Alabama Beach Mouse PHVA

Point Clear, Alabama
June 8-11, 2004

FINAL REPORT

Alabama Beach Mouse PHVA

Point Clear, Alabama
June 8-11, 2004

FINAL REPORT

Cover photo: United States Fish and Wildlife Service

A contribution of the IUCN/SSC Conservation Breeding Specialist Group

Traylor-Holzer, K., R. Lacy, D. Reed and O. Byers (eds.). 2005. *Alabama Beach Mouse Population and Habitat Viability Assessment: Final Report*. IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, MN.

Additional copies of *Alabama Beach Mouse Population and Habitat Viability Assessment* can be ordered through the IUCN/SSC Conservation Breeding Specialist Group, 12101 Johnny Cake Ridge Road, Apple Valley, MN 55124, www.cbsg.org.

Alabama Beach Mouse
Population and Habitat Viability Assessment

Point Clear, Alabama
June 8-11, 2004

CONTENTS

Alabama Beach Mouse PHVA

Point Clear, Alabama
June 8–11, 2004

FINAL REPORT

SECTION 1

Executive Summary

Executive Summary

Introduction

The Alabama beach mouse (*Peromyscus polionotus ammobates*) is one of several endangered subspecies of oldfield mice known as beach mice. Beach mice inhabit the coastal dune habitats of the southeastern U.S. and prefer sand slopes with patches of sea oats and other native coastal vegetation. They are primarily nocturnal, spending the day in burrows in the sand and emerging at night to feed on seeds and insects.

Endemic to the coastal dunes of Alabama, the Alabama beach mouse (ABM) is the most western beach mouse subspecies along the Gulf of Mexico coast. The distribution of this subspecies is restricted to the western tip of the Fort Morgan Peninsula eastward to Perdido Pass in Baldwin County. The historical range of this subspecies also included Ono Island; however no ABM are currently believed to exist there. ABM habitat consists of public lands (Fort Morgan and Perdue Units of the Bon Secour National Wildlife Refuge as well as Gulf State Park) and privately owned lands. Some level of connectivity is suspected across this range, although ABM are believed to avoid areas of human disturbance or habitation.

Coastal Baldwin County is an area of increasing recreational and residential development. Development on privately owned lands includes single family and duplex dwellings, condominiums, hotels and restaurants. Increased commercial and residential development has the potential to negatively impact beach mice populations through habitat loss and fragmentation, increased mortality, and increased vulnerability to the impacts of hurricanes.

As a step in assessing the effects of development and other factors on the viability of ABM populations, the U.S. Fish and Wildlife Service (FWS) initiated a Cumulative Impact Assessment (CIA) for this species and sought to develop a population viability analysis model. These evaluation tools will promote a better understanding of the population dynamics of the species and the expected impact of future development scenarios and management options.

CBSG’s Involvement

The Conservation Breeding Specialist Group (CBSG) was invited to conduct a Population and Habitat Viability Assessment (PHVA) workshop for the Alabama beach mouse to assist in the development of viability projections for the species. The PHVA workshop, sponsored by FWS, was held June 8-11, 2004 in Point Clear, Alabama. Thirty-one people from 13 agencies and organizations participated in the PHVA workshop (listed in Appendix I of this report).

At the PHVA, Alabama beach mouse population data were examined and discussed in detail. A computer population simulation model (*Vortex*) was used to evaluate current and future risk of population decline or extinction with no further actions or destruction of habitat and under alternative development and management scenarios. Participants developed detailed reports outlining these discussions and justification for those values chosen for the model. The main goal of this PHVA workshop was to develop an ABM population model and use this model to assess the current status of ABM habitat and populations and projections for continued existence.

The specific objectives of the workshop were to assist the FWS, ABM Recovery Team, and other stakeholders to:

1. Develop an agreed upon risk analysis and population simulation model for the ABM based on the best available data;
2. Evaluate probability of population extinction under various development scenarios; and
3. Identify research and management needs linked to preservation of the subspecies.

A briefing book including taxonomic information, distribution maps, field study synopsis, life history information and relevant, current published and unpublished materials was distributed to participants. This workshop report addresses the objectives listed above and reports all findings and updated information on ABM in connection with this workshop.

A draft baseline model was developed prior to the PHVA workshop using input data provided by the FWS and the ABM Recovery Team. This draft model was presented in the opening plenary session of the PHVA workshop and served as a springboard for discussion and a template for development of the consensus model by workshop participants.

The PHVA Process

CBSG was invited to serve as a neutral workshop facilitator and organizer. CBSG is a part of the Species Survival Commission of the IUCN - World Conservation Union, and for more than 15 years has been developing and applying a series of science-based tools and processes to assist species management decision-making. One tool CBSG employs is use of neutral facilitators to moderate small working groups, as the success of the workshop is based on the cooperative process of dialogue, group meetings, and detailed modeling of alternative management scenarios.

Effective conservation action is best built upon critical examination and use of available biological information, but also depends heavily upon the actions of humans living within the range of the threatened species. Motivation for organizing and participating in a PHVA comes from hope for the recovery, as well as a fear of loss, of a particular species.

At the beginning of the PHVA workshop, there was agreement among the participants that the general desired outcome is to maintain a viable population(s) of ABM. Each participant was asked to provide an introductory statement on his or her personal goal for the workshop and what they hoped to contribute (responses can be found in Appendix I). Nearly universal among the participants was their interest in improving their understanding of the current situation facing the ABM and using the PHVA process to assist in the critical and imminent decision-making facing the ABM Recovery Team and FWS. Information sharing is at the heart of the PHVA workshop process, which takes an in-depth look at the species' life history, history, status, and dynamics, and assesses the threats that may put the species at risk. One crucial by-product of a PHVA workshop is that an enormous amount of information can be gathered and considered that, to date, has not been published. This information can be from many sources; the contributions of all people with a stake in the future of the species are considered.

To obtain the entire picture concerning a species, all of the information that can be gathered is discussed by the workshop participants with the aim of first reaching agreement on the state of current information. These data then are incorporated into computer simulation models to determine: 1) risk of population extinction under current conditions; 2) those factors that make persistence of the species problematic; and 3) which factors, if changed or manipulated, may have the greatest effect on improving the prospects for survival. In essence, these computer-modeling activities provide a neutral way to examine the current situation and what needs to be changed to meet defined goals.

Complementary to the modeling process is a communication process, or deliberation, that takes place during a PHVA. Workshop participants work together to identify the data parameters to be entered into the *Vortex* model. During the PHVA process, participants work in small groups to discuss key issues. Each working group produces a report, which is included in the PHVA final report. A successful PHVA workshop depends on determining an outcome where all participants, coming to the workshop with different interests and needs, "win" in developing a model that best represents the reality for the species and is reached by consensus. The workshop report is developed by the participants and is considered advisory to the FWS and ABM Recovery Team.

The ABM PHVA workshop began with a series of presentations. The first was on CBSG and the process that had been designed for this particular workshop. This was followed by an overview on the current situation facing FWS regarding the ABM and then an introduction to the computer modeling tools to be used during the workshop and input parameters used in development of the preliminary ABM population model. The participants worked in plenary to review the data and build the initial baseline ABM model and also to identify areas of uncertainty needing additional discussion in small groups.

The next task was conducted in three working groups and involved the compilation and discussion of information to determine values for the following model parameters: 1) population structure (subpopulation designations, size, carrying capacity and dispersal rates); 2) demographic rates (reproductive and mortality rates); and 3) catastrophes. These discussions were necessary to quantify the status and population dynamics of the subspecies in order to build an ABM population model. Areas of uncertainty were identified for sensitivity testing within a range of plausible values to assess the effects on the results. Each group presented the results of its work in a plenary session to provide everyone with the opportunity to contribute to the work of the other groups and to assure that issues were carefully reviewed and consensus achieved.

Initial baseline models and limited sensitivity testing of demographic parameters were run overnight and presented to the group on the morning of the third day. This led to the refinement of the conclusions of the three working groups for recommended population, demographic and catastrophic input values for the ABM baseline model.

The remainder of the workshop was devoted to outlining alternative future scenarios for ABM populations and habitat. Two working groups were formed: one focused on potential future development scenarios along the Fort Morgan Peninsula, while the other addressed the potential effects of invasive species and management strategies to mitigate hurricane effects. These issues were brought back to plenary for further discussion and revision before closure of the workshop. Due to the complexity of the ABM model and the difficulty of this task, some of the discussions regarding model input values continued via a post-workshop internet-based listserv to refine the model. All workshop participants were included on the listserv and had the opportunity to review and/or respond to all topics. The results of these discussions led to revision of the working group reports and completion of the ABM baseline model and alternative scenarios. Sections 2 through 6 of this report contain detailed results from each of the working groups. Summaries of the results of each working group report are presented below.

Working Group and Model Results

The *Population Structure Working Group* defined the population structure to be used in the ABM *Vortex* model, including the description of population units to be analyzed, estimates of the current population size and carrying capacity for each unit, and estimates of the rate of movement of mice among these units. To maximize the ability to model alternative management and development scenarios, the group chose to structure the ABM metapopulation into eight subpopulations, or model units. Population and carrying capacity estimates were extrapolated from trapping data and estimates of ABM habitat, which resulted in an estimated total carrying capacity of 22,913 mice. Development to the west of Gulf State Park was considered to be a barrier to mouse movement; otherwise, mice were assumed to have some connectivity throughout existing ABM habitat. Although accurate estimates of population size, carrying capacity and movement are not currently available, the working group members used all available data and expertise to provide the best estimates possible for use in developing the *Vortex* model. The same can be said for all of the working groups.

The *Demographic Rates Working Group* examined all available published and unpublished information on beach mice to develop the best estimates of mortality rates, seasonal reproductive rates, and litter size and distribution for use in the *Vortex* model. Mouse populations were modeled using four-week time steps to correspond to the interval between major life history events. ABM populations fluctuate seasonally, peaking in late winter/early spring and dropping in late summer. Reproduction, and to a lesser extent mortality, were modeled as fluctuating seasonally, and reproduction was assumed to be density dependent. In general, ABM populations have the biological potential for rapid growth when densities are not close to carrying capacity as long as additional sources of mortality (natural or anthropogenic) are not too great.

The impact of hurricanes was discussed by the *Catastrophe Working Group*. Tropical storms and hurricanes were divided into five categories of intensity matching the Saffir-Simpson scale and were modeled to occur seasonally (August through October). The National Hurricane Center provided estimates for the frequency of occurrence of each category storm for the Gulf Shores area. Hurricanes impact beach mice populations by killing mice directly and by reducing ABM habitat and carrying capacity. These two effects vary throughout the eight model units and were estimated based on the SLOSH inundation model. The habitat and carrying capacity were assumed to recover at a logistic rate (i.e., slowly at first, followed by most rapid recovery in the middle years), with stronger storms having a greater impact and leading to longer recovery times.

The results of the baseline model suggest that the ABM metapopulation has an 18% to 21% probability of extinction over 100 years, depending on whether fast or slow recovery of habitat following hurricanes is assumed. Sensitivity tests of alternative values for uncertain model parameters yielded probabilities of ABM extinction ranging from 13% to 36%, with the strongest impacts observed when habitat carrying capacity, juvenile survival, or adult survival was varied.

The Perdue and Multi-Family model units appear to be the stabilizing portion of the overall metapopulation. These relatively large areas contain high elevation habitat that is less affected by hurricanes, and are centrally located relative to the linear array of subpopulation model units along the coast. Both the metapopulation and these two central units are projected to lose about 27% (with fast recovery) to 31% (with slow recovery) of their initial gene diversity over 100 years, which would result in an accumulated level of inbreeding approximately equivalent to a generation of mating between full siblings. As expected, hurricanes are a major influence on the population dynamics of this subspecies.

On the eastern part of the range, the Gulf State Park and Orange Beach units suffered local extinctions, typically within about 5 to 10 years. ABM subpopulations in these units have a high probability of extinction when hurricanes occur, particularly with more severe storms. Because these two units are completely isolated from the units to the west, they do not get recolonized naturally after local extirpation; translocation will likely be needed to sustain the ABM population in these areas. Subopulations at the Fort Morgan, Single Family, and West Beach model units also frequently do not survive hurricanes (with median times to extirpation of 11 to 23 years), but they are often recolonized from adjacent units.

The *Mitigation and Invasive Species Working Group* addressed potential management strategies for mitigating the effects of hurricanes on ABM populations. These strategies fell into two categories: those related to habitat restoration (sand fencing, vegetation planting/fertilization, beach nourishment) and others directly aimed at ABM populations (supplemental feeding, translocation). Restoration was modeled as a reduction in recovery times following hurricanes and led to an increase in mean population size for all model units, but little or no reductions in the probabilities that local and metapopulation extinction will occur at or immediately following a hurricane. Translocation of mice (modeled as supplementation of extirpated populations with 25 pairs of mice) resulted in larger mean population sizes and is the only scenario tested that was forecast to be able to eliminate the possibility of metapopulation extinctions. Full implementation of this strategy would depend on the continual availability of a source of mice to be used for release.

This working group also discussed the potential effects of several invasive species on ABM populations – cogongrass (*Imperata cylindrica*), domestic cats (*Felis sylvestris catus*) and house mice (*Mus musculus*). Cogongrass is an exotic Asian grass species that replaces native plants in ABM habitat and has become established on the Fort Morgan Peninsula. Cogongrass invasion was modeled as a 1% annual reduction in ABM carrying capacity, which would lead to steady population decline and metapopulation extinction in about 100 years. Lower ABM reproduction at low densities, as could happen if there is corralling of females by male house mice (modeled as an increased Allee effect), had little effect on ABM populations. Predation on mice by domestic cats had serious effects. When modeled as each cat killing one ABM per day, even the continual presence of one cat per model unit resulted in virtually certain extinction of ABM.

Future development scenarios were discussed by the *Development Working Group*. Potential scenarios included additional residential development in the Single Family and West Beach model units, additional development in the Multi-Family model unit, and increased park infrastructure in Fort Morgan and Gulf State Park. Most were modeled with and without management to minimize impacts upon ABM subpopulations, such as native landscaping and predator control. Each development option was modeled by estimating impacts on carrying capacity and survival.

Many of the development options examined had at most only minor impacts on estimates of probabilities of overall ABM extinction and mean metapopulation sizes. The development scenarios that did cause significant reductions in the simulation projections (either with respect to the probability of extinction or mean population size) were those that included large (20% or more) reductions in the habitat within Single Family or Multi-Family units, or the case of 10% reductions in both Single Family and West Beach units. Some of the other scenarios with minimal impacts at the metapopulation level did, however, result in smaller or more vulnerable local subpopulations within the affected habitat units and sometimes in adjacent units.

ABM populations – both in the simulation models and in nature – are subject to considerable fluctuations due to seasonal variation in breeding and survival, fluctuations in habitat quality across years, and the impacts of hurricanes. The fate of the ABM as a single, interconnected metapopulation is therefore intrinsically unpredictable, although the *probabilities* of population decimation and the long-term mean numbers of mice can be projected. With the number of repeats of the simulation model that were used in these analyses, general trends can be observed (as described above), but fine discrimination among scenarios that overlap considerably in the distribution of possible outcomes is not possible. More extensive modeling of specific cases of concern could be used to refine the analyses presented in this report. In addition, the accuracy of model results depend upon the accuracy of the values entered into the model. For many of the ABM model parameters, the best available data allow only approximate estimates of the true values. If these estimates are incorrect, the model results can be misleading regarding the most likely fate of the ABM population.

Post-Workshop Modeling Efforts

Several events occurred in the months following the June 2004 PHVA workshop that had implications for the model results reported here. The FWS approved several Incidental Take Permits to allow additional development in the Single Family model unit (resulting in a loss of 0.4% of ABM habitat in that model unit). A more significant event was the impact of Hurricane Ivan, a Category 3 hurricane whose eye passed over the Fort Morgan Peninsula on September 16, 2004, resulting in a major loss of primary and secondary dunes throughout ABM habitat. Finally, as work with ABM and the CIA continued, new data and ideas arose for refinement and expansion of the ABM *Vortex* model. On December 9, 2004 the FWS closed the discussion associated with the June 2004 ABM PHVA workshop.

At the invitation of the FWS, CBSG met with FWS staff from local and regional offices in December 2004 to discuss building upon the PHVA model. This discussion included developing a set of development scenarios that more closely match those outlined in the CIA. One of the modifications included building the occurrence of a Category 3 hurricane into the first time step of the model to simulate the effects of Ivan. Another significant change was to slightly reduce the impact of hurricanes on ABM habitat, as the original values (based on storm surge estimates according to the National Hurricane Center's SLOSH model) were thought to overestimate habitat loss. Recovery from hurricanes for this model was taken as the values labeled "slow logistic recovery" in this report. Restoration efforts were modeled in what is believed to be a more realistic manner. The results of this revised model will be available in spring 2005 and will be distributed by the FWS.

Alabama Beach Mouse PHVA

Point Clear, Alabama
June 8-11, 2004

FINAL REPORT

SECTION 2

Population Structure Working Group Report

Population Structure Working Group Report

This working group was tasked with developing the population structure to be used in the Alabama beach mouse *Vortex* model, including the description of population units to be analyzed, estimates of the current population size and carrying capacity for each unit, and estimates of the rate of movement of mice among these units**. Throughout the discussion it was recognized that accurate estimates of these parameters are not currently available. Therefore, the working group members used all available data and the expertise of the workshop participants to develop the best estimates possible for use in developing the *Vortex* model. Model parameter values can be modified as new and better data become available.**

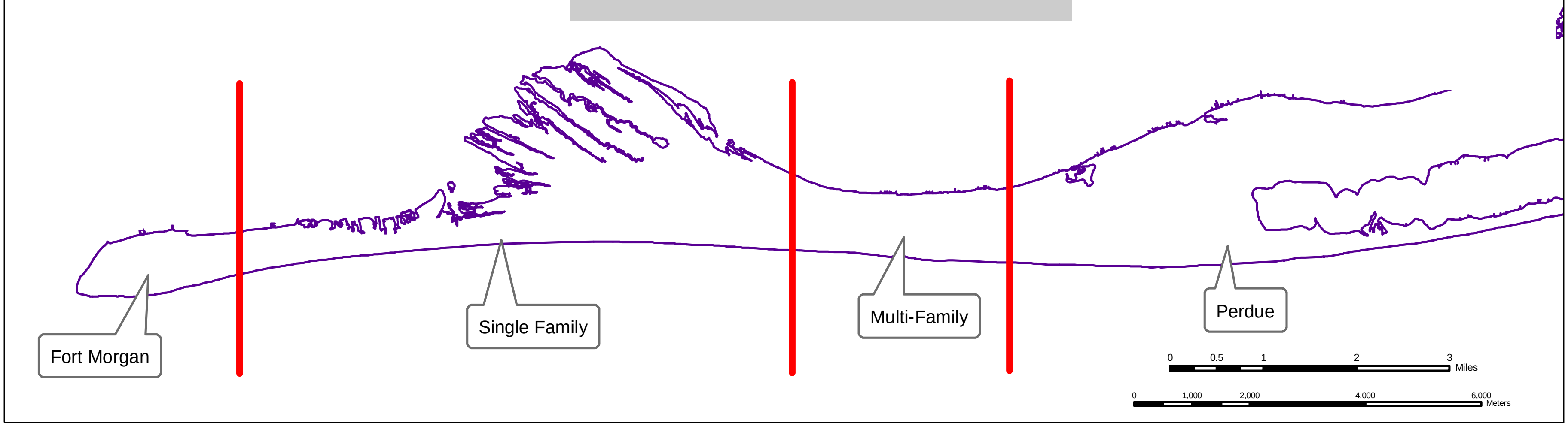
Delineation of Model Units

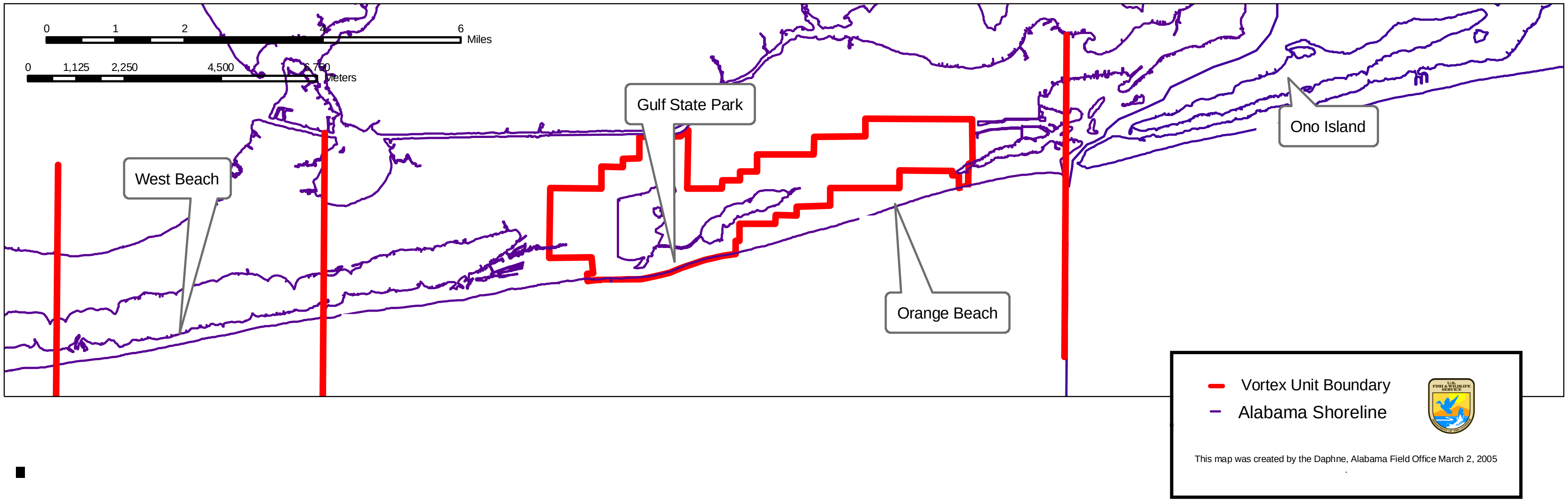
The range of the Alabama beach mouse (ABM) stretches across the Fort Morgan Peninsula of Alabama and the adjacent mainland beaches, from Fort Morgan State Historic Site at the western tip of the peninsula to Perdido Pass in Baldwin County, Alabama to the east. The historical range of this subspecies also included Ono Island, where no ABM are currently believed to exist. Within these geographic boundaries, ABM habitat consists of public lands (Fort Morgan State Historic Site and Perdue Unit of the Bon Secour National Wildlife Refuge, Gulf State Park) separated by privately owned lands. In most areas mice are thought to move to some extent between adjacent habitat patches. A barrier to dispersal is believed to exist west of Gulf State Park, dividing the mouse population into two separate biological subpopulations.

Many of these ABM habitat patches differ in terms of current and potential future management, development, hurricane impacts, and other factors that may influence ABM population viability. For instance, portions of the privately held lands are zoned for single family residential development, while other areas are zoned for multi-family development. Fort Morgan State Historic Site consists of public lands and contains higher elevation areas that may act as refugia for ABM during storm events, while the adjacent area to the east consists of private lands zoned primarily for single family development that are more intensively impacted by storms due to overall lower elevations. Habitat in public lands could be improved for ABM, or state-owned lands could be considered for alternate uses such as development or conference facilities. It was therefore decided to divide various segments of public and privately held lands into subpopulations within the ABM *Vortex* model to allow these geographical and management differences to be incorporated and to make it possible to test different future scenarios with respect to these areas. Since these areas do not describe biologically isolated populations but instead reflect geographical management units, the working group decided to term them *model units* to avoid confusion. Model units were defined as discrete ABM habitats having distinct geographic features and/or similar threats within the historic range of ABM.

The six model units used in the pre-PHVA workshop preliminary modeling efforts were discussed. The boundaries between these units run north to south, dividing the peninsula and adjacent mainland beaches into a string of model units from west to east (see Figure 2A). It was decided to subdivide the original model unit constituting privately held lands between Fort Morgan State Historic Site and Perdue Unit due to differences in land use (divided into Single

Vortex Model Units





— Vortex Unit Boundary

— Alabama Shoreline

This map was created by the Daphne, Alabama Field Office March 2, 2005

Family and Multi-Family model units). A portion of the former range, Ono Island, was initially added to broaden alternative scenario options but was subsequently dropped from the model. Consideration was given to making highway SR 180 a distinct model unit. This area runs west to east along the north side of the peninsula and provides a travel corridor for ABM between units. The working group decided not to define this area as a separate unit since this strategy does not offer any increased modeling capabilities. This resulted in the final delineation of the following eight model units for use in the *Vortex* model:

Fort Morgan Unit: This unit includes the western tip of Fort Morgan Peninsula consisting of the Fort Morgan State Historic Site, also known as the Fort Morgan Unit (FMU) of Bon Secour National Wildlife Refuge (BSNWR). The Service has identified through aerial photography, ground truthing, and trapping surveys that approximately 173 acres of ABM habitat exists within this model unit comprised of primary and secondary dunes. Extensive wetlands occur within this unit, which separate secondary and primary dunes from the escarpment to the north.

Single Family: This unit begins at the eastern boundary of the FMU and extends east approximately 7-8 miles, ending at the western boundary of the Kiva Dunes Development. Residential structures are primarily single family and duplex residences with a few multi-family developments interspersed among the Single Family neighborhoods. Situated from east to west, developments/subdivisions include Surfside Shores, Morgantown, Heritage Shores, Ponce de Leon Subdivision, Bay to Breakers, Fort Morgan Town Homes and The Dunes. This is a low-lying area with higher scrub dunes and relic escarpment at the eastern boundary, near the multi-family unit. Approximately 677 acres have been identified by the Service as habitat for ABM.

Multi-Family: This unit begins at the western boundary of Kiva Dunes and extends east to the western boundary of the Perdue unit of BSNWR. Developments within this unit include Kiva Dunes (condominiums, residences, and golf course), the Gulf Shores Plantation, Plantation Palms, Beach Club, Martinique, and Cabana Beach. This is the unit in which Beach Club West and Gulf Highlands are proposed to be developed. The escarpment begins just east of the western boundary of this unit near Kiva Dunes and extends eastward through the Perdue Unit. The FWS has identified approximately 513 acres of ABM habitat within this unit.

Perdue Unit: This unit includes the Perdue Unit (PU) of the BSNWR, which begins at the eastern boundary of Martinique and extends east to the western boundary of Laguna Key. This model unit contains approximately 1,036 acres of ABM habitat consisting of a matrix of primary and secondary dunes, escarpment, interior scrub, and some intermittent wetland swales.

West Beach: This unit extends from the western boundary of Laguna Key to Little Lagoon Pass. The characteristics of this unit are different from the other units in that there is little topographic relief from the low elevation, with average dune height of 5.5 feet. Based on trapping surveys, ground truthing, and aerial photography, the Service has identified approximately 188 acres of ABM habitat within this unit.

Gulf State Park: The Gulf State Park (GSP) western boundary begins immediately east of the Royal Palms Condominium on West Beach Boulevard and extends west 2.18 miles to the Orange Beach City limits. Approximately 4,321 acres exist within the entire GSP; however most of this is north of Highway 182 and does not provide ABM habitat. Trapping within the northern portion of the park has not been done to determine the extent of ABM occupancy; however, based on aerial photography and limited ground truthing, it is estimated that there are 111 acres that currently provide habitat for ABM.

Orange Beach: The Orange Beach Unit begins at the eastern boundary of Gulf State Park at the Orange Beach City limits, and extends eastward to Perdido Pass. This is a highly developed area extending approximately 5 miles. Multi-family condominiums, hotels, restaurants, and recreational developments dominate the area. Based on trapping surveys at two HCP sites (Tidewater and Phoenix) the Service believes that ABM have been extirpated from most of this area. However, since the reintroduction of ABM into Gulf State Park, ABM may have dispersed to the east to some extent. A recent trapping survey captured two ABM within this unit on the north side of Highway 182.

Ono Island: Ono Island is the eastern-most historic range of ABM and is connected to Alabama east of Perdido Pass via a two-lane vehicular bridge. Historically, a land bridge connected the island to Alabama and ABM occupied the island. No evidence of ABM occupancy has been discovered, although little trapping has been done. It is believed that ABM were extirpated from the island by introduced red foxes and cats, coupled with human development. This model unit was not included in the final model.

The amount of ABM habitat was previously calculated in each of these areas by the FWS based upon the presence of adequate forage, cover and burrowing sites. Areas that were not considered to be ABM habitat and were excluded from these calculations include wetlands, overgrown areas of dense vegetation, developed areas, wet beaches, small isolated areas of habitat, and maritime forests (see FWS 2003 for details on methods and results).

Estimation of Carrying Capacity

Once the model units were defined, the next task was to estimate the ABM current population size and carrying capacity for each unit. Good estimates for either of these parameters are not available. The working group adopted a strategy of using trapping data (both line and grid data) to estimate densities in each model unit; these density estimates were applied to the entire acreage of each model unit to estimate carrying capacity and current population size.

It was recognized that the carrying capacity (K) of each unit varies seasonally, with the peak in late winter/early spring and the low in late summer/early fall. The working group considered having K vary seasonally in the *Vortex* model, but abandoned this strategy for two reasons. Although K varies seasonally due to fluctuations in the production of food resources, this has the effect of causing the reproductive and survival rates of ABM to vary seasonally. Since seasonal breeding and survivorship are already incorporated into the *Vortex* baseline model, it should not be added as seasonal fluctuations in K as well to avoid “double counting” this effect on the population. Secondly, since better data were available with regard to seasonality in demographic rates vs seasonality in K, it was decided that this phenomenon would be modeled better in the demographic rates rather than by imposing fluctuations in K. Results of the baseline model demonstrate a reasonable seasonal fluctuation in population size due to seasonal reproduction and survival and appeared to simulate observed fluctuations in wild ABM populations.

The highest estimate of density within each model unit based upon trapping data was used to estimate the maximum carrying capacity for each unit. For the most part these data are fairly recent (2003 and 2004), when ABM numbers have been high, and were thought to be reasonable for use in estimating maximum K. It was acknowledged that some species go above carrying capacity and then crash. Consideration was given to incorporating this into the estimation of K by reducing the calculated K by 20%. However, there is no evidence that ABM were above carrying capacity at the time of trapping. Also, density-dependent reproduction is incorporated into the *Vortex* model such that the population will never grow substantially above K. Therefore the maximum density calculated from trap data was multiplied by the area of each unit to estimate K for that unit.

ABM densities not only vary seasonally, but would also be expected to vary among habitat types. ABM occupy very linear habitat that often changes relatively abruptly. This includes some areas of scrub habitat that are not generally trapped as they are thought to support only low population densities of mice. The working group recognized that much of the trapping data does not include scrub habitat. For comparison, the group considered data from Lynn (pers. comm.), who trapped across habitat types, to see if density estimates looked reasonable. Recorded high densities were 10.36 mice/acre in 1995 and 7.4 mice/acre in 1996. These estimates are similar to those used by the working group for the eight model units. It was also noted that what Swilling called ‘scrub’ is actually on the line between dune and scrub habitat.

Trapping estimates for three years were available for the Perdue unit, two in scrub habitat and one in dunes. A suggestion was made to use only the scrub data to estimate carrying capacity, since scrub areas are less affected than the frontal dunes by seasonal changes. There was concern that high numbers can be deceptive since some trapping may have occurred immediately after a storm, when some individuals may have moved from one area to another, consequently inflating the density for particular trapping sessions. The group discussed taking an average of trapping data for Perdue Unit and then reconsidered, since this was not done for other model units, and decided to use only the high number for Perdue (taken from scrub habitat).

Table 2A gives the density, habitat and carrying capacity estimates for each model unit. Unless otherwise indicated, density estimates were derived from trapping data using the CAPTURE software program. The highest density estimate for each unit was then used to calculate the estimated K. The working group recognized that K is an important parameter in the ABM *Vortex* model and therefore recommended sensitivity testing of carrying capacity at 100%, 85%, 70% and 50% of these calculated values to evaluate the impact of overestimating K on the long-term viability of ABM populations. Consideration was also given to testing higher levels of K, but this was not considered necessary once the K calculations were finalized and the estimates reviewed.

Although carrying capacity varies seasonally (and is also affected by storms), the annual environmental variation in K is thought to be low (i.e., K is the same from June to June, from July to July, etc.). Therefore no additional variation (SD) was added for K. Likewise, K was set to be constant in the baseline model (i.e., no ecologically-based future trend in K). Carrying capacity may decline in the future in relation to various development scenarios, but such changes in K will be incorporated into alternative scenario models and not in the baseline model. The group also recommended that drought be incorporated in some way into the model, perhaps as a catastrophe rather than through variations in K. However, when the group considered that the past several years have been drought years and that the numbers of ABM seem to be stable or increasing, it was decided that it may not be necessary to include drought as a catastrophe.

Table 2A. Habitat, density, and carrying capacity estimates for each ABM model unit.

Model unit	ABM habitat (ac)	CAPTURE estimates	Density (ABM/ac)	Estimated K
Fort Morgan	173	70 ABM/6.0 ac	11.67	2019
Single Family	677	14 ABM/1.57 ac 79 ABM/21.34 ac	8.92	6039
Multi-Family	513	148 ABM/35.54 ac[1] 53 ABM/23.87 ac 36 ABM/35.4 ac	6.5	3335
Perdue	1036	270 ABM/28.8 ac	9.38	9713
West Beach	188	56 ABM/8.43 ac	6.64	1249
Gulf State Park	111	48 ABM/10.75 ac	4.47	496
Orange Beach[2]	75	2 ABM/2.4 ac	0.83	62
Ono Island	263	0	0	0[3]
Total				22,913

[1] This is the actual number of mice captured, while for the rest of the units these numbers are CAPTURE estimates. The group estimated that the CAPTURE estimate would result in a slightly higher density of 6.5 ABM/ac.

[2] There is little trapping for this area; therefore, this density estimate needs to be revised when more trapping is completed and a better estimate of true carrying capacity can be made.

[3] The group decided not to estimate K for Ono Island since no data are available on habitat quality. This unit historically had ABM and likely includes some ABM habitat. However, ABM are not thought to be present on Ono Island at this time.

Estimation of Initial Population Size

As outlined above, there are no accurate estimates of ABM population size in which the working group had confidence. Population estimates have been relatively high in recent years, suggesting that perhaps the ABM population has recovered from past storms and is approaching the carrying capacity of the environment. ABM have also been documented moving into habitat not typically occupied at low ABM population levels, which suggests that they are near or at carrying capacity. Therefore the working group made the assumption that the current ABM population is at carrying capacity.

ABM population numbers have been observed to fluctuate seasonally, with the highest numbers in early spring and the lowest in early fall. The ABM *Vortex* model begins at a point in the seasonal cycle at which the population is at its midpoint and is increasing (approximately late December). Initially the working group attempted to calculate the seasonal peaks and valleys of population numbers (and carrying capacities) for each model unit. This could be done, however, only by extrapolating densities from trapping in one area, as such data are not available for all model units. This method would allow an estimation of the midpoint of the seasonal variation in population size to match the start of the *Vortex* model. The working group was not comfortable with this methodology and lack of data and so abandoned it, deciding instead to set the initial population size for each model unit to equal K as given in Table 2A. It was recognized that it is not essential that the estimated initial population be at its midpoint because seasonal reproduction will quickly bring the population under seasonal control. Sensitivity testing of the initial population size with respect to K (for N=K, N=80%K, N=50%K) was recommended to confirm this point.

Inter-Unit Dispersal Rates

The term dispersal can be used to describe a variety of situations in which an individual moves from one area to another. To avoid confusion the working group used the term *inter-unit dispersal* to describe the movement of ABM from one model unit to another model unit. It was necessary to estimate the rate of inter-unit dispersal among model units in order to incorporate genetic exchange and the possibility of recolonization of extirpated units into the *Vortex* model.

It was decided that sub-adults are the primary age class that establish new home ranges and therefore would possibly move across inter-unit boundaries. Very few adults are likely to leave their home ranges and disperse to establish others except perhaps in association with storm events. There is some published literature on adult exploratory behavior, but there is no true evidence of adult dispersal. Therefore, only sub-adults (i.e., those in the 29-56 days age class) were included in inter-unit dispersal in the model.

Another decision discussed by the working group was whether or not to impose additional mortality on individuals exhibiting inter-unit dispersal. Although Van Zant and Wooten (2003) suggest that there is an additional risk of mortality associated with long-distance dispersal, such dispersal is believed to be rare and is not incorporated into this model. Rather the assumption is that inter-unit dispersal represents normal dispersal by sub-adults to establish a home range outside of their natal home range and in cases in which such dispersal causes them to cross an inter-unit boundary. In most cases inter-unit boundaries are defined by land use and management differences rather than by hard ecological boundaries. Movement across these boundaries therefore is assumed to be no riskier than movement within model units. Swilling and Wooten (2002) suggest that of those individuals that dispersed from their home range, mortality is 27.1%. After consultation with the Demographic Rates Working Group it was the consensus opinion that mortality associated with dispersal is accounted for in the standard mortality rates in the model and that it would be inappropriate to add an additional mortality penalty for inter-unit dispersal.

The final task was to estimate the percent of each model unit sub-adult population that disperses into the next model unit. Swilling and Wooten (2002) found that 55% of individuals disperse up to one home range (average diameter = 68 m) from their natal area, and that 45% of individuals disperse greater than one home range from their natal site (average dispersal distance is 160 m). Using these estimates, the following strategy was adopted to estimate dispersal percentages:

1. GIS map data (from the FWS Daphne Office) were used to calculate the area of ABM habitat within 160 m of each north-south inter-unit boundary. This was then divided by the total ABM habitat in the model unit to determine the percent of the unit's ABM habitat lying along each border. Note: GIS data were not available for Orange Beach and Ono Island; these areas of ABM habitat were estimated from visual examination of habitat maps for these areas.
2. It was assumed that ABM distribution is uniform within the habitat in each model unit. Therefore, the percent area along the edge was also taken to be the percent of ABM population in the model unit living in that area ("border population").

3. It was assumed that 45% of the sub-adults living in the 160 m border area would disperse an average of 160 m, and that 50% of these (22.5%) would disperse in the direction of the adjacent model unit and therefore cross the inter-unit boundary. Thus the ratio of border population to model unit population was multiplied by 22.5% to estimate the percent of inter-unit dispersal across each model unit boundary by this portion of the population.
4. Only 42.5% of the 160 m border area lies within 68 m of the inter-unit border. It was assumed that 55% of the sub-adult population living within this 68 m border area would disperse 68 m, and that 50% of these (27.5%) would disperse in the direction of and therefore cross the inter-unit boundary. Thus the percent of habitat lying within the 160 m border was multiplied by 42.5% and then by 27.5% to estimate the percent of inter-unit dispersal across each model unit boundary by this portion of the population.
5. These two dispersal estimates (for dispersers moving within one home range and those moving greater than one home range) were then combined to produce an estimated dispersal rate from each model unit to each adjacent model unit.
6. Since ABM habitat was not necessarily equal on both sides of an inter-unit boundary due to existing development, and because carrying capacities and subpopulation numbers differ among model units, dispersal rates (%) differ across a single boundary depending upon the direction of movement. For example, a larger proportion of mice would live along a boundary (and therefore a larger percentage would be likely to migrate to the adjacent model unit) in a small model unit than in a large model unit.

The resulting estimated inter-unit dispersal rates are given in Table 2B. While the percent of the sub-adult population that disperses across unit boundaries is relatively small, this dispersal takes place in the *Vortex* model each 28 days (*Vortex* “year” – see Section 7). This is believed to represent an adequate flow of individuals among model units to allow for recolonization of areas where ABM are extirpated due to stochastic events. The boundary between Gulf State Park and West Beach is believed to be a barrier to ABM movement, effectively dividing the ABM population into two non-interacting populations. The working group recommended that a sensitivity analysis be conducted for this parameter, perhaps testing twice the suggested dispersal rates if recolonization appears to be insufficient.

Cautions

There is a paucity of information regarding ABM densities, population numbers, carrying capacity of ABM habitat, and dispersal rates among various areas within the ABM range. In most cases, available data are not sufficient to produce reliable estimates that take into account all factors. Some of the specific concerns with the estimates made for carrying capacity (which in turn affects estimates of population size and number of mice moving between model units), include the following:

- Limited data were used for estimating densities.
- Data were from both trapping grids and trap lines rather than a consistent methodology.
- Some trapping areas may not have been randomly placed but may have been placed in “good habitat” to maximize trapping success.
- ABM density is likely to vary by habitat type and quality. Due to limited data, density estimates made here were extrapolated from the trapping area across all habitat types.

The working group recognized that its members had access to sufficient information and expertise to make plausible estimates couched by certain assumptions, which were necessary to construct a population viability model for the ABM population. Once this model has been constructed, it can be refined with new and more accurate information as it becomes available. **Caution must be exercised when citing these estimates of population numbers, densities and carrying capacities outside of the context of this ABM *Vortex* model.**

Table 2B. Inter-unit dispersal estimates between adjacent ABM model units.

