sassafras	885	P	101	200
North Still Pond	4356157	402311	Sassafras	998	NP	182	286
West Betterton	4358587	406269	Sassafras	2758	NP	91	184
East Betterton	4358316	409848	Sassafras	540	NP	32	68
East Lloyd Creek	4357462	412008	Sassafras	202	NP	523	1426
Sassafras NRMA	4357976	413245	Sassafras	1656	P	576	984
East Turner	4357565	415860	Sassafras	237	NP	23	70

* Also known as Warrior's Rest

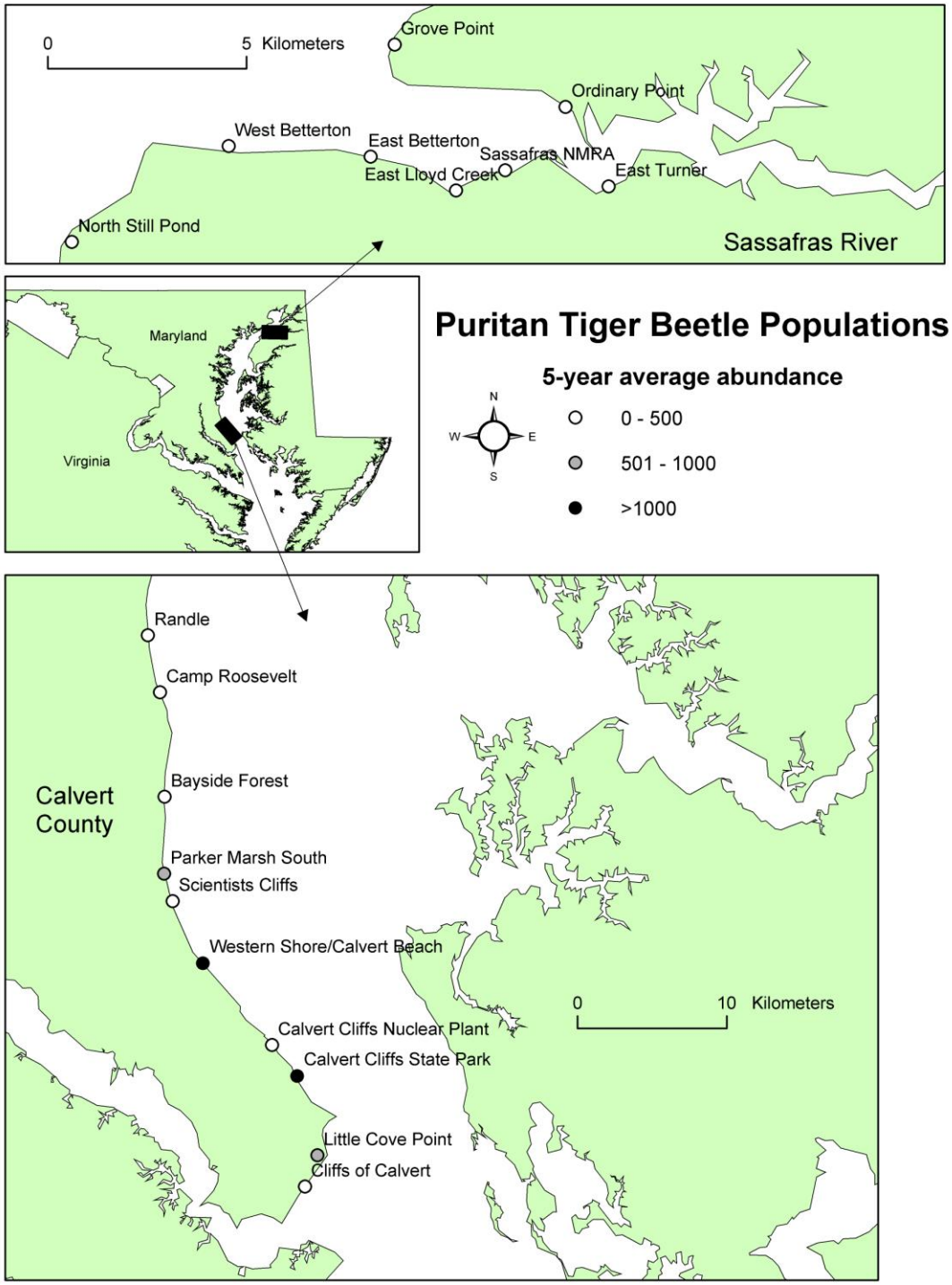


Figure 1. Puritan tiger beetle populations located near the Sassafras River (upper panel) and in Calvert County, Maryland (lower panel).

Modeling population growth within sub-populations

Population viability analyses are usually based on age- or stage-based population models requiring input data such as transition and survival probabilities between lifestages, and stage-specific fecundity rates. Because this information was not available for the Puritan tiger beetle, an alternative approach was developed based on empirical observations of sub-population dynamics in sub-populations monitored annually between 1988 and 2009 (Figure 2). The basic concept was to model future dynamics for all sub-populations based on statistics obtained from six sub-populations monitored intensively between 1988-2009. Although some monitoring occurred at other sites, we feel data from these six sites are the most reliable for quantifying population growth because these sites were consistently monitored since 1988. Where necessary, expert opinion of the second author was used to supplement available information.