Model unit	**Adjacent model unit**	**% ABM habitat w/i 160 m of boundary**	**% dispersal**		**Total dispersal**
			From 160 m area	**From 68 m area**	
Fort Morgan	Single Family	6.68	1.50	0.78	2.28% to E to Single Family
Single Family	Fort Morgan	1.74	0.39	0.20	0.59% to W to Fort Morgan
	Multi-Family	3.83	0.86	0.45	1.31% to E to Multi-Family
Multi-Family	Single Family	3.35	0.75	0.39	1.15% to W to Single Family
	Perdue	3.23	0.73	0.38	1.10% to E to Perdue
Perdue	Multi-Family	3.36	0.76	0.39	1.15% to W to Multi-Family
	West Beach	1.23	0.28	0.14	0.42% to E to West Beach
West Beach	Perdue	5.65	1.27	0.66	1.93% to W to Perdue
	Gulf State Pk	n/a	n/a	n/a	No dispersal to E to Gulf State Pk
Gulf State Park	West Beach	n/a	n/a	n/a	No dispersal to W to West Beach
	Orange Bch	2.77	0.62	0.32	0.95% to E to Orange Beach
Orange Beach	Gulf State Pk	0.99	0.22	0.12	0.34% to W to Gulf State Park
	Ono Island	n/a	n/a	n/a	No dispersal to E to Ono Island
Ono Island	Orange Bch	n/a	n/a	n/a	No dispersal to W to Orange Bch

References

FWS. 2003. Alabama Beach Mouse Habitat in Baldwin County, Alabama. Prepared by the U.S. Department of the Interior, U.S. Fish and Wildlife Service, Daphne Field Office, Daphne, AL. November 2003.

Swilling, W.R. and M.C. Wooten. 2002. Subadult dispersal in a monogamous species: The Alabama beach mouse. *Journal of Mammalogy* 83(1): 252-259.

Van Zant, J.L. and M.C. Wooten. 2003. Translocation of Choctawhatchee beach mice (*Peromyscus polionotus allophrys*): Hard lessons learned. *Biological Conservation* 112: 405-413.

Alabama Beach Mouse PHVA

Point Clear, Alabama
June 8–11, 2004

FINAL REPORT

SECTION 3

Demographic Rates Working Group Report

Demographic Rates Working Group Report

This working group was formed to more thoroughly discuss the values of various demographic rates to be used in the ABM baseline *Vortex* model and to identify parameters in need of sensitivity testing. Four parameters were addressed by this group:

1. Mortality rates (adult, sub-adult, juvenile)
2. Seasonal reproductive rates
3. Density-dependent reproduction
4. Litter size and distribution

Mortality Rates

The discussion of ABM mortality rates began in plenary and was then assigned to a working group for further investigation and discussion. Preliminary estimates made in plenary were based on a mix of data from both laboratory studies and biologically plausible estimates. One study of *P. maniculatus* suggests 30% mortality for neonates (in captive conditions) and 25% monthly mortality for sub-adults and adults (Citta, 1999). The following values were recommended in plenary as a starting point for group discussion:

Age class	Mortality (%)	SD (%)
Juvenile	30	10
Sub-adult	25	10
Adult	25	10

Adult Mortality

The working group searched for better data to refine the mortality estimates. Rave and Holler (1992) report a mean monthly probability of mortality as 0.322 based on data from wild populations after first capture. This study began 17 months after Hurricane Elena; dunes were present, suggesting that some recovery had occurred. In the 1987 and 1988 field seasons, 87% of mice survived four months or less beyond first capture; when the 1989 field season data were added, survival for the same time period dropped to 63%. Rave and Holler quote Blair (1951) as showing 81.5% loss of a beach mouse population on Santa Rosa Island over a four-month period. The working group also calculated mortality estimates from data provided by Swilling *et al*. (1998), which suggests 22% monthly mortality (SD = 12%).

During the first day of discussions the working group recommended using 27.1% as the monthly adult mortality, an average of the Rave and Holler (1992) estimate of 32.2% and the Swilling *et al*. (1998) estimate of 22%. The group was comfortable accepting the only SD estimate that could be calculated from the literature (12%), meaning that about 70% of the time monthly adult mortality would range between 15% and 39%.

Sub-Adult Mortality

As an initial starting point sub-adult and adult mortality rates were set to be the same. No data were available for separate sub-adult and adult mortalities; however, the working group believed that sub-adult mortality is probably higher than adult mortality. Sub-adults are the primary dispersers, are less experienced at avoiding predators, and less experienced at finding food; therefore it is likely that sub-adults may suffer higher mortality than adults that have established home ranges and burrows. The mortality estimate of 27.1% is derived from combined adult and sub-adult age class data. It is difficult to know how to partition this mortality for sub-adults and adults. One possibility is to weight mortality by the proportion of each age group in the population, but this may not be defensible.

The initial decision of the working group was to use 27.1% mortality (with 12% SD) for both sub-adults and adults. Sensitivity testing was recommended for the range of 22 – 32% mortality.

Revised Adult and Sub-Adult Mortality Rates

Later during the workshop the working group gained access to unpublished data from Holler *et al*. for ABM monthly survival rates from BSNWR (PU and FMU). Results were similar across these two study areas and so the data were combined to estimate mortality across all model units. These estimates of monthly adult and sub-adult mortality are:

Age class	Mortality (%)	SD (%)
Sub-adult	22.54	14.85
Adult	17.93	10.77

The higher mortality in sub-adult individuals encompasses expected additional mortality due to dispersal from the natal area. These estimates of mortality were preferred over the other estimates because these were the only data that did not include hurricane effects.

The working group discussed the need to include seasonal differences in mortality rates for ABM. ABM populations typically reach their lowest numbers in late summer, possibly due to the impact of reduced food resources in winter and spring and increased risk of predation. The Holler *et al*. data were examined for seasonal trends in sub-adult and adult mortality. Mortality was observed to be highest in summer, although this trend was not found to be statistically significant. The working group decided to include higher mortality rates for all age classes during the summer and recommended using the following mortality rates in the final baseline ABM *Vortex* model based on the Holler *et al*. data:

	Fall/Winter/Spring		Summer	
Age class	Mortality (%)	SD (%)	Mortality (%)	SD (%)
Sub-adult	21.1	14.4	30.3	14.4
Adult	16.1	10.6	23.7	10.6

Juvenile Mortality (birth to weaning)

Estimates of pre-weaning mortality could not be found in the literature for any wild beach mouse populations. Laboratory mortality rates (day 0-21) at Auburn University suggest up to 55% mortality. Kaufman and Kaufman (1987) report that mortality rates in the lab (to day 21) average 25% but vary greatly from 0 to 50%. Lacy *et al*. (1996) reported 14% pre-weaning (0-20 day) mortality for a laboratory population of *P. p. leucocephalus*, and 44% pre-weaning mortality from data in Brewer *et al*. (1990). Captive mortality rates are in all likelihood lower than those in natural populations because captive individuals do not have to forage for food or avoid predators.

In the absence of data on juvenile mortality in wild populations, the working group initially decided to use 30% mortality (birth to weaning), 10% SD, based primarily on laboratory data discussed in plenary. After further discussion, however, the group revised its decision and recommended 40% juvenile mortality, making the assumption that mortality would be higher in wild populations than under laboratory conditions. Sensitivity testing was recommended for this parameter to test the effect of 30 – 50% juvenile mortality. The standard deviation for juvenile mortality was thought to be at least as large as that for sub-adults.

It was decided to include the same degree of seasonality in juvenile mortality as that used for sub-adult and adults, which resulted in the following rates to be used in the baseline model:

	Fall/Winter/Spring		Summer	
Age class	Mortality (%)	SD (%)	Mortality (%)	SD (%)
Juvenile	36.2	14.4	52.5	14.4
Sub-adult	21.1	14.4	30.3	14.4
Adult	16.1	10.6	23.7	10.6

Seasonal Reproductive Rates

ABM populations have been observed to fluctuate seasonally, with the highest populations observed in the late winter/early spring and the lowest numbers in late summer/early fall. This is likely due to seasonal fluctuations in food availability (with a lag time between low food availability and resulting lower ABM population size) and possibly other factors, which in turn may affect reproduction and/or survival. There is stronger evidence for seasonality in reproductive rates than in survival rates. Data for the percent of females reproducing throughout the year were compiled and reviewed by the working group (see Table 3A). The working group decided to use the ABM data (first row) to develop the oscillating sine wave representing seasonal fluctuations in reproduction.

The sine wave used to represent seasonality in breeding, over five years of cycles, is shown in Figure 3A. The x-axis shows the four-week interval, so that breeding is at a peak in the first few

Table 3A. Data on seasonality in reproduction for wild beach mice populations.

		Percent of reproductively active females			
Source	**Taxon**	**Fall**	**Winter**	**Spring**	**Summer**
Rave & Holler 1992; Swilling *et al*. 1998	*P.p. ammobates*	79.9	90.9	54.6	38.2
Lynn 2001-03 (unpublished data) from GINS – Johnson Beach	*P.p. trissyllepsis*	81.0	66.0	62.0	86.0
Lynn 2001-03 (unpublished data) from GINS – PKSP	*P.p. trissyllepsis*	55.0	87.0	69.0	89.0
Moyers et al. 1999 (6/95 – 6/98; mostly post-Hurricane Opal)	*P.p. allophrys*	29.0	17.0	36.0	52.0

Note: Winter = Jan.-Mar.; Spring = Apr.-Jun.; Summer = Jul.-Sept.; Fall = Oct.-Dec.

months of each year and is at a low point in the summer. Note that the mean (elevation) of this sine wave will shift up or down to account for density-dependent effects.

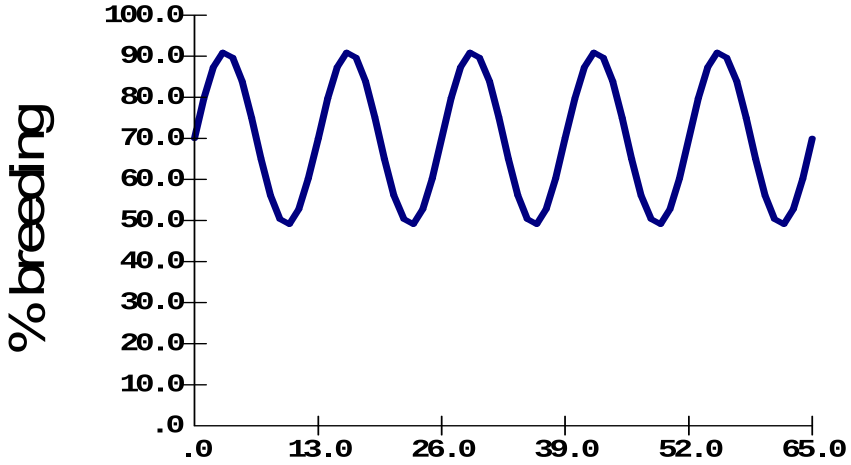


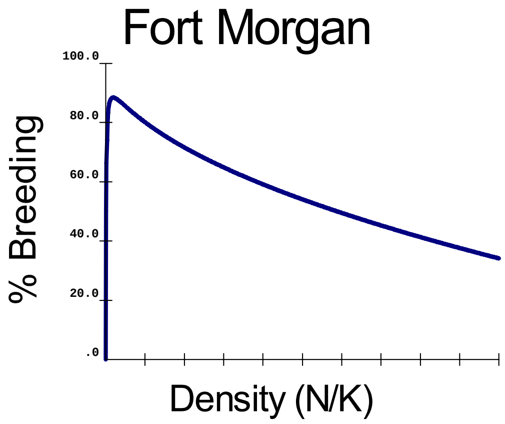
Fig. 3A. Sine wave representing seasonal cycles in percent of females breeding.

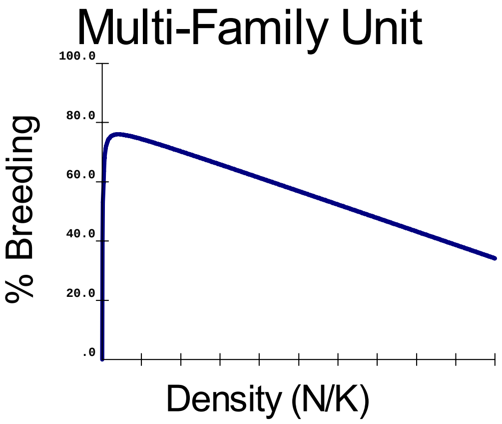
Density-Dependent Reproduction

Density dependence refers to a change in demographic rates in relation to the density of individuals in the habitat. In a typical density-dependent reproductive system, reproduction is low when the density of individuals is very low, due to difficulty in finding mates, etc. (Allee effect), increases quickly as density increases and more mates become available in the presence of abundant resources, and then drops off as density continues to increase due to competition for limited resources. Density-dependent reproduction has been observed in *Peromyscus*, although the exact nature of the relationship (shape of the density-dependence curve) differs among different species. Swilling *et al.* (1998) showed that ABM populations can recover very quickly after disturbance as long as dunes are present. Mice may use back scrub areas as refugia during storms and later repopulate dunes (Swilling *et al*. 1998, Sneckenberger 2001).

Two of the values needed to define this relationship are the maximum percent of females breeding under the best conditions (low density, with abundant resources and no Allee effect), termed P(0), and the minimum percent breeding at carrying capacity under crowded conditions, termed P(K). The preliminary estimates for these values were P(0) = 62% and P(K) = 31%. A literature search of 13 populations of *Peromyscus* found similar estimates of percent breeding at low and high density (63% and 28%, respectively). Unpublished data for Perdido Key and Choctawhatchee beach mice suggest a high reproductive rate of 90% and a low of 14% (Lynn, pers. comm.). The working group decided to use P(0) = 70% and P(K) = 30% for most of the population units. There is evidence that ABM populations at Fort Morgan Unit recover very quickly after disturbance and may reproduce at higher rates under low density conditions; therefore, for the Fort Morgan model unit P(0) was set at 90%. The rate of decrease in reproduction with increasing density was set to a steeper value (B = 0.5) for Fort Morgan, so that at densities above very low values, the reproductive rate in that population would be similar to that in other populations. For the Multi-Family Unit, a linear decrease in reproduction with increasing density (B = 1) was used; while for Perdue Unit and other populations, reproduction was specified to remain better until high densities were reached (B = 3). For all populations, a small Allee effect (A = 1) was imposed, to account for reduced reproduction when numbers within an area dropped below about 10 mice.

The three patterns of density dependence that were believed to represent the somewhat different dynamics in the population units are shown below in Figure 3B.





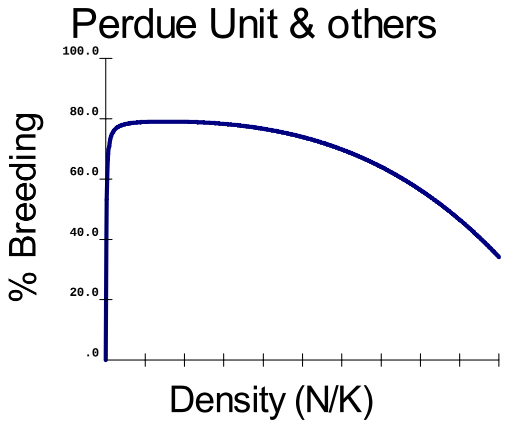


Fig. 3B. Density-dependent reproduction curves used for the model units in the *Vortex* model.

Litter Size and Distribution

Bowen (1968) states the litter size for beach mice to be 2-7 young. Kaufman and Kaufman (1987) report a maximum litter size of 8 with a mean of 4.1 young per litter. For the modeling, we used the distribution of litter sizes observed for 413 non-inbred litters of *P.p. leucocephalus* in the study by Lacy *et al*. (1996). This distribution was 3.15%, 5.09%, 20.34%, 27.84%, 28.09%, 12.35%, 2.91%, and 0.24% litters of 1, 2, …, up to 8 pups, respectively, resulting in a mean litter size of 4.23.

Cautions

Although there have been several studies of various beach mouse wild and captive populations, many of the specific demographic parameters needed for the Alabama beach mouse *Vortex* model have not been well studied for this subspecies. To develop the ABM *Vortex* model, this working group developed demographic rate estimates through discussions during and immediately following the PHVA workshop based on the available data. As with all of the model input values, the demographic rates can be refined with new and more accurate information as it becomes available. **Caution is advised in referencing these values beyond the scope of this PHVA *Vortex* model.**

References

Bowen, W.W. 1968. Variation and evolution of Gulf Coast populations of beach mice, *Peromyscus polionotus*. *Bulletin of the Florida State Museum* 12:1-91.

Brewer, B.A., R.C. Lacy, M.L. Foster and G. Alaks. 1990. Inbreeding depression in insular and central populations of *Peromyscus* mice. *Journal of Heredity* 81(4): 257-266.

Citta, J. 1999. How to change the growth of wildlife populations: Applications and experimental tests of demographic sensitivity analysis. Masters Thesis, University of Montana, Missoula, MT.

Kaufman, D.W. and G.A. Kaufman. 1987. Reproduction of *Peromyscus polionotus* number size and survival of offspring. *Journal of Mammalogy* 68(2): 275-280.

Lacy, R.C., G.A. Alaks and A. Walsh. 1996. Hierarchical analysis of inbreeding depression in *Peromyscus polionotus*. *Evolution* 50(6): 2187-2200.

Rave, E.H. and N.R. Holler. 1992. Population dynamics of beach mice (*Peromyscus polionotus ammobates*) in southern Alabama. *Journal of Mammalogy* 73(2): 347-355.

Sneckenberger, S.I. 2001. Factors influencing habitat use by the Alabama beach mouse (*Peromyscus polionotus ammobates*). Masters thesis. Auburn University, Auburn, AL. 101pp.

Swilling, W.R. 2000. Ecological dynamics of the endangered Alabama beach mouse (*Peromyscus polionotus ammobates).* Masters thesis. Auburn University, Auburn, AL. 91pp.

Swilling, W.R., M.C. Wooten, N.R. Holler, and W.J. Lynn. 1998. Population dynamics of Alabama beach mice (*Peromyscus polionotus ammobates*) following Hurricane Opal. *American Midland Naturalist* 140(2): 287-298.

Alabama Beach Mouse PHVA

Point Clear, Alabama
June 8-11, 2004

FINAL REPORT

SECTION 4

Catastrophe Working Group Report

Catastrophe Working Group Report

This working group addressed the various types of catastrophes that potentially affect wild Alabama beach mouse populations to determine which to include in the ABM *Vortex* model and to estimate the input values (in terms of frequency and impact) to be used in the model.

Hurricanes

Hurricanes were considered by all to be the primary catastrophic threat to the ABM. They result in significant adverse effects to ABM and its habitat, and there is ample evidence of populations of beach mice being completely lost after a hurricane. The working group decided to use the Saffir-Simpson Hurricane Scale to define storm categories (see Table 4A). Tropical storms and Category 1 hurricanes result in the least severe impacts and Category 5 hurricanes result in the most severe impacts to beach mice and their habitat. The parameters that need to be considered for each storm category for the *Vortex* model include:

- Frequency (by category): The frequency of tropical storms and Category 1 hurricanes is higher than the frequency of Category 5 hurricanes.

- Seasonality: Hurricanes typically occur in the fall, primarily from August through October.

- Impacts on demographic parameters: For the model it is necessary to specify the estimated average impacts of a hurricane on reproduction, survival, and carrying capacity of habitat. In addition, the following issues were discussed to determine if and how to consider them in modeling hurricanes:

  Duration: Do the impacts occur only at the time of the storm, or are there lag effects that impact survival or reproduction months later? Delayed effects on mortality might reduce the severity of impact on ABM population viability, because the population can partly recover before the delayed impacts are felt.

  Variability: Within categories and landfall areas, the significance of any storm is highly variable and dependent on where exactly the storm hits land, how much rain is associated with it, how fast it moves through, etc. Additionally, more severe damage occurs on the east side of a storm as opposed to the west side. This variability will be entered into the model using a random impact within an agreed upon range.

  Site Specificity: The eight model units may be affected differently by hurricanes because of differences in habitat quality and differences of elevation or vegetation.

Impacts of hurricanes and tropical storms are known to include sand movement, flooding, and storm surges. The Federal Emergency Management Agency (FEMA) has modeled storm surges to determine the extent of flooding by hurricane category. The storm surge of a Category 5 hurricane is much greater than that of a Category 1 hurricane, and this variation among categories of hurricanes was considered in the working group’s estimates of impacts on the mice.

Since data are available from FEMA and the National Oceanic and Atmospheric Administration (NOAA) on the storm surge effects for each of the five hurricane categories, the working group decided to model each of these, as opposed to treating all hurricanes as a single class of catastrophe. This decision recognizes that there is high variability in the data available to estimate impacts of various categories of storms, as well as high variability in the impacts on mice even for different storms of a given category. The best available information was used.

Table 4A. Saffir-Simpson Hurricane Scale developed by the National Hurricane Center.

Storm Category	Wind Velocity	Typical Effects
Tropical storm	39 – 73 mph	
Category 1 Hurricane	74 – 95 mph	No real damage to buildings. Damage to unanchored mobile homes. Some damage to poorly constructed signs.
Category 2 Hurricane	96 – 110 mph	Some damage to roofs, doors, and windows. Some trees blown down.
Category 3 Hurricane	111 – 130 mph	Some structural damage to small residences and utility buildings. Large trees blown down. Mobile homes and poorly built signs destroyed.
Category 4 Hurricane	131 – 155 mph	Wall failures in homes and complete roof structure failures on small homes. Trees, shrubs, and signs blown down.
Category 5 Hurricane	156 mph and higher	Complete roof failure on homes and industrial buildings. Some complete building failures. Severe and extensive window and door damage.

Frequency

Data from the National Weather Service were available from the draft CIA (see below), but it was decided also to seek data from the National Weather Service website and from the National Hurricane Center.

It was recognized that it may be hard to directly match data from long-term weather records with the frequency of catastrophic impacts on the ABM, because the impacts on the mice will depend on how close (and on which side) of ABM habitat a storm makes landfall. However, this uncertainty, including the variability of local impacts among different sections of ABM habitats, can be considered within the variability of storm impacts that are built into the model.

Seasonality

Data indicate that the following major hurricanes made direct land hits over the last century:

NW FL: None in June, 1 in July, 0 in August, 5 in September, 1 in October.
AL: 0 in June, 1 in July, 0 in August, 4 in Sept, 0 in October.
MS: 0 in June, 1 in July, 1 in August, 4 in Sept., 0 in October

The group determined that hurricanes mostly occur from August – October, with the peak occurring in September. It was agreed to model the seasonality of hurricanes from August through October. The model will vary the actual dates of hurricane strikes by randomly choosing times of impact within the three-month range.

Impacts on Demography

Survival: Various sources of data were discussed, including observational data and losses measured following recent hurricane events. Hurricanes Opal and Georges both were Category 2 storms when they hit the Gulf Coast. Survival of beach mice through Opal was estimated to have been 80% to 85% in Alabama and 20% to 25% in Florida, and Opal led to the extirpation of the Florida Point population of the Perdido Key beach mouse. Survival estimates for Georges ranged from 10% to 90%. The wide range of estimated survival for these storms demonstrates the variability of impacts that can occur, based on the specific site of landfall and other factors. It was felt that less severe storms (tropical storms and Category 1 hurricanes) would have lesser impacts on the mice and a narrower range of impacts, and the decision was made to combine tropical storms and Category 1 hurricanes in the model, as the range of impacts were thought to be similar. More severe storms (Categories 3, 4, and 5) are also believed to have narrower ranges of impacts than Category 2 storms, because most mice would not survive more severe storms.

The working group briefly discussed whether mouse loss after the storm (indirect effects as opposed to direct effects) was a parameter modeled elsewhere in the model. Are these secondary impacts? The group decided that all impacts of the storm, direct and indirect, should be accounted for in the initial storm impacts in the model and chose not to show a lag time since it would not likely make a significant difference in the model results. A quick comparison of a few sample models run with simultaneous impacts vs. those with impacts spread over a few months supported this assumption.

<u>Reproduction</u>: Although historical data have shown that increases in reproduction can occur after a storm event, the assumption was that this was likely a result of greater breeding in response to the low density of mice. This factor is already built in the density-dependence parameter of the model. Another possible benefit to the mice of hurricanes is that vegetation is ultimately improved because native species survive or come back faster, while non-native species are removed.

Data from past hurricanes have, however, shown that survival of sub-adults may be affected. After Opal, a generation (cohort of mice born over a month or two) appeared to be missing from the population. An educated guess is this effect was due to pups being lost due to flooding of the burrows. Pre-weaning pups would not be able to escape from flooding the way that some adult mice would.

The group questioned whether reproduction was directly affected or was only a secondary consequence of the density-dependence already accounted for in the model. There was no consistent data on reproduction on which to base any reliable modeling of hurricane impacts on reproduction, and what little data were available (one storm) indicate that breeding following the storm was similar to that before the storm. The group decided to assume that hurricanes affect reproduction only through mortality of pups and density-dependent responses in breeding. These effects are accounted for elsewhere in the model. Although higher category storms may produce a higher Allee effect (low reproduction due to the few surviving mice having difficulty finding mates), this effect is also accounted for in other parts of the model. Therefore, the working group chose to only model effects on survival and did not include direct effects of hurricanes on reproduction in the model.

<u>Long-term Impacts on Carrying Capacity</u>: Initial discussions related observed data for Hurricanes Georges and Opal. Georges was more destructive to the landscape than other

hurricanes in recent times. The working group was hesitant to estimate how much carrying capacity was lost. It took two years before mice started coming back, but some of them were fed supplementally, so these data may not fully reflect the time for habitat recovery. Opal destroyed about 80 meters of frontal habitat, and the habitat took two to three years to recover.

The group agreed that many factors influence the rate of recovery of beach habitats following a storm. For example, drought on the heels of Georges probably slowed habitat recovery rates; the amount of rainfall during and following the storms will generally have an effect; and clustering of storm events compounds recovery rates. Post-storm cleanup efforts also can slow the recovery of habitat and ABM, but the effects of these activities were not included in this ABM model.

There are some data that show 5 to 8 years are required for dune recovery. At Johnson Beach, dune recovery occurred in about 3 to 8 years. This was not total recovery of the dunes, however, but recovery to something close to what it was pre-storm. The group agreed that dune recovery can be manipulated, and that this is also a factor that needs to be considered. Human intervention/mitigation is an option that will be considered for future scenarios, but not used in the baseline scenario.

It is important to remember that all observational data reported here are based on recent level C1 or C2 storms. Damage due to higher-category storms could be phenomenally higher. Immediate effects and times to recovery of a C4 or C5 storm would be significantly different from what has been observed with smaller storms, and would affect ABM populations very differently.

First estimates of amount of habitat lost and recovery times were based on educated guesses and some historical observations. The amount of habitat lost and the recovery time (to full return to pre-storm carrying capacities for mice) were initially estimated per category of storm as:

TS-C1: 15% of habitat lost, 3yrs recovery
C2: 50% of habitat lost, 3 yrs recovery
C3: 65% of habitat lost, 5yrs recovery
C4: 90% of habitat lost, 50yrs recovery
C5: 98% of habitat lost, 100yrs recovery (*but see revised estimates, below*)

The structural and vegetative components of escarpment/scrub dunes would be severely damaged for high Category 3, 4 and 5 storms, so recovery times would be much longer for these more severe storms. It should be recognized that there is a big difference between a low and a high storm event even within any of these categories.

There is also the caveat that C4s and C5s may result in a permanent loss of some habitat and lower carrying capacity. The impacts of C4 and C5 storms may be similar, as climax vegetation and escarpment are lost in both. If sand remains, however, scrub or coastal vegetation may return as quickly as 5 to 8 years. Food would be available, but topography would take a lot longer (decades) to be restored.

For modeling purposes, it was necessary to define what is meant by post-hurricane recovery. Does recovery mean that the food source returns? Or habitat is restored to the extent that there is an ability to withstand another storm (original height of dunes)? There is agreement that return of the seral community does not equate to recovery. Upon further discussion of what recovery means, it was concluded it equates to a return to the pre-storm carrying capacity of the unit.

The group discussed whether recovery is a linear or non-linear process, and determined that it may not be linear because of confounding factors. A logistic recovery curve was chosen for the baseline model; both linear and logistic recovery curves were explored in sensitivity testing. The logistic recovery curve represents the case in which relatively little habitat recovery occurs in the first 25% or so of the total interval needed for recovery, most of the capacity of the habitat recovers relatively quickly during the middle years of recovery, and the completion of the last components of recovery occur slowly in the final 25% or so of the recovery period.

Site Specificity: Are some areas (model units) more vulnerable to storms? There was consensus that localized habitat quality, the extent of development, and other factors make some areas more vulnerable to both loss of ABM and ABM habitat. The working group decided that a relative index of resilience to storm events was the easiest way to address this factor.

If everything is scaled relative to the Perdue Unit (which has the best resilience) on a scale of 1 to 5, Table 4B shows the mean survival rates for a Category 2 storm and the percent of carrying capacity remaining immediately after a Category 2 storm. For other storm categories, and for the high and low values of survival, these rates were scaled among units in the same ratios as the survival rates shown below. For example, for a Category 1 storm, Perdue Unit is modeled as having 50% to 90% survival, while Fort Morgan and Gulf State Park would experience survival rates in the range of 10% to 18%.

Table 4B. Estimates for relative impact of hurricanes for each ABM model unit.

Model Unit	Resilience	Survival	Carrying Capacity
Fort Morgan	4	0.10	0.10
Single Family	5	0.05	0.05
Multifamily	2	0.40	0.40
Perdue	1	0.50	0.50
West Beach	5	0.05	0.05
Gulf State Park	4	0.10	0.10
Orange Beach	3	0.20	0.20

As reflected in the above table, Multi-Family and Perdue Units will be the least affected as they are more resilient, while other areas would have greater vulnerability. Survival will be variable (within the ranges to be specified for each category of storm), and this variability is assumed to be independent among units because of the specific interaction between the location of landfall and the habitat characteristics. For example, a given Category 2 storm could cause mortality toward the high end of the predicted range at Fort Morgan but at the lower end of the range of mortality estimated for Gulf State Park.

Further Discussions of Data for the Baseline Model

Storm Frequency

Because of some discomfort with the initial estimates of the frequency of hurricanes, the working group examined the estimates in the draft Cumulative Impact Assessment document. New estimates were also obtained from the National Hurricane Center representing the likelihood of a storm hitting Gulf Shores based on 1886-2002 unpublished data (Lawrence, pers. comm.). These data are summarized in Table 4C. The working group decided to use the storm frequency data provided by the National Hurricane Center, as they were most appropriate and specific to ABM. Dr. Lawrence from the National Hurricane Center agreed that these data are appropriate for estimating the likelihood of impacts on ABM and ABM habitat.

The ABM model in *Vortex* was constructed to restrict hurricanes to three of the 13 four-week time intervals modeled in each year (e.g., hurricanes are assumed to occur August through October.) Thus, in the model, the frequency of occurrence of each category of storm per time interval was set at one-third the rates listed in Table 4C so that the annual frequency of hurricanes would be as specified. Because catastrophes are independent random occurrences in *Vortex*, it would be possible (although relatively unlikely) in the simulation for two hurricanes of different magnitude to occur (with compounded impacts) in the same month, or for two or more hurricanes to occur in subsequent months of a hurricane season.

Hurricanes were assumed to hit all ABM units synchronously, but the severity (within the specified ranges) was set to be independent across units.

Table 4C. Probability of occurrence estimates for Category 1 – 5 hurricanes for ABM habitat.

	Probability of occurrence per year		
Storm Category	**Initial Estimate**	**CIA Estimate**	**NHC Estimate***
C1	0.25	0.10	0.125
C2	0.10	0.05	0.0625
C3	0.05	0.03	0.04
C4	0.025	0.016	0.021
C5	0.01	0.007	0.01

**Estimates used in the ABM Vortex model.*

Survival During Hurricanes

Table 4D provides the survival data as determined by the working group by model unit (scaled as in Table 4B) and by storm category. The group determined that these ranges of survival rates were still appropriate and should be used in the model.

Table 4D. Survival estimates for Category 1 – 5 hurricanes for each ABM model unit.

Model Unit	**C1**	**C2**	**C3**	**C4**	**C5**
Fort Morgan	0.10 – 0.18	0.02 – 0.18	0.01 – 0.05	0.0 – 0.02	0.0 – 0.01
Single Family	0.05 – 0.09	0.01 – 0.09	0.005 – 0.025	0.0 – 0.01	0.0 – 0.005
Multifamily	0.40 – 0.72	0.08 – 0.72	0.04 – 0.20	0.0 – 0.08	0.0 – 0.04
Perdue	0.50 – 0.90	0.10 – 0.90	0.05 – 0.25	0.0 – 0.10	0.0 – 0.05
West Beach	0.05 – 0.09	0.01 – 0.09	0.005 – 0.025	0.0 – 0.01	0.0 – 0.005
Gulf State Park	0.10 – 0.18	0.02 – 0.18	0.01 – 0.05	0.0 – 0.02	0.0 – 0.01
Orange Beach	0.20 – 0.36	0.40 – 0.36	0.02 – 0.10	0.0 – 0.04	0.0 – 0.02

Recovery of Carrying Capacity

An extended discussion of recovery times occurred during and following the PHVA workshop. Some discomfort was expressed in the plenary discussion that the initial estimates for C4 and C5 storm recovery times (shown in the second column below) were too long. A proposed estimate from some of the group members is represented in the third column below:

Storm Category	Initial Estimates	Proposed Estimates
C1	2-3yrs	5 yrs
C2	2-3yrs	8 yrs
C3	5 yrs	15 yrs
C4	50 yrs	25 yrs
C5	100yrs	35 yrs

Further discussion ensued. Recovery of escarpment after a C4 or C5 storm could take longer than recovery of typical dune habitat. At what category of storm do we lose the escarpment? For example, there is still damage apparent from Category 3 Frederic after 25 years, but the habitat might be considered to be recovered for ABM, as it is functioning now as good ABM habitat. Recovery times could depend on whether root stock was lost, as the habitat could take much longer to recover from those more severe storms that cause loss of root stock. A further confounding factor is the effect of subsequent storms that occur before full recovery from a prior storm.

The group felt that the recovery times for C4 and C5 storms are the most uncertain, as few such storms have occurred in the past century. A Category 4 storm hit in1906, and by about 80 years later the dunes appeared to have recovered. Category 3 Frederic hit in 1979 and effects were still evident three years later, but the habitat appeared to be largely recovered by the mid-1990s. The effects of Camille (C5, in 1969) are still evident 35 years later. The working group considered a reasonable estimate of the average time for full recovery from C4 and C5 storms to be intermediate between the values in the two columns in the above table, and set the values to 40 and 80 years for the two most severe categories of storms.

Following the workshop, this discussion continued among workshop participants via listserv. Consensus on this issue could not be reached, so two sets of recovery times ultimately were chosen for analysis: one set representing relatively fast recovery and one representing slower recovery of ABM carrying capacity following storms (Table 4E).

Table 4E. Time to recovery of habitat back to original carrying capacity for ABM following hurricanes.

Storm Category	Fast Recovery (years)	Slow Recovery (years)
C1	1	5
C2	3	8
C3	6	12
C4	20	25
C5	30	40

The working group also revisited the estimates of the average decrease in carrying capacity for each category of storm. Although some estimates were suggested, it was recognized that at the time of the workshop GIS work was underway to determine the relative amounts of habitat in each unit that would likely be lost in each category of storm. Subsequent to the workshop, these estimates were obtained and used in the final ABM *Vortex* model (Table 4F).

Table 4F. Estimates of reduction in ABM carrying capacity immediately following Category 1 – 5 hurricanes for each ABM model unit.

Model Unit	**C1**	**C2**	**C3**	**C4**	**C5**
Fort Morgan	0.690	0.810	0.890	0.925	0.933
Single Family	0.360	0.820	0.932	0.971	0.982
Multifamily	0.030	0.300	0.700	0.860	0.922
Perdue	0.040	0.270	0.840	0.900	0.938
West Beach	0.410	0.790	0.987	0.990	0.998
Gulf State Park	0.680	0.750	0.957	0.988	0.996
Orange Beach	0.680	0.750	0.957	0.988	0.996

Sensitivity Tests

The group discussed which model parameters are most uncertain, most likely to affect population projections, and therefore most important to examine in sensitivity tests. The time to recovery (fast vs. slow) and the shape of the recovery curve (linear vs. logistic) were recommended for testing.

Cautions

Most of the parameters estimated with relation to hurricanes are uncertain and variable depending upon a multitude of factors, including the intensity, direction of movement, and landfall location of the storm. Particularly challenging to quantify are the impacts of hurricanes on ABM habitat, carrying capacity and populations. The working group chose to use what they believe to be the best current estimates of these parameters for the *Vortex* model; subsequent revision is likely and desirable as new storm damage models and additional data become available.

Other Potential Catastrophes

The following impacts were discussed, but none was determined to meet the definition of “catastrophe” as used in the *Vortex* model (a year in which rates of mortality or reproduction lie outside of the normal year-to-year variation in these rates) and so were considered components of the environmental variation incorporated into the model.

Drought

Primary and secondary dunes are more resilient in a drought, but food resources in the scrub may be more affected. Anecdotal information leads FWS Daphne Field Office staff to be concerned whether carrying capacity of those areas would be substantially reduced. This does not need to be modeled as a catastrophe in the model if this variation is captured in the environmental variability already in the model.

Fire

Would severe drought in scrub areas contribute to more severe wildfires? Fire does not spread well in dune habitat and could produce some positive as well as negative effects. On the positive side, fire would remove the duff layer that may be affecting seed production. A negative impact is the invasion of cogongrass, which provides no value to ABM. The presence of this introduced grass in Fort Morgan could produce very intense fires that are not natural. This in turn would open up other areas to cogongrass invasion, which benefits from disturbance. This scenario may be better addressed as a long-term carrying capacity issue, within one of the management scenarios to be modeled later (see Section 5).

Tornados

Tornados were not further discussed because they are assumed to be incorporated into tropical storm events and are not a likely phenomenon affecting ABM.

Prolonged Rain

While it is agreed that prolonged rains can have negative effects on ABM (some will be flooded out and food resources may temporarily decline), they are not considered to affect ABM populations significantly enough to require inclusion as a separate catastrophe in the model.

Disease

The group consensus was that disease is not an issue or threat for this species at this time. There is no evidence of any diseases decimating populations of ABM.

Feral Cats

Feral cats have a significant negative effect on ABM and all beach mice populations. There is ample evidence of feral cats predating beach mice, and several instances of known loss of populations that can be at least partially attributed to the presence of feral cats on or adjacent to beach mouse habitat at both Perdido Key and Gulf State Park. The working group determined, however, that feral cats do not fall under the category of a catastrophe, but rather fall under the realm of a long-term management and carrying capacity issue (see Section 5). If management of cats, through removal and trapping programs, is not routinely and comprehensively utilized, the effects of feral cats may become catastrophic.

Other Exotic Species

Currently exotics are being managed/controlled and, therefore, do not meet the definition of a current catastrophic event within our baseline scenario.

Loss of Fort Morgan Peninsula Lease

Currently Bon Secour National Wildlife Refuge manages the land at the Fort Morgan Peninsula even though it is owned by the State Park. This lease is due to expire soon and has not yet been renewed. The working group recommended that the current conditions should be used in the baseline model, as the land is currently secure and in public ownership. This potential future threat does not meet the definition of a catastrophe, although it was agreed that loss of this land from public ownership in the future could be significant. Further exploration of the effects of changing control of Fort Morgan or other areas can be considered within development/ management scenarios to be modeled (see Section 6).

Erosion

Many beaches where ABM and other beach mice exist are currently experiencing erosion, some significantly. However, serious erosion problems and management of this erosion on Cape San Blas, where there is a population of St. Andrew beach mice, indicate that human intervention in the form of beach nourishment is maintaining the beach area, and also that there is a change in building activity farther back from the water. Current erosion issues are being dealt with adequately and do not rise to the level of catastrophic events.

References

Lawrence, M. 2004. Personal communication. National Hurricane Center.

Alabama Beach Mouse PHVA

Point Clear, Alabama
June 8-11, 2004

FINAL REPORT

SECTION 5

Mitigation & Invasive Species WG Report

Hurricane Mitigation/Invasive Species Working Group Report

There are several alternative future scenarios that differ from the baseline model that might impact the ABM population. Some of these include future development, which were explored by the Development Working Group (see Section 6). Other possible alternative scenarios include mitigating the impacts of hurricanes through habitat restoration and other techniques, and the potential escalating effects of invasive species on ABM populations. This working group attempted to quantify these alternative scenarios for exploration using the ABM *Vortex* model.

Mitigation of Hurricane Impacts

These scenarios encompass a variety of methodologies that might be used in attempt to lessen the impacts of hurricanes on the viability of ABM populations. Methods identified for exploration including those addressing habitat restoration (sand fencing, planting and fertilization of vegetation, and beach nourishment) and others directly aimed at ABM populations (supplemental feeding and translocation).

Sand Fencing, Planting and Fertilization

This is a possible management scenario following a hurricane in which snow fencing is placed in an optimal location and pattern to promote dune development. Vegetation is planted, and a 13-13-13 fertilizer is applied to improve plant growth. Beach restoration with sand fencing, planting and fertilization can be very effective, improving dune habitat and shortening the time of habitat recovery. Sand fencing is not a one-time action but rather requires repeated maintenance and funding. Limited availability of fencing and plants can be a constraining factor. This technique is applicable to all model units and could include the restoration after a hurricane of areas that previously consisted of sod or palms.

Sand fencing would not provide much benefit with relation to Category 1 storms. A greater benefit would be expected with more severe storms in which the vegetation root system is lost. The working group suggested changes in recovery time for various hurricane levels for the modeling of this mitigation strategy:

Category 1: No effect (keep recovery time of 5 years)
Category 2: Change recovery time from 8 to 6 years
Category 3: Change recovery time from 15 to 10 years
Category 4: Change recovery time from 40 to 35 years
Category 5: Change recovery time from 80 to 70 years

Post-workshop discussions led to the development of two revised recovery schedules (see Section 4). Restoration was modeled by shortening recovery times as outlined in Table 5A.

It was noted that with Category 4 or 5 hurricanes there would be a need for massive beach nourishment. None of the nurseries may be able to provide all of the sea oats needed after a major hurricane event. The magnitude of effort that would be needed to bring an area back to pre-storm conditions would be massive and problematic (e.g., still problems with damage from Camille even after 35 years).

Table 5A. Years to recovery of habitat back to original carrying capacity with restoration.

	Fast Recovery		**Slow Recovery**	
Storm Category	**Baseline**	**Restoration**	**Baseline**	**Restoration**
C1	1	1	5	5
C2	3	2.5	8	6
C3	6	4	12	8
C4	20	15	25	20
C5	30	25	40	35

Beach Nourishment

This technique of adding sand to build beaches is more of a recreation management tool rather than a habitat-building tool but could possibly be used to promote habitat restoration, serving as a source of wind-blown sand for future dune growth. This action also could be considered a preventative measure by providing a buffer that would sustain storm surges that could affect existing ABM habitat; however it was thought that Category 4 or 5 storms would wash over nourished areas. There was some concern that beach nourishment could have an adverse effect on ABM populations by producing salt spray and perhaps using a different type of sand. This method would be applicable to all model units.

After some discussion the working group decided that the recovery times cited for the fencing and vegetation restoration efforts above would not change with beach nourishment. Therefore, this will not be modeling as a separate management strategy but lumped together with other habitat restoration efforts.

Supplemental Feeding

Supplemental feeding is the provisioning of sunflower seeds after a hurricane to augment food supplies for mice. Seeds are provided for about three months following a hurricane event. This is thought to improve ABM survival until natural food sources begin to recover; however, there are no data to support or refute this. This strategy would be applicable to all model units.

In effect, supplemental feeding artificially increases carrying capacity immediately following a hurricane. This could perhaps be modeled by reducing the impact of the storm event (i.e., reducing the reduction in K), but the working group felt that the effect would only be marginal and was not sure how to quantify this. It may be that if supplemental feeding were successful, it would just buffer against further decline in the resulting small ABM populations due to other stochastic events. As the impact on the ABM population is unsubstantiated and believed to be small, the working group chose not to assign values to model this strategy.

Translocation

This technique involves the translocation of ABM from a sufficiently large and viable donor population to augment or re-establish an extirpated ABM population. Such an effort would follow established guidelines and protocols for translocation. According to these guidelines a donor population must have at least 50 individuals, in which case three pairs could be removed.

The larger the donor population, the more individuals can be removed if needed, up to 60% of donor populations comprised of over 80 individuals.

It was decided to model this management scenario in the following manner:

1. Supplement a model unit when its ABM population has been extirpated. This would be a one-time supplementation occurring within one year after extirpation. The working group recommended that supplementation occur two years after extirpation (asserting that two years would be needed for the habitat to recover sufficiently from a hurricane to support an ABM population); however, this delay proved challenging to model. Supplementation was modeled more optimistically as occurring the next November following extirpation (Vortex time step 13, 26, etc.).

2. Supplement the model unit with male and female sub-adult mice. In reality, adults may also be used in translocation efforts, but for simplicity sub-adults will be used in the model. Trapping mortality should be very low, as well as mortality due to translocation into unoccupied habitat; therefore no additional mortality is included in this scenario.

3. Supplement with 19 male and 19 female mice in the model. This represents an actual translocation of 25 male and 25 female mice. In the *Vortex* model, supplementation occurs after mortality is imposed for that year. In the real world, if 50 sub-adult mice (25 pairs) were translocated, about 25% of them would be expected to die prior to breeding during the next 28 days (i.e., '*Vortex* year'), leaving 38 individuals (approximately 19 pairs). To match this life history, it is necessary to account for this mortality and enter the number of individuals that would survive to potentially breed. Therefore, in the *Vortex* model 19 male and 19 female sub-adult mice are supplemented.

4. For model simplification, the supplemented mice were not removed from an existing ABM model unit but were modeled as if available from an outside unrelated source population. The model assumes that mice used for supplementation are unrelated from mice in the recipient population or from each other.

The resulting mechanism used to simulate translocation in the model is a simplification of the many complexities of translocation activities (e.g., reduction in the lag time between extirpation and supplementation, unlimited availability of donor mice, no effects of the removal of mice on the donor population). These simplifications may portray an optimistic view of the potential impacts of translocation on ABM populations.

Invasive Species

Cogongrass

Cogongrass (*Imperata cylindrica*) is an exotic Asian grass species. This perennial is fire-tolerant and has the ability to dominate habitats quickly. It is high in silica and is not a food source for ABM, outcompeting other food species. Cogongrass is expensive to control and requires repeat applications of an expensive herbicide. This species has been observed in all parts of the ABM range and has been sited in the dune habitat this year for the first time.

Attempts continue to control the spread of cogongrass; however, it is possible that this species might not be completely contained. The working group recommended a modeling scenario in which the invasion of cogongrass results in the loss of 1% of ABM habitat each year, ultimately completely eliminating natural vegetation that can support ABM populations. This was modeled as a 1% reduction in K in each model unit per annual year continually into the future.

Domestic Cats

Predation by domestic cats can impact ABM populations. One of the problems is that cats do not kill necessarily for food; their predatory response can be triggered by a mouse regardless of their hunger level, and so even cats that are well fed may kill mice. The effect of predation by cats was not included in the baseline mortality rates and would be an additive source of mortality across all age classes.

Cat predation is more likely to be a problem in developed areas of ABM habitat, but it was recognized that some people may try to establish feral cat colonies on public lands, so all model units are vulnerable to this threat. Trap-neuter-release programs for feral cats are increasing along the Gulf Coast. The ABM population on Ono Island and the Perdido Key beach mouse populations at Florida Point may have been eradicated by cats.

The working group first considered modeling two scenarios: a low level of predation (few cats) and a high level of predation (large number of cats). Little data, however, are available both in terms of the number of cats present or likely to be present in the future. After some discussion the group recommended that sensitivity testing be used to determine the level of cat predation that would lead to extirpation of ABM populations. Based upon the experiences at Ono Island and Florida Point, ABM extirpation is considered to be a very possible outcome for a model unit.

Kill rates of ABM by cats are also unknown, particularly if cats are not killing for food. Pearson (1964) found that six cats were primarily responsible for the loss of 4200 mice from a 35-acre plot over an eight-month period, suggesting a kill rate of almost 3 mice per cat per day. In a study in Michigan one well-fed cat was observed to kill at least 60 birds and 1600 small mammals in an 18-month period, again averaging about 3 small mammals per day (Schaefer, 1999). The working group decided to model each cat killing one mouse per day as a reasonable estimate of possible cat predation levels on ABM. Cat predation scenarios were recommended to be modeled as the harvest of one mouse per cat per day in each model unit across all ABM age and sex classes. Suggested numbers of cats for sensitivity analysis are 5, 10, 15 and 20 cats per model unit.

House Mice

The house mouse (*Mus musculus*) is an introduced rodent species that is typically found in close proximity of areas of human development. House mice have been captured in many areas, including in the Fort Morgan model unit (along the road, in the fort and in the scrub habitat), in Gulf State Park (near the pier and motel units), and near the Single Family homes of Laguna Key. Individuals are usually euthanized by the trapper if encountered. Native mouse species usually outcompete house mice outside of human-inhabited areas, and ABM can probably outcompete them except under certain circumstances (e.g., low ABM population densities).

Some suspect that male house mice may be able to outcompete ABM males in low densities. This would be in the form of competition by males for females, with male house mice collaring females into harems. This could possibly be modeled as an increased Allee effect in density-dependent reproduction, whereby reproductive success declines in low density situations.

References

Pearson, O.P. 1964. Carnivore-mouse predation: An example of its intensity and bioenergetics. *Journal of Mammalogy* 45(2): 177-188.

Schaefer, J. 1999. Impacts of free-ranging pets on wildlife. Document WEC-136. Department of Wildlife Ecology and Conservation, Florida Cooperative Extension Service, University of Florida.

Alabama Beach Mouse PHVA

Point Clear, Alabama
June 8-11, 2004

FINAL REPORT

SECTION 6

Development Scenarios Working Group Report

Development Scenarios Working Group Report

Alternative Scenarios

This working group initially met to discuss and delineate the various categories of alternative scenarios that should be considered for modeling using the ABM *Vortex* model. The following types of scenarios were recommended:

1. Development
   Multiple development scenarios should be modeled, both with and without management/mitigation (e.g., predator control, landscaping with native vs. non-native species). The focus should be on the following model units: Fort Morgan, Single Family, Multi-Family, and West Beach. Resources for this discussion include the draft CIA and zoning maps. Possible development scenarios include: no further development; pending development; and 25%, 50%, 75% and 100% development of developable areas.

2. Hurricane Impact Mitigation and Restoration
   Existing conditions should be modeled with and without mitigation/restoration efforts, which include sand fencing, fertilizing on dunes, and beach nourishment. All model units should be considered.

3. Invasive Species Management
   Loss of habitat may occur due to invasive exotic species such as cogongrass, which has been observed in ABM habitat. Other exotic species that might negatively impact ABM populations include domestic cats and house mice. All model units should be considered.

At this point it became necessary to divide these topics for discussion in new working groups that included all workshop participants. It was decided to have one working group focus on development scenarios (presented in this report), while a second working group discussed hurricane mitigation/restoration and invasive species impacts (see Section 5). Both working groups considered the effects of each scenario on ABM carrying capacity, survival, reproduction, dispersal, and impacts from hurricane events.

Development Scenarios

The working group identified and discussed seven potential development scenarios to explore through modeling and to compare with the baseline model (which assumes no further development). For each scenario, the impacts that development would have on ABM were considered with respect to carrying capacity, survival and inter-unit dispersal.

It was noted that critical habitat designation may be possibly expanded in the future. Although only 500 feet from high tide is currently designated, ABM populations do use areas outside of this zone and could be negatively impacted by development in those areas.

The seven development scenarios that were identified are:

<u>For Single Family/West Beach model units:</u>

- **SF/WB – 1A**: Existing regulations with all lots developed with minimal footprint (to promote ABM protection).
- **SF/WB – 1B:** Existing regulations with all lots developed with no ABM protection.
- **SF/WB – 2A1:** Convert from low density Single Family to high density Single Family housing such as may occur when the sites transition from Baldwin County to Gulf Shores jurisdiction.
- **SF/WB – 2A2:** Rezoning to allow for multi-family condominiums. This can be broken down even further. Baldwin County has a maximum limit of six units per acre, while Gulf Shores has higher density but requires more landscaping.

<u>For Fort Morgan/Gulf State Park model units:</u>

- **FM/GSP – 3A**: Increased park infrastructure and improved ABM management (e.g., widening of road, parking lots in ABM habitat).

<u>For Multi-Family model unit:</u>

- **MF – 4A:** Gulf Highlands (196-acre site) condominium development only, with ABM management; remaining acreage of Multifamily model unit undeveloped.
- **MF – 4B:** Gulf Highlands condominium developed plus additional single- and multi-family homes, with management on the remaining 300 acres.

The following sections describe each development scenario, the estimated impacts on the ABM population, and the rationale used in estimating these impacts (see Table 6A for summary). An "A" designates scenario with management for ABM populations, while "B" designates those with no ABM management in developed areas. For each scenario, the impacts of development on carrying capacity and survival are described. The working group also discussed possible impacts on inter-unit dispersal, but it was decided that there was no additional effect beyond the reduction in survival already estimated.

Single Family and West Beach Model Unit Development

<u>Scenario SF/WB - 1A</u>

Description: All lots are developed according to existing regulations, with minimal footprint to promote ABM protection.

Carrying capacity: There will be a loss of carrying capacity (K) as lots are developed, even using minimal footprints. The loss of K is based on the development of 40 lots per year for 20 years with a loss of 0.1 acre of impacts per lot, resulting in an 80-acre loss (approximately 10%) in the Single Family model unit. In West Beach the working group estimated a 10% decrease in ABM carrying capacity.

Survival: There would be an estimated decrease of 10% in survival with the full build-out under this scenario. While there would still be remnant patch habitat and corridors, ABM would have to travel and disperse over greater distances and would be subject to increased predation.

Scenario SF/WB – 1B

Description: All lots are developed according to existing regulations, with no ABM protection.

Carrying capacity: The development of all lots would translate into about a 90% loss of habitat in the Single Family model unit, with about 10% of the habitat remaining in the area south of the CCCL (Coastal Construction Control Line). In West Beach the group estimated that 85% of the area could be developed since the lots are longer and more of the habitat would be preserved below the CCCL.

Survival: There would be a decline in survivability due to the fragmented nature of the habitat and the ability of private citizens to walk in the dunes and to bulldoze dunes below the CCCL that adversely affect the view of the ocean from the residences. Decline in survival is estimated at 80% in the Single Family model unit and 75% in the West Beach model unit.

Scenarios SF/WB – 2A1 and 2A2

Description: Under these scenarios, Single Family areas would be rezoned/redeveloped to allow more intensive multi-family development with ABM protection. This can be divided into two separate scenarios: 1) low density Single Family to higher density Single Family areas (2A1); and 2) redevelopment into multi-family condominiums (2A2). Scenario 2A2 can also be broken down even further. Baldwin County has an upper limit of six units per acre, while the city of Gulf Shores allows a higher density but requires more landscaping.

SF/WB – 2A1 (high density Single Family development)

Carrying Capacity: There would be an estimated loss in K of approximately 20% in the Single Family model unit if it goes from Single Family development under Baldwin County to Single Family development under Gulf Shores. Carrying capacity for West Beach model unit would remain the same since its already part of Gulf Shores and additional zoning changes are unlikely.

Survival: No effect on survival is anticipated under this scenario.

SF/WB – 2A2 (multi-family condominiums)

Carrying Capacity: Redevelopment of a previously developed Single Family area could result in a net increase of habitat due to the requirement for mitigation to maintain an excess of habitat acreage and could lead to an increase in K. It is anticipated that any professional developer would approach redevelopment with the clear understanding that any proposal would require mitigation in excess of minimization. On the other hand, such development might lead to a loss of K, since multi-family areas would have more individuals, more vehicles, more need for night lighting, more trash, and more people potentially traversing the remaining ABM habitat. Sensitivity testing is needed for this scenario to explore the possible range of impacts and should range from –10%, 0 and +15% change in K for Single Family and from –10%, 0 and +10% for West Beach model units.

Survival: No effect on survival is anticipated under this scenario.

Fort Morgan and Gulf State Park Model Unit Development

<u>Scenario FM/GSP – 3A</u>
Description: Increased park infrastructure and improved management.
Carrying capacity: Increases in infrastructure may result in either an increase or decrease in ABM and carrying capacity. With the current park proposal being discussed, there would be a net increase of 3% in K in Gulf State Park as a result of this project. The suggested impact of this scenario on K for modeling purposes is a 2% reduction in Fort Morgan model unit and a 3% increase in Gulf State Park.
Survival: No effect on survival is anticipated under this scenario.

Multi-Family Model Unit Development

<u>Scenario MF – 4A</u>
Description: Gulf Highlands condominium development (196-acre site) with management, with the remaining acreage of the Multi-Family model unit left undeveloped.
Carrying capacity: About 59 acres would be impacted under the current proposed development scenario, resulting in a loss in K of about 10% in this model unit.
Survival: No effect on survival is anticipated under this scenario.

<u>Scenario MF – 4B</u>
Description: Gulf Highlands condominium development (196-acre site) plus additional Single Family and multi-family homes with management on the remaining 313 acres in this unit.
Carrying capacity: Development of the remaining 313 acres in this model unit outside of Gulf Highlands would result in a loss of habitat and carrying capacity. If the portion of the Multi-Family model unit outside of the Gulf Highlands area were developed as Single Family homes, there would be an estimated decrease in K of 35% for the entire model unit.
Survival: No effect on survival is anticipated under this scenario.

Additional Vortex Scenarios

Each of the seven individual development scenarios listed above were run using the ABM *Vortex* model. In addition, the following combinations were run to represent development across multiple model units:

Anticipated development: 1A, 3A & 4A
Worst-case scenario: 1B & 4B

In addition, a scenario (K1) was run in which all model units lost 1% of ABM habitat (carrying capacity) to assess the effect of a widespread small reduction in K due to management or development activities (e.g., issuance of Incidental Take Permits).

Table 6A. *Vortex* input values for alternative development scenarios.

Development Scenario	**Effect on**	
	Carrying Capacity	**Survival**
SF/WB – 1A. Development (ABM protection) All lots developed under existing regulations with minimal footprint and ABM protection	SF: ↓10% WB: ↓10%	SF: ↓10% WB: ↓10%
SF/WB – 1B. Development (no protection) All lots developed under existing regulations with no ABM protection	SF: ↓90% WB: ↓85%	SF: ↓80% WB: ↓75%
SF/WB – 2A1. Multi-family rezoning Rezoning from Single Family low density to Single Family higher density (e.g., transition from Baldwin Co to Gulf Shores jurisdiction)	SF: ↓20% WB: No impact	No impact
SF/WB – 2A2. Redevelopment to condos Redevelopment to multi-family condominiums. Gulf Shores allows a higher density than Baldwin County but requires more landscaping.	Sensitivity tests SF: ↓10, 0, ↑15% WB: ↓10, 0, ↑10%	No impact
FM/GSP – 3A. Increased infrastructure Increased park infrastructure and improved management	FM: ↓2% GSP: ↑3%	No impact
MF – 4A. Gulf Highlands only Gulf Highlands Condominium development only, with management; remaining acreage of MF unit undeveloped	↓10%	No impact
MF – 4B. Gulf Highlands & additional homes Gulf Highlands Condominium developed PLUS additional SF and MF homes with management on the remaining 313 acres	↓35%	No impact

Cautions

The development scenarios described here and their impacts upon the ABM population have been estimated as accurately as possible at the time of the PHVA workshop. Reductions in K were extrapolated from anticipated reductions in ABM habitat due to development, and reductions in survival were based upon expected impacts of human disturbance in each scenario. The working group recognized that further development may impact ABM populations in other ways as well. Most notable of these is the possible increased vulnerability of ABM to hurricanes. If development occurs primarily in high elevation areas that are believed to act as refugia for ABM during storm events, then the number of ABM that survive storms may be further reduced. This effect is currently not incorporated into the *Vortex* model but could be added with a substantial increase in model complexity.

Alabama Beach Mouse PHVA

Point Clear, Alabama
June 8-11, 2004

FINAL REPORT

SECTION 7

Vortex Model Input and Results

Vortex Model Input and Results

Vortex Simulation Model

Computer modeling is a valuable and versatile tool for assessing risk of decline and extinction of wildlife populations. Complex and interacting factors that influence population persistence and health can be explored, including natural and anthropogenic causes. Models can also be used to evaluate the effects of alternative management strategies to identify the most effective conservation actions for a population or species. Such an evaluation of population extinction risk under current and varying conditions is commonly referred to as a population viability analysis (PVA).

To examine the viability of the Alabama beach mouse population, we used the *Vortex* simulation software program. *Vortex* is a Monte Carlo simulation of the effects of deterministic forces as well as demographic, environmental, and genetic stochastic events on wild populations. *Vortex* models population dynamics as discrete sequential events that occur according to defined probabilities. The program begins by creating individuals to form the starting population and stepping through life cycle events (e.g., births, deaths, dispersal, catastrophic events), typically on an annual basis. Events such as breeding success, litter size, sex at birth, and survival are determined based upon designated probabilities. Consequently, each run (iteration) of the model gives a different result. By running the model hundreds of times, it is possible to examine the probable outcome and range of possibilities. For a more detailed explanation of *Vortex* and its use in population viability analysis, see Appendix II.

Development of the Baseline Model

A draft baseline model was developed prior to the PHVA using input data provided by the FWS and the ABM Recovery Team. This draft model then was presented in the opening plenary session of the PHVA workshop and served as a springboard for discussion and a template for building of the consensus model by workshop participants.

The ABM *Vortex* model was first discussed in detail in plenary to determine as many input values as possible. During this process many areas of uncertainty were identified that required additional discussion in small groups. Working groups used available published and unpublished information as well as expert opinion to determine the best strategies and values for modeling population structure, demography and catastrophic events (see Sections 2 through 4 of this report). Some of these discussions continued after the PHVA workshop via listserv before the final model input values were agreed upon.

Working groups also convened to determine additional scenarios to model for comparison to the baseline model. These included the potential impacts of invasive species, possible management strategies, and future potential development of ABM habitat (see Sections 5 and 6). Again, these discussions were initiated during the workshop and were finalized via listserv composed of all workshop participants.

Model Input Values

The final values used in the baseline model are summarized below. Detailed explanations of input values can be found in the five working group reports (Sections 2 – 6).

Number of iterations: *1500, 500, or 250*
1500 independent iterations (runs) were completed for each baseline scenario (fast and slow logistic recovery rates); 250 iterations for the scenarios with linear fast and slow recovery); and 500 iterations for the other scenarios used for testing sensitivity to demographic rates, impacts of development scenarios, and effects of possible management actions. These numbers of iterations were sufficient to provide indications of which factors had large effects, but the model results do not distinguish among scenarios with small effects. For example, scenarios that differ in the probability of metapopulation extinction by 2% (e.g., a shift from 20% to 22% probability of extinction) cannot be reliably discriminated in our results, as the standard error of the difference was typically about 3%.

Number of years: *100 calendar years*
Due to the relatively short generation time for this species, life history events were modeled in four-week time steps rather than 365-day intervals. Therefore, iterations were run for 1300 time steps to project population trends for 100 years.

Extinction definition: *Only one sex remaining*

Number of populations: *7*
The ABM metapopulation was modeled as seven partially connected subpopulations to allow the geographical and management differences across the ABM range to be incorporated and to make it possible to test different future scenarios with respect to these areas. In most cases these areas do not describe biologically separate populations but instead reflect geographical management units, termed *model units*. Model units were defined as discrete ABM habitats having distinct geographic and/or similar threats within the historic range of ABM. Although Ono Island was originally identified as a potential model unit, it was removed from the analysis as it was not included in any of the defined scenarios to be tested (see Section 2 for details).

Inbreeding depression: *Yes*
Inbreeding is thought to have major effects on reproduction and survival, especially in small populations, and so was included in the model (as reduced survival of inbred offspring through their first year). The impact of inbreeding was modeled as 1.8 lethal equivalents, which is the value reported for the Santa Rosa beach mouse ((*P. p. leucocephalus*). The inbreeding effect was specified to be due entirely to recessive lethal alleles (100%). This optimistic assumption was made to allow the simulations to run much more quickly, as this parameter has little effect in large populations.

Concordance between environmental variation in reproduction and survival: *Yes*
It was believed that there is a correlation between environmental conditions that affect survival and reproduction for beach mouse (years that are good or bad for survival tend to also be good or bad for reproduction).

EV correlation among populations: *0.5*
The model includes a moderate correlation between variation in birth and death rates among all model units (populations). A correlation of 0.5 was selected as reasonable for this size species over the distance covered by ABM habitat across the Fort Morgan Peninsula.

Number of catastrophes: *5*
Hurricanes were the only catastrophe included in the model. Each category of storm (1-5) was modeled as a separate type of catastrophe to allow for differences in frequency of occurrence, severity of impacts, and habitat recovery time.

Dispersal Among Populations: *0 to 2.43%*
This parameter describes the movement of ABM from one model unit to another model unit. There is little evidence of long-distance movement in beach mice, so inter-unit movement represents normal dispersal by sub-adults to establish a home range outside of their natal home range and in cases in which such dispersal causes them to cross an inter-unit boundary. No additional mortality was imposed, as movement across these boundaries is assumed to be no riskier than movement within model units. The percent of each model unit sub-adult population that disperses into the next model unit was calculated based up the probability of dispersing distances less than or greater one home range and the percent of the ABM model unit population calculated to live within dispersal distance of inter-unit boundaries (see Section 2 for details and values). Inter-unit dispersal rates range from 0 to 2.43% of sub-adult mice.

Mating system: *Long-term polygyny*
Monogamy is modeled in *Vortex* such that one adult male and one adult female are paired for one (short-term) or many (long-term) breeding seasons. Unpaired females have no opportunity of mating, and so the population can be limited by a shortage of either sex. ABM are typically considered to be monogamous, with male mice contributing to parental care. However, males will also breed with unpaired females. To more accurately represent the consequences of the mating system in the ABM model, mating is modeled as long-term polygyny so that reproduction will not be male-limited.

Age of first reproduction: *3 time steps (84 days)*
Vortex defines reproduction onset as the time at which offspring are born, not the age of sexual maturity. The model uses the mean age of first reproduction (parturition) rather than the earliest recorded age of offspring production.

Maximum age of reproduction: *19 time steps (532 days, or approx. 1.5 years)*
Vortex assumes that animals can reproduce throughout their adult life. Mice can live and breed beyond 2 years in lab conditions, but few individuals are likely to live beyond one year in the wild. Although the maximum age of reproduction was set at 1.5 years, the mortality rates used in the model result in few mice surviving past one year.

Maximum litter size/litter distribution: *8*
Values for litter size were taken from the distribution of litter sizes observed for 413 non-inbred litters of *P.p. leucocephalus*. This distribution was 3.15%, 5.08%, 20.34%, 27.85%, 28.09%, 12.35%, 2.91%, and 0.23% for 1 to 8 pups, respectively, resulting in a mean litter size of 4.23.

Sex ratio at birth: *50% male*

Density-dependent reproduction: *Yes*

Density-dependent reproduction has been observed in *Peromyscus*. Density dependence is defined by specifying parameters of a particular functional shape for the relationship between population density and breeding success. The curve that is often used to represent the functional relationship is: % breeding = $[(P_0-(P_o-P_k)*(N/K)^B)] * (N/(N+A))$. The nature of this curve was thought to differ in Fort Morgan and Multi-Family model units than in the other five units. The following parameter values were used in the model (see Section 3 for further discussion):

P_0	Specifies the % of adult females breeding in an average year when population density is very low relative to the food supply and carrying capacity of the habitat. Set at 70% based on data from *Peromyscus* populations (90% for Fort Morgan).
$P_k=30$	Specifies the breeding rate (% females breeding each year) when the population is at its carrying capacity. Set at 30% based on data from *Peromyscus* populations.
$A=1$	Defines the Allee effect (difficulty in finding mates at low densities, < 10 mice).
B	Defines the steepness with which breeding decreases as population approaches K. Set at B = 3 for most model units; set to a steeper value for Fort Morgan (B = 0.5) and Multi-Family (B = 1) units.

Environmental variation in breeding rate: *17%*

ABM populations have been observed to fluctuate seasonally, with the highest populations observed in the late winter/early spring and the lowest numbers in late summer/early fall. An oscillating sine wave was used to represent seasonal fluctuations in reproduction (see Section 3).

Monopolization of breeding: *95%*

There is little evidence for social prevention of mating (e.g., dominance). Most males are believed to have the opportunity to breed; although only about 70% of males examined were reproductively active based on categorization of abdominal vs. scrotal males, abdominal males can quickly come into breeding condition if a female is available.

Mortality: *See below*

Sub-adult and adult mortality rates and environmental variation were calculated from data from ABM populations in Perdue and Fort Morgan units. Mortality was observed to be highest in summer. Juvenile mortality rates were taken from laboratory data and modified to include higher summer mortality, resulting in the following rates used in the model:

	Fall/Winter/Spring		Summer	
Age class	% Mortality	SD (%)	% Mortality	SD (%)
0 – 1 (0-28 days)	36.2	14.4	52.5	14.4
1 – 2 (29-56 days)	21.1	14.4	30.3	14.4
2+ (>56 days)	16.1	10.6	23.7	10.6

Catastrophes: *Yes (5), variable effects*

Five categories of storms were modeled as global catastrophes (i.e., hurricanes hit all model units synchronously) occurring only in August through October. Probability of occurrence was based on site-specific estimates by the National Hurricane Center. Hurricanes affect ABM survival and carrying capacity but not reproduction in the model. These effects differ by model unit, as some units are more resilient to storm damage. Impacts on carrying capacity are constant for each storm category and model unit combination; the effect on ABM survival is variable within a specified range (Section 4). Recovery of carrying capacity to pre-storm levels varies based on the storm category; two recovery timelines were modeled (fast and slow) using a logistic curve.

Category	Frequency	Fast Recovery (yrs)	Slow Recovery (yrs)
C1	1 in 8 years	1	5
C2	1 in 16 years	3	8
C3	1 in 25 years	6	12
C4	1 in 47 years	20	25
C5	1 in 100 years	30	40

Carrying capacity (K): *Subpopulation specific*
The carrying capacity for each model was based upon estimates of the amount of suitable ABM habitat and ABM density for each model unit, as listed below (see Section 2 for details). No environmental variation was included for carrying capacity, as year-to-year variation in K was not considered to be a factor in the absence of hurricane impacts and recovery. No future trend in K was added to the baseline model; a potential decline in K due to the invasion and spread of cogongrass was modeled as an alternative scenario.

Model unit	Carrying capacity
Fort Morgan	2019
Single Family	6039
Multi-Family	3335
Perdue	9713
West Beach	1249
Gulf State Park	496
Orange Beach	62

Initial Population Size (N): *Subpopulation specific*
There are no accurate estimates of ABM population sizes. High population estimates in recent years suggest that ABM may have been near or at carrying capacity prior to Hurricane Ivan. For the baseline model, initial population sizes were set at carrying capacity. *Vortex* distributes the specified initial population among age-sex classes according to a stable age distribution that is characteristic of the mortality and reproductive schedule described for the model.

Harvest: *None*
Trap mortality is negligible and does not need to be included in the model. There is no additional harvest. Predation by cats is modeled as a separate scenario and not included in the baseline.

Supplementation: *None*
The addition of individuals to the population from captivity or other sources was not included in the baseline model but was modeled as a potential management option (via translocation).

Parameters Varied During Sensitivity Testing

Due to the uncertainty surrounding many of the demographic and population values estimated for the ABM *Vortex* model, sensitivity testing was conducted to explore the sensitivity of the model results to a range of plausible values for mortality, population size, carrying capacity, inter-unit dispersal, and recovery from hurricanes. The following values were tested (baseline values are in **boldface**). All models were run with both fast and slow recovery times.

Initial population size:	50% K, 75% K, **100% K**
Carrying capacity:	50%, 60%, 70%, 80%, 90%, **100%** (of original estimated K)
Mean juvenile mortality:	30%, **40%**, 50%
Adult mortality (non-summer):	14.1%, **16.1%**, 18.1%
Inter-unit dispersal:	50%, **100%**, 200% (of original estimated rates)
Recovery curve:	**Logistic**, linear

Caveat Regarding Results of Simulation Modeling

It is important to recognize that the results presented in this workshop report will not be precise enough to reveal slight shifts in expected population viability, nor to allow discrimination among scenarios that produce largely overlapping distributions of projected outcomes. The populations of Alabama beach mice, both in nature and in the computer simulations, are subject to large, unpredictable fluctuations – due to the combination of seasonal changes in survival and breeding, large fluctuations in population performance due to random environmental variation over time, and periodic decimation of numbers of mice and habitat by hurricanes. Thus, even 500 iterations of a simulation (considered adequate for describing viability of most species) still results in an uncertainty of several percent in the probability of taxon extinction, an uncertainty of about ± 5% in the mean numbers of mice expected in the future, and greater uncertainty about the fates of subpopulations within specific habitat units.

The results presented below provide general indications about the expected population performance, the factors that have the greatest impact on population projections, and the development and management scenarios that have the greatest impact on trends. Sufficient precision to allow detection and demonstration of more subtle distinctions among the models examined would likely require several thousand iterations of the models of interest. (This can be done for any scenarios of particular interest, but will require many days of computer time for each model so refined.)

However, it is important also to recognize the difference between the precision of mean results, the accuracy of trends, and the predictability of projections. **With a sufficient number of independent iterations of a simulation model, the mean result can be obtained to any level of precision that might be desired. However, the accuracy of this result will depend on the correctness of the values that were put into the model. For many of the model parameters, available data allow only approximate estimates of the true values. Thus, simulation results can be very precise but still misleading regarding the most likely fate of a population.** Even if the mean prediction from a model is biased because of inaccurate values of some parameters describing the species biology or habitat, comparisons among models that change one or a few parameters (such as a test of the effect of a loss of some habitat, or the effect of disruption of a dispersal corridor) would still be expected to provide robust estimates of the relative shift in extinction probabilities or mean population size.

Even if mean results are both precise and accurate, the *mean* result of a model does not guarantee that the actual outcome in nature or in any one simulation will closely approximate that mean result. The high fluctuations in the ABM populations and the great variability among iterated simulations indicate that there is great inherent uncertainty in the future fate of the populations of beach mice. Thus, we may be able to estimate the probability of extinction to be, for example, 20% ± 2%, but the real population either will go extinct or it will persist for the specified time period. Similarly, we may project the population size in the future to be N = 5000 ± 100 s.e. (as the measure of precision), but the range of projected size may be SD = 2000 (as a measure of the uncertainty in individual outcomes), indicating that the final population size could (with about 95% probability) vary anywhere from 1000 to 9000. In many of the scenarios tested, the SD(N) among iterations was of approximately the same magnitude as the mean N, indicating that across years and across iterations the population sizes in the simulations often varied from 0 (extinction) to double the mean N or more.

Because of the lack of high precision for model results generated from the 500 iterations repeated for the scenarios testing development and management options, and because many of these results were generated after the PHVA workshop concluded as a physical meeting and moved to an electronic forum, we have not attempted to provide highly detailed text descriptions and extensive interpretations of results. Instead, we highlight below the general trends observed in the analyses concluded to date. Individual readers may wish to focus more carefully on the results shown in the tables to address specific questions of interest, and those using this report should examine the results presented to draw their own conclusions, rather than accepting our interpretations of trends and meanings without questioning.

All scenarios include the effect of hurricanes as an integral component of the baseline model. Alternative scenarios that model the effects of development, hurricane mitigation, and invasive species were analyzed as single factor effects; the interaction of these factors (e.g., development, house mice and cogon grass combined) were not evaluated in this analysis but may indeed occur in reality. The potential for such effects should be considered when reviewing these results.

Results of the Baseline Model and Sensitivity Testing

Deterministic Population Growth Rate

Traditional demographic analyses calculate a mean population growth rate based on the mean birth and death rates and assumptions of the population being at the stable age distribution, no fluctuations in demographic rates, no variation from a 1:1 sex ratio, and no impacts on demography from inbreeding depression, density dependent effects, or other factors. For the Alabama beach mouse, the deterministic growth rate calculated under these assumptions may not be particularly meaningful, because the birth and deaths rates vary seasonally (which impacts different generations), there are believed to be strong density-dependent effects on reproduction, and hurricanes periodically decimate the population. However, when the impacts of hurricanes are removed from our models, a deterministic growth rate expected for the population can be calculated separately for each season and at high (N = carrying capacity) and low (N near 0) densities. These growth rates will be only approximate, because seasonal shifts in the age structure will impact growth, and because the exact breeding rate will depend on the population size. The following table shows the expected mean four-week rates of population growth, as it is expected to vary by season and population density. These population growth rates can be considered to represent the biological potential for population growth, in the absence of factors such as hurricanes, inbreeding effects, fluctuations in the environmental conditions, or the inherent randomness (stochasticity) of demographic processes. These numbers seem plausible for a small rodent adapted to a variable environment that is often resource-limited. They indicate potential for rapid population recovery under good conditions, but marginal population growth or decline during the more harsh times of the year.

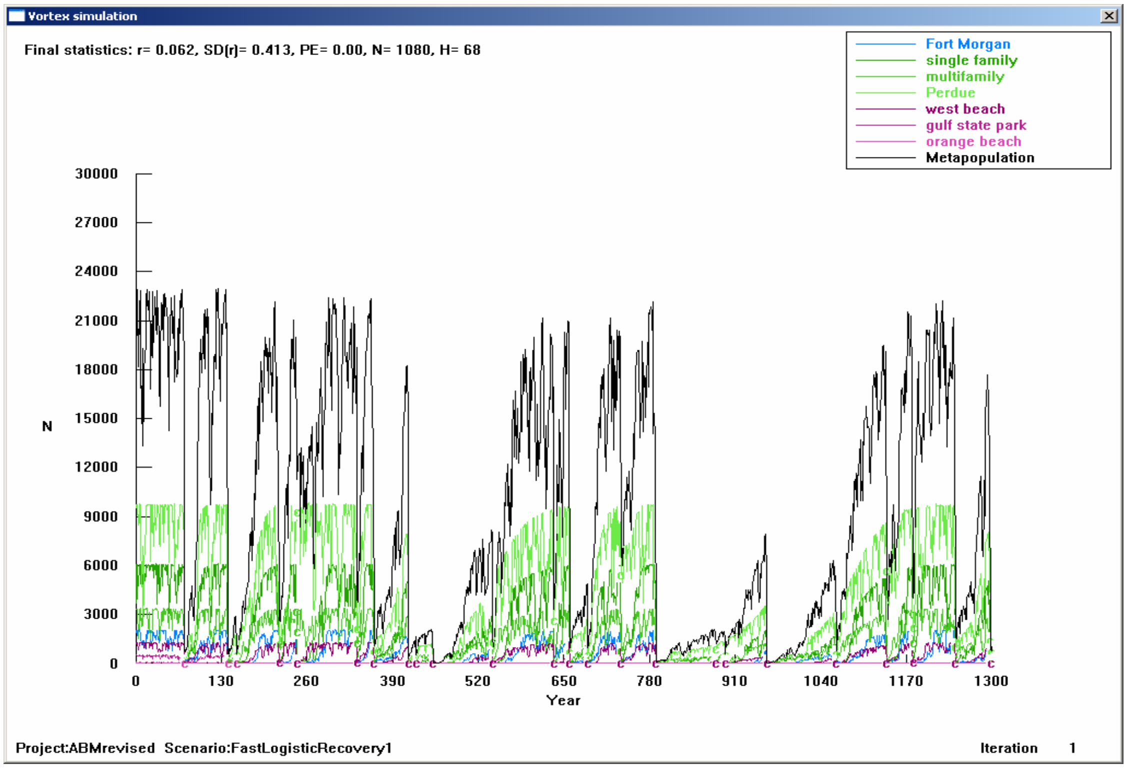
	Low Density	High Density
Winter	34%	12%
Spring/Fall	31%	7%
Summer	6%	-11%

Baseline Models

The results for the tests of the two baseline models (with fast or slow recovery of habitat following hurricanes) and the various sensitivity tests of alternative plausible model parameters are given in Table 7A, at the end of this section. These results are illustrated in the figures shown below (Figures 7A – 7K).

Figure 7A shows a sample run (iteration) for the baseline model with relatively fast (1, 3, 6, 20, and 30 year) recovery of habitat from hurricanes, following a logistic curve, with all other model parameters set to values deemed appropriate by the PHVA participants for the “baseline” model of ABM population dynamics. Population crashes followed by rapid recovery are instances of Category 1 or Category 2 hurricanes occurring 17 times in this simulation. Category 3 hurricanes occurred at about year 11 (time step 132, labeled as model “year” 132 on the graph), year 29, year 50, and year 96. Category 4 hurricanes occurred at about year 35 and year 73. A likely Category 5 hurricane occurred in year 61. The subpopulations at the Fort Morgan, Single Family, and West Beach units often suffered local extirpation after storms, but were then recolonized. The subpopulation unit at Orange Beach was extirpated by a Category 2 hurricane that occurred in year 6, and the Gulf State Park unit was extirpated by a Category 3 hurricane in year 11 of this simulation.

Figure 7B shows the probability of local extirpation of each of the seven subpopulation units over the 100-year (1300 time step) simulation, for the case with relatively fast (1, 3, 6, 20, and 30 year) recovery of habitat from hurricanes (top), or relatively slow (5, 8, 12, 25, and 40 year) recovery of habitat from hurricanes (bottom), following logistic curves, with all other model parameters set to values deemed appropriate by the PHVA participants for the “baseline” model of ABM population dynamics. In the baseline model, the ABM metapopulation is projected to go extinct with an 18% (with fast recovery of habitat) to 21% (with slow recovery of habitat) probability over 100 years. The subpopulations did suffer local extirpations in more of the iterations than those in which they were extirpated at the end of the 100-year simulation, but often these local extinctions were followed by recolonization from neighboring units except when the entire metapopulation went extinct.



Final statistics: r= 0.062, SD(r)= 0.413, PE= 0.00, N= 1080, H= 68

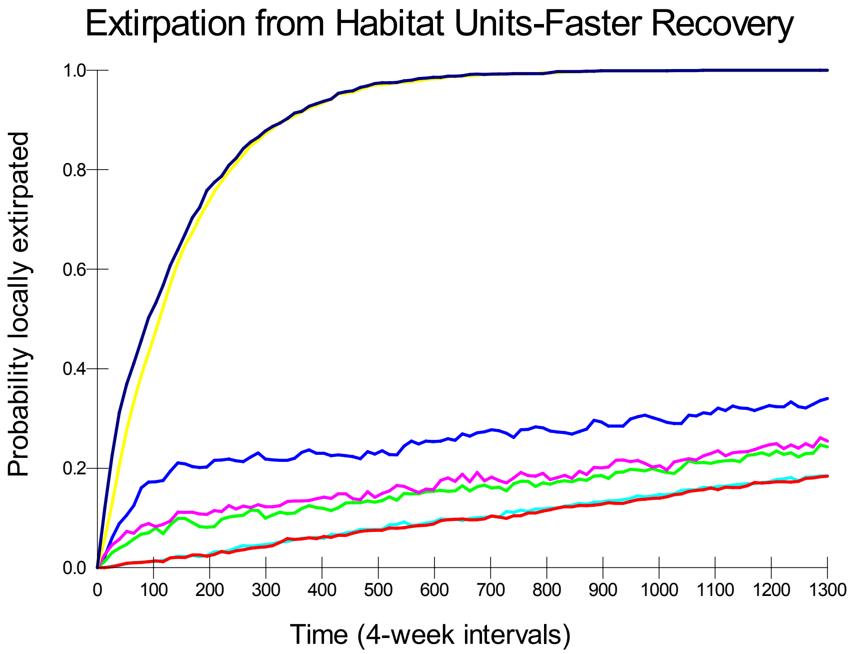
Project:ABMrevised Scenario:FastLogisticRecovery1

Fig. 7A. Sample iteration (run) of the simulation of ABM subpopulations in 7 habitat units over a period of 100 years (1300 four-week time steps), with fast recovery of habitat from hurricanes, following logistic curves.