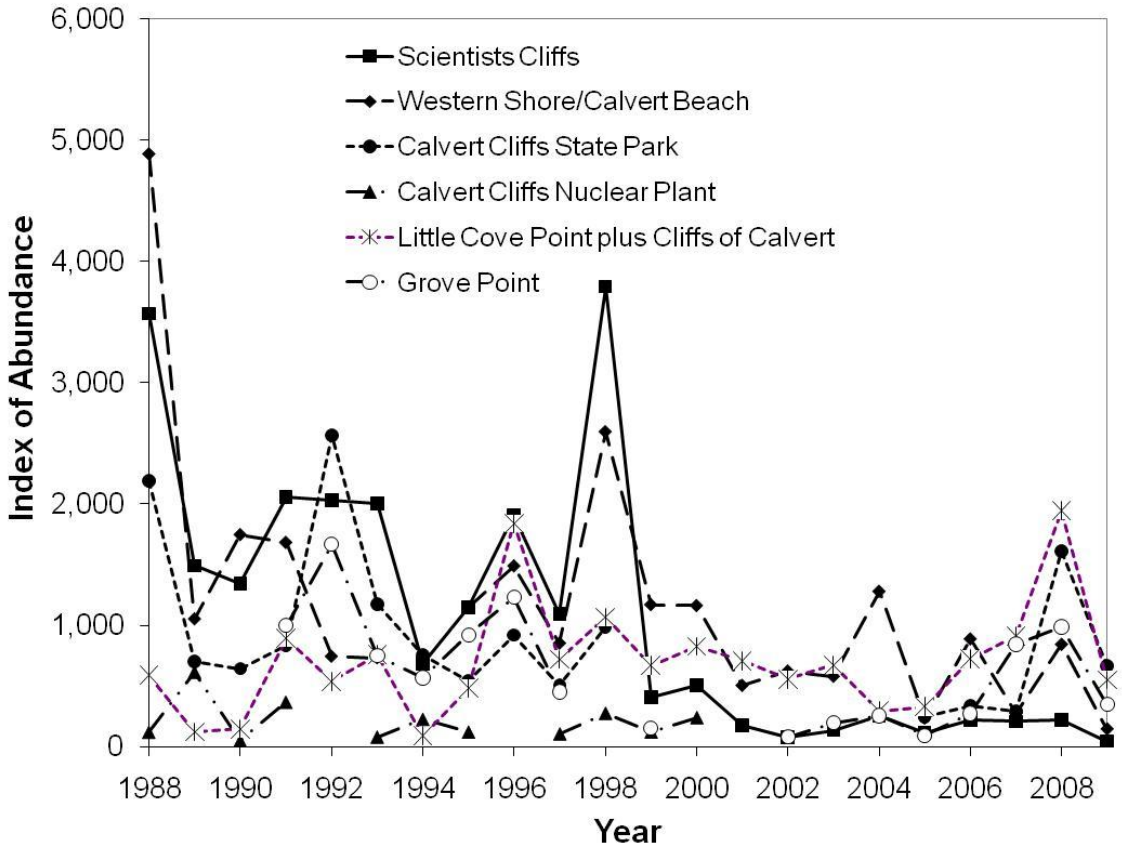


Figure 2. Index counts for adult tiger beetles in six sub populations, 1988-2009. Index counts were made by one observer moving along the entire length of beach habitat and counting all observed beetles during peak abundance and optimum conditions.

In selecting a population model, we first analyzed the observed dynamics to determine if each population exhibited density dependence. Because the beetles have a two-year lifecycle with distinct cohorts, density dependence could occur on either a one or two year interval. A two-year interval makes intuitive sense because it means that the density dependence is based on interactions between the same life stage (e.g., number of adults in one year affects number of

adults two-years later). If density dependent effects influenced population dynamics on a two-year interval, the slope of a regression of population abundance in year t (N_t, log-transformed) on the rate of growth between year t and year $t+2$ ($N_{t+2}/N_t = \lambda$, log-transformed) should be negative. The same analysis can be done on a one-year interval, except that N_{t+1} replaces N_{t+2}. Results for both analyses were similar, so only those from the two-year interval will be presented for brevity. Growth rates over two-year intervals will be referred to as "cohort growth rates".

There was strong evidence of density dependence (Figure 3; by linear regression; P <0.0001 for the analysis of all sites combined; when analyzed individually, five of the six sites showed evidence of density dependence (P<0.1), the exception being the Calvert Cliffs Nuclear Plant population (P=0.46)). Based on this, a logistic growth model was selected.

Maximum cohort growth rate (λ_{max}) for the logistic model was estimated based on the observed growth rates for the six sub-populations monitored between 1988-2009 (Table 2). Average cohort growth rate (N_{t+2}/N_t) varied from 0.81 at Calvert Cliffs Nuclear Plant to 1.96 at Grove Point. A value of 1.32 was selected for all sub-populations included in the metapopulation

Table 2. Cohort population growth rate (λ) of tiger beetle populations averaged over available cohorts for six sites.

Site	*n* Cohorts	Mean λ	Standard Deviation
Scientists Cliffs	20	1.036	0.8627
Western Shore Estates plus Calvert Beach	18	0.923	0.5483
Calvert Cliffs State Park	12	1.592	1.4173
Calvert Cliffs Nuclear Plant	7	0.806	0.4434
Little Cove Point plus Cliffs of Calvert	18	1.607	1.7578
Grove Point	12	1.958	2.5967
Average		1.320	1.2711

model because the growth rate in the metapopulation model is meant to represent the maximum rate that the population can achieve under ideal circumstances. The value used in the 2005 report was 1.30, and so the new parameter value is essentially identical to that used in the original report.

One of the most important aspects in PVA is to account for the effects of stochastic events on population growth rate. This is especially true for invertebrate populations wherein temporal variation in abundance is probably due more to stochastic events in the environment rather than density dependent effects. Environmental stochasticity was incorporated into the model by making annual population growth rate a random variable. That is, for each year in a simulation, the computer selected a random value for growth rate (λ_t where t indicates time) from a normal distribution with a user-specified mean (λ_{max}=1.32 as previously described) and standard deviation. If a higher value is selected for the standard deviation, then greater environmental stochasticity is incorporated in the metapopulation model because there is a greater potential for any given year to be extremely poor (λ_t is small) or extremely good (λ_t is large) in terms of population growth rate.

Appropriate values for the standard deviation of λ were based on the observed variation in sub-population growth rates between 1988-2009. The observed average standard deviation in sub-population growth rate was 1.27 (Table 2). However, this value may over-estimate actual variation because it includes variation in capture probability in different years. That is, because beetle abundance was estimated using index counts, some of the recorded variation in abundance was due to variation in the ability of the observers to detect and count beetles each year, and to variation in the number of beetles active at the time of the observations. Moreover, there is evidence of declining abundance over time (Figure 2), which would increase the estimated standard deviation of growth rate. Based on the opinion of the authors, a standard deviation of 0.6 (about 50% of the recorded value) was used in the metapopulation model. This value is very close to the value of 0.55 used in the 2005 report.

The same mean and standard deviation of population growth rate was used for all sub-populations. However, each sub-population was given a unique carrying capacity (K) and starting population (Table 1). The K and starting values for each sub-population were based on index counts made periodically since 1988 in all sub-populations. The average of index counts for the most recent five years available times 2 was taken as the starting population size. The maximum index count for the most recent five years times 2 was taken as the carrying capacity. The index counts were multiplied by 2 because various studies with several tiger beetle species showed that index counts underestimated true abundance by a factor of about 0.5.

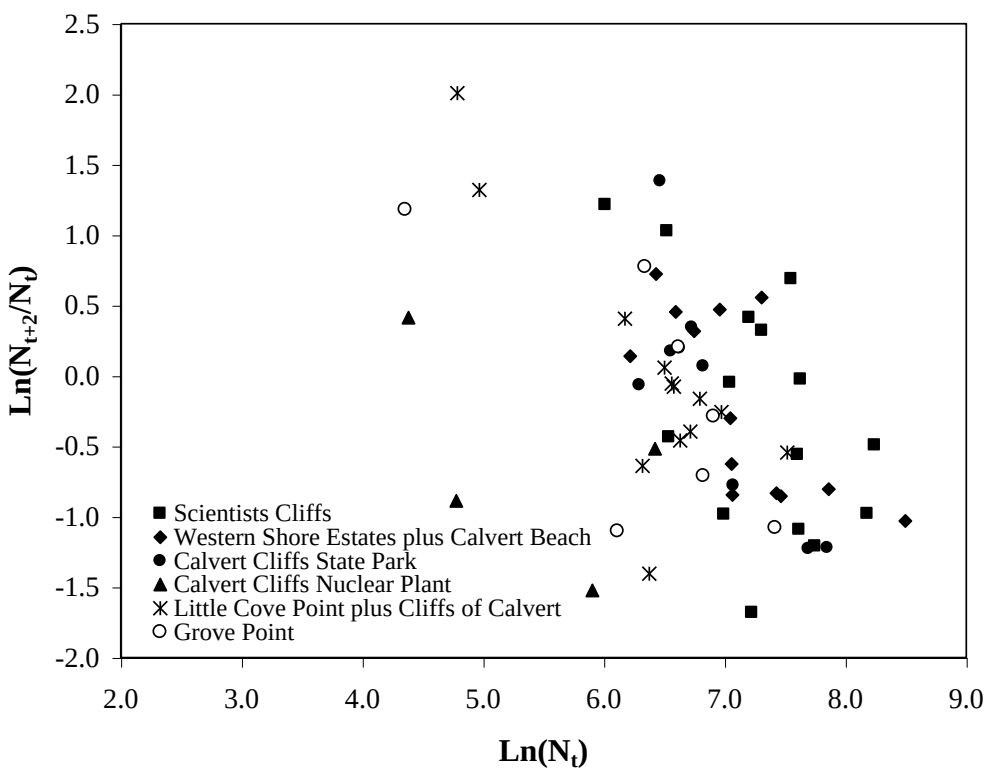


Figure 3. Regression of population growth rate ($\lambda = N_{t+2}/N_t$) on population size (N_t) for six populations of Puritan tiger beetles during the years 1988-2004.

Modeling correlation in population growth among sub-populations

Although each sub-population is geographically distinct, it is reasonable to assume that they will often experience similar environmental conditions, such as good and bad weather. As such, there should be some degree of correlation in annual population growth rates, meaning that if one population experiences poor growth in a cohort, nearby ones probably will as well. This effect was incorporated into the metapopulation model by specifying the degree to which population growth rate was correlated among sub-populations.

To determine the degree to which tiger beetle population growth rates were correlated, data from the six sub-populations (Figure 2) were examined with a view towards quantifying the relationship between distance separating two populations and correlation between them in population growth rate (under the assumption that sub-populations that are close to one another will be more correlated than those that are distant). To quantify the relationship between correlation and distance, the correlation in population growth rate was calculated for each of the six sub-population pairs, and the distance between them measured. Based on these data (Table 3), a line was fit to the equation,

$$\rho_{ij} = e^{-D_{ij}/b} \qquad \text{Equation 1}$$

where ρ_{ij} = the correlation coefficient between populations i and j,
D_{ij} = the distance (km) separating them, and,
b = a regression coefficient estimated from the data.

Table 3. Distance between six sub-populations and the correlation coefficient (p_{ij}) estimated by regressing λ_1 (cohort growth rate in sub-population 1) on λ_2 (cohort growth rate in sub-population 2) for the years 1988-2004. Negative correlations were assumed to be zero when analyzing the relationship between distance and correlation (see Figure 4).

Sub-population pair (sample size)	Distance (km)	p_{ij}, for cohort λ
Scientists Cliffs to Western Shore (*n*=12)	5.2	-0.14
Scientists Cliffs to Calvert Cliffs State Park (*n*=9)	14.8	0.39
Scientists Cliffs to Calvert Cliffs Nuclear Plant (*n*=4)	12.1	0.81
Scientists Cliffs to Little Cove Point (*n*=13)	20.4	0.22
Scientists Cliffs to Grove Point (*n*=7)	105.9	0.38
Western Shore to Calvert Cliffs State Park (*n*=6)	9.7	0.23
Western Shore to Calvert Cliffs Nuclear Plant (*n*=4)	7.1	0.51
Western Shore to Little Cove Point (*n*=12)	15.2	-0.18
Western Shore to Grove Point (*n*=5)	109.4	0.34
Calvert Cliffs State Park to Little Cove Point (*n*=7)	6.1	0.38
Calvert Cliffs State Park to Grove Point (*n*=5)	114.3	0.37
Calvert Cliffs Nuclear Plant to Little Cove Point (*n*=4)	8.5	-0.69
Little Cove Point to Grove Point (*n*=5)	119.8	-0.66

Based on the data in Table 3, the parameter b from Equation 1 was estimated to be 7.187, allowing us to predict the degree to which two sub-populations would be correlated based on the distance between them. Populations separated by >40 km were essentially uncorrelated, but

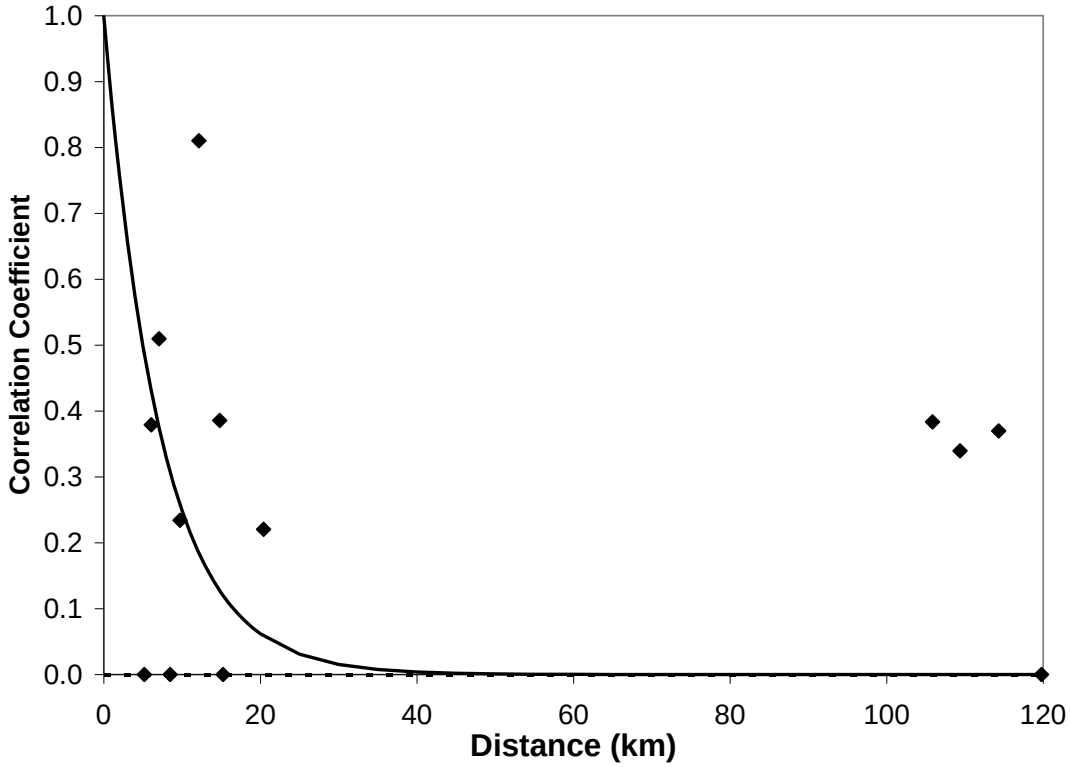


Figure 4. Relationship between distance separating two sub-populations and the correlation coefficient of growth rate estimated by regressing λ_1 (cohort growth rate in sub-population 1) on λ_2 (cohort growth rate in sub-population 2) for the years 1988-2004.

correlation increased to 1.0 (perfect correlation) as the distance between sub-populations decreased to 0 km (Figure 4). Equation 1 was incorporated into the metapopulation model and used to predict the correlation in growth rate among all possible sub-population pairs. The net result was that populations close together (<40 km apart) tended to fluctuate up and down together, increasing the risk of extinction due to a single poor year affecting those populations together. Populations separated by >40 km fluctuated independently of one another, reducing extinction risk. These parameter values are unchanged from the 2005 report.