The Perdue unit and Multi-Family unit subpopulations had about the same rate of local extinction at the end of the 100 years as did the metapopulation, as these two habitat units were usually the last to go extinct in the simulations. These two units appear to be the stabilizing part of the overall metapopulation, as they are large, less affected by hurricanes, and central relative to the linear array of population units along the coast. Both the metapopulation and these two central units are projected to lose about 27% (with fast recovery) to 31% (with slow recovery) of their initial gene diversity over the 100 years, which would result in an accumulated level of inbreeding approximately equivalent to a generation of mating between full siblings.

In contrast, the units at Gulf State Park and Orange Beach suffered local extinctions, typically in about 5 to 10 years. Given the frequency of hurricanes entered into the model (1/8, 1/16, 1/25, 1/47, and 1/100 years for C1, C2, C3, C4, and C5 hurricanes), this suggests that the Orange Beach unit is projected to not survive hurricanes about half of the time (and perhaps to sometimes go locally extinct even in the absence of a hurricane), while the Gulf State Park unit is predicted to survive the least severe (C1) hurricanes, but typically not survive more severe storms. Because these two units are completely isolated from the units to the west, they do not get recolonized naturally after local extirpation.

Populations at the Fort Morgan unit, the Single Family unit, and West Beach unit also frequently do not survive hurricanes (with median times to extirpation of 11-23 years), but they are often recolonized from adjacent population units. At the end of the 100 year simulation, these units are locally extinct in 24-38% of the iterations, which means that they are locally extinct in 6-17% of the cases in which the metapopulation did not go extinct.


Extirpation from Habitat Units-Faster Recovery

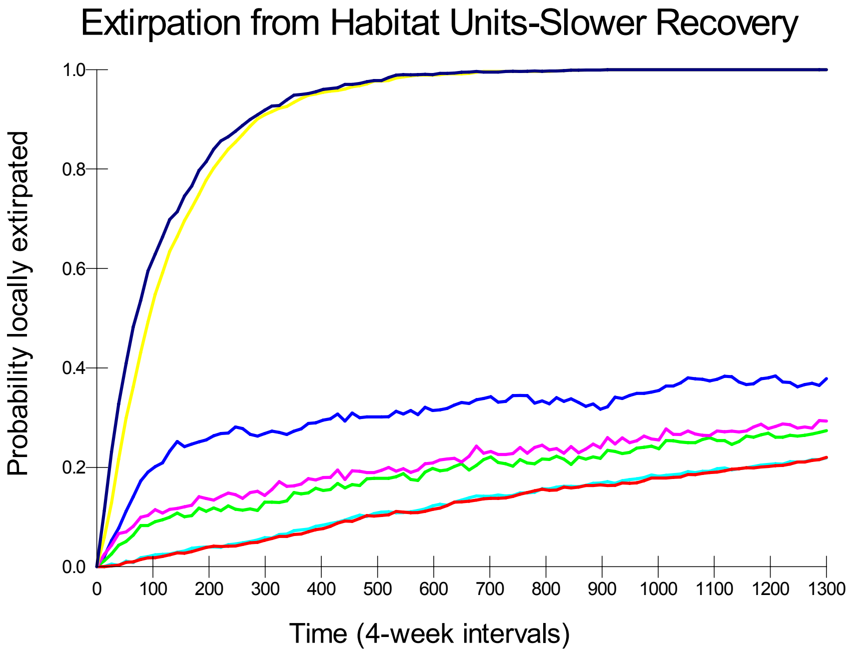
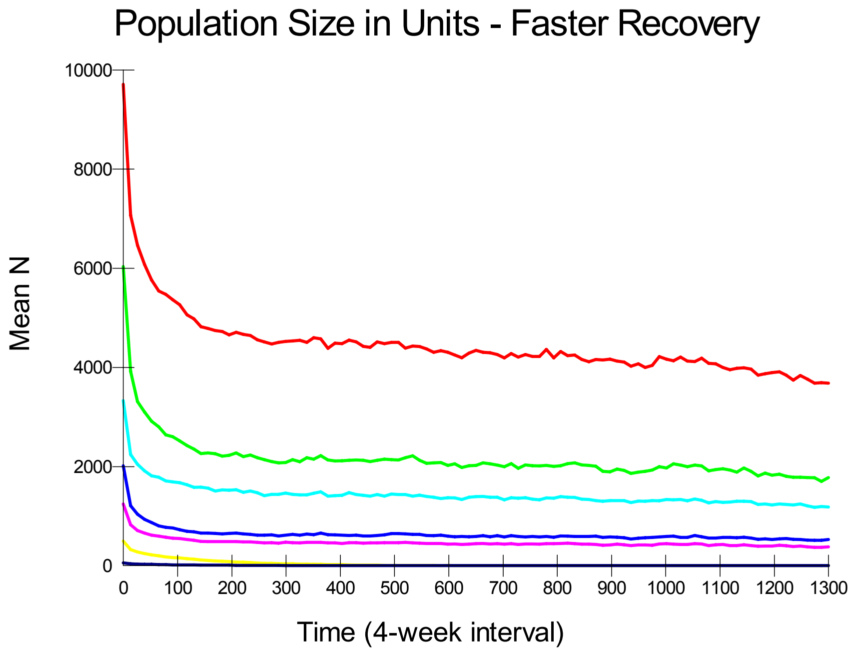

Extirpation from Habitat Units-Slower Recovery

Fig. 7B. Probability of extirpation from each of the seven subpopulation units over the100-year (1300 time step) simulation, for the case with relatively fast recovery (top graph) or relatively slow recovery (bottom graph) of habitat from hurricanes, following a logistic curve, with all other model parameters set to values deemed appropriate by the PHVA participants for the "baseline" model of ABM population dynamics. Lines show the proportion out of 1500 simulations in which the subpopulations in the Perdue, Multi-Family, Single Family, West Beach, Fort Morgan, Gulf State Park, and Orange Beach habitat units (bottom to top) were locally extirpated at each time step. Usually, when the Perdue subpopulation was extirpated, so were all of the others, and ABM was globally extinct).

Figure 7C shows the mean population sizes projected for each habitat unit over 100 years. For all populations in the simulations, there is a rapid initial decline in the mean N, simply because the simulations were started with the populations at carrying capacity, so that populations could decline but not increase. The rapid decline in the mean N does not indicate that every simulation showed an initial decline (nor that the real populations will necessarily decline in the next few years), but rather that the mean of simulated populations is initially declining, as those not remaining at capacity must show a decline. See Figure 7A for an example of a simulation in which population decline did not occur until a hurricane at about 5 years, and then the population recovered rapidly to K for another 5 years. As shown in Figure 7C, however, the typical population sizes in the model after the initial decline is about 50% of the carrying capacity. This means that the average population size was about half of the maximum possible. However, as illustrated in Figure 7A, this mean of N at about half of K resulted not from populations being stable at that size, but rather a long-term average of populations that fluctuate from being near K to being near extinction.

Figure 7D shows the loss of genetic diversity (measured as proportion of initial gene diversity or heterozygosity, averaged across those simulated populations that are not yet extinct) for the population in each habitat unit. Keeping losses of genetic diversity to less than 10% is sometimes used as a goal for endangered species programs. A loss of 25% of diversity would indicate that inbreeding over the generations had accumulated to a level equivalent to matings between siblings or between parent and offspring. Most local populations lost 10% of their genetic diversity in somewhat shorter times than the median times to first extinction. These losses of diversity are probably the consequence of population fluctuations and declines, but they may also be partly a cause of declines (due to inbreeding depression) in the simulations. Local populations lost 25 % of initial genetic diversity over time spans that ranged from about 10 years (for Orange Beach) to nearly 100 years (for Perdue and Multi-Family model units). The persistence of populations after the accumulation of this level of inbreeding suggests that the mice have a high enough fecundity to overcome or adapt to moderate levels of inbreeding (at least in the model). The genetic diversity in the total metapopulation declined by 26-30% after about 100 years in the simulation.



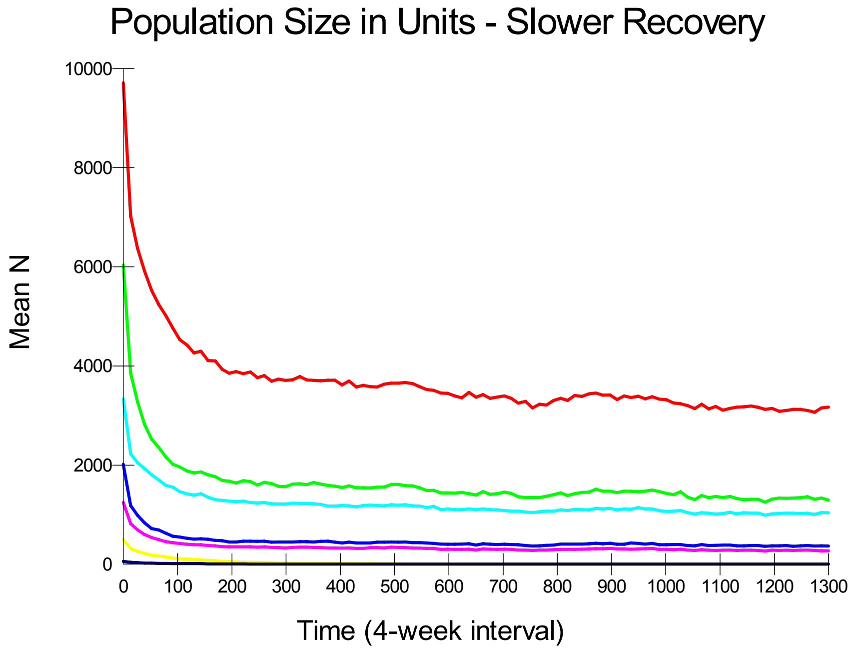
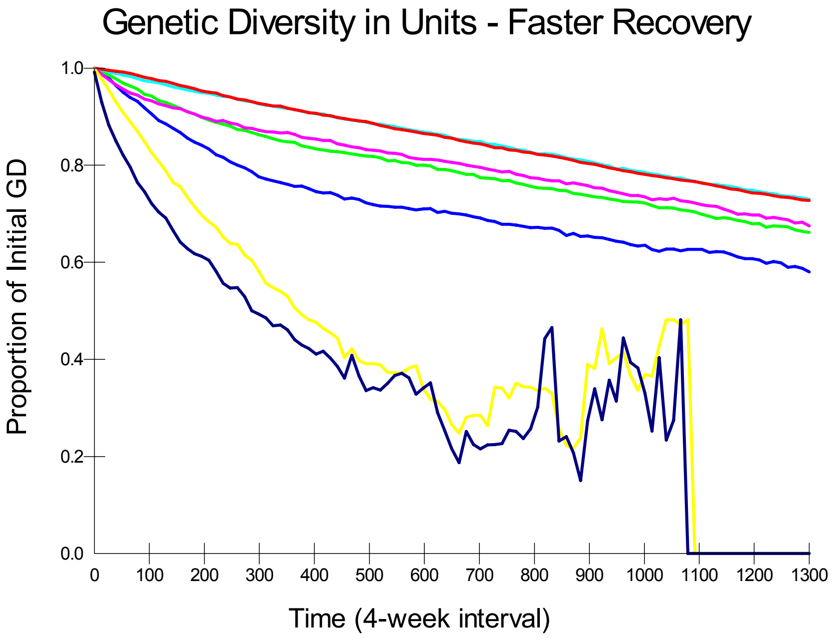


Fig. 7C. Mean population size projected for the seven population units (from top to bottom: Perdue, Single Family, Multi-Family, Fort Morgan, West Beach, Gulf State Park, and Orange Beach), for the case with relatively fast (1, 3, 6, 20, and 30 year) recovery (top graph) or relatively slow (5, 8, 12, 25, and 40 year) recovery (bottom graph) of habitat from hurricanes.



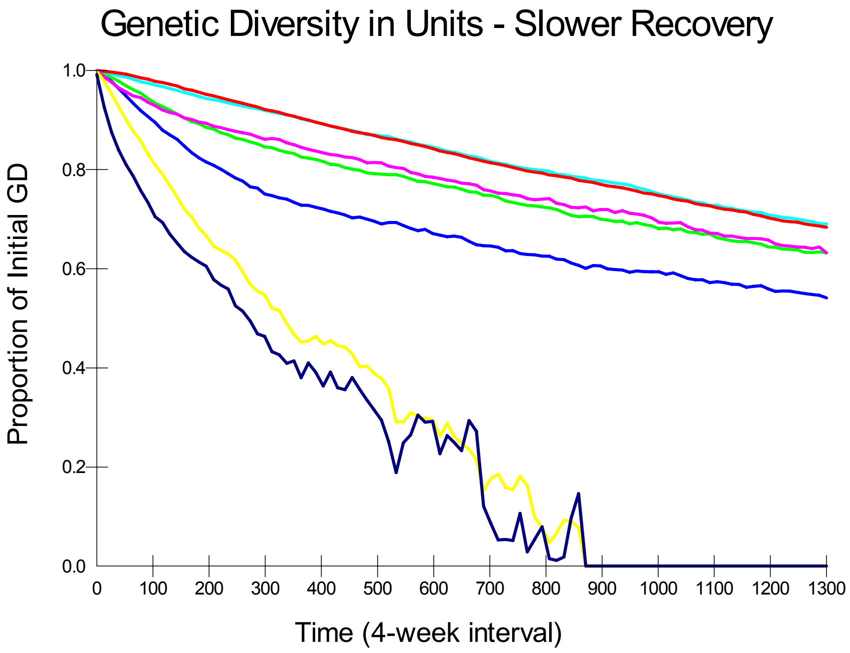


Fig. 7D. Mean proportion of initial gene diversity (heterozygosity) projected for the seven subpopulation units (from top to bottom: Perdue, Multi-Family, West Beach, Single Family, Fort Morgan, Gulf State Park, and Orange Beach), for the case with relatively fast (1, 3, 6, 20, and 30 year) recovery (top graph) or relatively slow (5, 8, 12, 25, and 40 year) recovery (bottom graph) of habitat from hurricanes.

Alternative Models of Rate and Shape of Habitat Recovery after Hurricanes

Four alternative models for the recovery of habitat from hurricanes were tested (Fig. 7E). In the “Fast” recovery models, it was assumed that habitat carrying capacity (K) returned to pre-storm levels within 1, 3, 6, 20, and 30 years for Category 1, 2, 3, 4, and 5 hurricanes, respectively. In the “Slow” recovery models, it was assumed that habitat carrying capacity returned to pre-storm levels within 5, 8, 12, 25, and 40 years. In the “Logistic” recovery models, it was assumed that the recovery of K followed a logistic curve, with a slow start to recovery, more rapid recovery in middle years, and a slow approach to maximum K near the end of the recovery period. In the “Linear” recovery models, it was assumed that the recovery of K was linear (constant rate).

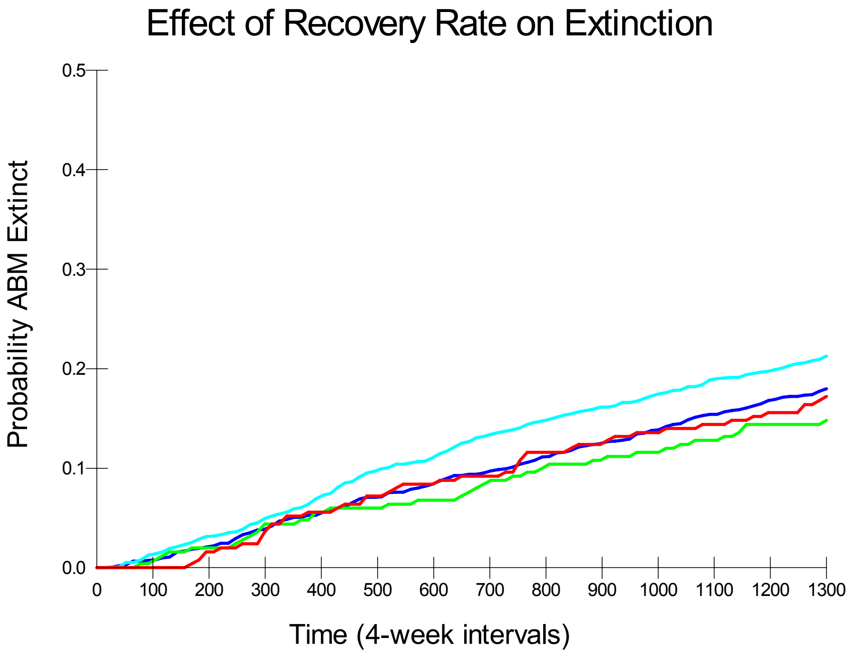
Faster recovery of habitat led to a 2-3% lower probability of ABM extinction, relative to the simulations with slower recovery of habitat. These results suggest that within the range of recovery rates tested initially in the baseline models, the rate of habitat recovery is a measurable but perhaps not dominant factor in determining population persistence. Linear recovery of habitat (which also means that there is more recovery in the year or two immediately following a hurricane) led to about 3-4% lower probability of population extinction, relative to the simulations with recovery following a logistic shape curve. This suggests that the speed of recovery in the period immediately following a hurricane (which is much less in the logistic model than in the linear model) may have a significant effect on the likelihood that a population will survive the effects of a hurricane. The long-term mean population size was modestly impacted by which model of recovery was used (see Fig. 7E-bottom and Table 7A).

Effect of Initial Population Size

Figure 7F shows the results for scenarios in which the initial population sizes were reduced to 50% or 75% of K (the starting point in the baseline models). The effect of initial N on long-term means was very small, and not even detectable within the random error in 500 repeats of the simulations. Thus, as long as the populations are initially at least 50% of the capacity, they are not at measurably greater risk of extinction. Lower initial population sizes were not recommended for testing by the working group but could be considered in future analyses.

Effect of Habitat Carrying Capacity

Figure 7G shows the effect of lower estimates of carrying capacity (set at 50% to 100% of that in the baseline model) for cases with fast recovery from hurricanes, while Figure 7H shows these effects when recovery from hurricanes is slower. The impact of lower K is to reduce mean population size approximately proportional to the reduction in K (which is expected), but also to noticeably increase the probabilities of extinction. Thus, a greater maximum population size afforded by more or higher quality habitat provides some buffering of populations from extinctions that are caused predominantly by occasional hurricanes. Although the results from 500 iterations of the simulations do not provide precise results, it appears that each 10% decline in habitat causes a small but measurable increase in extinction rates (see Table 7A).



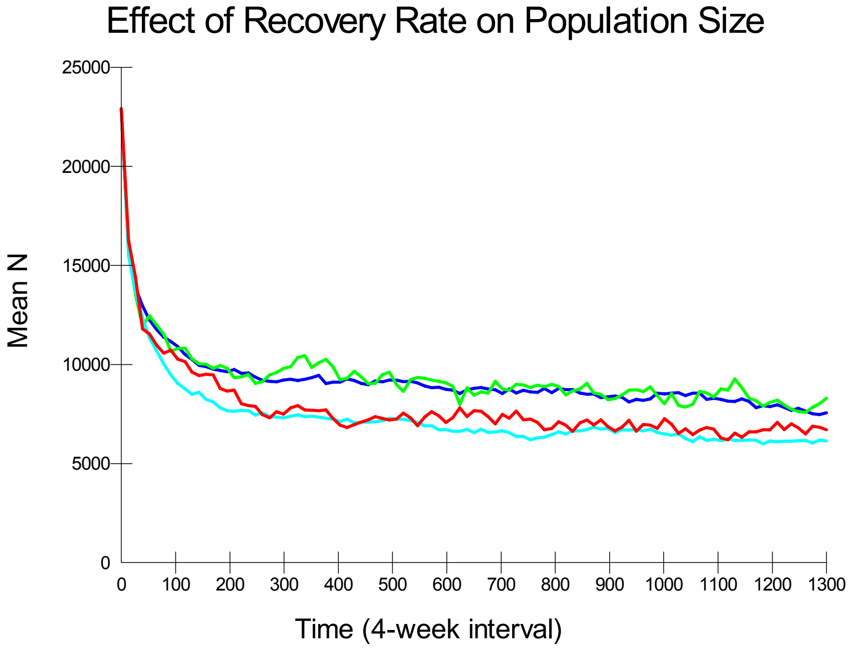
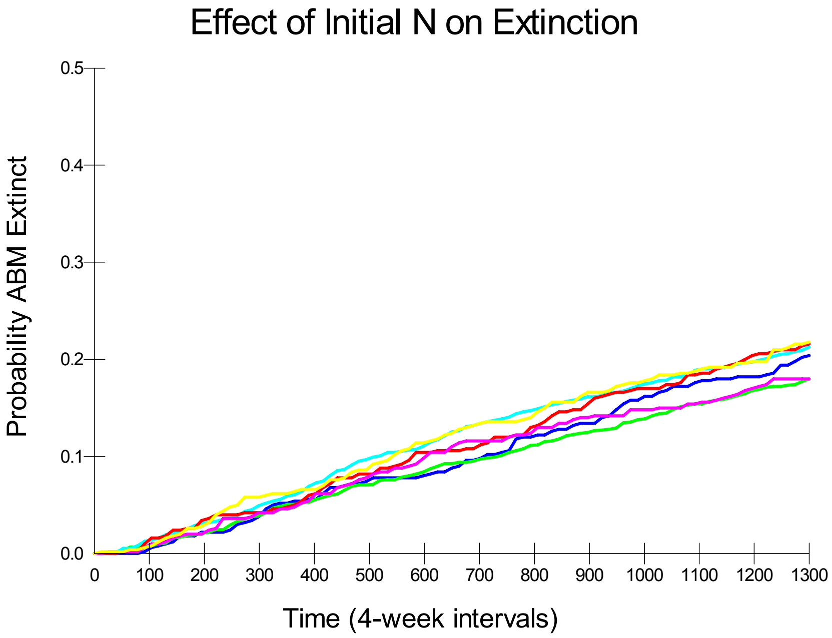


Fig. 7E. Effect of four models of recovery from hurricanes on (top graph) probabilities of ABM extinction (bottom to top: fast linear recovery, slow linear, fast logistic, slow logistic), and (bottom graph) mean size of the metapopulation (top to bottom: fast linear recovery, fast logistic, slow linear, slow logistic). The smoothness of lines and precision of mean results is greater for the logistic recovery models (with 1500 iterations) than for the linear recovery models (with 250 iterations each). Note that the y-axis for Probability ABM Extinct in this and many subsequent graphs ranges from 0.0 to 0.5.



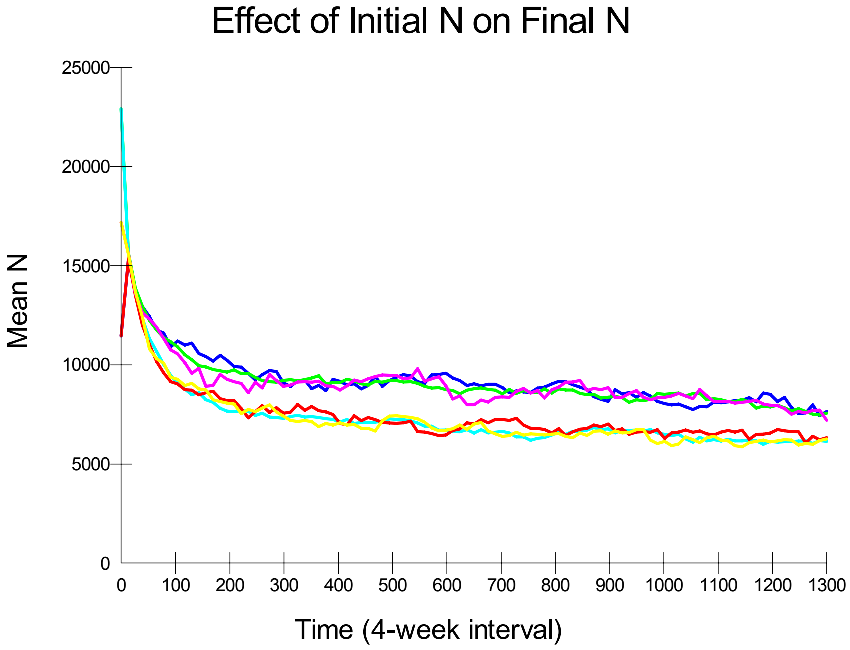
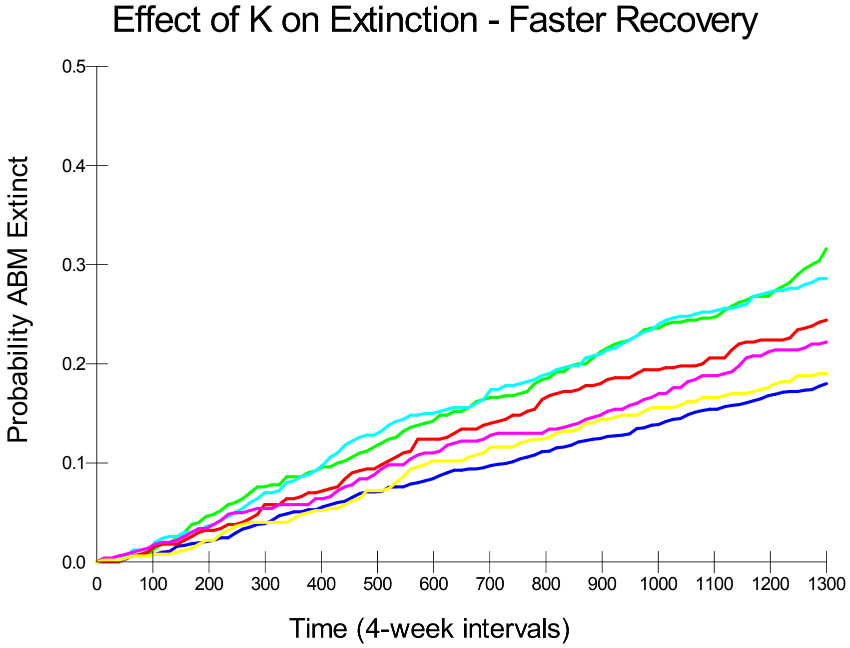


Fig. 7F. Effect of initial population size on (top graph) probabilities of ABM extinction (lines show cases of initial N = 50%, 75%, or 100% of K, for fast or slow recovery, but differences between lines are not usually significant), and (bottom graph) mean size of the metapopulation (top three lines: fast recovery; bottom lines: slow recovery).



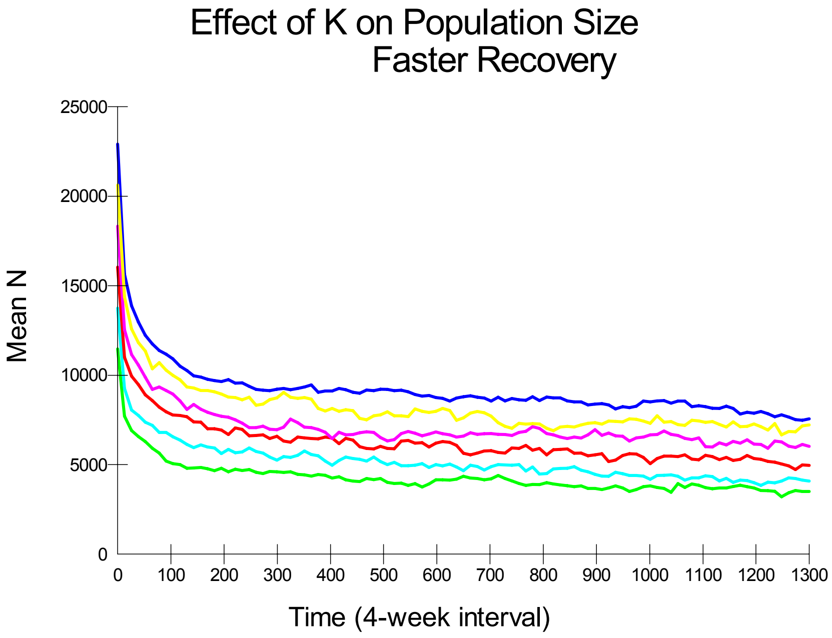
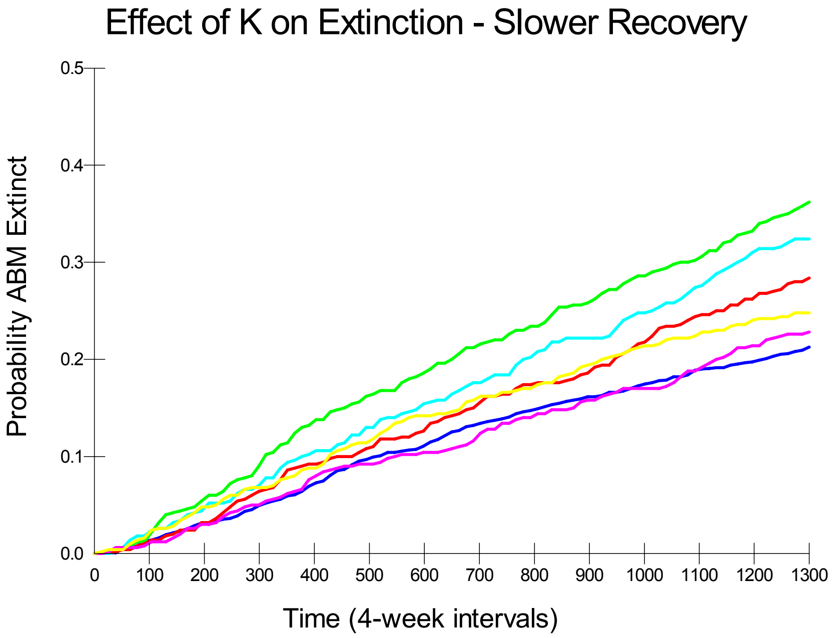


Fig. 7G. Effect of habitat carrying capacity (K) on (top graph) probabilities of ABM extinction, and (bottom graph) mean size of the metapopulation (best to worst: K = 100%, 90%, 80%, 70%, 60%, 50% of baseline, but differences between some adjacent lines are not significant), with fast recovery from hurricanes.



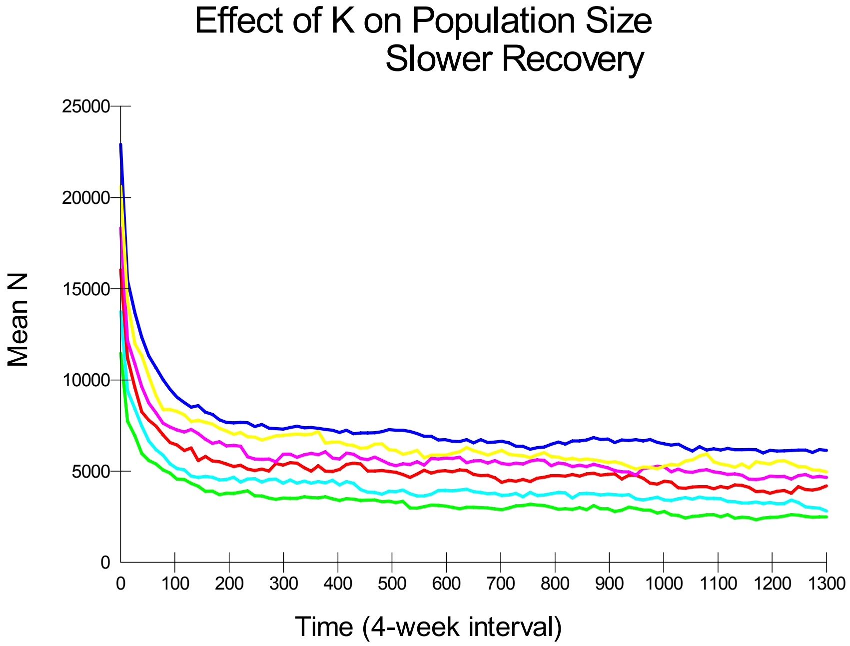


Fig. 7H. Effect of habitat carrying capacity (K) on (top graph) probabilities of ABM extinction, and (bottom graph) mean size of the metapopulation (best to worst, usually: K = 100%, 90%, 80%, 70%, 60%, 50% of baseline), with slow recovery from hurricanes.

Effect of Dispersal among Habitat Units

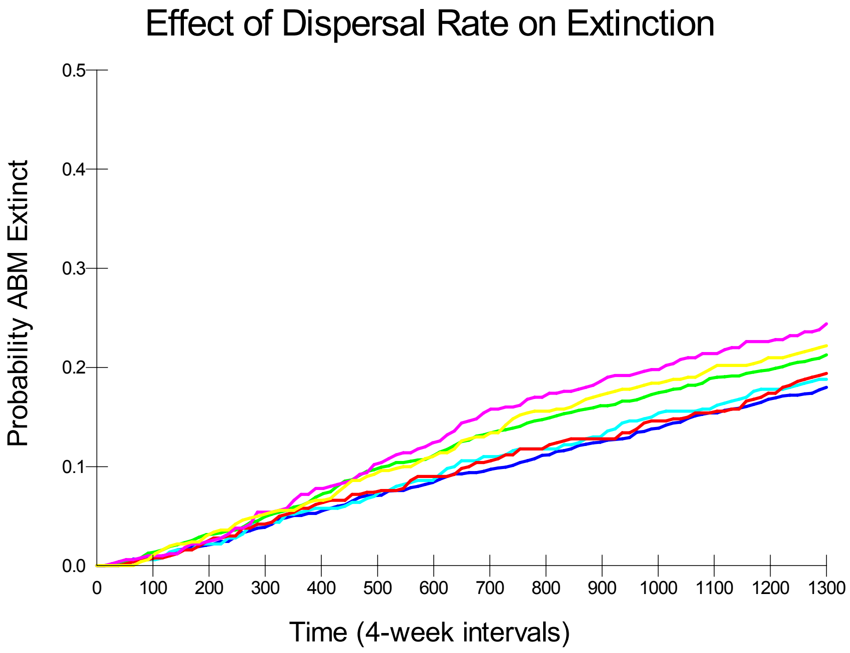
The rates of dispersal between adjacent units are difficult to estimate with confidence (see Section 2). As shown in Figure 7I, doubling or halving the dispersal rates that were estimated for the baseline model had weak but detectable effects on metapopulation extinction and mean size. However, as seen in Table 7A, this lack of effect is due to the dispersal rates having little impact on the subpopulations in the central habitat units (Perdue and Multi-Family units) that form the most stable portion of the metapopulation. Among the more peripheral subpopulations (Fort Morgan, Single Family, and West Beach), reduced interpopulation dispersal has weak and inconsistent effects on the median times to first extinction, but causes the local subpopulations to be extirpated at the end of 100 years in 5% to 13% more of the iterations than in scenarios with the higher rates of dispersal. This indicates that these subpopulations are more often recolonized after local extinctions by immigrants in those scenarios with higher inter-unit dispersal. The subpopulations in the two most eastern and isolated habitat units (Gulf State Park and Orange Beach) always go extinct in the model, as they cannot be recolonized from the other units and are not large enough to be individually (or jointly) stable.

Effect of Juvenile Mortality Rates

Increasing or decreasing the estimate of juvenile survival by 10% (i.e., changing mean four-week survival from 40% to 50% or 30%) had considerable effects on the probabilities of population extinction and noticeable effects on the projected mean population sizes (Figure 7J). Even with the higher rate of juvenile mortality, the beach mouse populations would be capable of rapid population growth, but the slower recovery after hurricanes (and perhaps lesser ability to withstand further reductions in survival due to inbreeding depression) led to higher (often doubling) probabilities of local extirpation (especially within the core habitat units, Perdue and Multi-Family) and of overall metapopulation extinction.

Effect of Adult Mortality Rates

More data are available of adult mortality rates, so the plausible range that was examined in the sensitivity tests was narrower than the range of juvenile mortality rates tested. Varying adult four-week (non-summer) mortality from 14.1% to 18.1% had effects on estimated probabilities of extinction (Fig. 7K) that were a little weaker than the impact observed when juvenile mortality was varied from 30% to 50%. The effect on mean population size was similar to the effect seen with varied juvenile mortality rates.



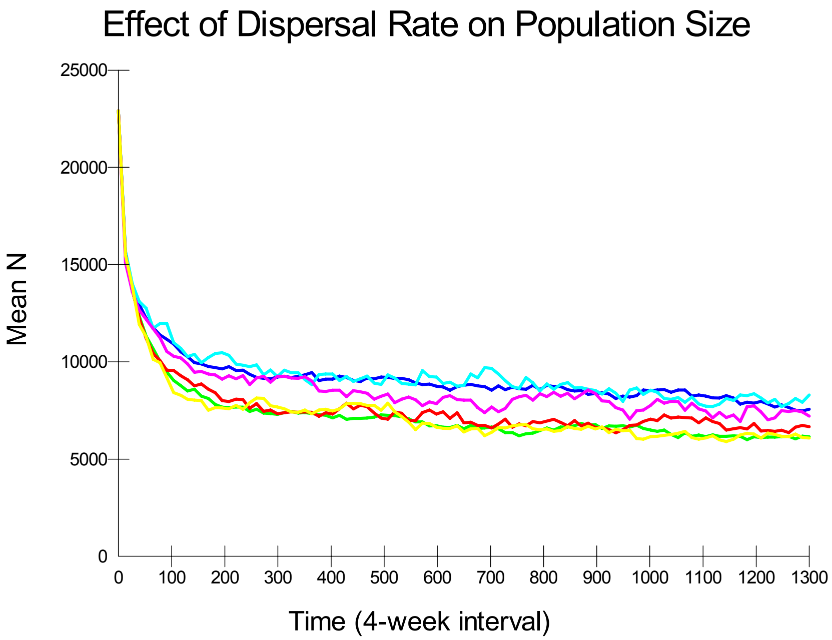
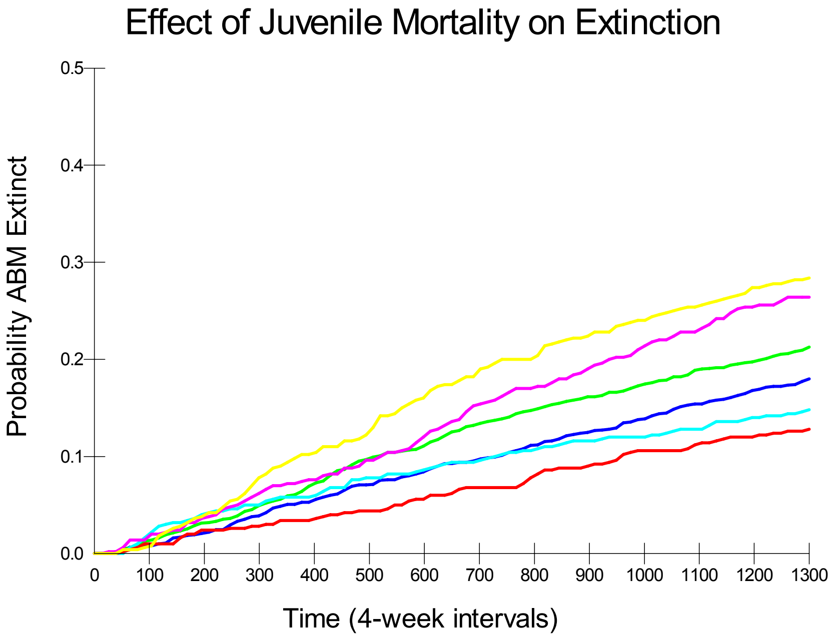


Fig 7I. Effect of inter-unit dispersal rate on (top graph) probabilities of ABM extinction (lines show cases of dispersal set to 50%, 100%, or 200% of baseline rates, for fast or slow recovery, but differences between lines are often not significant), and (bottom graph) mean size of the metapopulation (top three lines: fast recovery; bottom lines: slow recovery).