Modeling beetle dispersal among sub-populations

Metapopulations can sometimes persist longer than a single large population because extinct sub-populations (vacant habitat) can be recolonized by individuals from nearby extant ones. Thus, modeling dispersal is an important component in a metapopulation analysis.

An attempt was made to estimate beetle dispersal using a mark/recapture study conducted in 2003. A total of 651 beetles were marked at released at the Western Shores site between June 30 and July 7. Recaptures were attempted at Western Shores, Little Cove Point, Scientists Cliffs, Bayside Forest, Cliffs of Calvert, and Randle on July 15, 16, 20, 21, 25, 28, 29 and August 1, 2, 4, 5 and 11. However, a total of only 3 dispersers (one to Little Cove Point captured on July 15 and 2 to Scientists Cliffs captured on July 20th) were detected, a number too small to allow statistical analysis. Data provided by K. Omand from a population of *C. puritana* at sites on the

Connecticut River in Connecticut were also examined, but because beetles were not individually-marked in that study, it was not possible to separate probability of dispersal (the parameter of interest) from capture probability and mortality rate (nuisance parameters). Thus, we had no reliable data upon which to estimate dispersal in *C. puritana*.

In lieu of data for *C. puritana*, we used mark/recapture data collected for the northeastern beach tiger beetle (*Cicindela dorsalis dorsalis*) We believe using *C. dorsalis* dispersal data is reasonable because the species occur in the same geographic area, use similar linear shoreline habitats, have a similar 2-year life-cycle and share other aspects of basic biology, and show similar variation in abundance over time. The sample sites were all in the Smith Point area of Northumberland County, Maryland and separated by 1.3 to 13.9 km. Five capture occasions took place between July 6 and August 23, 1994, involving a total of 10,131 beetles (Table 4). All captured beetles were marked to indicate location and date and released.

Table 4. Number of beetles marked during a 1994 mark/recapture study of *C. dorsalis dorsalis* to evaluate dispersal among five sites.

Site	Number Marked	Percent Recaptured at All Sites	Number Detected at Another Site
Smith Point North	3,470	42%	42
Smith Point South	1,981	47%	12
Taskmakers Creek	2,637	59%	7
Sandy Point	365	42%	14
Dameron Marsh	1,678	22%	4

It is reasonable to assume that beetles more easily disperse to nearby rather than distant sites. Thus, data from the dispersal study were examined with a view towards quantifying the relationship between distance separating two sub-populations and the probability that a beetle would disperse from one to the other. To quantify the relationship between dispersal and distance, dispersal rate between each sub-population pair (a total of 10 pairs) was estimated and the distance between them measured. Based on these data, a line was fit to the equation,

$$m_{ij} = e^{-D_{ij}/b} \qquad \text{Equation 2}$$

where m_{ij} = probability that a beetle will disperse between populations i and j, D_{ij} = the distance (km) separating them, and b = a regression coefficient that was estimated from the mark/recapture data.

Estimating dispersal based on mark/recapture data is difficult because the number of dispersers detected is a function of not only dispersal rate, but also capture probability and mortality. Thus, in order to obtain reliable estimates of dispersal rate, an open-population survival rate model was used. Such models are called multi-strata models (Brownie et al. 1993) because they simultaneously estimate capture, survival, and movement probabilities based on the model where:

p_i^s = probability of capture at time i, for an animal in location s at time i.

ϕ_i^{rs} = probability of being alive and in location s at time $i+1$ for an animal alive and in location r at time i.

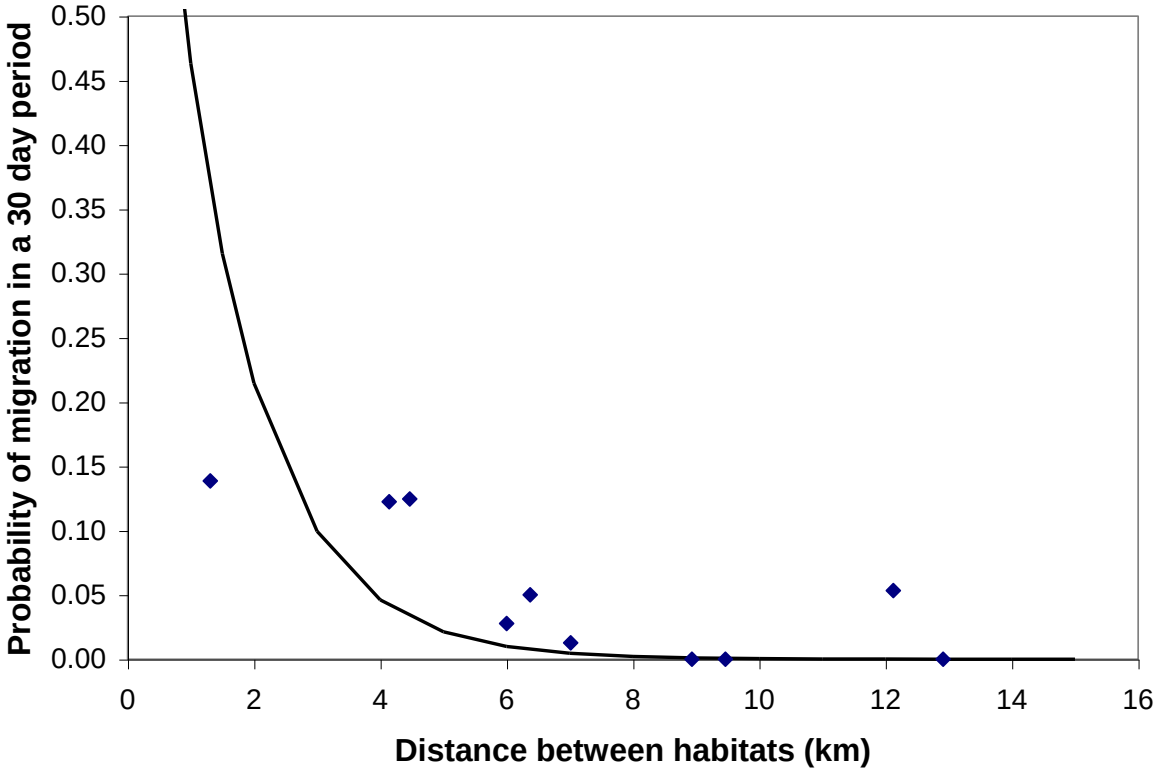


Figure 5. Relationship between distance separating two sub-populations and the probability that an adult beetle will migrate between them during a 30 day period.