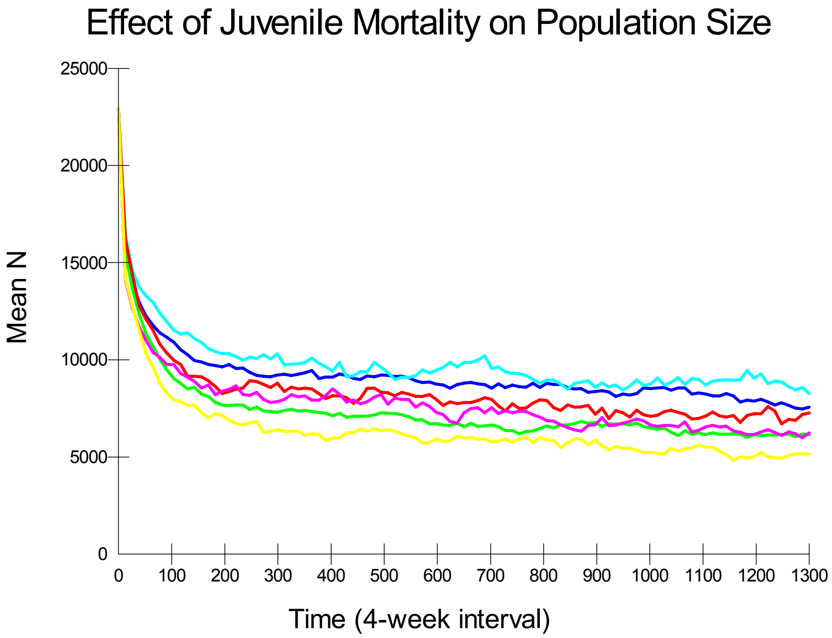
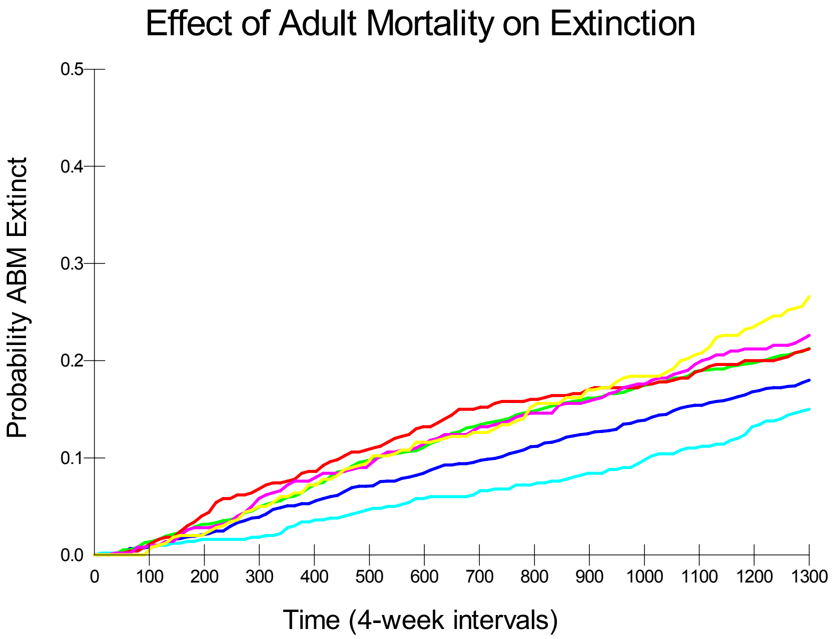


Fig. 7J. Effect of juvenile mortality rate on (top graph) probabilities of ABM extinction (bottom to top: 30% mortality and slow recovery, 30% mortality and fast recovery, 40% mortality and fast recovery, 40% mortality and slow recovery, 50% mortality and fast recovery, 50% mortality and slow recovery, but some differences between adjacent lines are not significant), and (bottom graph) mean size of the metapopulation (top to bottom, with respect to endpoints: 30% mortality and fast recovery, 40% mortality and fast recovery, 30% mortality and slow recovery, 50% mortality and fast recovery, 40% mortality and slow recovery, 50% mortality and slow recovery, but often differences between adjacent lines are not significant).



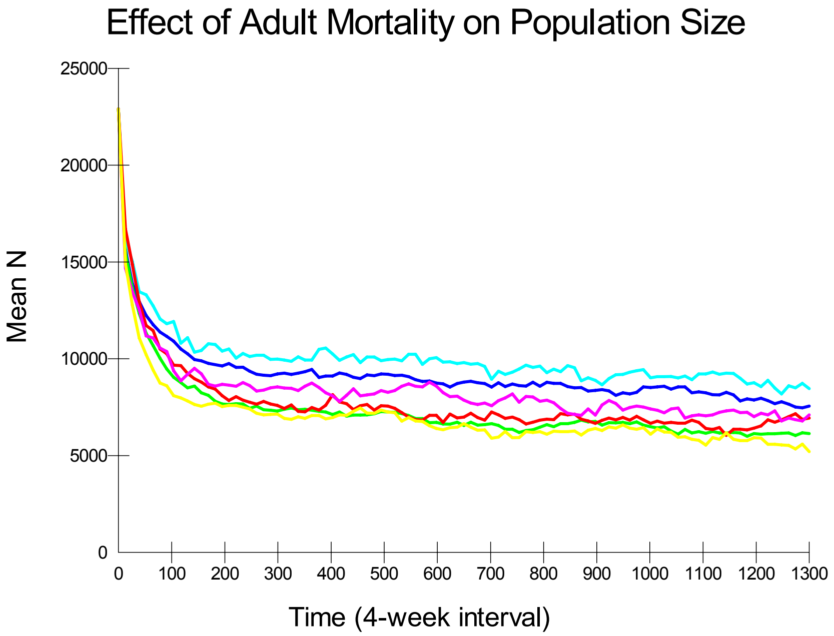


Fig. 7K. Effect of adult mortality rate on (top graph) probabilities of ABM extinction (bottom to top, with respect to endpoints: 14.1% mortality/fast recovery, 16.1% mortality/fast recovery, 14.1% mortality/slow recovery, 16.1% mortality/slow recovery, 18.1% mortality/fast recovery, 18.1% mortality/slow recovery, but often differences between adjacent lines are not significant), and (bottom graph) mean size of metapopulation (top to bottom: 14.1% mortality/fast recovery, 16.1% mortality/fast recovery, 18% mortality/fast recovery, 14.1% mortality/slow recovery, 16.1% mortality/slow recovery, 18.1% mortality/slow recovery, but often differences between adjacent lines are not significant).

Table 7A. Results for each model unit and the metapopulation for the baseline scenarios and various sensitivity tests of alternative parameter values. For the two baseline scenarios, the results are from 1,500 independent iterations of the simulation. For the tests of linear recovery of habitat following hurricanes, 250 iterations were used. Subsequent scenarios for testing sensitivity to parameter values were repeated for 500 simulations, and often similar values in the results are not significantly divergent.

Prob. Extinct = the probability that the population is extinct after 100 years, estimated from the proportion of simulation iterations in which the population did not have animals of both sexes.

SE(PE) = standard error of probability of extinction

Mean N = mean population size projected at the end of 100 years

SD(N) = standard deviation of final N across iterations

SE(N) = standard error of mean N

Gene Diversity = mean gene diversity (expected heterozygosity) at 100 years, as a proportion of the initial diversity

Median Time to Extinction = median year at which the population first goes extinct (blank if the population goes extinct in fewer than 50% of the iterations). Note that often locally extinct populations are later recolonized.

Model Unit	Prob. Extinct	SE(PE)	Mean N	SD(N)	SE(N)	Gene Diversity	Median Time to Extinction
Baseline, fast logistic recovery							
Fort Morgan	0.34	0.012	530	682	18	0.58	18
Single Family	0.24	0.011	1777	2233	58	0.66	23
Multi-Family	0.19	0.010	1186	1149	30	0.73	
Perdue	0.18	0.010	3682	3530	91	0.73	
West Beach	0.26	0.011	384	466	12	0.68	14
Gulf St. Park	1.00	0.000	0	0	0	0.00	10
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.18	0.010	7558	7533	195	0.74	
Baseline, slow logistic recovery							
Fort Morgan	0.38	0.013	366	553	14	0.54	14
Single Family	0.27	0.012	1296	1840	48	0.63	17
Multi-Family	0.22	0.011	1039	1066	28	0.69	71
Perdue	0.22	0.011	3172	3267	84	0.68	
West Beach	0.29	0.012	271	378	10	0.63	11
Gulf St. Park	1.00	0.000	0	0	0	0.00	8
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.21	0.011	6144	6599	170	0.70	
Baseline, fast linear recovery							
Fort Morgan	0.25	0.027	584	628	40	0.62	16
Single Family	0.18	0.025	1920	2041	129	0.70	21
Multi-Family	0.15	0.023	1278	1058	67	0.77	96
Perdue	0.15	0.022	4084	3275	207	0.77	
West Beach	0.18	0.024	431	423	27	0.71	14
Gulf St. Park	1.00	0.000	0	0	0	0.00	9
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.15	0.022	8297	6863	434	0.77	

Model Unit	Prob. Extinct	SE(PE)	Mean N	SD(N)	SE(N)	Gene Diversity	Median Time to Extinction
	Baseline, slow linear recovery						
Fort Morgan	0.29	0.029	447	556	35	0.61	15
Single Family	0.22	0.026	1500	1746	110	0.67	19
Multi-Family	0.17	0.024	1063	931	59	0.73	73
Perdue	0.18	0.024	3375	2981	189	0.73	
West Beach	0.24	0.027	315	361	23	0.68	14
Gulf St. Park	1.00	0.000	0	0	0	0.00	8
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.17	0.024	6700	6075	384	0.74	
	initial N = 50% of K, fast recovery						
Fort Morgan	0.37	0.022	542	712	32	0.60	17
Single Family	0.28	0.020	1764	2233	100	0.67	20
Multi-Family	0.22	0.018	1213	1192	53	0.74	85
Perdue	0.21	0.018	3756	3661	164	0.74	
West Beach	0.29	0.020	380	469	21	0.69	13
Gulf St. Park	1.00	0.003	1	18	1	0.00	9
Orange Beach	1.00	0.003	0	0	0	0.00	5
Metapopulation	0.20	0.018	7657	7747	346	0.75	
	initial N = 75% of K, fast recovery						
Fort Morgan	0.35	0.021	509	683	31	0.58	17
Single Family	0.27	0.020	1655	2182	98	0.67	17
Multi-Family	0.18	0.017	1135	1143	51	0.73	94
Perdue	0.19	0.017	3536	3484	156	0.73	
West Beach	0.28	0.020	376	464	21	0.68	13
Gulf St. Park	1.00	0.000	0	0	0	0.00	8
Orange Beach	1.00	0.000	0	0	0	0.00	6
Metapopulation	0.18	0.017	7211	7432	332	0.74	
	initial N = 50% of K, slow recovery						
Fort Morgan	0.38	0.022	358	547	24	0.53	14
Single Family	0.28	0.020	1318	1850	83	0.63	16
Multi-Family	0.23	0.019	1058	1097	49	0.69	70
Perdue	0.22	0.018	3319	3357	150	0.68	
West Beach	0.28	0.020	272	375	17	0.64	11
Gulf St. Park	1.00	0.000	0	0	0	0.00	8
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.22	0.018	6325	6737	301	0.69	
	initial N = 75% of K, slow recovery						
Fort Morgan	0.39	0.022	392	594	27	0.53	13
Single Family	0.28	0.020	1383	1971	88	0.62	17
Multi-Family	0.22	0.019	996	1056	47	0.68	68
Perdue	0.22	0.019	3204	3341	149	0.67	
West Beach	0.29	0.020	292	406	18	0.63	11
Gulf St. Park	1.00	0.000	0	0	0	0.00	8
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.22	0.018	6266	6860	307	0.69	

Model Unit	Prob. Extinct	SE(PE)	Mean N	SD(N)	SE(N)	Gene Diversity	Median Time to Extinction
K = 50% of baseline, fast recovery							
Fort Morgan	0.50	0.022	237	346	15	0.44	12
Single Family	0.39	0.022	839	1154	52	0.52	16
Multi-Family	0.32	0.021	555	615	27	0.59	48
Perdue	0.33	0.021	1695	1864	83	0.59	
West Beach	0.41	0.022	181	241	11	0.54	9
Gulf St. Park	1.00	0.000	0	0	0	0.00	7
Orange Beach	1.00	0.000	0	0	0	0.00	4
Metapopulation	0.32	0.021	3506	3994	179	0.60	
K = 60% of baseline, fast recovery							
Fort Morgan	0.44	0.022	271	394	18	0.49	13
Single Family	0.35	0.021	934	1273	57	0.57	16
Multi-Family	0.29	0.020	640	675	30	0.63	54
Perdue	0.29	0.020	2037	2127	95	0.62	
West Beach	0.37	0.022	201	264	12	0.58	10
Gulf St. Park	1.00	0.000	0	0	0	0.00	7
Orange Beach	1.00	0.000	0	0	0	0.00	4
Metapopulation	0.29	0.020	4083	4401	197	0.64	
K = 70% of baseline, fast recovery							
Fort Morgan	0.43	0.022	328	474	21	0.52	14
Single Family	0.31	0.021	1127	1532	69	0.61	17
Multi-Family	0.25	0.019	807	831	37	0.68	66
Perdue	0.25	0.019	2438	2509	112	0.68	
West Beach	0.33	0.021	252	327	15	0.63	13
Gulf St. Park	1.00	0.000	0	0	0	0.00	8
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.24	0.019	4951	5335	239	0.69	
K = 80% of baseline, fast recovery							
Fort Morgan	0.37	0.022	396	528	24	0.53	15
Single Family	0.28	0.020	1429	1801	81	0.62	18
Multi-Family	0.23	0.019	958	954	43	0.69	73
Perdue	0.23	0.019	2925	2881	129	0.69	
West Beach	0.29	0.020	307	373	17	0.63	11
Gulf St. Park	1.00	0.000	0	0	0	0.00	8
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.22	0.019	6016	6095	273	0.70	
K = 90% of baseline, fast recovery							
Fort Morgan	0.36	0.021	470	620	28	0.57	16
Single Family	0.25	0.019	1706	2073	93	0.65	20
Multi-Family	0.20	0.018	1134	1084	48	0.71	81
Perdue	0.19	0.018	3547	3307	148	0.71	
West Beach	0.26	0.020	358	418	19	0.66	12
Gulf St. Park	1.00	0.000	0	0	0	0.00	8
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.19	0.018	7215	7047	315	0.72	

Model Unit	Prob. Extinct	SE(PE)	Mean N	SD(N)	SE(N)	Gene Diversity	Median Time to Extinction
K = 50% of baseline, slow recovery							
Fort Morgan	0.60	0.022	144	274	12	0.37	11
Single Family	0.45	0.022	513	862	39	0.46	14
Multi-Family	0.38	0.022	423	515	23	0.53	47
Perdue	0.37	0.022	1303	1646	74	0.54	93
West Beach	0.48	0.022	113	189	8	0.49	10
Gulf St. Park	1.00	0.000	0	0	0	0.00	7
Orange Beach	1.00	0.000	0	0	0	0.00	3
Metapopulation	0.36	0.021	2495	3290	147	0.55	
K = 60% of baseline, slow recovery							
Fort Morgan	0.57	0.022	169	318	14	0.43	15
Single Family	0.45	0.022	584	1023	46	0.50	15
Multi-Family	0.34	0.021	453	578	26	0.57	
Perdue	0.34	0.021	1494	1886	84	0.58	
West Beach	0.46	0.022	127	218	10	0.52	10
Gulf St. Park	1.00	0.000	0	0	0	0.00	8
Orange Beach	1.00	0.000	0	0	0	0.00	4
Metapopulation	0.32	0.021	2826	3760	168	0.59	
K = 70% of baseline, slow recovery							
Fort Morgan	0.47	0.022	240	385	17	0.48	12
Single Family	0.35	0.021	904	1323	59	0.57	15
Multi-Family	0.29	0.020	695	768	34	0.64	66
Perdue	0.29	0.020	2165	2328	104	0.63	
West Beach	0.35	0.021	194	283	13	0.58	10
Gulf St. Park	1.00	0.000	0	0	0	0.00	7
Orange Beach	1.00	0.000	0	0	0	0.00	4
Metapopulation	0.28	0.020	4197	4758	213	0.65	
K = 80% of baseline, slow recovery							
Fort Morgan	0.48	0.022	283	461	21	0.49	13
Single Family	0.32	0.021	1003	1502	67	0.57	15
Multi-Family	0.24	0.019	768	846	38	0.64	61
Perdue	0.24	0.019	2386	2682	120	0.64	
West Beach	0.34	0.021	220	319	14	0.59	11
Gulf St. Park	1.00	0.000	0	0	0	0.00	7
Orange Beach	1.00	0.000	0	0	0	0.00	4
Metapopulation	0.23	0.019	4660	5450	244	0.65	
K = 90% of baseline, slow recovery							
Fort Morgan	0.45	0.022	275	477	21	0.54	13
Single Family	0.32	0.021	1069	1664	74	0.61	16
Multi-Family	0.25	0.019	805	902	40	0.68	69
Perdue	0.25	0.019	2604	2914	130	0.68	
West Beach	0.35	0.021	221	341	15	0.64	11
Gulf St. Park	1.00	0.000	0	0	0	0.00	7
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.25	0.019	4975	5916	265	0.69	

Model Unit	Prob. Extinct	SE(PE)	Mean N	SD(N)	SE(N)	Gene Diversity	Median Time to Extinction
2x Dispersal, fast recovery							
Fort Morgan	0.28	0.020	597	724	32	0.65	15
Single Family	0.22	0.019	1982	2314	104	0.71	21
Multi-Family	0.19	0.018	1269	1155	52	0.75	91
Perdue	0.19	0.017	4022	3641	163	0.74	
West Beach	0.24	0.019	427	475	21	0.72	15
Gulf St. Park	1.00	0.000	0	0	0	0.00	9
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.19	0.017	8297	7752	347	0.75	
0.5x Dispersal, fast recovery							
Fort Morgan	0.41	0.022	472	672	30	0.49	15
Single Family	0.32	0.021	1645	2209	99	0.60	17
Multi-Family	0.25	0.019	1161	1194	53	0.69	68
Perdue	0.25	0.019	3578	3540	158	0.70	
West Beach	0.32	0.021	353	459	21	0.63	10
Gulf St. Park	1.00	0.000	0	0	0	0.00	8
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.24	0.019	7207	7500	335	0.71	
2x Dispersal, slow recovery							
Fort Morgan	0.30	0.021	440	598	27	0.62	14
Single Family	0.24	0.019	1495	1963	88	0.69	20
Multi-Family	0.20	0.018	1098	1071	48	0.72	88
Perdue	0.20	0.018	3315	3330	149	0.72	
West Beach	0.25	0.019	312	417	19	0.69	13
Gulf St. Park	1.00	0.000	0	0	0	0.00	7
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.19	0.018	6661	6920	309	0.73	
0.5x Dispersal, slow recovery							
Fort Morgan	0.41	0.022	372	570	26	0.44	13
Single Family	0.29	0.020	1264	1775	79	0.56	15
Multi-Family	0.23	0.019	1008	1020	46	0.67	66
Perdue	0.23	0.019	3164	3184	142	0.67	
West Beach	0.33	0.021	267	382	17	0.58	10
Gulf St. Park	1.00	0.000	0	0	0	0.00	8
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.22	0.019	6074	6391	286	0.68	
30% juvenile mortality, fast recovery							
Fort Morgan	0.29	0.020	600	719	32	0.60	18
Single Family	0.21	0.018	1913	2309	103	0.70	21
Multi-Family	0.15	0.016	1290	1179	53	0.75	
Perdue	0.15	0.016	4058	3691	165	0.75	
West Beach	0.22	0.019	407	473	21	0.70	13
Gulf St. Park	1.00	0.000	0	0	0	0.00	8
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.15	0.016	8267	7896	353	0.76	

Model Unit	Prob. Extinct	SE(PE)	Mean N	SD(N)	SE(N)	Gene Diversity	Median Time to Extinction
50% juvenile mortality, fast recovery							
Fort Morgan	0.45	0.022	385	607	27	0.54	14
Single Family	0.36	0.021	1365	1985	89	0.63	17
Multi-Family	0.28	0.020	966	1093	49	0.68	65
Perdue	0.27	0.020	3204	3503	157	0.68	
West Beach	0.37	0.022	309	434	19	0.64	11
Gulf St. Park	1.00	0.000	0	0	0	0.00	8
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.26	0.020	6228	7064	316	0.69	
30% juvenile mortality, slow recovery							
Fort Morgan	0.27	0.020	469	594	27	0.55	15
Single Family	0.18	0.017	1560	1940	87	0.66	20
Multi-Family	0.14	0.015	1203	1066	48	0.74	92
Perdue	0.13	0.015	3696	3365	150	0.73	
West Beach	0.20	0.018	340	409	18	0.68	13
Gulf St. Park	1.00	0.000	0	0	0	0.00	9
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.13	0.015	7268	6899	309	0.74	
50% juvenile mortality, slow recovery							
Fort Morgan	0.49	0.022	324	552	25	0.53	11
Single Family	0.36	0.021	1123	1782	80	0.60	14
Multi-Family	0.29	0.020	838	1003	45	0.65	53
Perdue	0.29	0.020	2603	3082	138	0.65	
West Beach	0.37	0.022	252	378	17	0.62	11
Gulf St. Park	1.00	0.000	0	0	0	0.00	7
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.28	0.020	5140	6322	283	0.66	
14% adult mortality, fast recovery							
Fort Morgan	0.30	0.020	597	727	33	0.60	17
Single Family	0.22	0.018	1935	2292	103	0.67	20
Multi-Family	0.16	0.016	1358	1230	55	0.74	87
Perdue	0.15	0.016	4146	3770	169	0.73	
West Beach	0.25	0.019	424	480	21	0.69	14
Gulf St. Park	1.00	0.000	0	0	0	0.00	9
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.15	0.016	8461	7960	356	0.75	
18% adult mortality, fast recovery							
Fort Morgan	0.39	0.022	445	617	28	0.56	14
Single Family	0.28	0.020	1608	2164	97	0.63	17
Multi-Family	0.23	0.019	1106	1127	50	0.69	76
Perdue	0.23	0.019	3591	3551	159	0.68	
West Beach	0.29	0.020	359	451	20	0.65	11
Gulf St. Park	1.00	0.000	0	0	0	0.00	7
Orange Beach	1.00	0.000	0	0	0	0.00	4
Metapopulation	0.23	0.019	7110	7375	330	0.69	

Model Unit	Prob. Extinct	SE(PE)	Mean N	SD(N)	SE(N)	Gene Diversity	Median Time to Extinction
14% adult mortality, slow recovery							
Fort Morgan	0.33	0.021	451	623	28	0.55	14
Single Family	0.25	0.019	1533	1988	89	0.65	17
Multi-Family	0.22	0.019	1150	1113	50	0.70	78
Perdue	0.21	0.018	3492	3348	150	0.70	
West Beach	0.26	0.020	309	396	18	0.66	11
Gulf St. Park	1.00	0.000	0	0	0	0.00	8
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.21	0.018	6936	6960	311	0.71	
18% adult mortality, slow recovery							
Fort Morgan	0.49	0.022	281	485	22	0.51	18
Single Family	0.33	0.021	1103	1803	81	0.59	20
Multi-Family	0.27	0.020	870	1000	45	0.65	99
Perdue	0.27	0.020	2718	3192	143	0.65	
West Beach	0.36	0.021	232	358	16	0.61	12
Gulf St. Park	1.00	0.000	0	0	0	0.00	8
Orange Beach	1.00	0.000	0	0	0	0.00	4
Metapopulation	0.27	0.020	5204	6364	285	0.66	

Development Scenarios

Figures 7L and 7M, and Table 7B, show the projected effects of some scenarios of possible development (see Section 6 for details.) The trends observed in these analyses are summarized briefly below. The trends relative to the baseline scenarios are largely the same under an assumption of faster or slower recovery of habitat following hurricanes (although the scenarios with faster recovery uniformly perform better than the comparable scenarios with slower recovery). Therefore, to discern effects of each development scenario, we examined the impact on both the fast and slow recovery models, and considered the average effect to provide the best representation of the likely impacts. In a few cases, the simulation results for development scenarios under fast and slow recovery models deviated considerably (although not greater than could be explained by the random sampling error observed with the number of iterations that we ran). For these development scenarios, we re-ran the simulation for the case (Dev4AFast and Dev1A3A4ASlow) that appeared to have by chance deviated from the overall patterns. The results from the re-run of 500 iterations for these scenarios are shown in the figures and tables below, as they seem more in line with the patterns across scenarios and the two models of recovery rate. However, because 500 iterations were not enough to provide precise estimates about moderate impacts of some development scenarios, any judgments about the impacts of specific scenarios (as opposed to more general information obtained from the overall patterns across the set of scenarios tested) should be made with caution and perhaps only after a larger number (1,000 to 2,000) of iterations are completed for the scenarios of particular interest.

Scenario 1A

The projected reduction of Single Family and West Beach model units, in accordance with existing regulations, minimal footprints, and ABM protection, caused an increase in the probability of metapopulation extinction that borders on being statistically detectable. Reductions in the metapopulation size were more noticeable, and mean Ns were significantly below the baseline values. These effects on the metapopulation are mirrored by (and primarily determined by) the impacts on the two largest and most stable subpopulations in Multi-Family and Perdue units. The Single Family and West Beach units show somewhat more rapid and increased risk of extirpation and lower mean population size, as does the subpopulation in the Fort Morgan unit that is partly dependent for stability on its linkage to the Single Family unit.

Scenario 1B

A much larger reduction of the Single Family and West Beach habitat units, as expected if all lots are developed and no protection is provided to the mice, is still projected to result in at most a small increase in the vulnerability of the metapopulation to extinction, because the Multi-Family and Perdue units continue to provide a relatively stable reserve. However, the West Beach and Single Family units were extinct at the end of about half of the scenarios, and when they are not extinct they harbor very few mice (occasional immigrants from Multi-Family and Perdue units). The Fort Morgan subpopulation rarely persists in this scenario, as it is not adjacent to a stable subpopulation that can serve as a source of immigrants.

Scenario 2A1

A reduction in habitat in the Single Family unit that could result from rezoning to higher density housing had little impact on the metapopulation viability (with no significant change under the fast recovery model, and small but just significant reductions in the slow recovery model), but caused a reduction in the number of mice in the Single Family model unit.

Scenario 2A2
Three possible effects were examined to represent changes expected if there is redevelopment of Single Family and West Beach areas for condominiums. One possibility is that there would be no net effect (the same as the baseline scenario), another possibility is that there would be modest reductions in capacity of Single Family and West Beach units (the same as 1A), and a third possibility is that there would be increases in the capacity of Single Family and West Beach units (the case shown in Table 7B and Figures 7L & 7M). This last possibility, with improved habitat, did not result in metapopulation extinction or size noticeably different from the baseline case (although the sizes of Single Family and West Beach subpopulations were increased moderately). As shown in Scenario 1A, a reduction in the capacity of these units slightly increases risk of extinction and decreases mean population size of the units.

Scenario 3A
The modest changes modeled in this scenario, representing effects of increased park infrastructure and improved management, did not measurably alter the model projections.

Scenario 4A
The 10% decrease in the Multi-Family unit if the Gulf Highlands condominium is developed but remaining acreage of the unit is left undeveloped did not cause a significant change in simulation results for the metapopulation.

Scenario 4B
The greater reduction in Multi-Family unit that is expected if the Gulf Highlands condominium is developed and additional homes are built on the remaining acres caused the probability of extinction in the Multi-Family unit and in other units to increase by amounts that are marginally significant under the fast recovery model, and resulted in significant reductions in local subpopulation size and the metapopulation size under the slow recovery model.

Scenario 1A+3A+4A
Combining the effects of development scenarios 1A, 3A, and 4A results in a cumulative effect that reduces mean metapopulation size, but does not cause an observable change in the likelihood of extinction.

Scenario 1B+4B
Combining these development scenarios results in an increased chance of metapopulation extinction, and (similarly to scenario 1B) leaves only the Perdue and Multi-Family units with more than a few mice.

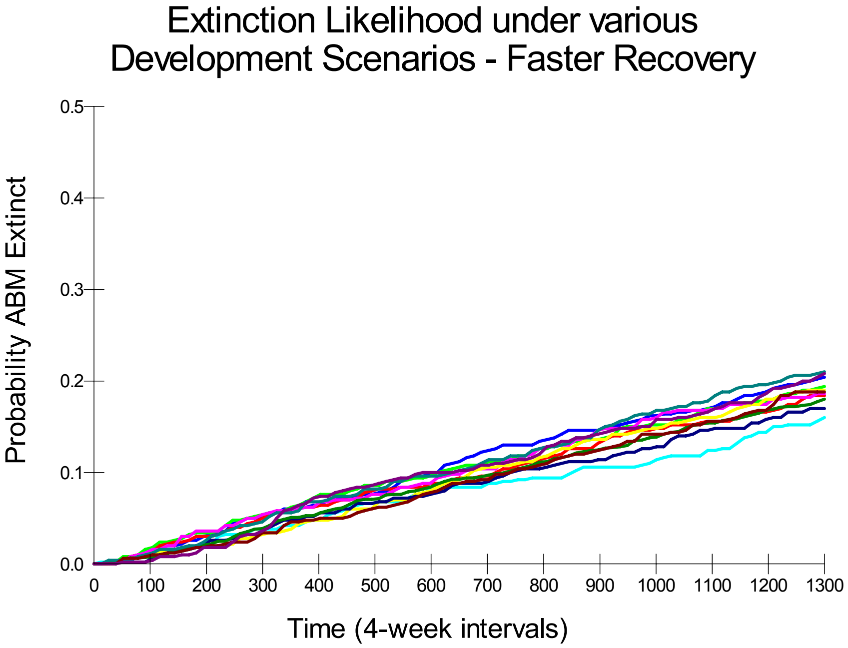
Scenario K1
A reduction of 1% of habitat across all units did not result in an impact that could be detected in our models.

Summary

Overall, the results from these tests of development alternatives indicate that scenarios that include:

- Scenario 1B (large reductions in the Single Family and West Beach units) led to reduced metapopulation size but had minor effects on metapopulation extinction (because these units are not the stabilizing core of the range);
- Scenario 4B (reductions in the amount and quality of habitat in the Multi-Family model unit) resulted in a noticeable increase in the probability of extinction of the metapopulation and reductions in population size in the Multi-Family unit;
- the combination of development scenarios 1B and 4B resulted in the poorest projections of both population size and risk of extinction of any of the development scenarios that we examined;
- Scenario 1A (reduction of Single Family and West Beach units, as expected under existing regulations) caused modest but usually detectable increases in the probabilities of extinction of local subpopulations and the metapopulation, and cause reductions in mean population sizes.

Most other scenarios caused at most local reductions within some of the model units but little impact within the core of the range.



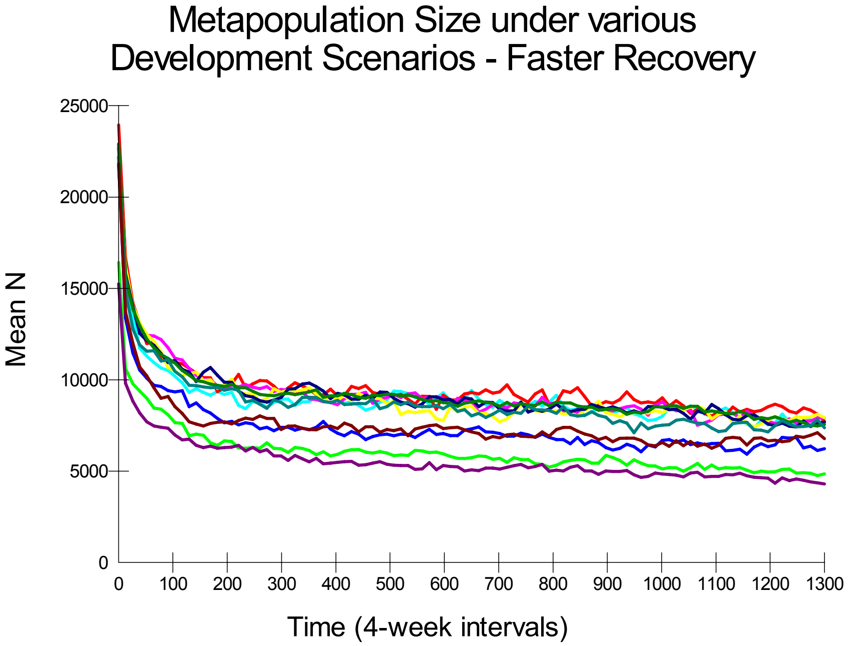


Fig. 7L. Projections of (top graph) probabilities of ABM extinction (the bottom cluster of 9 lines, including the Baseline, are statistically indistinguishable; top two lines are 4B and 1B4B), and (bottom graph) mean size of the metapopulation (the top cluster of 7 lines are not significantly divergent from the baseline; the bottom four lines, significantly below the baseline, are, from best to worst, 1A3A4A, 1A, 1B, and 1B4B) under various scenarios of development, with relatively fast recovery of habitat following hurricanes.

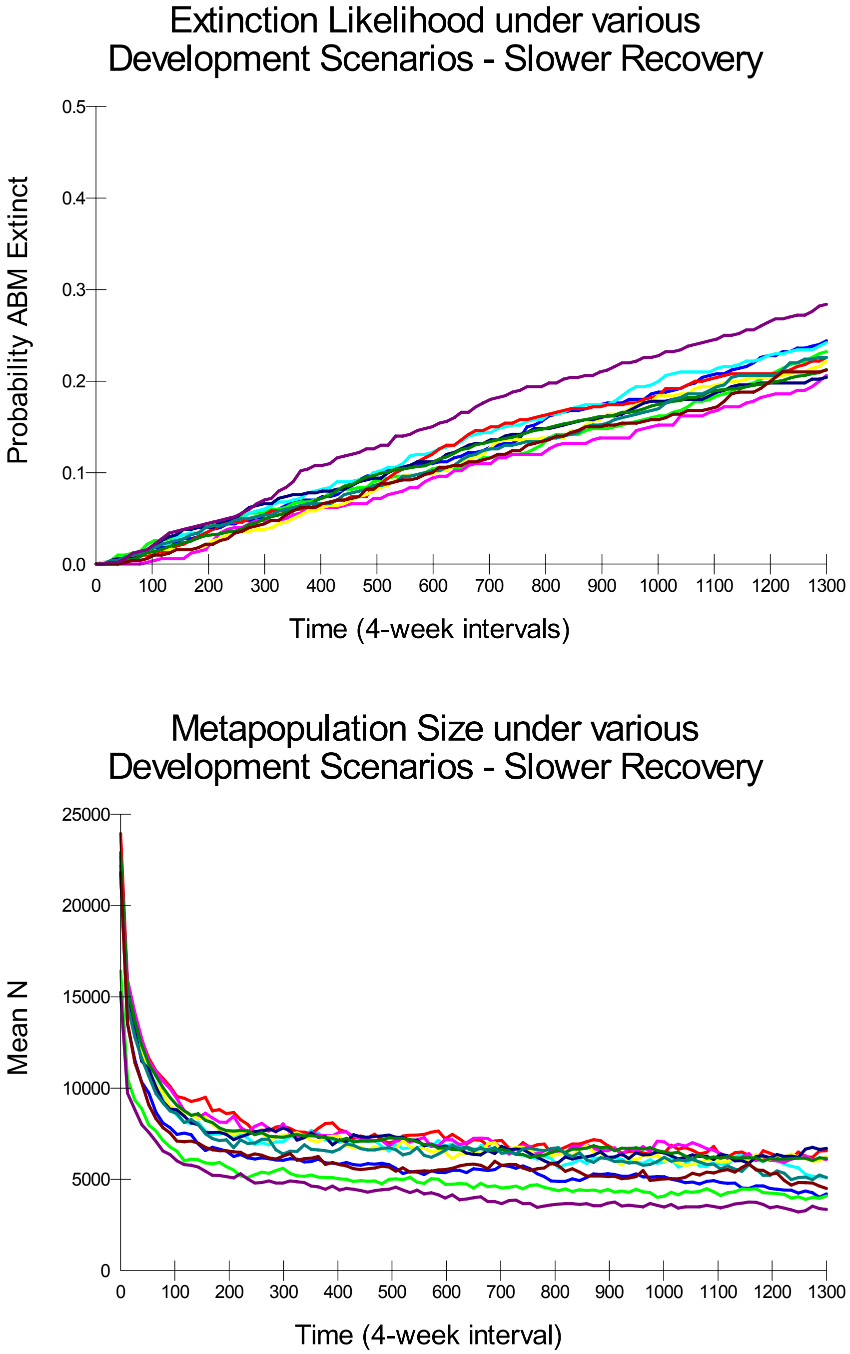


Fig. 7M. Projections of (top graph) probabilities of ABM extinction (the bottom 8 lines, including the Baseline scenario, are statistically indistinguishable; top three lines are 1A, 2A1, and 1B4B), and (bottom graph) mean size of the metapopulation (top five line are indistinguishable; subsequent lines are 2A1, 4B, 1A3A4A, 1A, 1B, and 1B4B) under various scenarios of development, with relatively slow recovery of habitat following hurricanes.

Table 7B. Results for each model unit and the metapopulation for scenarios testing effects of some possible development activities. For the two baseline scenarios, the results are from 1,500 independent iterations of the simulation. Scenarios for testing effects of development were repeated for 500 simulations, and often similar values in the results are not significantly divergent.