The multi-strata survival and movement model included in Program MARK (written by Gary White, Colorado State University) was used to estimate movement probability between tiger beetle locations. A capture history was developed for each beetle included in the 1994 study based on the location/date marks each received. This capture history was input to Program MARK, and a series of models was developed by constraining various parameters to be equal to one another. For example, some models were constrained such that all capture probabilities were equal among locations, but varied by capture occasion. By developing a large number of models and testing them against one another, the most parsimonious model was identified. This model had the properties that it adequately explained the capture history data with the fewest parameters. Akaike's Information Criterion (AIC) was used to identify the most parsimonious model (see Burnham and Andersen (1998) for a complete discussion of model selection theory). Once the most parsimonious model was identified, it was used to estimate daily movement probability between each sub-population pair involved in the 1994 study.

Because the metapopulation model uses a time step of one cohort, not one day, the binomial distribution was used (binomial parameter p set equal to daily movement rate) to estimate the probability that an adult beetle would migrate between two locations once within a 30 day period. It was judged that this was the approximate time period during which an individual is an active disperser, and that if a beetle dispersed within this period, it could successfully colonize and breed in the new location.

Estimates of 30-day movement probability were used to determine a best fit line for Equation 2 (i.e., to estimate the value of *b*). The best fit line was obtained with $b = 1.30$ (Figure 5). It should be noted that it is not strictly correct to regress movement probability on distance because the movement probability estimates from Program MARK are not independent. However, for the purpose of getting a rough estimate of the relationship between distance and dispersal, this approach was judged adequate. Equation 2 was incorporated into the metapopulation model and used to predict the probability that a beetle would migrate from one location to another, based on the distance between the locations. The net result was that populations close together (<6 km apart) tended to exchange individuals, decreasing the risk of extinction by allowing extant sub-populations to "rescue" nearby extinct ones. These parameter values are unchanged from the 2005 report.

Predicting Probability of Extinction Under Various Management Strategies

Program RAMAS Metapop (Applied Biomathematics, Inc., Setauket, New York) was used to model metapopulation dynamics and predict extinction probability over two planning horizons: 50 cohorts (100 years; a typical horizon used in PVA) and 5 cohorts (10 years; a horizon

Table 5. Management strategies developed for Puritan tiger beetles in the Chesapeake Bay region. Each strategy was evaluated based on predicted extinction risk as determined by a metapopulation model. PMS=Parker Marsh South, CCSP=Calvert Cliffs State Park, CCNP=Calvert Cliffs Nuclear Plant, SC=Scientists Cliffs, WS=Western Shore/Calvert Beach, CC=Cliffs of Calvert, R=Randle, LCP=Little Cove Point, BF=Bayside Forest, SNRMA=Sassafras NRMA, GP=Grove Point, GPWMA=Grove Point Wildlife Management Area, OP=Ordinary Point, ET=East Turner, EL=East Lloyd Creek, EB=East Betterton, WB=West Betterton, NS= North Still Pond.

Strategy	Calvert County	Sassafras River
1	All sites preserved	All sites preserved
2	All sites but one preserved. Remove each site individually to judge its influence	All sites but one preserved. Remove each site individually to judge its influence.
3	Preserve protected sites only (CCSP, PMS)	Preserve protected sites only (SSRMA, OP, GPWMA)
4	Preserve protected sites only, and increase carrying capacity of each*	Preserve protected sites only and increase carrying capacity of each*
5	Preserve all sites, but reduce K at certain "at risk" sites by 50%**	Preserve all sites, but reduce K at certain "at risk" sites by 50%**
6	Preserve all sites, and reduce K at all sites with houses by 50%†	Preserve all sites, and reduce K at all sites with houses by 50%†
7	Preserve protected sites (CCSP, PMS), but add WS with K reduced by 50%	No Strategy 7
8	Preserve protected sites (CCSP, PMS), plus CCNP, BF, and R at full K, plus WS at 50% K	No Strategy 8

* K=5130 for CCSP and 3628 for PMS. K=984 for SNRMA, 3334 for GP, and 20 for GPWMA.
** Sites with K set at 50% of the value shown in Table 1: LCP, CC, SC, and GP.
† Sites with K set at 50% of the value shown in Table 1: SC, WS, CCNP, LCP, CC, GP, EL, WB, NS.

pertinent for short-term planning). At the beginning of a given horizon, the starting size for each sub-population was specified (Table 1). Population abundance one cohort later was predicted based on the model-generated λ for each sub-population (generated from a normal distribution with mean λ [=1.32] and the specified standard deviation [=0.60] and accounting for correlation among sub-populations based on the distance between them); the amount of dispersal among sub-populations (also based on distance); and the specified carrying capacity for each sub-population (Table 1). This produced a predicted abundance in each sub-population at the beginning of the next cohort. The process was repeated for the desired number of cohorts (50 or 5), producing a time series of abundance for that planning horizon. When a simulation was complete, original parameter values were reset to the specified initial conditions, and the model rerun. Predictions from each individual run, even if started from the same initial conditions, produced different abundance time series because of the environmental stochasticity incorporated in to the model. In order to predict extinction probability under a specified set of initial conditions, 1000 replicate model runs were made for each planning horizon. The percentage of runs that produced an extinction sometime during each planning horizon (population size reaching 0 as some point during the planning horizon) was the predicted probability of extinction for Puritan tiger beetles over that horizon.

In order to evaluate the potential effectiveness of different management strategies, a range of strategies were developed based on the judgement of the second author in consultation with the Maryland Department of Natural Resources and other resource management agencies (Table 5). Each strategy represented a different set of sub-populations being protected from shoreline alteration. The metapopulation model was adjusted for each strategy to include only the sub-populations that would be protected under that strategy (i.e., all other sub-populations were assumed to be lost to shoreline alteration or other habitat impacts). The goal was to determine which strategy produced the lowest extinction probability. To provide a baseline for comparison, a default strategy was used that included all sub-populations known to be extant in 2009. Modeling was completed for the Calvert County and Sassafras River metapopulations individually.

Results and Discussion

General Results

In order to compare management strategies, interval extinction risks were summarized graphically (Figures 6 and 7). Interval extinction risk is defined as the probability that beetle abundance will drop below a specified threshold population size sometime during the next specified number of cohorts. If the threshold is set at 0, then interval extinction risk is equal to the risk of extinction. However, if thresholds above 0 are considered, then the ability of a given management strategy to maintain beetle abundance above certain critical thresholds can be examined. The easiest way to use the figures is to look for lines shifted as far to the right as possible. Those lines represent strategies that reduce extinction risk the most (notice that the "All Sites" strategy is generally the right-most line). By looking at the spacing of the lines, one can judge the relative effectiveness of a given strategy. Although not shown, lines shift to the right as the planning horizon is shortened (50 versus 5 cohorts) because there is a lower probability that the metapopulation will go extinct over the next 5 cohorts as compared to the next 50.

If all currently-extant populations are protected, extinction risk for the Calvert metapopulation is 0.1% over the next 100 years (Figure 6, Strategy 1), and essentially zero for the next 10. For Sassafras, extinction risk is somewhat higher but still low: 2.6% for the next 100 years (Figure 6, Strategy 1), and 0.4% for the next 10.

Influence of Individual Sub-populations on Extinction Risk

The influence of individual sub-populations on overall metapopulation survival was assessed by removing each sub-population sequentially and calculating interval extinction risk for the remaining sub-populations (Figure 6). In the Calvert metapopulation, the most important individual sub-populations are Calvert Cliffs State Park, Parker Marsh South, Western Shore/Calvert Beach, Little Cove Point, and Cliffs of Calvert. Removal of any one of these sub-populations results in a substantial increase in extinction risk (Figure 6). For example, the risk of the population falling below 500 organisms over the next 100 years is about 40% when all sites are protected, but the risk increases to about 60% when any one of the most important sub-populations are removed. Conversely, removal of Randle or Bayside Forest has a minimal effect on risk. Scientists Cliffs and Calvert Cliffs Nuclear Plant have an intermediate effect (risk of falling below 500 organisms over the next 100 years if either of these sub-populations is lost equals about 50%).

Extinction risks at the Sassafras metapopulation are higher than those at Calvert. The most important single subpopulation in the Sassafras metapopulation is Grove Point (Figure 6). If that single subpopulation is removed, the risk of the population falling below 500 is about 99%, compared to a risk of about 92% if all sub-populations are protected. Other important sites include Sassafras NRMA, East Lloyd, West Betterton, North Still Pond. Subpopulations with relatively little influence on extinction risk are East Turner and Ordinary Point. Interestingly, removal of the East Betterton sub-population is predicted to reduce extinction risk, probably because it has a low carrying capacity and so serves as a “sink” for nearby, larger sites.

Influence of Management Strategy on Extinction Risk

As just reported, extinction risks for both the Calvert and Sassafras metapopulations are relatively low if all extant populations are protected. However, the probability of extinction within each metapopulation over the next 100 years is very high if no additional sites are protected beyond those already included under state, federal, or private plans to preserve beach habitat (Figure 7; Strategy 3). The two protected sites in Calvert County are Calvert Cliffs State Park and Parker Marsh South (also known as Warrior’s Rest). If only these sites remain protected (and the other populations lost to habitat alteration), the metapopulation model predicts a 73% chance that the metapopulation will go extinct within the next 100 years, and a 2.9% chance in the next 10. In the Sassafras River metapopulation, protected sites include the Sassafras NRMA, Grove Point WMA, and Ordinary Point. If only these sites are protected, the model predicts a 49% chance of extinction within 100 years and 8.4% chance within the next 10.

All the remaining management strategies fall between the two ends of the spectrum just presented: at one end is a management strategy that preserves all existing beetle habitat, and at

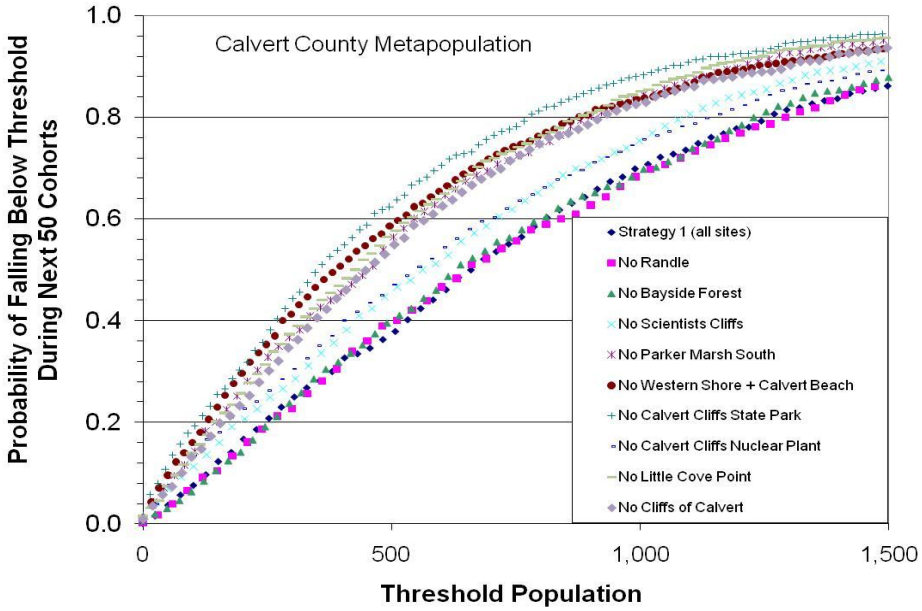
the other is one that preserves beetles only in those locations that are already receiving some form of protection.

Comparison of extinction risk under the various management strategies provides important information regarding the efficacy of different generalized approaches to protecting the beetle. For example, strategies aimed at increasing carrying capacity at just a few "important" sites perform poorly (compare Strategies 3 and 4 in Figure 7) relative to strategies involving protection of more sites even if some of those sites suffer a reduced carrying capacity due to habitat loss (compare Strategies 1, 5, and 6 in Figure 7). All else being equal, it is much more important to preserve at least some habitat at many sites, rather than providing much habitat at just a few.

Sensitivity Analysis

Because important parameters in the model were only roughly estimated, a sensitivity analysis was conducted to evaluate if using different parameter values changed conclusions regarding which management strategies were best. The metapopulation was adjusted to include a higher level of annual stochasticity in population growth rate (standard deviation of annual growth rate = 0.8 rather than 0.6), no dispersal, or no correlation in growth rate among populations. All management strategies in each metapopulation were re-run under each condition. The relative effectiveness of each management strategy was compared for both models in order to determine if alternative parameter values in the model changed conclusions about which strategy is optimum.