Scenario Model Unit	Prob. Extinct	SE(PE)	Mean N	SD(N)	SE(N)	Gene Diversity	Median Time to Extinction
Baseline Fast							
Fort Morgan	0.34	0.012	530	682	18	0.58	18
Single Family	0.24	0.011	1777	2233	58	0.66	23
Multi-Family	0.19	0.010	1186	1149	30	0.73	
Perdue	0.18	0.010	3682	3530	91	0.73	
West Beach	0.26	0.011	384	466	12	0.68	14
Gulf St. Park	1.00	0.000	0	0	0	0.00	10
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.18	0.010	7558	7533	195	0.74	
Dev1AFast							
Fort Morgan	0.47	0.022	428	659	29	0.52	15
Single Family	0.27	0.020	684	1267	57	0.65	12
Multi-Family	0.21	0.018	1223	1163	52	0.70	68
Perdue	0.21	0.018	3711	3510	157	0.70	
West Beach	0.28	0.020	191	276	12	0.66	10
Gulf St. Park	1.00	0.000	0	0	0	0.00	8
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.20	0.018	6237	6122	274	0.71	
Dev1BFast							
Fort Morgan	0.99	0.004	4	78	3	0.16	14
Single Family	0.50	0.022	5	7	0	0.67	2
Multi-Family	0.20	0.018	1189	1171	52	0.72	75
Perdue	0.20	0.018	3649	3605	161	0.73	
West Beach	0.46	0.022	6	7	0	0.66	1
Gulf St. Park	1.00	0.000	0	0	0	0.00	9
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.19	0.018	4853	4656	208	0.73	
Dev2A1Fast							
Fort Morgan	0.33	0.021	552	688	31	0.57	19
Single Family	0.22	0.019	1489	1812	81	0.67	22
Multi-Family	0.16	0.016	1280	1171	52	0.73	
Perdue	0.17	0.017	3944	3601	161	0.73	
West Beach	0.24	0.019	414	478	21	0.70	15
Gulf St. Park	1.00	0.003	1	14	1	0.00	10
Orange Beach	1.00	0.003	0	1	0	0.00	5
Metapopulation	0.16	0.016	7679	7249	324	0.74	

Scenario Model Unit	Prob. Extinct	SE(PE)	Mean N	SD(N)	SE(N)	Gene Diversity	Median Time to Extinction
Dev2A2Fast							
Fort Morgan	0.36	0.021	517	694	31	0.60	15
Single Family	0.25	0.019	1958	2581	115	0.66	19
Multi-Family	0.19	0.018	1142	1145	51	0.72	83
Perdue	0.18	0.017	3709	3570	160	0.72	
West Beach	0.27	0.020	400	507	23	0.68	12
Gulf St. Park	1.00	0.000	0	0	0	0.00	8
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.18	0.017	7727	7957	356	0.73	
Dev3AFast							
Fort Morgan	0.35	0.021	545	692	31	0.58	18
Single Family	0.25	0.019	1876	2245	100	0.66	21
Multi-Family	0.19	0.018	1246	1172	52	0.72	80
Perdue	0.19	0.017	3842	3563	159	0.72	
West Beach	0.26	0.020	408	478	21	0.68	14
Gulf St. Park	1.00	0.000	0	0	0	0.00	10
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.19	0.017	7916	7673	343	0.73	
Dev4AFast							
Fort Morgan	0.32	0.021	524	677	30	0.58	16
Single Family	0.24	0.019	1953	2368	106	0.66	19
Multi-Family	0.19	0.018	1123	1068	48	0.72	76
Perdue	0.20	0.018	3931	3622	162	0.72	
West Beach	0.26	0.020	403	472	21	0.67	13
Gulf St. Park	1.00	0.000	0	0	0	0.00	9
Orange Beach	1.00	0.000	0	0	0	0.00	6
Metapopulation	0.19	0.018	7933	7676	343	0.73	
Dev4BFast							
Fort Morgan	0.34	0.021	562	683	31	0.59	15
Single Family	0.27	0.020	1890	2281	102	0.66	20
Multi-Family	0.22	0.018	809	763	34	0.73	69
Perdue	0.21	0.018	3695	3598	161	0.73	
West Beach	0.28	0.020	416	488	22	0.69	13
Gulf St. Park	1.00	0.000	0	0	0	0.00	9
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.21	0.018	7373	7353	329	0.74	
Dev1A3A4AFast							
Fort Morgan	0.39	0.022	507	684	31	0.54	14
Single Family	0.26	0.020	831	1355	61	0.66	11
Multi-Family	0.19	0.018	1159	1039	46	0.71	75
Perdue	0.19	0.018	4047	3711	166	0.71	
West Beach	0.29	0.020	236	317	14	0.68	9
Gulf St. Park	1.00	0.000	0	0	0	0.00	9
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.19	0.017	6781	6409	287	0.71	

Scenario Model Unit	Prob. Extinct	SE(PE)	Mean N	SD(N)	SE(N)	Gene Diversity	Median Time to Extinction
Dev1B4BFast							
Fort Morgan	0.99	0.003	5	94	4	0.18	15
Single Family	0.59	0.022	3	4	0	0.62	1
Multi-Family	0.22	0.019	737	748	33	0.69	61
Perdue	0.21	0.018	3558	3518	157	0.69	
West Beach	0.44	0.022	6	7	0	0.65	1
Gulf St. Park	1.00	0.000	0	0	0	0.00	8
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.21	0.018	4309	4207	188	0.69	
DevK1Fast							
Fort Morgan	0.34	0.021	525	674	30	0.58	18
Single Family	0.24	0.019	1797	2215	99	0.66	22
Multi-Family	0.18	0.017	1220	1163	52	0.73	97
Perdue	0.17	0.017	3750	3535	158	0.73	
West Beach	0.24	0.019	393	465	21	0.68	14
Gulf St. Park	1.00	0.000	0	0	0	0.00	9
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.17	0.017	7685	7546	337	0.74	
Baseline Slow							
Fort Morgan	0.38	0.013	366	553	14	0.54	14
Single Family	0.27	0.012	1296	1840	48	0.63	17
Multi-Family	0.22	0.011	1039	1066	28	0.69	71
Perdue	0.22	0.011	3172	3267	84	0.68	
West Beach	0.29	0.012	271	378	10	0.63	11
Gulf St. Park	1.00	0.000	0	0	0	0.00	8
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.21	0.011	6144	6599	170	0.70	
Dev1ASlow							
Fort Morgan	0.60	0.022	232	478	21	0.47	13
Single Family	0.37	0.022	339	848	38	0.62	10
Multi-Family	0.25	0.019	899	1022	46	0.68	70
Perdue	0.25	0.019	2632	2966	133	0.68	
West Beach	0.37	0.022	105	202	9	0.63	8
Gulf St. Park	1.00	0.000	0	0	0	0.00	8
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.24	0.019	4207	4950	221	0.68	
Dev1BSlow							
Fort Morgan	1.00	0.002	0	6	0	0.50	13
Single Family	0.57	0.022	4	6	0	0.63	2
Multi-Family	0.24	0.019	985	1082	48	0.67	71
Perdue	0.24	0.019	3103	3394	152	0.68	
West Beach	0.53	0.022	5	7	0	0.66	1
Gulf St. Park	1.00	0.000	0	0	0	0.00	7
Orange Beach	1.00	0.000	0	0	0	0.00	4
Metapopulation	0.23	0.019	4097	4393	196	0.68	

Scenario Model Unit	Prob. Extinct	SE(PE)	Mean N	SD(N)	SE(N)	Gene Diversity	Median Time to Extinction
Dev2A1Slow							
Fort Morgan	0.46	0.022	328	541	24	0.53	13
Single Family	0.33	0.021	945	1457	65	0.62	15
Multi-Family	0.26	0.020	909	1026	46	0.70	64
Perdue	0.25	0.019	2703	3158	141	0.69	
West Beach	0.33	0.021	242	370	17	0.64	11
Gulf St. Park	1.00	0.000	0	0	0	0.00	8
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.24	0.019	5127	6174	276	0.70	
Dev2A2Slow							
Fort Morgan	0.37	0.022	412	586	26	0.56	13
Single Family	0.28	0.020	1609	2204	99	0.63	19
Multi-Family	0.23	0.019	1028	1057	47	0.70	71
Perdue	0.23	0.019	3188	3350	150	0.70	
West Beach	0.30	0.020	328	444	20	0.65	13
Gulf St. Park	1.00	0.000	0	0	0	0.00	8
Orange Beach	1.00	0.000	0	0	0	0.00	4
Metapopulation	0.23	0.019	6566	7171	321	0.71	
Dev3ASlow							
Fort Morgan	0.41	0.022	369	565	25	0.53	15
Single Family	0.29	0.020	1352	1942	87	0.63	20
Multi-Family	0.22	0.018	1009	1083	48	0.71	
Perdue	0.21	0.018	3081	3255	146	0.70	
West Beach	0.31	0.021	280	390	17	0.65	14
Gulf St. Park	1.00	0.000	0	0	0	0.00	10
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.21	0.018	6090	6806	304	0.72	
Dev4ASlow							
Fort Morgan	0.40	0.022	398	582	26	0.54	13
Single Family	0.29	0.020	1387	1938	87	0.62	16
Multi-Family	0.22	0.019	928	963	43	0.68	67
Perdue	0.23	0.019	3235	3384	151	0.67	
West Beach	0.29	0.020	297	409	18	0.63	11
Gulf St. Park	1.00	0.000	0	0	0	0.00	8
Orange Beach	1.00	0.000	0	0	0	0.00	4
Metapopulation	0.22	0.019	6246	6826	305	0.69	
Dev4BSlow							
Fort Morgan	0.43	0.022	302	487	22	0.52	13
Single Family	0.29	0.020	1134	1726	77	0.58	16
Multi-Family	0.23	0.019	620	666	30	0.66	59
Perdue	0.23	0.019	2800	3172	142	0.66	
West Beach	0.31	0.021	244	362	16	0.62	11
Gulf St. Park	1.00	0.000	0	0	0	0.00	8
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.23	0.019	5100	6003	268	0.67	

Scenario Model Unit	Prob. Extinct	SE(PE)	Mean N	SD(N)	SE(N)	Gene Diversity	Median Time to Extinction
Dev1A3A4ASlow							
Fort Morgan	0.54	0.022	259	501	22	0.49	13
Single Family	0.35	0.021	418	934	42	0.62	9
Multi-Family	0.22	0.019	848	903	40	0.67	81
Perdue	0.22	0.019	2865	3130	140	0.68	
West Beach	0.34	0.021	121	216	10	0.63	8
Gulf St. Park	1.00	0.000	0	0	0	0.00	7
Orange Beach	1.00	0.000	0	0	0	0.00	4
Metapopulation	0.21	0.018	4511	5088	228	0.69	
Dev1B4BSlow							
Fort Morgan	1.00	0.003	1	26	1	0.36	13
Single Family	0.64	0.021	3	4	0	0.61	1
Multi-Family	0.30	0.020	605	683	31	0.66	53
Perdue	0.28	0.020	2741	3103	139	0.66	
West Beach	0.53	0.022	4	6	0	0.62	1
Gulf St. Park	1.00	0.000	0	0	0	0.00	7
Orange Beach	1.00	0.000	0	0	0	0.00	4
Metapopulation	0.28	0.020	3354	3723	166	0.67	
DevK1Slow							
Fort Morgan	0.36	0.021	425	586	26	0.53	12
Single Family	0.26	0.020	1523	1979	89	0.63	15
Multi-Family	0.21	0.018	1064	1059	47	0.69	73
Perdue	0.21	0.018	3372	3369	151	0.70	
West Beach	0.27	0.020	318	411	18	0.65	11
Gulf St. Park	1.00	0.000	0	0	0	0.00	7
Orange Beach	1.00	0.000	0	0	0	0.00	4
Metapopulation	0.20	0.018	6701	6945	311	0.70	

Management Scenarios

Several scenarios were tested to examine the likely impacts of changes in management or in habitat impacts not directly related to land development activities (see Section 5 for details). The projections for some of these scenarios are shown in Figures 7N and 7O, while the results for these and for cases of increased cat predation are given in Table 7C. Each factor was analyzed separately; combinations of these factors were not considered in this analysis.

Restoration (Restore)

Restoration of dunes includes sand fencing and the planting and fertilization of vegetation to promote dune development. This was modeled by shortening the recovery time of the habitat (K) following hurricanes. In the model, restoration resulted in about a 10% to 15% increase in mean population size – experienced throughout the model units – but no measurable reductions in probabilities of local and metapopulation extinction. It may be that the probability of extinction is determined more by the extent of population decimation caused by hurricanes than by the rate of recovery of the mouse populations following hurricanes that to do not diminish the populations to such small sizes that recovery does not occur.

Translocation (Trans)

Translocation of mice was modeled as the supplementation of 25 pairs of mice to extirpated ABM subpopulations. For model simplification, the supplemented mice were not removed from an existing ABM model unit but were modeled as if available from an outside unrelated source population. This scenario yielded about 20% to 30% larger mean population sizes and is the only scenario tested that resulted in no extinctions of the metapopulation in the simulations. Local subpopulations occasionally go extinct in this model, but augmentation prevents widespread extinctions, and the Multi-Family, Perdue, and adjacent model units are usually populated with large numbers of mice. Logistical restrictions on actual translocation activities (e.g., timing following extirpation, availability of donor population) may reduce the magnitude of this effect. For example, for this translocation strategy to be able to prevent or reverse all extinctions would require that an external source of mice always be available for restocking beach habitats as needed.

House Mice (Mice2 and Mice4)

There is the possibility that male house mice prevent breeding by female beach mice at low population densities. This scenario was modeled as an increased Allee effect (A = 2 or 4) in density-dependent reproduction. (A given Allee effect, A, reduces reproduction by half when a local population is reduced to that size, reduces reproduction by a percent about equal to the Allee parameter when N = 100, and causes diminishing effects at larger population sizes.)When the Allee effect was set to 2, there were no detectable impacts on population size and extinction risk. When A = 4, there were measurable increases in the probability of extinction, and perhaps weak effects on mean population sizes.

Cogongrass Invasion (Cogon)

Based on the observed rate of cogongrass invasion in areas of the southeastern U.S., the possible spread of cogongrass through ABM habitat was modeled as a loss of 1% of the original K each year, resulting in no remaining ABM habitat after 100 years. Under this level of invasion, the ABM populations in each model unit and the metapopulation are expected to decline steadily in size, resulting in final extinction in a median of about 100 years.

Domestic Cats (Cat1 to Cats20)

Cat predation on ABM was modeled as each cat killing one ABM per day across all ABM age and sex classes. Killing rate was modeled as constant independent of ABM population size. Scenarios tested 1, 2, 3, 4, 5, 10, 15, and 20 cats per model unit. Thus, for example, the scenario *Cat2* with 2 cats per model unit was modeled as the harvest of 56 ABM in each model unit during each Vortex time step of 28 days (1 ABM killed per day x 28 days x 2 cats). Increased predation by cats, even at the lowest level tested (one cat per model unit), resulted in extinction of ABM throughout the habitats in virtually all (> 99%) or all of the iterations of the simulation models. The levels of cat predation modeled are wholly unsustainable, with the metapopulations usually being driven extinct in less than 20 years. With a large number of cats per unit, extinction can occur within a very few years.

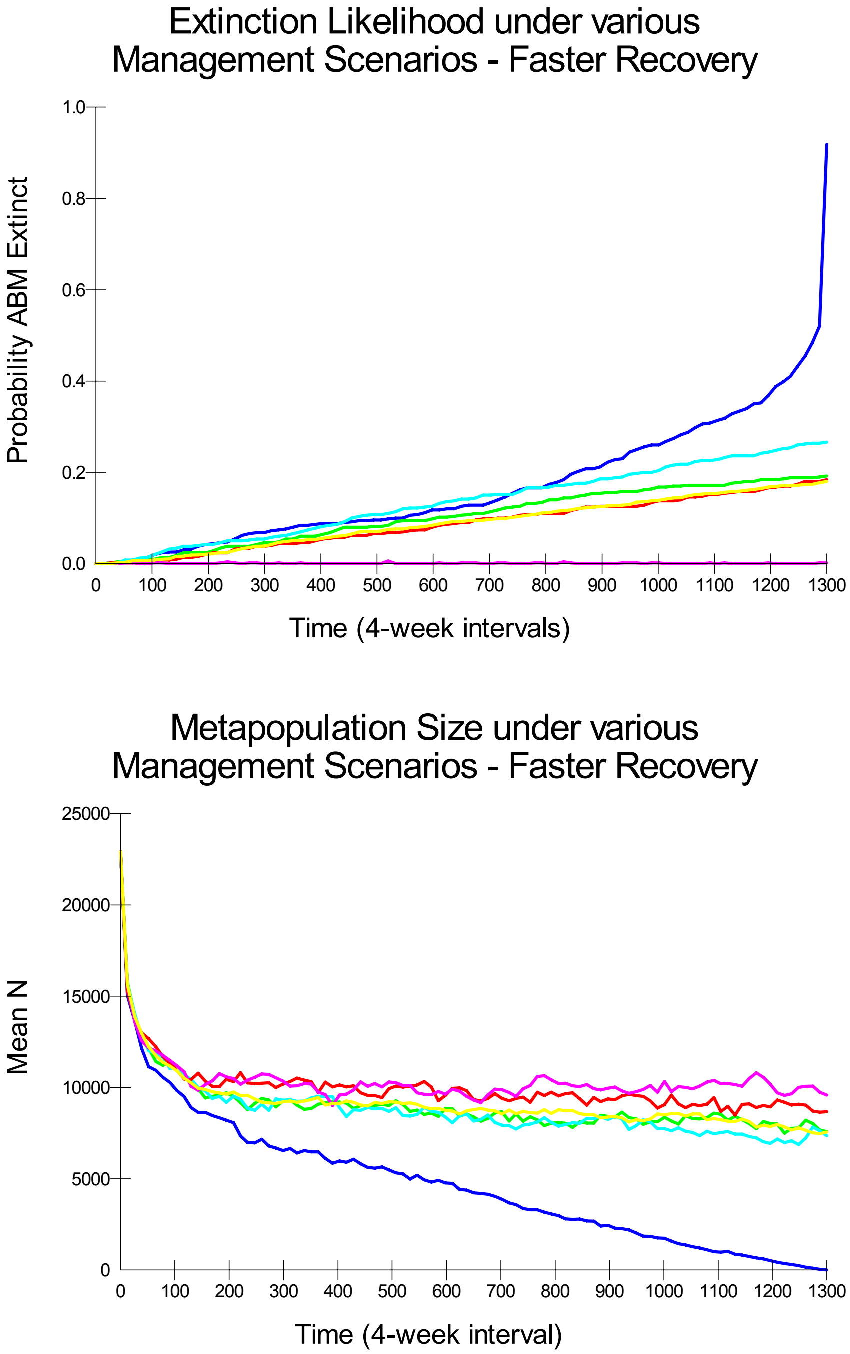


Fig. 7N. Projections of (top graph) probabilities of ABM extinction (bottom line is Trans; cluster of next three indistinguishable lines are Restore, Baseline, and Mice2; top two lines are Mice4 and Cogon), and (bottom graph) mean size of the metapopulation under various management scenarios (top is Trans; followed by Restore; Baseline, Mice2, and Mice4 are indistinguishable; Cogon is at the bottom), with relatively fast recovery of habitat following hurricanes.

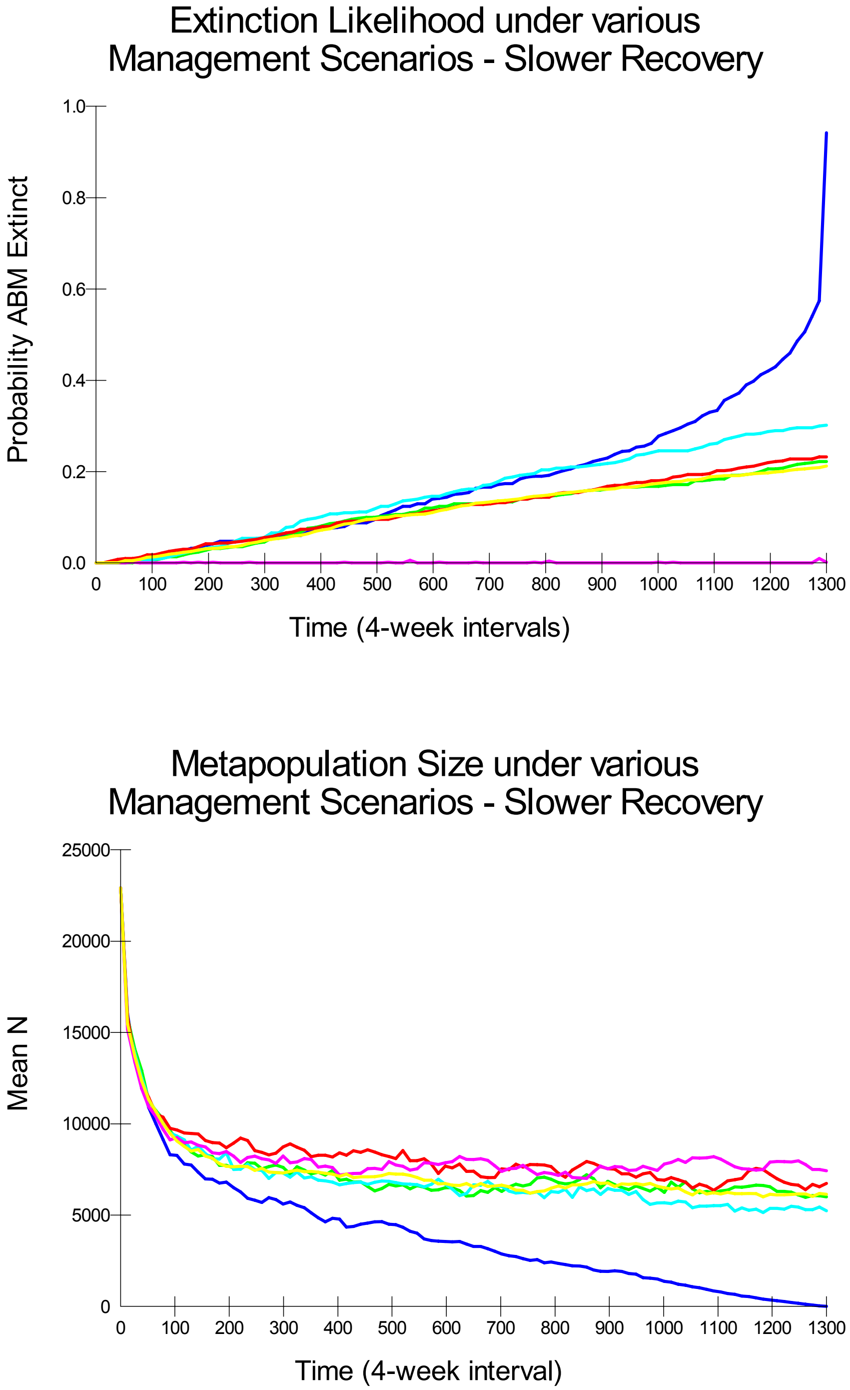


Fig. 7O. Projections of (top graph) probabilities of ABM extinction (bottom to top: Trans; a cluster of Restore, Baseline, and Mice2; Mice4; and Cogon), and (bottom graph) mean size of the metapopulation under various management scenarios (top to bottom, with respect to endpoints: Trans; Restore; Baseline and Mice2; Mice4; Cogon), with relatively slow recovery of habitat following hurricanes.

Table 7C. Results for each model unit and the metapopulation for scenarios testing effects of some possible management activities and changes in the environment. For the two baseline scenarios, the results are from 1,500 independent iterations of the simulation. Scenarios for testing effects of management actions were repeated for 500 simulations, and often similar values in the results are not significantly divergent.

Scenario Model Unit	Prob. Extinct	SE(PE)	Mean N	SD(N)	SE(N)	Gene Diversity	Median Time to Extinction
Baseline Fast							
Fort Morgan	0.34	0.012	530	682	18	0.58	18
Single Family	0.24	0.011	1777	2233	58	0.66	23
Multi-Family	0.19	0.010	1186	1149	30	0.73	
Perdue	0.18	0.010	3682	3530	91	0.73	
West Beach	0.26	0.011	384	466	12	0.68	14
Gulf St. Park	1.00	0.000	0	0	0	0.00	10
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.18	0.010	7558	7533	195	0.74	
Mice2Fast							
Fort Morgan	0.34	0.021	511	693	31	0.58	14
Single Family	0.26	0.020	1763	2262	101	0.67	19
Multi-Family	0.20	0.018	1214	1200	54	0.73	77
Perdue	0.20	0.018	3716	3552	159	0.72	
West Beach	0.27	0.020	380	462	21	0.69	12
Gulf St. Park	1.00	0.000	0	0	0	0.00	8
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.19	0.018	7585	7651	342	0.73	
Mice4Fast							
Fort Morgan	0.41	0.022	485	687	31	0.62	13
Single Family	0.33	0.021	1691	2224	99	0.69	17
Multi-Family	0.28	0.020	1172	1163	52	0.74	71
Perdue	0.27	0.020	3640	3606	161	0.74	
West Beach	0.34	0.021	370	459	21	0.70	12
Gulf St. Park	1.00	0.000	0	0	0	0.00	8
Orange Beach	1.00	0.000	0	0	0	0.00	4
Metapopulation	0.27	0.020	7358	7582	339	0.75	
CogonFast							
Fort Morgan	1.00	0.000	0	0	0	0.00	16
Single Family	0.99	0.004	0	0	0	0.27	18
Multi-Family	1.00	0.002	0	0	0	0.75	58
Perdue	0.97	0.007	0	1	0	0.46	90
West Beach	1.00	0.000	0	0	0	0.00	11
Gulf St. Park	1.00	0.000	0	0	0	0.00	9
Orange Beach	1.00	0.000	0	0	0	0.00	4
Metapopulation	0.92	0.012	0	1	0	0.46	99

Scenario Model Unit	Prob. Extinct	SE(PE)	Mean N	SD(N)	SE(N)	Gene Diversity	Median Time to Extinction
RestoreFast							
Fort Morgan	0.31	0.021	607	718	32	0.61	15
Single Family	0.23	0.019	2065	2374	106	0.69	20
Multi-Family	0.18	0.017	1379	1223	55	0.76	84
Perdue	0.19	0.017	4182	3696	165	0.75	
West Beach	0.26	0.020	440	484	22	0.71	12
Gulf St. Park	1.00	0.000	0	0	0	0.00	9
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.18	0.017	8673	7908	354	0.76	
TransFast							
Fort Morgan	0.06	0.010	676	674	30	0.83	20
Single Family	0.04	0.008	2098	2217	99	0.88	22
Multi-Family	0.01	0.003	1488	1123	50	0.88	
Perdue	0.01	0.003	4653	3494	156	0.84	
West Beach	0.06	0.011	459	464	21	0.83	15
Gulf St. Park	0.13	0.015	186	182	8	0.67	9
Orange Beach	0.33	0.021	23	23	1	0.71	5
Metapopulation	0.00	0.002	9584	7523	336	0.90	
Baseline Slow							
Fort Morgan	0.38	0.013	366	553	14	0.54	14
Single Family	0.27	0.012	1296	1840	48	0.63	17
Multi-Family	0.22	0.011	1039	1066	28	0.69	71
Perdue	0.22	0.011	3172	3267	84	0.68	
West Beach	0.29	0.012	271	378	10	0.63	11
Gulf St. Park	1.00	0.000	0	0	0	0.00	8
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.21	0.011	6144	6599	170	0.70	
Mice2Slow							
Fort Morgan	0.39	0.022	357	539	24	0.54	14
Single Family	0.29	0.020	1304	1892	85	0.62	16
Multi-Family	0.23	0.019	1004	1058	47	0.68	62
Perdue	0.23	0.019	3074	3276	147	0.69	
West Beach	0.30	0.020	269	384	17	0.64	11
Gulf St. Park	1.00	0.000	0	0	0	0.00	8
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.22	0.019	6006	6691	299	0.69	
Mice4Slow							
Fort Morgan	0.48	0.022	313	528	24	0.56	13
Single Family	0.35	0.021	1114	1762	79	0.62	17
Multi-Family	0.31	0.021	894	1031	46	0.68	65
Perdue	0.30	0.021	2685	3148	141	0.67	
West Beach	0.38	0.022	238	374	17	0.63	11
Gulf St. Park	1.00	0.000	0	0	0	0.00	7
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.30	0.021	5244	6413	287	0.68	

Scenario Model Unit	Prob. Extinct	SE(PE)	Mean N	SD(N)	SE(N)	Gene Diversity	Median Time to Extinction
CogonSlow							
Fort Morgan	1.00	0.000	0	0	0	0.00	13
Single Family	1.00	0.003	0	0	0	0.41	16
Multi-Family	1.00	0.000	0	0	0	0.00	54
Perdue	0.97	0.007	0	1	0	0.42	85
West Beach	1.00	0.000	0	0	0	0.00	11
Gulf St. Park	1.00	0.000	0	0	0	0.00	8
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.94	0.010	0	1	0	0.44	97
RestoreSlow							
Fort Morgan	0.38	0.022	428	610	27	0.58	14
Single Family	0.29	0.020	1504	1974	88	0.65	17
Multi-Family	0.24	0.019	1114	1128	50	0.72	76
Perdue	0.23	0.019	3379	3397	152	0.71	
West Beach	0.31	0.021	319	417	19	0.67	12
Gulf St. Park	1.00	0.000	0	0	0	0.00	8
Orange Beach	1.00	0.000	0	0	0	0.00	5
Metapopulation	0.23	0.019	6744	7019	314	0.72	
TransSlow							
Fort Morgan	0.07	0.011	482	560	25	0.83	21
Single Family	0.04	0.009	1549	1911	85	0.87	24
Multi-Family	0.01	0.004	1220	1037	46	0.85	
Perdue	0.00	0.002	3712	3206	143	0.80	
West Beach	0.08	0.012	330	402	18	0.80	13
Gulf St. Park	0.20	0.018	124	153	7	0.63	9
Orange Beach	0.45	0.022	15	19	1	0.64	5
Metapopulation	0.00	0.002	7433	6727	301	0.88	
1CatFast							
Fort Morgan	1.00	0.000	0	0	0	0.00	3
Single Family	1.00	0.003	0	0	0	0.75	5
Multi-Family	0.99	0.003	3	38	2	0.92	11
Perdue	0.99	0.003	33	481	22	0.91	16
West Beach	0.99	0.003	0	2	0	0.88	4
Gulf St. Park	1.00	0.000	0	0	0	0.00	2
Orange Beach	1.00	0.000	0	0	0	0.00	0
Metapopulation	0.99	0.003	35	504	23	0.91	17
2CatsFast							
Fort Morgan	1.00	0.000	0	0	0	0.00	3
Single Family	1.00	0.000	0	0	0	0.00	4
Multi-Family	1.00	0.000	0	0	0	0.00	9
Perdue	1.00	0.000	0	0	0	0.00	11
West Beach	1.00	0.000	0	0	0	0.00	4
Gulf St. Park	1.00	0.000	0	0	0	0.00	1
Orange Beach	1.00	0.000	0	0	0	0.00	0
Metapopulation	1.00	0.000	0	0	0	0.00	11

Scenario Model Unit	Prob. Extinct	SE(PE)	Mean N	SD(N)	SE(N)	Gene Diversity	Median Time to Extinction
3CatsFast							
Fort Morgan	1.00	0.000	0	0	0	0.00	3
Single Family	1.00	0.000	0	0	0	0.00	4
Multi-Family	1.00	0.002	0	3	0	0.94	7
Perdue	1.00	0.002	17	372	17	0.95	9
West Beach	1.00	0.002	0	1	0	0.94	3
Gulf St. Park	1.00	0.000	0	0	0	0.00	1
Orange Beach	1.00	0.000	0	0	0	0.00	0
Metapopulation	1.00	0.002	17	375	17	0.95	9
4CatsFast							
Fort Morgan	1.00	0.000	0	0	0	0.00	2
Single Family	1.00	0.000	0	0	0	0.00	3
Multi-Family	1.00	0.000	0	0	0	0.00	6
Perdue	1.00	0.000	0	0	0	0.00	7
West Beach	1.00	0.000	0	0	0	0.00	3
Gulf St. Park	1.00	0.000	0	0	0	0.00	1
Orange Beach	1.00	0.000	0	0	0	0.00	0
Metapopulation	1.00	0.000	0	0	0	0.00	7
5CatsFast							
Fort Morgan	1.00	0.000	0	0	0	0.00	2
Single Family	1.00	0.000	0	0	0	0.00	3
Multi-Family	1.00	0.000	0	0	0	0.00	6
Perdue	1.00	0.000	0	0	0	0.00	6
West Beach	1.00	0.000	0	0	0	0.00	3
Gulf St. Park	1.00	0.000	0	0	0	0.00	0
Orange Beach	1.00	0.000	0	0	0	0.00	0
Metapopulation	1.00	0.000	0	0	0	0.00	6
10CatsFast							
Fort Morgan	1.00	0.000	0	0	0	0.00	2
Single Family	1.00	0.000	0	0	0	0.00	2
Multi-Family	1.00	0.000	0	0	0	0.00	4
Perdue	1.00	0.000	0	0	0	0.00	5
West Beach	1.00	0.000	0	0	0	0.00	2
Gulf St. Park	1.00	0.000	0	0	0	0.00	0
Orange Beach	1.00	0.000	0	0	0	0.00	0
Metapopulation	1.00	0.000	0	0	0	0.00	5
15CatsFast							
Fort Morgan	1.00	0.000	0	0	0	0.00	1
Single Family	1.00	0.000	0	0	0	0.00	1
Multi-Family	1.00	0.000	0	0	0	0.00	3
Perdue	1.00	0.000	0	0	0	0.00	3
West Beach	1.00	0.000	0	0	0	0.00	2
Gulf St. Park	1.00	0.000	0	0	0	0.00	0
Orange Beach	1.00	0.000	0	0	0	0.00	0
Metapopulation	1.00	0.000	0	0	0	0.00	3

Scenario Model Unit	Prob. Extinct	SE(PE)	Mean N	SD(N)	SE(N)	Gene Diversity	Median Time to Extinction
20CatsFast							
Fort Morgan	1.00	0.000	0	0	0	0.00	1
Single Family	1.00	0.000	0	0	0	0.00	1
Multi-Family	1.00	0.000	0	0	0	0.00	2
Perdue	1.00	0.000	0	0	0	0.00	2
West Beach	1.00	0.000	0	0	0	0.00	2
Gulf St. Park	1.00	0.000	0	0	0	0.00	0
Orange Beach	1.00	0.000	0	0	0	0.00	0
Metapopulation	1.00	0.000	0	0	0	0.00	2
1CatSlow							
Fort Morgan	1.00	0.000	0	0	0	0.00	3
Single Family	0.99	0.003	0	1	0	0.88	5
Multi-Family	0.99	0.005	13	164	7	0.90	9
Perdue	0.99	0.005	84	789	35	0.91	14
West Beach	0.99	0.004	0	3	0	0.90	4
Gulf St. Park	1.00	0.000	0	0	0	0.00	2
Orange Beach	1.00	0.000	0	0	0	0.00	0
Metapopulation	0.99	0.005	97	920	41	0.91	15
2CatsSlow							
Fort Morgan	1.00	0.000	0	0	0	0.00	3
Single Family	1.00	0.000	0	0	0	0.00	4
Multi-Family	1.00	0.002	0	1	0	0.93	8
Perdue	1.00	0.002	19	414	19	0.93	11
West Beach	1.00	0.002	0	1	0	0.90	4
Gulf St. Park	1.00	0.000	0	0	0	0.00	1
Orange Beach	1.00	0.000	0	0	0	0.00	0
Metapopulation	1.00	0.002	19	416	19	0.93	11
3CatsSlow							
Fort Morgan	1.00	0.000	0	0	0	0.00	3
Single Family	1.00	0.000	0	0	0	0.00	4
Multi-Family	1.00	0.000	0	0	0	0.00	7
Perdue	1.00	0.000	0	0	0	0.00	9
West Beach	1.00	0.000	0	0	0	0.00	3
Gulf St. Park	1.00	0.000	0	0	0	0.00	1
Orange Beach	1.00	0.000	0	0	0	0.00	0
Metapopulation	1.00	0.000	0	0	0	0.00	9
4CatsSlow							
Fort Morgan	1.00	0.000	0	0	0	0.00	3
Single Family	1.00	0.000	0	0	0	0.00	3
Multi-Family	1.00	0.000	0	0	0	0.00	7
Perdue	1.00	0.000	0	0	0	0.00	7
West Beach	1.00	0.000	0	0	0	0.00	3
Gulf St. Park	1.00	0.000	0	0	0	0.00	1
Orange Beach	1.00	0.000	0	0	0	0.00	0
Metapopulation	1.00	0.000	0	0	0	0.00	8

Scenario Model Unit	Prob. Extinct	SE(PE)	Mean N	SD(N)	SE(N)	Gene Diversity	Median Time to Extinction
5CatsSlow							
Fort Morgan	1.00	0.000	0	0	0	0.00	2
Single Family	1.00	0.000	0	0	0	0.00	3
Multi-Family	1.00	0.000	0	0	0	0.00	5
Perdue	1.00	0.000	0	0	0	0.00	6
West Beach	1.00	0.000	0	0	0	0.00	3
Gulf St. Park	1.00	0.000	0	0	0	0.00	0
Orange Beach	1.00	0.000	0	0	0	0.00	0
Metapopulation	1.00	0.000	0	0	0	0.00	6
10CatsSlow							
Fort Morgan	1.00	0.000	0	0	0	0.00	2
Single Family	1.00	0.000	0	0	0	0.00	2
Multi-Family	1.00	0.000	0	0	0	0.00	4
Perdue	1.00	0.000	0	0	0	0.00	4
West Beach	1.00	0.000	0	0	0	0.00	2
Gulf St. Park	1.00	0.000	0	0	0	0.00	0
Orange Beach	1.00	0.000	0	0	0	0.00	0
Metapopulation	1.00	0.000	0	0	0	0.00	4
15CatsSlow							
Fort Morgan	1.00	0.000	0	0	0	0.00	1
Single Family	1.00	0.000	0	0	0	0.00	1
Multi-Family	1.00	0.000	0	0	0	0.00	3
Perdue	1.00	0.000	0	0	0	0.00	3
West Beach	1.00	0.000	0	0	0	0.00	2
Gulf St. Park	1.00	0.000	0	0	0	0.00	0
Orange Beach	1.00	0.000	0	0	0	0.00	0
Metapopulation	1.00	0.000	0	0	0	0.00	3
20CatsSlow							
Fort Morgan	1.00	0.000	0	0	0	0.00	1
Single Family	1.00	0.000	0	0	0	0.00	1
Multi-Family	1.00	0.000	0	0	0	0.00	2
Perdue	1.00	0.000	0	0	0	0.00	2
West Beach	1.00	0.000	0	0	0	0.00	1
Gulf St. Park	1.00	0.000	0	0	0	0.00	0
Orange Beach	1.00	0.000	0	0	0	0.00	0
Metapopulation	1.00	0.000	0	0	0	0.00	2

Alabama Beach Mouse PHVA

Point Clear, Alabama
June 8–11, 2004

FINAL REPORT

APPENDIX I

Workshop Participant Information

MEMORANDUM

TO: Alabama Beach Mouse Recovery Team Members

FROM: Larry Goldman

DATE: April 19, 2004

SUBJECT: Alabama Beach Mouse Population and Habitat Viability Analysis Workshop

---

We are pleased to confirm that a workshop will be held June 7-11, 2004 to analyze data in an effort to predict the viability of Alabama beach mouse population(s) and required habitat(s). The workshop will be conducted and facilitated by Conservation Breeding Specialists Group.

This workshop will be held in Point Clear, Alabama at the Marriott Grand Hotel. The week will begin Monday, June 7 with an afternoon field visit to ABM habitat along Alabama's Gulf Coast and the Fort Morgan Peninsula. The rest of the workshop will be conducted indoors at the hotel (Tuesday-Thursday, June 8-10 from 8:00 am until 5:00 pm and Friday, June 11 from 8:00 am until 12:00 pm). The hotel is holding a block of rooms for our event and you will be responsible for making your own reservations with the hotel.

We need to gather information that may be useful in the workshop so that it can be compiled into a briefing book for use by workshop participants. We request your assistance in compiling this information. Any published or non-published information that you have should be submitted to Lori McNease or Rob Tawes ***by close of business Monday, May 17, 2004***. Lori may be reached via e-mail at lori_mcnease@fws.gov or 251-441-5867. Rob may be reached via e-mail at robert_tawes@fws.gov or 251-441-5830. Printed materials may also be mailed to our office at P. O. Drawer 1190, Daphne, AL 36526 or shipped to our office at 1208-B Main Street, Daphne, AL 36526.

To help us in finalizing plans for the workshop, we need to confirm your attendance (or that of someone you think might need to attend). Please notify Lori or Rob by e-mail or telephone with ***attendance information by close of business Monday May 24, 2004***.

ALABAMA BEACH MOUSE PHVA WORKSHOP

Participant List

Barbara Allen
USFWS
1208-B Main Street
Daphne, AL 36526
barbara_allen@fws.gov

Gloria Bell
USFWS
1875 Century Blvd, Suite 200
Atlanta, GA 30345
gloria_bell@fws.gov

Brett Bowen
FEMA
US Dept. Homeland Security
3003 Chamblee Tucker Rd.
Atlanta, GA 30341
Brett.bowen@dhs.gov

Onnie Byers
CBSG
12101 Johnny Cake Ridge Rd
Apple Valley, MN 55124
onnie@cbsg.org

Tracy Bush
USFWS
1208-B Main Street
Daphne, AL 36526
tracy_bush@fws.gov

Roger Clay
ADCNR
PO Box 247
Daphne, AL 36526
rclay@dcnr.state.al.us

Michelle Clendenin
USFWS
1208-B Main Street
Daphne, AL 36526
michelle_clendenin@fws.gov

David Cooper
PO Box 1096
Gulf Shores, AL 36547
david.ddc@gulftel.com

Brent Danielson
Iowa State Univ., Dept EEOB
353 Bessey
Ames, IA 50211
Jessie@iastate.edu

David Flemming
USFWS
1875 Century Blvd, Ste 200
Atlanta, GA 30345
dave_flemming@fws.gov

Flo Gardipee
934 Rimini Court
Missoula, MT 59801
flo.gardipee@mso.umt.edu

Ralph Gilges
Pres. Friends of BSNWR
6939 Driftwood Dr.
Gulf Shores, AL 36542-8089
rngilges@aol.com

Larry Goldman
USFWS
1208-B Main Street
Daphne, AL 36526
larry_goldman@fws.gov

Mike Groutt
USFWS
1208-B Main Street
Daphne, AL 36526
mike_groutt@fws.gov

Amber Houston
US Army Corps of Engineers
109 St. Joseph St.
Mobile, AL 36602
amber.m.houston@
sam.usace.army.mil

Jenny Jacobson
US Army Corps of Engineers
109 St. Joseph St.
Mobile, AL 36602
jennifer.l.jacobson@
sam.usace.army.mil

Scott James
Mobile Bay Sierra Club
PO Box 852102
Mobile, AL 36685
ssjames@gulftel.com

Bob Lacy
CBSG
12101 Johnny Cake Ridge Rd
Apple Valley, MN 55124
rlacy@ix.netcom.com

Bill Lynn
St. Joe Timberland/
WindMark Beach Naturalist
P. O. Box 908
Port St. Joe, FL 32457
Blynn@joe.comm

Will McDearman
USFWS
6578 Dogwood View Pkwy
Jackson, MS 39213
will_mcdearman@fws.gov

Lori McNease
USFWS
1208-B Main Street
Daphne, AL 36526
lori_mcnease@fws.gov

Jim Moyers
14500 School Drive
Panama City, FL 32413
jmoyers@joe.com

Janet Mizzi
USFWS
1601 Balboa Ave
Panama City, FL 32405
janet_mizzi@fws.gov

Wendell Neal
ESACS, LLC
316 Remington Dr.
Brandon, MS 39042
waneal4543@aol.com

Lorna Patrick
USFWS
1601 Balboa Ave
Panama City, FL 32405
lorna_patrick@fws.gov

Jereme Phillips
BSNWR
12295 St. Hwy. 180
Gulf Shores, AL 36542
jereme_phillips@fws.gov

Kent Prior
Canadian Wildlife Service
Place Vincent Massey, 4th Floor
351 St. Joseph Blvd.
Gatineau, Quebec
CANADA K1A 0H3
kent.prior@ec.gc.ca

David Reed
Department of Biology
University of Mississippi
PO Box 1848
University, MS 38677
dreed@olemiss.edu

Kelly Reetz
20115 St. Hwy 135
Gulf Shores, AL 36542
gspnc@gulftel.com

Tony Rivera
PO Box 299
Gulf Shores, AL 36547
cogs@gulftel.com

Sandra Sneckenberger
USFWS
1601 Balboa Ave
Panama City, FL 32405
sandra_sneckenberger@fws.gov

Rob Tawes
USFWS
1208-B Main Street
Daphne, AL 36526
robert_tawes@fws.gov

Kathy Traylor-Holzer
CBSG
12101 Johnny Cake Ridge Rd
Apple Valley, MN 55124
kathy@cbsg.org

Aaron Valenta
USFWS
1875 Century Blvd, Suite 200
Atlanta, GA 30345
aaron_valenta@fws.gov

Noreen Walsh
USFWS
1875 Century Blvd, Suite 200
Atlanta, GA 30345
noreen_walsh@fws.gov

Short Biographical Information

PHVA Workshop Participants

Barbara Allen holds a Biology degree from the University of South Alabama (emphasis on wetland ecology with chemistry minor). Her career as a biologist began in 1981 with the US Army Corps of Engineers. She served as a project manager in the Regulatory Branch with responsibility for evaluating permit applications under the Clean Water Act. In 1998, Barbara began her career with the US Fish and Wildlife Service in the Daphne Field Office. Since that time she has worked primarily on endangered species issues, including development of an endangered species mitigation bank for gopher tortoises (*Gopherus polyphemus*) and Habitat Conservation Plans for Red Hill salamanders (*Phaeognathus hubrichti*). Her primary responsibility for the past several years has been administration of Section 10 of the Endangered Species Act and dealing with controversial issues related to the Alabama beach mouse.

Gloria Bell works for the US Fish and Wildlife Service Regional Office in Atlanta, GA and is chief of Endangered Species for the Southeastern U.S. She previously worked in listing and recovery in the Southeast Regional Office.

Brett Bowen works for FEMA, US Department of Homeland Security in Atlanta, GA.

Tracy Bush has worked for the US Fish and Wildlife Service from 1992 to present. Her duties primarily include developing, implementing, analyzing and maintaining complex Geographical Information System (GIS) databases for endangered species management, protection, recovery and conservation efforts throughout the state of Alabama with emphasis on Alabama and Perdido Key beach mouse.

Roger Clay works for the Alabama Department of Conservation and Natural Resources in Daphne, AL.

Michelle Clendenin is an endangered species biologist for the Daphne (Alabama) Field Office of the US Fish and Wildlife Service. She has been with the Service since 1997, and has experience working with endangered species in Colorado, California and throughout the southeastern US. Currently, she is assisting proponents of development projects in habitat conservation planning and other recovery efforts associated with actions affecting the Alabama beach mouse and marine sea turtles. She received her Bachelor of Science degree in Botany from the University of Arkansas and Master of Science in Forest Ecology from Stephen F. Austin State University.

Brent Danielson is an associate professor in the Department of Ecology, Evolution, and Organismal Biology at Iowa State University. He has conducted research on the spatial population dynamics of many species, including the mainland subspecies of *Peromyscus polionotus* over the last 25 years. He has conducted large-scale experiments on the effects of landscape features on the behavior, dispersal, and population dynamics of these species and has modeled these effects as well. He holds a Bachelors of Science degree from Michigan State University and a Doctorate from the University of Kansas.

David Flemming is a biologist in the US Fish and Wildlife Service (Service) Regional Office in Atlanta, Georgia. He has been working with the Service since 1979 in the Ecological Services program , primarily with endangered species. Currently, he is an Ecological Services Supervisor, supervising field offices in Alabama, Georgia, Florida, Puerto Rico, and the U.S. Virgin Islands. Dave received a Bachelor of Science from Grove City College in 1975 with a major in biology and a Master of Science in biology from Bowling Green State University in 1977. He did graduate work on *Peromyscus leucopus* and has worked with most of the HCPs for the Alabama beach mouse.

Flo Gardipee is a graduate student at the University of Montana and served as an intern for the Bon Secour National Wildlife Refuge during the summer of 2004.

Ralph Gilges is the President of Friends of Bon Secour National Wildlife Refuge.

Larry Goldman is Field Supervisor of the US Fish and Wildlife Service Field Office at Daphne, Alabama. He has a Bachelor of Science Degree in Fisheries from the University of Washington. He has worked for over 36 years for the Service. His entire career has dealt with environmental impact analysis and effects of development on fish and wildlife resources. He has worked in California, Oregon, Washington, Mississippi, Florida, Georgia, Puerto Rico. U.S. Virgin Islands, Alabama, and spent two years in the Service's Washington, DC office. Mr. Goldman has been involved with administration of the Endangered Species Act, including consideration of activities affecting the Alabama beach mouse (ABM), since 1988. The Daphne Field Office has had lead responsibility for the ABM since 1997.

Mike Groutt serves as the Public Affairs specialist for the US Fish and Wildlife Service Daphne Field Office, and is responsible for outreach and education activities. Mike came to the Service in 2003 from the Centers for Disease Control and Prevention in Atlanta, where he worked with the news media on issues related to environmental health. Mike has a wide variety of communications experience with the federal government, including work with the United States Army and the U.S. Department of Agriculture. His educational background includes a B.A. in Journalism from Memphis State University, as well as the Army Advanced Public Affairs Course at the University of South Carolina.

Amber Houston attended the PHVA workshop while interning for the US Army Corps of Engineers in Mobile, AL.

Jenny Jacobson is a Biologist for the US Army Corps of Engineers, Mobile District in Mobile, AL. Jenny is responsible for preparing and coordinating EIS, ROD, EA, Section 404(b)1, and FONSI documents according to National Environmental Policy Act. She came to the District in 1998 from the National Oceanic and Atmospheric Administration (NOAA). Jenny holds a B.A. in Biology from the University of Louisville, Kentucky and a M.S. in Marine Biology and Coastal Zone Management from Nova Southeastern University, Florida.

Scott James works for the Sierra Club.

Bill Lynn completed his master's work on the Alabama Beach Mouse while attending Auburn University. His thesis work was entitled "The Social Organization and Burrow-Site Selection of the Alabama Beach Mouse." Collectively, Mr. Lynn has more than 10 years of research for all beach mice subspecies on the Gulf Coast of Florida and Alabama. Mr. Lynn worked four years for the US Fish and Wildlife Service and recently joined the St. Joe Timberland Company.

Will McDearman works for the US Fish and Wildlife Service in Jackson, MS.

Lori McNease received a B.S. in Biology (zoology emphasis with botany minor) from Northwestern State University and an M.S. in Forestry (wildlife ecology emphasis) from Mississippi State University. She worked for USDA, Natural Resources Conservation Service on wetland and wildlife habitat conservation with private landowners in Mississippi and coastal wetlands restoration in Louisiana. Lori has worked for US Fish and Wildlife Service since 1999, with duties concentrating on endangered species protection and enhancement on Forest Service lands in Alabama, migratory bird conservation efforts through Partners in Flight, and Alabama and Perdido Key beach mouse recovery efforts.

Janet Mizzi is the Deputy Field Supervisor for the US Fish and Wildlife Service's Panama City Field Office where she oversees the Endangered Species Program for northwest Florida. Janet has a Bachelors Degree in Fish and Wildlife Management, with a minor in Chemistry, and a Masters Degree from South Dakota State University in Fish and Wildlife Science. Janet has 14 years experience working with endangered species in Utah and California and as a regional coordinator in Denver, Colorado prior to assuming her current position in 2003.

Wendell Neal received his B.S. in Biology from Northwestern State College and M.S. in Wildlife from Louisiana State University. He retired from US Fish and Wildlife Service in 1994 where he supervised Section 7 activities for Alabama, Arkansas, Louisiana and Mississippi until reorganization, then supervised Section 10 activity for the same area, plus listing activity (LA. black bear, green pitcher plant, and reclassification of American alligator). Since retirement, Wendell has done all Section 10 activity for all major developments in Alabama beach mouse habitat, with the single exception of the currently ongoing application on Gulf Shores State Park. He conducts permit required beach mouse trapping on all the major developments. He has served as a consultant on other Section 10 permit applications, including the red-cockaded woodpecker and American burying beetle.

Lorna Patrick is a Fish and Wildlife Biologist in the US Fish and Wildlife Service Panama City, Florida Field Office. She has been working for the Service since 1978 and has been working with upland coastal endangered species since the late 1980s. Lorna conducts recovery projects and consultations for projects that could affect species such as sea turtles, beach mice and shorebirds. She received her Bachelor of Arts degree from Florida State University in 1978 with a major in biology and a minor in chemistry.

Jereme Phillips is a wildlife biologist with the US Fish and Wildlife Service at Bon Secour National Wildlife Refuge in Gulf Shores, Alabama. He has been working with endangered species for the Service since 1999 at refuges in Mississippi and Alabama. His responsibilities include coordinating research and management of wildlife and habitats on the refuge with particular emphasis on endangered species, including sea turtles and beach mice, and neotropical migratory birds. Jereme received his B.S. in wildlife biology from Texas State University in 1996.

Kent Prior works for the Canadian Wildlife Service and is interested in applying the PHVA process to high priority species at risk in Canada.

Kelly Reetz is a naturalist at Gulf State Park in Gulf Shores, Alabama. She received her B.S. in Zoology at Auburn University and has been with Gulf State Park since 2000. Her responsibilities include educating the park guests and locals about native wildlife and the importance of habitat management and preservation within the park and surrounding coastal areas.

Tony Rivera served as a City Administrator for the City of Gulf Shores with 33 years of experience in Municipal Administration. He has a B.S. in Business Administration from Northeastern State and a M.S. in Human Resources from East Central University, both in Oklahoma. As City Manager, he was particularly interested in the ABM and the impact of development and municipal expansion on its habitat and sustainability. As of February 2005, Tony is no longer a city employee of Gulf Shores.

Sandra Sneckenberger is a Fish and Wildlife Biologist at the US Fish and Wildlife Service South Florida Ecological Services Office in Vero Beach. While her current position focuses on Everglades restoration, Sandra studied habitat use of the Alabama beach mouse for her Master's degree. Her studies concentrated on the different roles and uses of frontal dune and scrub habitat by beach mice.

Rob Tawes graduated from the University of Georgia in 1993 with a B.S. in Zoology and from the University of Montana in 1998 with an M.S. in Resource Conservation. He has worked in the Peace Corps in Costa Rica (1995-97) and worked as an ecologist with the Georgia Department of Transportation for 2.5 years. Rob started working for the FWS Endangered Species Program in the Cookeville, Tennessee Field Office in January 2001. He transferred to the Daphne (AL) Field Office in January 2004 and has been working on endangered species issues, especially regarding the Alabama beach mouse.

Aaron Valenta has been a Southeast Regional HCP coordinator with the US Fish and Wildlife Service for over two years. His area of responsibility extends from Arkansas to North Carolina and from Kentucky to the Gulf Coast. Aaron assists Field Offices with the development of HCPs, provides technical assistance, and ensures compliance with all Federal laws and regulations. Aaron previously assisted the Southeast Regional NEPA Coordinator and Federal Projects/Permits Coordinators in the effective implementation of various acts and regulations across the region. Prior to joining the Fish and Wildlife Service, he worked as a Project Manager with the Corps of Engineers in the Wetland Regulatory Branch and also worked as senior ecologist for the Georgia Department of Transportation.

Noreen Walsh works for the US Fish and Wildlife Service Regional Office in Atlanta, GA.

CBSG Facilitators and Modelers

Onnie Byers is the Executive Officer of the Conservation Breeding Specialist Group in Apple Valley, MN. She earned her Ph.D. in Reproductive Physiology from the University of Minnesota and completed a post-doctoral fellowship at the Smithsonian Institution's National Zoo in Washington, DC. Onnie joined the CBSG staff in 1991 as a Program Officer. She is responsible for the organization, design and facilitation of CBSG's Population and Habitat Viability Assessment and Conservation Assessment and Management Plan workshops and has developed a Comprehensive Conservation Plan process for US National Wildlife Refuges. Onnie also collaborates with the SSC and the IUCN Red List office to develop a process for incorporating CAMP threat assessments into the global IUCN Red List.

Bob Lacy holds a B.A and M.A. in Biology from Wesleyan University and a Ph.D. in Evolutionary Biology from Cornell University. After working for 17 years as a CBSG member and Strategic Associate, he accepted the position of CBSG Chairman in 2003. Bob also works as a population geneticist in the Conservation Biology Department of the Chicago Zoological Society and holds a faculty position in Evolutionary Biology at the University of Chicago. He has published more than 100 scientific papers on genetics, population biology, evolutionary theory, ecology, behavior, physiology, taxonomy, and conservation. His current scientific interests include the effects of inbreeding on fitness and population viability, genetic management of small populations, and the use of simulation models to understand interactions among demographic, genetic, and environmental processes in wildlife populations and to project the impacts of human activities on population dynamics. Bob developed the *Vortex* software for population viability analysis, and is now working with collaborators to link the *Vortex* model to epidemiological models of disease and spatial landscape models.

David Reed is an Assistant Professor at the University of Mississippi. He received his Ph.D. in Ecology and Evolution from the University of Houston in 1998. His Bachelor of Science degree is from Lincoln Memorial University (1988) with a major in Economics and Statistics. David publishes regularly in the scientific literature on such subjects as minimum viable population size, conservation genetics, and population modeling and dynamics. He provides modeling expertise as a member of CBSG and hopes to apply his expertise to conservation efforts around the world.

Kathy Traylor-Holzer is a Program Officer for the Conservation Breeding Specialist Group. Kathy worked in the research and conservation department of the Minnesota Zoo for 18 years before coming to CBSG in 2002. As a zoo employee she worked closely with CBSG for over 10 years as a facilitator and population biologist for a variety of species in North America and Asia, including wolves, tigers, giant pandas and black-footed ferrets. Her professional interests include genetic management of small populations and human/wildlife conflicts. Kathy holds a B.S. in Biology/Psychology from the College of William and Mary, a M.S. in Animal Behavior from North Dakota State University, and a Ph.D. in Conservation Biology from the University of Minnesota.

Participant Introductions

At the beginning of the PHVA workshop, the participants were asked to respond to the following two questions. Their responses are listed below.

1. What is your personal goal for this workshop?

- To gain information and contribute to this group.
- To see some resolution to ABM management direction based on agreed upon model parameters. This will set a precedent for beach mouse issues in Florida.
- To help determine the viability of the Alabama beach mouse. To find gaps in our knowledge of the species.
- To define a series of models that may converge on predicating the viability of the ABM.
- To understand the PVA process and how it may affect development activity.
- To develop relationships with all stakeholders involved with the recovery of ABM and to understand more about the species so that I can be an effective team player in my office toward ABM conservation.
- To complete the ABM PHVA because it should be applicable for BM subspecies in NW Florida. We have similar development and issues along our beachfront.
- To ensure that all equipment functions effectively and that everyone is comfortable with the workshop outcome.
- To form a PHVA using the best data available and to use this information for scientific decision-making.
- To learn more about ABM and Gulf State Park’s role in recovery and public education.
- Since I have no true experience on the animal itself I hope to continue my education on the species with the hopes of contributing something worthy and valid to the management of the ABM.
- To learn what the actual situation is for the ABM and the real impact of development on it.
- To learn more about the process – to gain a better understanding of population viability and how we determine an answer.
- To gain a clearer understanding of long-term viability of species.
- To develop a modeling effort to assist in our recovery goals and expectations of the count for this species.
- To assess viability of ABM and develop management strategies so that FWS can better inform our decisions regarding recovery and permitting.
- To better understand strengths and weaknesses of stage/age-based beach mouse model.
- To get answers to questions I am currently attempting to answer in an environmental assessment for the Fort Morgan Peninsula.

- To learn more about viability analysis and help with this pressing issue as much as I can; to develop a sound model.
- Interested in all of the presented data regarding ABM; to determine sustainability between development and ABM survival.
- To assess viability with different development scenarios.
- To understand better the PHVA workshop process to see how it might apply to my work in Canada.
- To learn more about different aspects of PVA and take home something beneficial to my studies.
- To advance conservation and recovery of BM subspecies in a sound, science-based approach. Results must weather challenges from either side.
- To get a better handle on number of populations/mice and amount of supporting habitat needed to prevent extinction of AL beach mouse.

2. What do you hope to contribute to the workshop?

- Open mind to a working solution.
- I hope to contribute my experience in conflict resolution, mice and recovery issues; practical experience.
- My expertise on population dynamics and modeling. Help elicit answers useful for building the best model possible.
- Multiple and different ways of analyzing a problem.
- Field level experience and history with ABM.
- Other experiences, especially urban planning. Past and most immediate experience in southern CA-urban planning and development.
- The Florida beach mouse perspective relative to development of the Gulf Coast beachfront and conservation of BM and other coastal species.
- I hope to answer questions relating to ABM GIS projects, particularly the habitat maps.
- My scientific and personal experience with beach mice.
- Lots of questions to promote abstract thinking.
- Perhaps an unbiased or neutral view of the issues at hand –whatever those issues may be.
- A local government perspective different from “academia,” which will result in a balanced situation.
- Not absolutely sure, being a non-technical participant, but possibly can contribute a wider view… a way of looking at questions and answers…as the public will see them.
- Knowledge of Endangered Species Act; experience in working with imperiled species.

- Provide input on this effort based on background with this issue (historically) and having participated in PHVA workshops with other species in the region in past years.
- Provide input on endangered species policy issues as appropriate and experience as a participant in PVAs for other listed species.
- To better understand strengths and weaknesses of stage/age-based beach mouse model.
- Current knowledge of development pressures, ABM biology and list of unanswered questions.
- Knowledge of beach mice populations on the peninsula when densities were low – right after a hurricane; that perspective might be particularly helpful, as densities are currently greater.
- Views from an environmental standpoint while also being aware of coastal development pressures.
- My input, enthusiasm and knowledge of ABM and section 10/NEPA needs.
- Objective perspective; ‘out of the box’ viewpoint; planning experience.
- My knowledge and experience as a graduate student studying PVA and population genetics.
- In the field, on the ground experience with beach mice: trapping, behavior, habitat management, as well as knowledge of developer’s attitudes, opinions and goals.
- Assure comfort of participants and arrange for workshop needs; knowledge of recent (last 1.5 years) recovery planning activities.

Alabama Beach Mouse PHVA

Point Clear, Alabama
June 8-11, 2004

FINAL REPORT

APPENDIX II

Definitions of Terms and Abbreviations

ABM-Related Terms and Abbreviations

ABM – Alabama beach mouse
BSNWR – Bon Secour National Wildlife Refuge
Carrying capacity (K) – the maximum number of individuals of a species that can be sustained indefinitely by a particular environment
CBSG – Conservation Breeding Specialist Group
CCCL – Coastal Construction Control Line
CIA – Cumulative Impact Assessment
Fecundity – birth rate
FEMA – Federal Emergency Management Agency
FMU – Fort Morgan Unit of BSNWR
FWS – Fish and Wildlife Service
Gene diversity (GD) – a measure of genetic variation in a population (expected heterozygosity)
GSP – Gulf State Park
HCP – Habitat Conservation Plan
Inbreeding – mating between related individuals (defines the probability that alleles at a particular locus at identical by descent)
IUCN – The World Conservation Union
Mortality – death rate (inverse of survival rate)
N – population size
NHC – National Hurricane Center
NOAA – National Oceanic and Atmospheric Administration
PD – Perdue Unit of BSNWR
PE – probability of extinction
PHVA – Population and Habitat Viability Assessment
PVA – Population Viability Analysis
SLOSH – a model of inundation from storm surges estimated by the National Hurricane Center
Standard deviation (SD) – a measure of variability among iterations (defined as the square root of the variance)
Standard error (SE) – a measure of precision of the estimated mean across iterations
Vortex – computer simulation program used to model populations (Lacy, Borbat and Pollak, 2005); available for download at: www.vortex9.org/vortex

Alabama Beach Mouse PHVA

Point Clear, Alabama
June 8-11, 2004

FINAL REPORT

APPENDIX III

Overview of PVA Using *Vortex*

An Overview of Population Viability Analysis Using *VORTEX*

Introduction

This Appendix presents an overview of processes threatening the health and persistence of wildlife populations, the methods of population viability analysis, the *VORTEX* simulation program for PVA, and the application of such techniques to wildlife conservation. Much of the following material is adapted from Lacy (1993a) and Lacy (1993/4).

The Dynamics of Small Populations

Many wildlife populations that were once widespread, numerous, and occupying contiguous habitat have been reduced to one or more small, isolated populations. The primary causes of the decline of many species are obvious and deterministic: Populations are over-harvested; natural habitat is converted and lost to the species, often involving the replacement of diverse ecological communities with monocultures; environments are polluted, with the dumping of toxins into the air, water, and soil; local and now even global climates are modified by the actions of humans; and numerous exotic competitors, predators, parasites and diseases are introduced into communities that have never evolved defenses to the new invaders. The primary causes of species decline are usually easy to understand, and often easy to study and model, but usually, though not always, difficult to reverse. Even if the original causes of decline are removed, a small isolated population is vulnerable to additional forces, intrinsic to the dynamics of small populations, which may drive the population to extinction (Shaffer 1981; Soulé 1987; Clark and Seebeck 1990).

Of particular impact on small populations are stochastic, or random or probabilistic, processes. Indeed, the final extinction of most populations often occurs not so much because of a continuation of the pressures that led to the initial decline, but because of bad luck. Chance, or stochastic, processes usually have little impact on long-term population dynamics, as long as the population is abundant and spread over a wide geographic range and a number of habitats. Deterministic processes, such as those listed above, predominate in widespread, still common species, while local chance events impacting subsets of the population will average out across the broader, diverse range. When a population becomes small, isolated, and localized, however, chance events can become important, even dominating the long-term dynamics and fate of a population.

Many stages in the life history of an organism, and the processes that define the history of a biological population, are essentially stochastic sampling phenomena. Births, deaths, dispersal, disease, sex determination, and transmission of genes between generations all are largely probabilistic phenomena. Small samples intrinsically have greater variance around the probabilistic mean or expectation than do large samples, and therefore small populations will experience greater fluctuations in births, deaths, sex ratio, and genetic variation than will larger populations. The fundamental problem facing small populations is that the fluctuations they experience due to the multiple stages of sampling each generation make it increasingly likely that the populations will, unpredictably, decline to zero. Once populations are small, the probability that they will become extinct can become more strongly determined by the amount of fluctuations in population size than in the mean, deterministic population growth rate. Thus, extinction can be viewed as a process in which once common and widespread populations become reduced to small, isolated fragments due to extrinsic factors, the small remnant populations then become subjected to large fluctuations due to intrinsic processes, the local populations occasionally and unpredictably go extinct, and the cumulative result of local extinctions is the eventual extinction of the taxon over much or all of its original range (Gilpin and Soulé 1986; Clark et al. 1990).

The stochastic processes impacting on populations have been usefully categorized into demographic stochasticity, environmental variation, catastrophic events, and genetic drift (Shaffer 1981). Demographic stochasticity is the random fluctuation in the observed birth rate, death rate, and sex ratio of a population even if the probabilities of birth and death remain constant. Assuming that births and deaths and sex determination are stochastic sampling processes, the annual variations in numbers that are born, die, and are of each sex can be specified from statistical theory and would follow binomial distributions. Such demographic stochasticity will be most important to population viability perhaps only in populations that are smaller than a few tens of animals (Goodman 1987), in which cases the annual frequencies of birth and death events and the sex ratios can deviate far from the means.

Environmental variation is the fluctuation in the probabilities of birth and death that results from fluctuations in the environment. Weather, the prevalence of enzootic disease, the abundances of prey and predators, and the availability of nest sites or other required microhabitats can all vary, randomly or cyclically, over time. The fluctuations in demographic rates caused by environmental variation is additive to the random fluctuations due to demographic stochasticity. Thus, the difference between the observed variation in a demographic rate over time and the distribution describing demographic variation must be accounted for by environmental variation.

Catastrophic variation is the extreme of environmental variation, but for both methodological and conceptual reasons rare catastrophic events are analyzed separately from the more typical annual or seasonal fluctuations. Catastrophes such as epidemic disease, hurricanes, large-scale fires, and floods are outliers in the distributions of environmental variation. As a result, they have quantitatively and sometimes qualitatively different impacts on wildlife populations. (A forest fire is not just a very hot day.) Such events often precipitate the final decline to extinction (Simberloff 1986, 1988). For example, one of two populations of whooping crane was decimated by a hurricane in 1940 and soon after went extinct (Doughty 1989). The only remaining population of the black-footed ferret (*Mustela nigripes*) was being eliminated by an outbreak of distemper when the last 18 ferrets were captured (Clark 1989).

Genetic drift is the cumulative and non-adaptive fluctuation in allele frequencies resulting from the random sampling of genes in each generation. This can impede the recovery or accelerate the decline of wildlife populations for several reasons (Lacy 1993b). Inbreeding, not strictly a component of genetic drift but correlated with it in small populations, has been documented to cause loss of fitness in a wide variety of species, including virtually all sexually reproducing animals in which the effects of inbreeding have been carefully studied (Wright 1977; Falconer 1981; O'Brien and Evermann 1988; Ralls et al. 1988; Lacy et al. 1993; Lacy 1997). Even if the immediate loss of fitness of inbred individuals is not large, the loss of genetic variation that results from genetic drift may reduce the ability of a population to adapt to future changes in the environment (Fisher 1958; Robertson 1960; Selander 1983).

Thus, the effects of genetic drift and consequent loss of genetic variation in individuals and populations negatively impact on demographic rates and increase susceptibility to environmental perturbations and catastrophes. Reduced population growth and greater fluctuations in numbers in turn accelerates genetic drift (Crow and Kimura 1970). These synergistic destabilizing effects of stochastic process on small populations of wildlife have been described as “extinction vortices” (Gilpin and Soulé 1986).

What is Population (and Habitat) Viability Analysis?

Analyses which have used the *VORTEX* simulation for guiding conservation decisions refer variously to “Population Viability Analysis (PVA)”, “Population and Habitat Viability Analysis (PHVA),” “Population Vulnerability Analysis”, “Population Viability (or Vulnerability) Assessment”, and other variants on the name. This diversity of terminology has caused some confusion among practitioners of the PVA (or PHVA) approach, and probably even more confusion among wildlife managers who have tried to understand what analysis was being described, and whether it could be a useful tool in their efforts to conserve biodiversity. The diversity of perceptions about the PVA approach is not limited to its name. Different people mean different things by PVA, and the definitions and practice of PVA are constantly evolving. We don’t think it is not the case, as has sometimes been suggested, that some people are doing PVA correctly, and others incorrectly, but rather that people are using different (if related) kinds of analyses and labeling them with the same (or similar) terms. What analysis is correct depends on the need and the application. Below, we attempt to clarify what PVA is, by suggesting a more consistent terminology and by describing the features that characterize the application of the PVA approach to conservation. The perspective offered here is necessarily biased by personal experiences in conservation; we will not attempt an exhaustive historical account of this field.

Population viability analysis originally described methods of quantitative analysis to determine the probability of extinction of a population. Shaffer (1981) first defined a minimum viable population (MVP) as the size at which a population has a 99% probability of persistence for 1000 years, but it might be more meaningful biologically to consider it to be the size below which a population's fate becomes determined largely by the stochastic factors that characterize extinction vortices. One concept of population viability analysis is any methodology used to determine an MVP (Shaffer 1990). More broadly, PVA is the estimation of extinction probabilities and other measures of population performance by analyses that incorporate identifiable threats to population survival into models of the extinction process (Brussard 1985; Gilpin and Soulé 1986; Burgman et al. 1993; Lacy 1993/1994).

Shaffer's (1981) original term “minimum viable population” (MVP) has fallen into disfavor (Soulé 1987), even as the PVA approach has risen in popularity. Shaffer stressed that an MVP was an estimate of the population size below which the *probability* of extinction was unacceptably high, that different populations would have different MVPs, and that the MVP determined for a population would depend on the threatening factors that were considered. However, the term implied to some people that there was a well-defined number below which extinction was certain and above which persistence was assured. Re-emphasizing the probabilistic nature of the extinction process, a number of conservation biologists have focused on methods for estimating the probability of extinction over defined time periods for a designated population exposed to a specific scenario of environmental conditions, threats to persistence, and future management actions and other foreseeable events (Brussard 1985; Starfield and Bleloch 1986; Soulé 1987; Simberloff 1988; Gilpin 1989; Shaffer 1990; Boyce 1992; Burgman et al. 1993). Thus, “Population Viability Analysis” (or the synonymous “Population Viability Assessment” and “Population Vulnerability Analysis”) came to describe any of the array of methods for quantifying the probability of extinction of a population. Although PVA has been extended by some to encompass a broader approach to conservation (see below), the term “Population Viability Analysis”, or PVA, should perhaps be reserved for its original, yet still rather broad, meaning.

Beginning in about 1989 (Lacy et al. 1989; Seal and Lacy 1989; Seal et al. 1990), it became increasingly recognized that PVA can often be most usefully incorporated into a strategy for the conservation of a taxon if it is part of, and often central to, a conservation workshop that mobilizes collaboration among the array of people with strong interest in or responsibility for a conservation effort (e.g., governmental wildlife agencies, conservation NGOs, and the local people who interact with the species or its habitat) or with particular expert knowledge about the species, its habitats, or the threats it faces (e.g., academic biologists, conservation professionals, other wildlife biologists, experts on human demographics and resource use). Conservation problems are almost always multi-faceted, involving not only complex dynamics of biological populations, but also interactions with human populations, the past, present, and future impacts of humans on habitats, and human political, social, and economic systems (Alvarez 1993; Bormann and Kellert 1991; Clark 1989, 1993). Many people need to contribute knowledge, expertise, and ideas in order to achieve the recovery of threatened species. Population viability analyses can provide a framework for incorporating the many needed kinds of knowledge into species conservation efforts, because PVAs do allow the assessment of many kinds of factors that threaten the persistence of populations (Lacy 1993a; Lindenmayer et al. 1993).

The Conservation Breeding Specialist Group (CBSG) of the IUCN's Species Survival Commission especially has advocated and used workshops centered on PVAs to provide guidance to conservation assessment and planning (see references to CBSG workshops in Appendix III). Over the past few years, the PVA workshop as an approach to species conservation has expanded considerably beyond the quantitative analysis of extinction probabilities as advanced by Shaffer (1981, 1990), Soulé (1987), Gilpin (1989), Clark et al. (1991), Boyce (1992), and others. PVA workshops have incorporated consideration of resource use and needs by local human populations (Seal et al. 1991; Bonaccorso et al. 1999), education programs for the local human populations (Odum et al. 1993), trade issues (Foose et al. 1993), and trends in human demographics and land use patterns (Walker and Molur 1994; Herrero and Seal 2000). Recognizing that the conservation assessment workshops increasingly incorporated more than just the population biology modeling (which still formed a core organizing and analysis framework for the workshop), the CBSG has termed their workshops Population *and Habitat* Viability Analyses (PHVA). We would recommend that the term Population and Habitat Viability Analysis (PHVA) be used to describe the collaborative workshop approach to species conservation that centers on, but encompasses more than, a Population Viability Analysis (in the narrow sense). The concept of a PHVA continues to expand and evolve, as it should considering the need for more holistic and flexible approaches to conservation (e.g., Ruggiero et al. 1994). Thus, in the usage I recommend, PVA is a quantitative analysis of the probability of population persistence under defined sets of assumptions and circumstances. PHVA is a workshop process that brings to bear the knowledge of many people on species conservation, eliciting and assessing multiple options for conservation action, principally by using the tool of PVA as a way evaluate present threats to population persistence and likely fates under various possible scenarios.

Population Viability Analysis (PVA)

Two defining characteristics of a PVA are an explicit model of the extinction process and the quantification of threats to extinction. These features set PVA apart from many other analyses of the threats facing species, including, for example, the IUCN Red Books of Threatened Species. As a methodology to estimate the probability of extinction of a taxon, PVA necessarily must start with an understanding, or model, of the extinction process (Clark et al. 1990).

Generally, the model of extinction underlying a PVA considers two categories of factors: deterministic and stochastic. Deterministic factors, those that can shift species from long-term average population growth to population decline include the well-known threats of over-harvest, habitat destruction, pollution or other degradation of environmental quality, and the introduction of exotic predators, competitors, and diseases. Singly or combined, these forces have driven many wildlife populations to low numbers and, for some, to extinction. Once a population becomes small, and isolated from conspecific populations that might serve as sources for immigrants that could stabilize demographics and genetics, its dynamics and fate can become dominated by a number of random or stochastic processes (as outlined above and by Shaffer 1981). Thus, even if the original deterministic causes of decline are stopped or reversed, the instability caused by the action of stochastic processes acting on small populations can cause the extinction of a population.

In nature, most threatening processes have both deterministic and stochastic features. For example, a high level of poaching might be seen as a deterministic factor driving a wildlife population toward extinction, but whether an individual animal is killed might be largely a matter of chance. In a PVA, poaching might be modeled as a deterministic process by killing a determined proportion of the animals, or it might be modeled as a stochastic process by giving each animal that probability of being killed but allowing the exact numbers killed to vary over time. If the population is large and the percent of animals killed is high, then these two ways of modelling the effects of poaching will yield the same results: the deterministic component of poaching dominates the population dynamics. If the population is small or the percent of animals killed is very low, then the numbers killed in a stochastic model (and in nature) might vary substantially from year to year: the stochastic nature of poaching further destabilizes the population.

Which of the various deterministic and stochastic factors are important to consider in a PVA will depend on the species biology, the present population size and distribution, and the threats it faces. For example, orang utans may be threatened by forest destruction and other largely deterministic processes, but inbreeding and randomly skewed sex ratios resulting from highly stochastic processes are unlikely to be problems, at least not on a species-wide basis. On the other hand, even if the remnant Atlantic coastal rainforest of Brazil is secured for the future, the populations of golden lion tamarins (*Leontopithecus rosalia*) which can persist in that remnant forest are not sufficiently large to be stable in the face of stochastic threats (Seal et al. 1990; Rylands 1993/4; Ballou et al. 1997). The identification of the primary threats facing a taxon via a comprehensive PVA is important for conservation planning. For example, tamarin populations might be stabilized by the translocations and reintroductions that are underway and planned, but an orang utan PHVA recognized that releases of confiscated “pet” orang utans are unlikely to have a conservation benefit for those populations which are facing habitat destruction, not stochastic fluctuations and inbreeding. For many species, such as the whooping crane (*Grus americana*), the temporarily extinct-in-the-wild black-footed ferret (*Mustela nigripes*), and the Puerto Rican parrot (*Amazona vitatta*), only a single population persisted in the wild. Although those populations may have been maintained or even increased for a number of years, the principal threat was that a local catastrophe (e.g., disease epidemic, severe storm) could decimate the population (Clark 1989; Lacy et al. 1989; Mirande et al. 1991). The primary recovery actions therefore needed to include the establishment of additional populations. Tragically, some taxa, such the eastern barred bandicoot (*Perameles gunnii*) in Australia, may be critically threatened simultaneously by deterministic factors and stochastic processes (Lacy and Clark 1990).

PVA is formally an assessment of the probability of extinction, but PVA methods often focus on other indicators of population health. Mean and variance in population growth (Lindenmayer and Lacy 1995a, 1995b, 1995c), changes in range, distribution, and habitat occupancy (Hanski and Gilpin 1991, 1997), and losses of genetic variability (Soulé et al. 1986; Lande and Barrowclough 1987; Seal 1992; Lacy and Lindenmayer 1995) can be analyzed and monitored. Although not yet common, monitoring of population health could also utilize measures of developmental stability (Clarke 1995), physiological parameters such as body condition (Altmann et al. 1993) or levels of the hormones related to stress and reproduction (Sapolsky 1982, 1986), or the stability of behavior and the social structure of the population (Samuels and Altmann 1991).

The interactions and synergism among threatening processes will often cause numerical, distributional, physiologic, behavioral, and genetic responses to concordantly reflect species decline and vulnerability. It remains important, however, to understand and target the primary causal factors in species vulnerability. The recent proposal to base IUCN categories of threat on quantified criteria of probability of extinction, or changes in such indicators as species range, numbers, and trends (Mace and Lande 1991; Mace et al. 1992; Mace and Stuart 1994; IUCN Species Survival Commission 1994) reflects the increased understanding of the extinction process that has accompanied the development of PVA, and simultaneously demands that much more progress be made in developing predictive models, gathering relevant data on status and threats, and applying the PVA techniques.

Population and Habitat Viability Analysis (PHVA)

Population and Habitat Viability Analysis is a multi-faceted process or framework for assisting conservation planning, rather than a singular technique or tool. It is often interwoven with other techniques for managing complex systems, such as decision analysis (Maguire 1986; Maguire et al. 1990). Even when viewed as *the* PHVA workshop, all such conservation workshops involved and required substantial pre-workshop and post-workshop activities. Some PHVA workshops have been extended into multiple workshops and less formal, smaller collaborative meetings, often focused on subsets of the larger problems of species conservation.

Although PHVAs are diverse and not well defined, the PHVA process contains a number of critical components. First, it is essential to gather an array of experts who have knowledge of the species or problem. A PHVA is not required to bring together experts, but it often facilitates such sharing of expertise because the collective knowledge of many is essential for a useful PVA (in the narrow sense) to be completed. In addition to a diversity of people, a PHVA workshop also requires and therefore facilitates the involvement of a number of agencies and other concerned organizations. For example, the PVA on the two endemic primates of the Tana River Primate Reserve in Kenya (Seal et al. 1991) was convened by the Kenya Wildlife Service, facilitated by the IUCN SSC Captive Breeding Specialist Group, benefited from the expertise contributed by members of the IUCN SSC Primate Specialist Group, and was sponsored by the World Bank. The involvement of many agencies and interested parties is critical to endangered species recovery.

An early requirement, or prerequisite, of a PHVA workshop is to determine the conservation problem to be addressed, and to state the goals of the management plan. Many endangered species programs have not clearly identified their goals. For example, at a PHVA and Conservation Assessment and Management Plan workshop on the forest birds of the Hawaiian islands (Ellis et al. 1992a, 1992b), it became apparent that the agencies responsible for the conservation of Hawaii's bird fauna had not determined whether their goal was to prevent species extinctions, prevent taxa (species or subspecies) from becoming extirpated on any of the islands they presently inhabit, preserve species in sufficient numbers and distribution to allow them to continue to fill ecological roles in the biological communities, or the restoration of taxa to most or all parts of the original ranges. The management actions required to achieve these various levels of conservation are quite different. In contrast, a PHVA on the Grizzly Bear in the Central Rockies of Canada (Herrero and Seal 2000) clearly identified that provincial policy called for maintenance of stable or growing populations of the species. Thus, the criterion against which alternative management scenarios were judged was whether the PVA projections indicated that the populations would not decline.

PHVA workshops facilitate the assembly of all available data. Often, important information is found in the field notes of researchers or managers, in the heads of those who have worked with and thought about the problems of the species, and in unpublished agency reports, as well as in the published scientific literature. A pending PHVA can be the impetus that encourages the collection of data in anticipation of presentation, review, and analysis at the workshop. For example, a Sumatran Tiger PHVA helped stimulate the systematic collection of data on sightings and signs of tigers in protected areas throughout the island of Sumatra, and collation and integration with a Geographic Information System (GIS) map of habitats and human pressures on those habitats. The PHVA on the Grizzly Bear in the Central Canadian Rockies Ecosystem provided the opportunity for detailed habitat mapping data to be integrated with population biology data on the bears, resulting in the development of models which would allow projection of the impacts of habitat changes on the bear populations.

It is important to specify the assumptions that underlay a PHVA, and any consequent management recommendation. For example, the Hawaiian bird conservation efforts are constrained by a belief that no birds bred outside of the islands should ever be brought back to the islands for release. While this position derives from a reasonable concern for disease transmission (much of the decline of Hawaii's native birds is thought to be due to introduced avian diseases) as much as from any political or philosophical stand, any justification for the restriction must be questioned in light of the fact that wildlife agencies import and release, without quarantine, 1000s of exotic gamebirds onto the islands annually.

Once experts are assembled, problems stated and goals set, data gathered, and assumptions specified, then the PHVA process can proceed with what I describe as PVA in the narrow sense: estimation of the probability of population persistence. The available data are used to estimate the parameters that are needed for the model of population dynamics to be applied. Often, data are not available from which to estimate certain key parameters. In those cases, subjective and objective, but non-quantified, information might be solicited from the assembled experts, values might be obtained from data on related species, or a factor might simply be omitted from the model. While such a non-precise process might consist simply of intuitive judgements made by experts, it is important to specify how values for the parameters in the model were obtained. The resulting limitations of the analyses should be acknowledged, and a decision made if, how, by whom, and when the missing data would be collected so that more refined analyses could be conducted. With the PVA model, projections of the most likely fate, and distribution of possible fates, of the population under the specified assumptions are made.

Because so much of a PVA – the data, the model, and even the interpretation of output – is uncertain, a PVA that provides an estimate of the probability of extinction under a single scenario is of very limited usefulness. An essential component of the PHVA process, therefore, is sensitivity testing. Ranges of plausible values for uncertain parameters should be tested, to determine what effects those uncertainties might have on the results. In addition, several different PVA models might be examined at a PHVA workshop, or the same general model tested under different structural assumptions. Different participants in the process should assess and interpret the results. Such sensitivity testing reveals which components of the data, model, and interpretation have the largest impact on the population projections. This will indicate which aspects of the biology of the population and its situation contribute most to its vulnerability and, therefore, which aspects might be most effectively targeted for management. In addition, uncertain parameters that have a strong impact on results are those which might be the focus of future research efforts, to better specify the dynamics of the population. Close monitoring of such parameters might also be important for testing the assumptions behind the selected management options and for assessing the success of conservation efforts.

Closely parallel to the testing of uncertainties in the present situation is the testing of options for management. PVA modeling allows one to test the expected results of any given management action, under the assumptions of the model and within the limitations of present knowledge, on the computer before implementation in the field. This process can guide selection of the management options most likely, given current knowledge, to be effective, and will define target recovery goals that should be obtained if our knowledge is adequate and the recommended actions are followed. A PHVA workshop on the Black Rhinoceros in Kenya's 11 rhino sanctuaries (Foose et al. 1993) suggested that periodic movement of rhinos between fenced sanctuaries to reduce inbreeding and demographic fluctuations would be necessary to stabilize the populations in the smaller parks. Moreover, the modeling provided estimates of the rate at which the larger populations would be able to provide surplus animals for translocation.

It would be an error to assume that any PVA model incorporates everything of interest. A PVA simulation program can only include those processes that are known to the programmer. This will likely be a subset of what might be known to the field biologists, which in turn will definitely be a subset of those processes that impact natural populations. A number of variables affecting population dynamics and viability are not yet commonly examined in PVA models. These include: social and ecological determinants of dispersal; complex social processes, such as the role of non-breeders in group stability and the impacts of other aspects of the social environment on reproductive success and survival; competitive, exploitative, or mutualistic interactions with other species experiencing their own population dynamics; and the effects of changes in the global environment. To date, most PVA models treat organisms as independent actors in spatially homogeneous physical, biotic, and social environments. There is tremendous opportunity and need for elaboration of PVA models, and it is likely that increasingly sophisticated models will also become more specific to the individual taxa and environments under study.

PHVA workshops must incorporate consideration of the assumptions of the PVA model used and the biases or limitations in interpretation that could result. PHVAs consider only those threatening processes of which we have knowledge, for which we can develop algorithms for modeling or other methods for analysis, and for which we have some data. As a result, it is likely that PVAs will underestimate the vulnerability of most populations to extinction, and that PHVA workshops will be less comprehensive than is desirable. We need always to be cognizant of the limits of our understanding of wildlife populations, and to include appropriate margins for error in our conservation strategies.