That different parameter values influence predicted extinction risks is not surprising and reinforces the fact that predicted risks presented in this report should not be taken as literally true. Instead, the main intent is to identify management strategies that work better than others to reduce extinction risk, regardless of the exact numerical value of the predicted risk. Therefore, what is most important is to identify those strategies which consistently rank as the best regardless of which particular parameter values are used. The ideal strategy would be one that worked well under a wide-range of model parameters, meaning that even if we were wrong about certain parameter values, we could still correctly identify which management strategies worked best. To examine this issue, we compared predicted extinction probabilities for each strategy under each alternative model. For each model, we ranked strategies (rank 1= lowest risk of extinction) and compared average rankings across models (Table 6). As expected, the strategy that includes protection of all sub-populations (Strategy 1) ranks as best (average rank =1.5) under all models. In the Calvert County metapopulation, Strategies 5 and 6 (average ranks =2 and 2.3, respectively) also worked consistently well under all models. In the Sassafras River metapopulation, Strategy 5 (average rank = 1.5) is the only strategy that worked consistently well under all models. As previously reported, the best strategies all involve protection of the largest number of sub-populations possible, even if some of those sub-populations have reduced carrying capacities due to habitat loss.



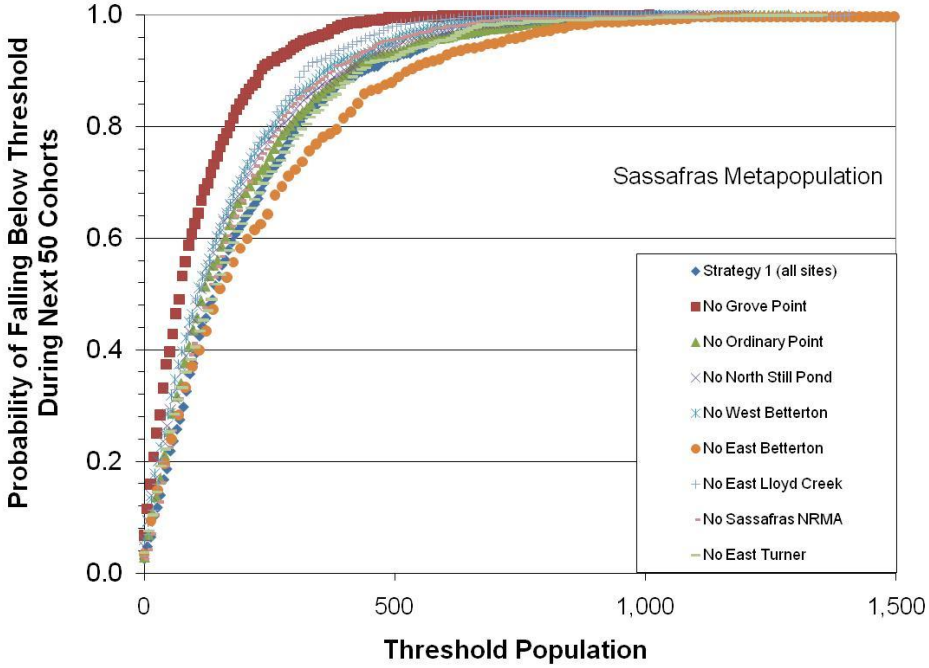


Figure 6. Interval extinction risks for Puritan tiger beetles in the Calvert County (upper panel) and Sassafras River (lower panel) metapopulation in the Chesapeake Bay region. Risks are shown for a period of 50 cohorts (100 years) with each sub-population removed from the metapopulation.

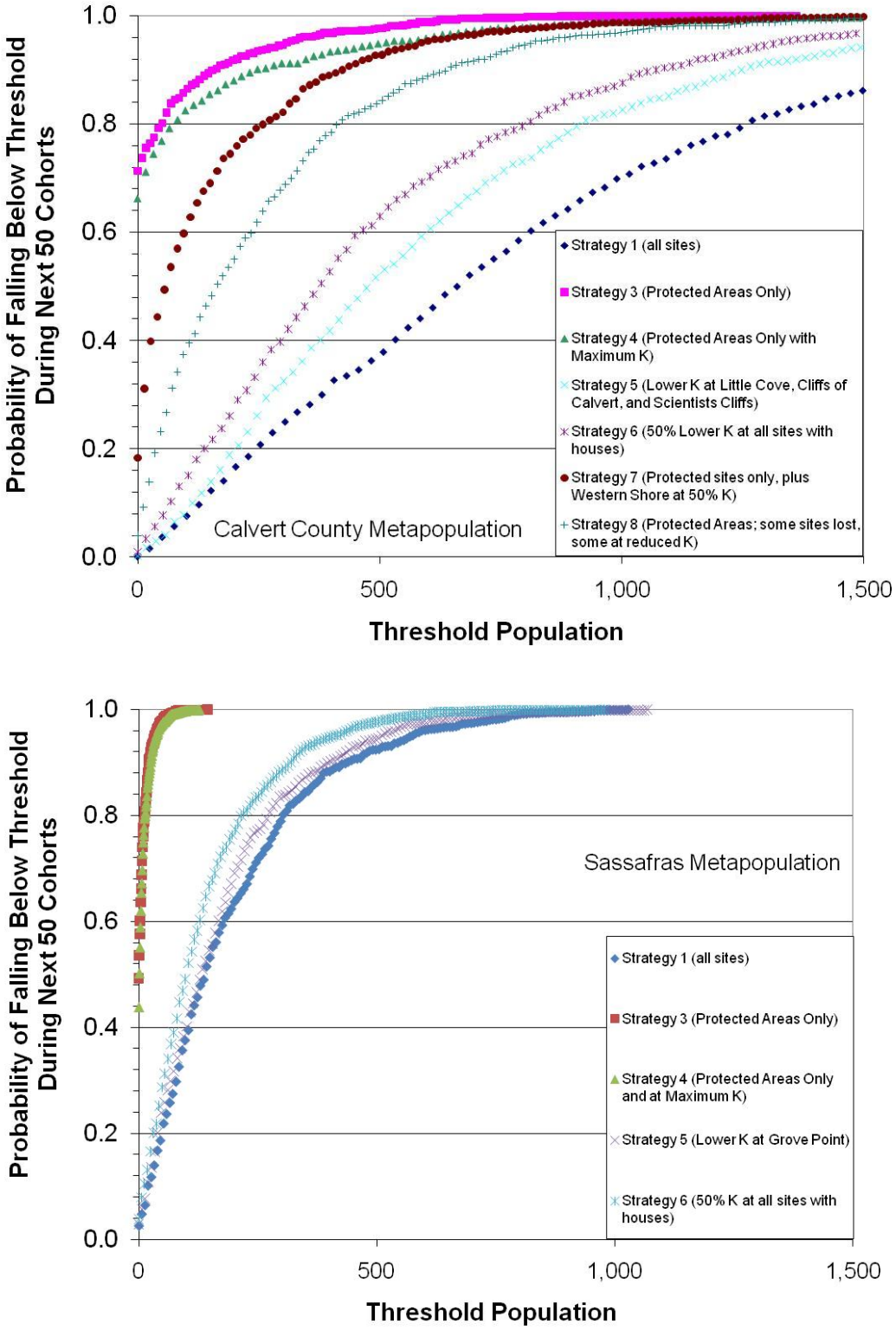


Figure 7. Interval extinction risks for Puritan tiger beetles in the Calvert County (upper panel) and Sassafras River (lower panel) metapopulation in the Chesapeake Bay region under various management strategies (see Table 5 for details). Risks are shown for a period of 50 cohorts (100 years).

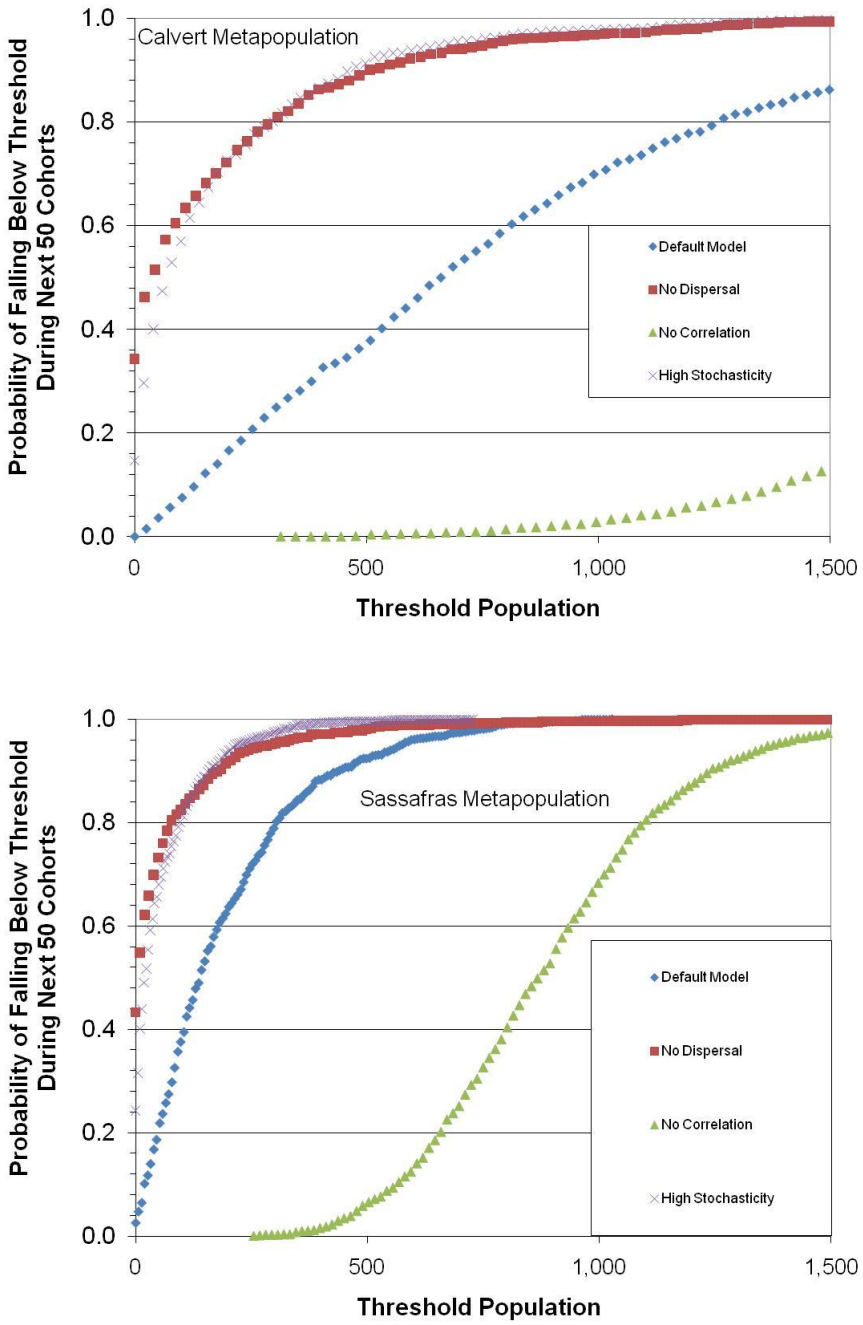


Figure 8. Interval extinction risks over 100 cohorts for Puritan tiger beetles in the Calvert Count (upper panel) and Sassafras River (lover panel) metapopulations in the Chesapeake Bay region. Risks were predicted using four models, including one with best-estimates for each parameter ("default model"), one with no dispersal among sub-populations, one with no correlation in growth rates among sub-populations, and one with high stochasticity (variation) in cohort growth rates.

Table 6. Extinction-probability predictions for various management strategies (see Table 5) using four metapopulation models. The Default Model includes best estimates for parameters related to dispersal, correlation in growth rates, and stochasticity in growth rates. The No Dispersal model assumes that there is no dispersal among sub-populations. The No Correlation model assumes that there is no correlation in cohort growth rates among sub-populations. The High Stochasticity model uses 0.8 as the standard deviation of cohort growth rates (default model=0.6). Simulations were made for two metapopulations existing in Chesapeake Bay. The overall best strategy for a metapopulation is the one with the lowest Average Rank because it performs well regardless of which model parameters are used.

	Default Model		No Dispersal		No correlation		High Stochasticity		
Strategy	Extinction Probability	Strategy Rank	Extinction Probability	Strategy Rank	Extinction Probability	Strategy Rank	Extinction Probability	Strategy Rank	Average Rank
Calvert County Metapopulation									
1	0.001	1	0.343	1	0.001	3	0.15	1	1.5
3	0.713	7	0.709	7	0.697	7	0.97	6	6.8
4	0.663	6	0.673	6	0.665	6	0.98	7	6.3
5	0.002	2	0.366	3	0.000	1	0.18	2	2.0
6	0.010	3	0.363	2	0.000	1	0.20	3	2.3
7	0.183	5	0.635	5	0.091	5	0.74	5	5.0
8	0.040	4	0.503	4	0.002	4	0.51	4	4.0
Sassafras River Metapopulation									
1	0.0260	1	0.433	1	0.000	1	0.24	2	1.3
3	0.4930	5	0.752	2.5	0.025	5	0.89	5	4.4
4	0.4380	4	0.726	2.5	0.022	4	0.89	4	3.6
5	0.0290	2	0.476	2	0.000	1	0.23	1	1.5
6	0.0380	3	0.517	3	0.000	1	0.28	3	2.5

Summary and Recommendations

Strategies that include only protected sites provide almost no protection from extinction. It is vital that sites beyond those currently protected be included in future management strategies. The overall best strategies of those examined are Strategies 1 (protection of all sites at current carrying capacities) and 5 and 6 (protection of all sites, but with some at reduced carrying capacity). In all, every effort should be made to protect as many sub-populations as possible.

Sensitivity analysis indicates, as expected, that dispersal, correlation, and stochasticity all have a strong influence on predicted extinction rates. If management options existed to increase dispersal (perhaps via scheduled translocations of adults from large sub-populations to smaller, distant ones), or to decrease correlation (it is difficult to imagine how this could be done), or to decrease stochasticity (translocation may also be a way to achieve this), then extinction risks could be lowered. Exploring these options may be the next logical step in evaluating how best to protect the beetles.

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