PVA is, by definition, an assessment of the probability of persistence of a population over a defined time frame. Yet, persistence of a population, while a necessary condition for effective conservation of natural systems, is often not sufficient. Prevention of extinction is the last stand of conservationists, but the goals should be higher: conservation of functional biological communities and ecosystems. PVA usually ignores the functional role of a species in a community, but a PHVA workshop should consider much more than the prevention of the final biological extinction of the taxon. A species, such as the American Bison (*Bison bison*), can be functionally extinct in terms of no longer filling its original role in nature, even as it is praised as a conservation success story and would be considered safe from extinction and viable.

The use of the PHVA process to help guide conservation decisions is not a singular event, in which an analysis can be completed, management actions recommended and implemented, and conservation thereby assured. The many uncertainties in the process mandate that PVA be used as a tool in an adaptive management framework, and a PHVA workshop is just one stage of an effective conservation strategy. In adaptive management, the lack of knowledge adequate to predict with certainty the best course of action is recognized, management actions are designed in such a way that monitoring will allow testing of the adequacy of our model and understanding, and corrective adjustments to management plans are made whenever the accumulating data suggest that the present course is inadequate to achieve the goals and that a better strategy exists (Holling 1978). The urgency of the biodiversity crisis will not permit us ethically to refrain from aggressive conservation action until we have scientifically sound understanding of all the factors that drive population, community, and ecosystem dynamics. PHVA provides a forum for making use of the information we do have, in a well-documented process that is open to challenge and improvement. PHVA workshops can, therefore, assist wildlife managers in the very difficult and important job of using science to safeguard the future of wildlife populations.

In summary, Population Viability Analysis (PVA) and Population and Habitat Viability Analysis (PHVA) refer to an array of interrelated and evolving techniques for assessing the survival probability of a population and possible conservation actions. It might be useful to restrict the term PVA to its original meaning -- the use of quantitative techniques to estimate the probability of population persistence under a chosen model of population dynamics, a specified set of biological and environmental parameters, and enumerated assumptions about human activities and impacts on the system. PHVA refers to a workshop approach to conservation planning, which elicits and encourages contributions from an array of experts and stakeholders, uses PVA and other quantitative and non-quantitative techniques to assess possible conservation actions, and strives to achieve consensus on the best course of action from competing interests and perspectives, incomplete knowledge, and an uncertain future.

Many of the components of PVAs and PHVAs, even when used in isolation, can be effective educational and research tools. To be a useful framework for advancing the conservation of biodiversity, however, PHVA must incorporate all of: (1) collection of data on the biology of the taxon, status of its habitat, and threats to its persistence, (2) quantitative analysis of available data, (3) input of population status and identifiable threats to persistence into analytical or simulation models of the extinction process, (4) assessment of the probability of survival over specified periods of time, given the assumptions and limitations of the data and model used, (5) sensitivity testing of estimates of extinction probability across the range of plausible values of uncertain parameters, (6) specification of conservation goals for the population, (7) identification of options for management, (8) projection of the probability of population survival under alternative scenarios for future conservation action, (9) implementation of optimal actions for assuring accomplishment of conservation goals, (10) continued monitoring of the population, (11) reassessment of assumptions, data, models, and options, and (12) adjustment of conservation strategies to respond to the best information available at all times. There are many uncertain aspects of population dynamics, especially of endangered taxa, including few data on species biology and habitats, uncertain political and social climate for implementing conservation actions, and the unpredictability inherent in small populations due to the many stochastic forces that drive population dynamics.

The rapid development of PVA as a research and management tool, and the concurrent but not always parallel expansion of the scope of what conservation threats, options, and actions are considered in PHVA workshops, has led to confusion. Different people can describe rather distinct kinds of analyses with the same terminology, while others use different terms to describe nearly identical approaches. The ever-changing concepts of PVA and PHVA are confusing, but the flexibility of the processes is also their strength. Current tools are inadequate to address fully the challenges of stemming the losses of biodiversity. The PVA/PHVA framework allows and encourages rapid application of new tools, data, and interpretations into increasingly effective conservation programs.

Methods for Analyzing Population Viability

An understanding of the multiple, interacting forces that contribute to extinction vortices is a prerequisite for the study of extinction-recolonization dynamics in natural populations inhabiting patchy environments (Gilpin 1987), the management of small populations (Clark and Seebeck 1990), and the conservation of threatened wildlife (Shaffer 1981, 1990; Soulé 1987; Mace and Lande 1991).

Shaffer (1981) suggested several ways to conduct PVAs. Perhaps the most rigorous method, and the one that would produce the most defensible estimates, would be an empirical observation of the stability and long term fates of a number of populations of various sizes. Berger (1990) presented a good example of this approach, in which he observed that populations of bighorn sheep in the mountains of the western USA persisted only when the populations consisted of more than 100 animals. A few other studies of wildlife populations have provided empirical data on the relationship between population size and probability of extinction (e.g., Belovsky 1987; Thomas 1990), but presently only order of magnitude estimates can be provided for MVPs of vertebrates (Shaffer 1987). More empirical studies are needed, but the time and numbers of populations required for such studies are precluded in the cases of most species threatened with extinction -- exactly those for which estimates of population vulnerability are most urgently needed.

A more elegant and general approach to PVA is to develop analytical models of the extinction process that will allow calculation of the probability of extinction from a small number of measurable parameters. Goodman's (1987) model of demographic fluctuations, and applications to conservation of the classic population genetic models of loss of genetic diversity by genetic drift (Franklin 1980; Soulé et al. 1986; Lande and Barrowclough 1987) are valuable efforts in this direction. Unfortunately, our understanding of population biology is not yet sufficient to provide fully adequate analytical models of the extinction process. For example, none of the existing analytical models incorporate all three of demographic, environmental, and genetic fluctuations, and thus they do not begin to model the array of extinction vortices described by Gilpin and Soulé (1986). Moreover, the analytical models make extremely simplifying assumptions about a number of the intricacies of population structure. For example, social groupings or preferences are often assumed to be invariant or lacking, resulting in random mating; and dispersal is usually assumed to be random between all sites (the "island model") or only to occur between adjacent sites (the "stepping stone model"). Much more work is needed either to develop more complex and flexible models or to demonstrate that the simple models are sufficient to provide guidance for conservation.

A third method of conducting a PVA is the use of computer simulation modeling to project the probability distribution of possible fates of a population. Simulation models can incorporate a very large number of threatening processes and their interactions, if the processes can be described in terms of quantitative algorithms and parameterized. Although many processes affecting small populations are intrinsically indeterminate, the average long-term fate of a population and the variance around the expectation can be studied with computer simulation models. The focus is on detailed and explicit modeling of the forces impinging on a given population, place, and time of interest, rather than on delineation of rules (which may not exist) that apply generally to most wildlife populations.

Modeling and Population Viability Analysis

A model is any simplified representation of a real system. We use models in all aspects of our lives, in order to: (1) extract the important trends from complex processes, (2) permit comparison among systems, (3) facilitate analysis of causes of processes acting on the system, and (4) make predictions about the future. A complete description of a natural system, if it were possible, would often decrease our understanding relative to that provided by a good model, because there is "noise" in the system that is extraneous to the processes we wish to understand. For example, the typical representation of the growth of a wildlife population by an annual percent growth rate is a simplified mathematical model of the much more complex changes in population size. Representing population growth as an annual percent change assumes constant exponential growth, ignoring the irregular fluctuations as individuals are born or immigrate, and die or emigrate. For many purposes, such a simplified model of population growth is very useful, because it captures the essential information we might need regarding the average change in population size, and it allows us to make predictions about the future size of the population. A detailed description of the exact changes in numbers of individuals, while a true description of the population, would often be of much less value because the essential pattern would be obscured, and it would be difficult or impossible to make predictions about the future population size.

In considerations of the vulnerability of a population to extinction, as is so often required for conservation planning and management, the simple model of population growth as a constant annual rate of change is inadequate for our needs. The fluctuations in population size that are omitted from the standard ecological models of population change can cause population extinction, and therefore are often the primary focus of concern. In order to understand and predict the vulnerability of a wildlife population to extinction, we need to use a model which incorporates the processes which cause fluctuations in the population, as well as those which control the long-term trends in population size. Many processes can cause fluctuations in population size: variation in the environment (such as weather, food supplies, and predation), genetic changes in the population (such as genetic drift, inbreeding, and response to natural selection), catastrophic effects (such as disease epidemics, floods, and droughts), decimation of the population or its habitats by humans, the chance results of the probabilistic events in the lives of individuals (sex determination, location of mates, breeding success, survival), and interactions among these factors (Gilpin and Soulé 1986).

Models of population dynamics which incorporate causes of fluctuations in population size in order to predict probabilities of extinction, and to help identify the processes which contribute to a population's vulnerability, are used in Population Viability Analysis (PVA). For the purpose of predicting vulnerability to extinction, any and all population processes that impact population dynamics can be important. Much analysis of conservation issues is conducted by largely intuitive assessments by biologists with experience with the system. Assessments by experts can be quite valuable, and are often contrasted with "models" used to evaluate population vulnerability to extinction. Such a contrast is not valid, however, as *any* synthesis of facts and understanding of processes constitutes a model, even if it is a mental model within the mind of the expert and perhaps only vaguely specified to others (or even to the expert himself or herself).

A number of properties of the problem of assessing vulnerability of a population to extinction make it difficult to rely on mental or intuitive models. Numerous processes impact population dynamics, and many of the factors interact in complex ways. For example, increased fragmentation of habitat can make it more difficult to locate mates, can lead to greater mortality as individuals disperse greater distances across unsuitable habitat, and can lead to increased inbreeding which in turn can further reduce ability to attract mates and to survive. In addition, many of the processes impacting population dynamics are intrinsically probabilistic, with a random component. Sex determination, disease, predation, mate acquisition -- indeed, almost all events in the life of an individual -- are stochastic events, occurring with certain probabilities rather than with absolute certainty at any given time. The consequences of factors influencing population dynamics are often delayed for years or even generations. With a long-lived species, a population might persist for 20 to 40 years beyond the emergence of factors that ultimately cause extinction. Humans can synthesize mentally only a few factors at a time, most people have difficulty assessing probabilities intuitively, and it is difficult to consider delayed effects. Moreover, the data needed for models of population dynamics are often very uncertain. Optimal decision-making when data are uncertain is difficult, as it involves correct assessment of probabilities that the true values fall within certain ranges, adding yet another probabilistic or chance component to the evaluation of the situation.

The difficulty of incorporating multiple, interacting, probabilistic processes into a model that can utilize uncertain data has prevented (to date) development of analytical models (mathematical equations developed from theory) which encompass more than a small subset of the processes known to affect wildlife population dynamics. It is possible that the mental models of some biologists are sufficiently complex to predict accurately population vulnerabilities to extinction under a range of conditions, but it is not possible to assess objectively the precision of such intuitive assessments, and it is difficult to transfer that knowledge to others who need also to evaluate the situation. Computer simulation models have increasingly been used to assist in PVA. Although rarely as elegant as models framed in analytical equations, computer simulation models can be well suited for the complex task of evaluating risks of extinction. Simulation models can include as many factors that influence population dynamics as the modeler and the user of the model want to assess. Interactions between processes can be modeled, if the nature of those interactions can be specified. Probabilistic events can be easily simulated by computer programs, providing output that gives both the mean expected result and the range or distribution of possible outcomes. In theory, simulation programs can be used to build models of population dynamics that include all the knowledge of the system which is available to experts. In practice, the models will be simpler, because some factors are judged unlikely to be important, and because the persons who developed the model did not have access to the full array of expert knowledge.

Although computer simulation models can be complex and confusing, they are precisely defined and all the assumptions and algorithms can be examined. Therefore, the models are objective, testable, and open to challenge and improvement. PVA models allow use of all available data on the biology of the taxon, facilitate testing of the effects of unknown or uncertain data, and expedite the comparison of the likely results of various possible management options.

PVA models also have weaknesses and limitations. A model of the population dynamics does not define the goals for conservation planning. Goals, in terms of population growth, probability of persistence, number of extant populations, genetic diversity, or other measures of population performance must be defined by the management authorities before the results of population modeling can be used. Because the models incorporate many factors, the number of possibilities to test can seem endless, and it can be difficult to determine which of the factors that were analyzed are most important to the population dynamics. PVA models are necessarily incomplete. We can model only those factors which we understand and for which we can specify the parameters. Therefore, it is important to realize that the models probably underestimate the threats facing the population. Finally, the models are used to predict the long-term effects of the processes presently acting on the population. Many aspects of the situation could change radically within the time span that is modeled. Therefore, it is important to reassess the data and model results periodically, with changes made to the conservation programs as needed.

Dealing with uncertainty

It is important to recognize that uncertainty regarding the biological parameters of a population and its consequent fate occurs at several levels and for independent reasons. Uncertainty can occur because the parameters have never been measured on the population. Uncertainty can occur because limited field data have yielded estimates with potentially large sampling error. Uncertainty can occur because independent studies have generated discordant estimates. Uncertainty can occur because environmental conditions or population status have been changing over time, and field surveys were conducted during periods which may not be representative of long-term averages. Uncertainty can occur because the environment will change in the future, so that measurements made in the past may not accurately predict future conditions.

Sensitivity testing is necessary to determine the extent to which uncertainty in input parameters results in uncertainty regarding the future fate of the population. If alternative plausible parameter values result in divergent predictions for the population, then it is important to try to resolve the uncertainty with better data. Sensitivity of population dynamics to certain parameters also indicates that those parameters describe factors that could be critical determinants of population viability. Such factors are therefore good candidates for efficient management actions designed to ensure the persistence of the population.

The above kinds of uncertainty should be distinguished from several more sources of uncertainty about the future of the population. Even if long-term average demographic rates are known with precision, variation over time caused by fluctuating environmental conditions will cause uncertainty in the fate of the population at any given time in the future. Such environmental variation should be incorporated into the model used to assess population dynamics, and will generate a range of possible outcomes (perhaps represented as a mean and standard deviation) from the model. In addition, most biological processes are inherently stochastic, having a random component. The stochastic or probabilistic nature of survival, sex determination, transmission of genes, acquisition of mates, reproduction, and other processes preclude exact determination of the future state of a population. Such demographic stochasticity should also be incorporated into a population model, because such variability both increases our uncertainty about the future and can also change the expected or mean outcome relative to that which would result if there were no such variation. Finally, there is "uncertainty" which represents the alternative actions or interventions that might be pursued as a management strategy. The likely effectiveness of such management options can be explored by testing alternative scenarios in the model of population dynamics, in much the same way that sensitivity testing is used to explore the effects of uncertain biological parameters.

Often, the uncertainty regarding a number of aspects of the population biology, current status, and threats to persistence is too large to allow scientifically accurate and reliable projections of population dynamics. Therefore, the predictions made from PVA models should be considered to be projections about what would most likely happen to the population *if* various hypotheses about the status of the populations and the threats are true. Conservation and management decisions must be made based on the most plausible hypotheses about the population status, before sufficient data could be collected to test those hypotheses scientifically. An important advantage of PVA models is that they forced systematic consideration and specification of the assumptions and hypotheses that must be made in the absence of adequate data. This facilitates careful reassessment and improvement in the analyses, as better data become available.

Questions that can be explored with PVA models

Below are some of the conservation and management questions that can be explored by Population Viability Analysis modeling. References describing uses of *VORTEX* give many examples of these and other applications of PVA techniques to guide conservation.

Using the best current information on the biology of the taxon and its habitat, are the populations projected to persist if conditions remain as they are now? Beyond just the persistence of the population, what is the most likely average population size, range of population sizes across years, and rate of loss of genetic variation? If the population is at risk of extinction, is the extinction expected to result primarily from negative average population growth (mean deaths exceeding mean births), from large fluctuations in numbers, from effects of accumulated inbreeding, or from a combination of these factors?

Given that there is considerable uncertainty about several aspects of the species biology and its habitat, is the population likely to persist across the plausible ranges of parameters that might characterize the population? In particular, how sensitive are the population dynamics to varying estimates of reproductive success, juvenile survival, adult survival, effects of natural catastrophes, initial population size, carrying capacity of the habitat, and dispersal among populations? Are there critical values for any of these parameters which demarcate a transition from a population that would be considered viable to one that is not?

Which factors have the greatest influence on the projected population performance? If important factors are identified, management actions might be designed to improve these factors or ameliorate the negative effects. How much change would be required in aspects of the population in order to ensure population survival?
What would be the effect of removing some individuals from the population? Would there be a significant benefit from supplementing the population with individuals translocated from other populations or released from captive breeding stocks? Can the population sustain controlled harvest? Can it sustain poaching?

Would a corridor connecting fragmented habitats improve long-term viability? Could the same effect be achieved by translocating a few individuals? What will happen to population viability if mortality increases for individuals dispersing between habitat patches?

What will happen to the wildlife population if trends in human populations and human impacts on the environment continue unabated?

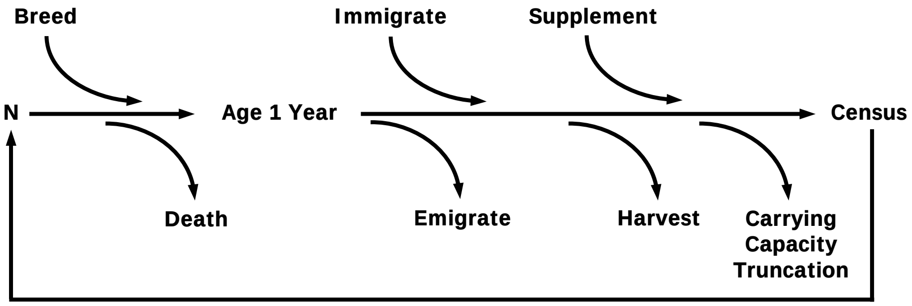
The *VORTEX* Population Viability Analysis Model

The *VORTEX* computer program is a simulation of the effects of deterministic forces as well as demographic, environmental and genetic stochastic events on wildlife populations. It is an attempt to model many of the extinction vortices that can threaten persistence of small populations (hence, its name). *VORTEX* models population dynamics as discrete, sequential events that occur according to probabilities that are random variables following user-specified distributions. *VORTEX* simulates a population by stepping through a series of events that describe an annual cycle of a typical sexually reproducing, diploid organism: mate selection, reproduction, mortality, increment of age by one year, migration among populations, removals, supplementation, and then truncation (if necessary) to the carrying capacity. Although *VORTEX* simulates life events on an annual cycle, a user could model "years" that are other than 12 months duration. The simulation of the population is iterated many times to generate the distribution of fates that the population might experience.

VORTEX is an individual-based model. That is, it creates a representation of each animal in its memory and follows the fate of the animal through each year of its lifetime. *VORTEX* keeps track of the sex, age, and parentage of each animal. Demographic events (birth, sex determination, mating, dispersal, and death) are modeled by determining for each animal in each year of the simulation whether any of the events occur. (See figure below.)

VORTEX requires a lot of population-specific data. For example, the user must specify the amount of annual variation in each demographic rate caused by fluctuations in the environment. In addition, the frequency of each type of catastrophe (drought, flood, epidemic disease) and the effects of the catastrophes on survival and reproduction must be specified. Rates of migration (dispersal) between each pair of local populations must be specified. Because *VORTEX* requires specification of many biological parameters, it is not necessarily a good model for the examination of population dynamics that would result from some generalized life history. It is most usefully applied to the analysis of a specific population in a specific environment.

VORTEX Simulation Model Timeline



Events listed above the timeline increase N, while events listed below the timeline decrease N.

In the program explanation that follows, demographic rates are described as constants specified by the user. Although this is the way the program is most commonly and easily used, *VORTEX* does provide the capability to specify most demographic rates as functions of time, density, and other parameters (see Chapter 5).

Demographic stochasticity

VORTEX models demographic stochasticity by determining the occurrence of probabilistic events such as reproduction, litter size, sex determination, and death with a pseudo-random number generator. For each life event, if the random value sampled from a specified distribution falls above the user-specified probability, the event is deemed to have occurred, thereby simulating a binomial process. Demographic stochasticity is therefore a consequence of the uncertainty regarding whether each demographic event occurs for any given animal.

The source code used to generate random numbers uniformly distributed between 0 and 1 was obtained from Maier (1991), based on the algorithm of Kirkpatrick and Stoll (1981). Random deviates from binomial distributions, with mean p and standard deviation s, are obtained by first determining the integral number of binomial trials, N, that would produce the value of s closest to the specified value, according to:

$$N = \frac{p(1-p)}{s^2}$$

N binomial trials are then simulated by sampling from the uniform 0-1 distribution to obtain the desired result, the frequency or proportion of successes. If the value of N determined for a desired binomial distribution is larger than 25, a normal approximation is used in place of the binomial distribution. This normal approximation must be truncated at 0 and at 1 to allow use in defining probabilities, although, with such large values of N, s is small relative to p and the truncation would be invoked only rarely. To avoid introducing bias with this truncation, the normal approximation to the binomial (when used) is truncated symmetrically around the mean. The algorithm for generating random numbers from a unit normal distribution follows Latour (1986).

Environmental variation

VORTEX can model annual fluctuations in birth and death rates and in carrying capacity as might result from environmental variation. To model environmental variation, each demographic parameter is assigned a distribution with a mean and standard deviation that is specified by the user. Annual fluctuations in probabilities of reproduction and mortality are modeled as binomial distributions. Environmental variation in carrying capacity is modeled as a normal distribution. Environmental variation in demographic rates can be correlated among populations.

Catastrophes

Catastrophes are modeled in *VORTEX* as random events that occur with specified probabilities. A catastrophe will occur if a randomly generated number between zero and one is less than the probability of occurrence. Following a catastrophic event, the chances of survival and successful breeding for that simulated year are multiplied by severity factors. For example, forest fires might occur once in 50 years, on average, killing 25% of animals, and reducing breeding by survivors 50% for the year. Such a catastrophe would be modeled as a random event with 0.02 probability of occurrence each year, and severity factors of 0.75 for survival and 0.50 for reproduction. Catastrophes can be local (impacting populations independently), or regional (affecting sets of populations simultaneously).

Genetic processes

VORTEX models loss of genetic variation in populations, by simulating the transmission of alleles from parents to offspring at a hypothetical neutral (non-selected) genetic locus. Each animal at the start of the simulation is assigned two unique alleles at the locus. Each offspring created during the simulation is randomly assigned one of the alleles from each parent. *VORTEX* monitors how many of the original alleles remain within the population, and the average heterozygosity and gene diversity (or "expected heterozygosity") relative to the starting levels. *VORTEX* also monitors the inbreeding coefficients of each animal, and can reduce the juvenile survival of inbred animals to model the effects of inbreeding depression.

Inbreeding depression is modeled as a loss of viability of inbred animals during their first year. The severity of inbreeding depression is commonly measured by the number of "lethal equivalents" in a population (Morton et al. 1956). The number of lethal equivalents per diploid genome estimates the average number of lethal alleles per individual in the population if all deleterious effects of inbreeding were due entirely to recessive lethal alleles. A population in which inbreeding depression is one lethal equivalent per diploid genome may have one recessive lethal allele per individual, it may have two recessive alleles per individual, each of which confer a 50% decrease in survival, or it may have some other combination of recessive deleterious alleles which equate in effect with one lethal allele per individual.

VORTEX partitions the total effect of inbreeding (the total lethal equivalents) into an effect due to recessive lethal alleles and an effect due to loci at which there is heterozygote advantage (superior fitness of heterozygotes relative to all homozygote genotypes). To model the effects of lethal alleles, each founder starts with a unique recessive lethal allele (and a dominant non-lethal allele) at up to five modeled loci. By virtue of the deaths of individuals that are homozygous for lethal alleles, such alleles can be removed slowly by natural selection during the generations of a simulation. This diminishes the probability that inbred individuals in subsequent generations will be homozygous for a lethal allele.

Heterozygote advantage is modeled by specifying that juvenile survival is related to inbreeding according to the logarithmic model:

$$\ln(S) = A - BF$$

in which S is survival, F is the inbreeding coefficient, A is the logarithm of survival in the absence of inbreeding, and B is the portion of the lethal equivalents per haploid genome that is due to heterozygote advantage rather than to recessive lethal alleles. Unlike the situation with fully recessive deleterious alleles, natural selection does not remove deleterious alleles at loci in which the heterozygote has higher fitness than both homozygotes, because all alleles are deleterious when homozygous and beneficial when present in heterozygous combination with other alleles. Thus, under heterozygote advantage, the impact of inbreeding on survival does not diminish during repeated generations of inbreeding.
Unfortunately, for relatively few species are data available to allow estimation of the effects of inbreeding, and the magnitude of these effects apparently varies considerably among species (Falconer 1981; Ralls et al. 1988; Lacy et al. 1993) and even among populations of the same species (Lacy et al. 1996). Even without detailed pedigree data from which to estimate the number of lethal equivalents in a population and the underlying nature of the genetic load (recessive alleles or heterozygote advantage), PVAs must make assumptions about the effects of inbreeding on the population being studied. If genetic effects are ignored, the PVA will overestimate the viability of small populations. In some cases, it might be considered appropriate to assume that an inadequately studied species would respond to inbreeding in

accord with the median (3.14 lethal equivalents per diploid) reported in the survey by Ralls et al. (1988). In other cases, there might be reason to make more optimistic assumptions (perhaps the lower quartile, 0.90 lethal equivalents), or more pessimistic assumptions (perhaps the upper quartile, 5.62 lethal equivalents). In the few species in which inbreeding depression has been studied carefully, about half of the effects of inbreeding are due recessive lethal alleles and about half of the effects are due to heterozygote advantage or other genetic mechanisms that are not diminished by natural selection during generations of inbreeding, although the proportion of the total inbreeding effect can vary substantially among populations (Lacy and Ballou 1998).

A full explanation of the genetic mechanisms of inbreeding depression is beyond the scope of this manual, and interested readers are encouraged to refer to the references cited above.

VORTEX can model monogamous or polygamous mating systems. In a monogamous system, a relative scarcity of breeding males may limit reproduction by females. In polygamous or monogamous models, the user can specify the proportion of the adult males in the breeding pool. Males are randomly reassigned to the breeding pool each year of the simulation, and all males in the breeding pool have an equal chance of siring offspring.

Deterministic processes

VORTEX can incorporate several deterministic processes, in addition to mean age-specific birth and death rates. Density dependence in mortality is modeled by specifying a carrying capacity of the habitat. When the population size exceeds the carrying capacity, additional morality is imposed across all age classes to bring the population back down to the carrying capacity. Each animal in the population has an equal probability of being removed by this truncation. The carrying capacity can be specified to change over time, to model losses or gains in the amount or quality of habitat.

Density dependence in reproduction is modeled by specifying the proportion of adult females breeding each year as a function of the population size. The default functional relationship between breeding and density allows entry of Allee effects (reduction in breeding at low density) and/or reduced breeding at high densities.

Populations can be supplemented or harvested for any number of years in each simulation. Harvest may be culling or removal of animals for translocation to another (unmodeled) population. The numbers of additions and removals are specified according to the age and sex of animals.

Migration among populations

VORTEX can model up to 50 populations, with possibly distinct population parameters. Each pairwise migration rate is specified as the probability of an individual moving from one population to another. Migration among populations can be restricted to one sex and/or a limited age cohort. Emigration from a population can be restricted to occur only when the number of animals in the population exceeds a specified proportion of the carrying capacity. Dispersal mortality can be specified as a probability of death for any migrating animal, which is in addition to age-sex specific mortality. Because of between-population migration and managed supplementation, populations can be recolonized. *VORTEX* tracks the dynamics of local extinctions and recolonizations through the simulation.

Output

VORTEX outputs: **(1)** probability of extinction at specified intervals (e.g., every 10 years during a 100 year simulation), **(2)** median time to extinction, if the population went extinct in at least 50% of the simulations, **(3)** mean time to extinction of those simulated populations that became extinct, and **(4)** mean size of, and genetic variation within, extant populations.

Standard deviations across simulations and standard errors of the mean are reported for population size and the measures of genetic variation. Under the assumption that extinction of independently replicated populations is a binomial process, the standard error of the probability of extinction is reported by *VORTEX* as:

$$\mathrm{SE}(p) = \sqrt{\frac{p(1-p)}{n}}$$

in which the frequency of extinction was *p* over *n* simulated populations. Demographic and genetic statistics are calculated and reported for each subpopulation and for the metapopulation.

Sequence of program flow

(1) The seed for the random number generator is initialized with the number of seconds elapsed since the beginning of the 20th century.

(2) The user is prompted for an output file name, duration of the simulation, number of iterations, the size below which a population is considered extinct, and a large number of population parameters.

(3) The maximum allowable population size (necessary for preventing memory overflow) is calculated as:

$$K_{\max} = (K + 3s)(1 + L)$$

in which *K* is the maximum carrying capacity (carrying capacity can be specified to change during a simulation, so the maximum carrying capacity can be greater than the initial carrying capacity), *s* is the annual environmental variation in the carrying capacity expressed as a standard deviation, and *L* is the specified maximum litter size.

(4) Memory is allocated for data arrays. If insufficient memory is available for data arrays then N_{max} is adjusted downward to the size that can be accommodated within the available memory and a warning message is given. In this case it is possible that the analysis may have to be terminated because the simulated population exceeds N_{max}. Because N_{max} is often several-fold greater than the likely maximum population size in a simulation, a warning that it has been adjusted downward because of limiting memory often will not hamper the analyses.

(5) The deterministic growth rate of the population is calculated from mean birth and death rates that have been entered. Algorithms follow cohort life-table analyses (Ricklefs 1979). Generation time and the expected stable age distribution are also calculated. Life-table calculations assume constant birth and death rates, no limitation by carrying capacity, no limitation of mates, no loss of fitness due to inbreeding depression, and that the population is at the stable age distribution. The effects of catastrophes are incorporated into the life table analysis by using birth and death rates that are weighted averages of the values in years with and without catastrophes, weighted by the probability of a catastrophe occurring or not occurring.

(6) Iterative simulation of the population proceeds via steps 7 through 26 below.

(7) The starting population is assigned an age and sex structure. The user can specify the exact age-sex structure of the starting population, or can specify an initial population size and request that the population be distributed according to the stable age distribution calculated from the life table.

Individuals in the starting population are assumed to be unrelated. Thus, inbreeding can occur only in second and later generations.

(8) Two unique alleles at a hypothetical neutral genetic locus are assigned to each individual in the starting population and to each individual supplemented to the population during the simulation. *VORTEX* therefore uses an infinite alleles model of genetic variation. The subsequent fate of genetic variation is tracked by reporting the number of extant neutral alleles each year, the expected heterozygosity or gene diversity, and the observed heterozygosity. The expected heterozygosity, derived from the Hardy-Weinberg equilibrium, is given by

$$H_e = 1 - \sum \left(p_i^2\right)$$

in which p_i is the frequency of allele i in the population. The observed heterozygosity is simply the proportion of the individuals in the simulated population that are heterozygous. Because of the starting assumption of two unique alleles per founder, the initial population has an observed heterozygosity of 1.0 at the hypothetical locus and only inbred animals can become homozygous. Proportional loss of heterozygosity through random genetic drift is independent of the initial heterozygosity and allele frequencies of a population (Crow and Kimura 1970), so the expected heterozygosity remaining in a simulated population is a useful metric of genetic decay for comparison across scenarios and populations. The mean observed heterozygosity reported by *VORTEX* is the mean inbreeding coefficient of the population.

(9) For each of the10 alleles at five non-neutral loci that are used to model inbreeding depression, each founder is assigned a unique lethal allele with probability equal to 0.1 x the mean number of lethal alleles per individual.

(10) Years are iterated via steps 11 through 25 below.

(11) The probabilities of females producing each possible size litter are adjusted to account for density dependence of reproduction (if any).

(12) Birth rate, survival rates, and carrying capacity for the year are adjusted to model environmental variation. Environmental variation is assumed to follow binomial distributions for birth and death rates and a normal distribution for carrying capacity, with mean rates and standard deviations specified by the user. At the outset of each year a random number is drawn from the specified binomial distribution to determine the percent of females producing litters. The distribution of litter sizes among those females that do breed is maintained constant. Another random number is drawn from a specified binomial distribution to model the environmental variation in mortality rates. If environmental variations in reproduction and mortality are chosen to be correlated, the random number used to specify mortality rates for the year is chosen to be the same percentile of its binomial distribution as was the number used to specify reproductive rate. Otherwise, a new random number is drawn to specify the deviation of age- and sex-specific mortality rates from their means. Environmental variation across years in mortality rates is always forced to be correlated among age and sex classes.

The carrying capacity (K) for the year is determined by first increasing or decreasing the carrying capacity at year 1 by an amount specified by the user to account for changes over time. Environmental variation in K is then imposed by drawing a random number from a normal distribution with the specified values for mean and standard deviation.

(13) Birth rates and survival rates for the year are adjusted to model any catastrophes determined to have occurred in that year.

(14) Breeding males are selected for the year. A male of breeding age is placed into the pool of potential breeders for that year if a random number drawn for that male is less than the proportion of adult males specified to be breeding. Breeding males are selected independently each year; there is no long-term tenure of breeding males and no long-term pair bonds.

(15) For each female of breeding age, a mate is drawn at random from the pool of breeding males for that year. If the user specifies that the breeding system is monogamous, then each male can only be paired with a single female each year. Males are paired only with those females which have already been selected for breeding that year. Thus, males will not be the limiting sex unless there are insufficient males to pair with the successfully breeding females.

If the breeding system is polygynous, then a male may be selected as the mate for several females. The degree of polygyny is determined by the proportion of males in the pool of potential breeders each year.

The size of the litter produced by that pair is determined by comparing the probabilities of each potential litter size (including litter size of 0, no breeding) to a randomly drawn number. The offspring are produced and assigned a sex by comparison of a random number to the specified birth sex ratio. Offspring are assigned, at random, one allele at the hypothetical genetic locus from each parent.

(16) The genetic kinship of each new offspring to each other living animal in the population is determined. The kinship between new animal *A*, and another existing animal, *B*, is

$$f_{AB} = 0.5(f_{MB} + f_{PB})$$

in which f_{ij} is the kinship between animals *i* and *j*, *M* is the mother of *A*, and *P* is the father of *A*. The inbreeding coefficient of each animal is equal to the kinship between its parents, $F = f_{MP}$, and the kinship of an animal to itself is $f_A = 0.5(1 + F)$. (See Ballou 1983 for a detailed description of this method for calculating inbreeding coefficients.)

(17) The survival of each animal is determined by comparing a random number to the survival probability for that animal. In the absence of inbreeding depression, the survival probability is given by the age and sex-specific survival rate for that year. If a newborn individual is homozygous for a lethal allele, it is killed. Otherwise, the survival probability for individuals in their first year is multiplied by

$$e^{-b(1-\Pr[Lethals])F}$$

in which *b* is the number of lethal equivalents per haploid genome, and Pr[*Lethals*] is the proportion of this inbreeding effect due to lethal alleles.

(18) The age of each animal is incremented by 1.

(19) If more than one population is being modeled, migration among populations occurs stochastically with specified probabilities.

(20) If population harvest is to occur that year, the number of harvested individuals of each age and sex class are chosen at random from those available and removed. If the number to be removed do not exist for an age-sex class, *VORTEX* continues but reports that harvest was incomplete.

(21) Dead animals are removed from the computer memory to make space for future generations.

(22) If population supplementation is to occur in a particular year, new individuals of the specified age-class are created. Each immigrant is assumed to be genetically unrelated to all other individuals in the population, and it carries the number of lethal alleles that was specified for the starting population.

(23) The population growth rate is calculated as the ratio of the population size in the current year to the previous year.

(24) If the population size (N) exceeds the carrying capacity (K) for that year, additional mortality is imposed across all age and sex classes. The probability of each animal dying during this carrying capacity truncation is set to $(N - K)/N$, so that the expected population size after the additional mortality is K.

(25) Summary statistics on population size and genetic variation are tallied and reported.

(26) Final population size and genetic variation are determined for the simulation.

(27) Summary statistics on population size, genetic variation, probability of extinction, and mean population growth rate are calculated across iterations and output.

Literature Cited

Altmann, J., D. Schoeller, S.A. Altmann, P. Muruthi and R.M. Sapolsky. 1993. Body size and fatness of free-living baboons reflect food availability and activity levels. *American Journal of Primatology* 30:149-161.

Ballou, J.D. 1997. Ancestral inbreeding only minimally affects inbreeding depression in mammalian populations. *Journal of Heredity* 88:169-178.

Belovsky, G.E. 1987. Extinction models and mammalian persistence. Pages 35-57 in: Soulé, M.E. (ed.). *Viable Populations for Conservation*. Cambridge: Cambridge University Press.

Berger, J. 1990. Persistence of different-sized populations: an empirical assessment of rapid extinctions in bighorn sheep. *Conservation Biology* 4:91-98.

Bonaccorso, F., P. Clark, P.S. Miller, and O. Byers (eds.). 1999. *Conservation Assessment and Management Plan for the Tree Kangaroos of Papua New Guinea and Population and Habitat Viability Assessment for Matschie's Tree Kangaroo: Final Report*. Apple Valley, MN: Conservation Breeding Specialist Group (SSC/IUCN).

Bormann, F.H. and S.R. Kellert. 1991. *Ecology, Economics, and Ethics. The Broken Circle*. New Haven: Yale University Press.

Boyce, M.S. 1992. Population viability analysis. *Annual Review of Ecology and Systematics* 23:481-506.

Brussard, P. 1985. Minimum viable populations: how many are too few? *Restoration and Management Notes* 3:21-25.

Burgman, M., S. Ferson and H.R. Akçakaya. 1993. *Risk Assessment in Conservation Biology*. New York: Chapman and Hall.

Clark, T.W. 1989. *Conservation Biology of the Black-Footed Ferret.* Philadelphia: Wildlife Preservation Trust International.

Clark, T.W. 1993. Creating and using knowledge for species and ecosystem conservation: Science, organizations, and policy. *Perspectives in Biology and Medicine* 36:497-525.

Clark, T.W., R.M. Warneke and G.G. George. 1990. Management and conservation of small populations. Pages 1-18 in: Clark, T.W. and J.H. Seebeck (eds.). *Management and Conservation of Small Populations*. Brookfield, Illinois: Chicago Zoological Society.

Clark, T.W., G.N. Backhouse and R.C. Lacy. 1991. The population viability assessment workshop: A tool for threatened species management. *Endangered Species Update* 8:1-5.

Clark, T.W., and Seebeck, J.H. (eds.) 1990. *Management and Conservation of Small Populations*. Brookfield, Illinois: Chicago Zoological Society.

Ellis, S., K. Hughes, C. Kuehler, R.C. Lacy and U.S. Seal (eds.). 1992a. *Alala, Akohekohe, and Palila Population and Habitat Viability Assessment Reports*. Apple Valley, MN: Captive Breeding Specialist Group (SSC/IUCN).

Ellis, S., C. Kuehler, R.C. Lacy, K. Hughes and U.S. Seal (eds.). 1992b. *Hawai`ian Forest Birds Conservation Assessment and Management Plan*. Apple Valley, MN: Captive Breeding Specialist Group (SSC/IUCN).

Falconer, D.S. 1981. *Introduction to Quantitative Genetics*. 2nd ed. New York: Longman.

Fisher, R.A. 1958. *The Genetical Theory of Natural Selection*. 2nd ed. New York; Dover.

Fowler, C.W. 1981. Density dependence as related to life history strategy. *Ecology* 62:602-610.

Franklin, I.R. 1980. Evolutionary change in small populations. Pages 135-149 in: Soulé, M.E. and B.A. Wilcox (eds.). *Conservation Biology: An Ecological/Evolutionary Perspective.* Sunderland, MA: Sinauer Associates.

Foose, T.J., R.C. Lacy, R. Brett and U.S. Seal (eds.). 1993. *Kenyan Black Rhino Metapopulation Workshop Report*. Apple Valley, MN: Captive Breeding Specialist Group (SSC/IUCN).

Gilpin, M.E. 1987. Spatial structure and population vulnerability. Pages 125-139 in: Soulé, M.E. (ed.). *Viable Populations for Conservation*. Cambridge: Cambridge University Press.

Gilpin, M.E. 1989. Population viability analysis. *Endangered Species Update* 6:15-18.

Gilpin, M.E., and M.E. Soulé. 1986. Minimum viable populations: processes of extinction. Pages 19-34 in: Soulé, M.E. (ed.). *Conservation Biology: The Science of Scarcity and Diversity*. Sunderland, MA: Sinauer Associates.

Goodman, D. 1987. The demography of chance extinction. Pages 11 – 34 in: Soulé, M.E. (ed.). *Viable Populations for Conservation*. Cambridge: Cambridge University Press.

Herrero, S., P.S. Miller and U. S. Seal (eds.). 2000. *Population and Habitat Viability Assessment Workshop for the Grizzly Bear of the Central Rockies Ecosystem (*Ursus arctos horribilis). Apple Valley, MN: Conservation Breeding Specialist Group (SSC/IUCN).

Hobbs, N.T., and D.M. Swift. 1985. Estimates of habitat carrying capacity incorporating explicit nutritional constraints. *Journal of Wildlife Management* 49:814-822.

Holling, C.S. (ed.). 1978. *Adaptive Environmental Assessment and Management*. International Series on Applied Systems Analysis 3, International Institute for applied systems analysis. Toronto: John Wiley and Sons.

Kirkpatrick, S, and Stoll, E. 1981. A very fast shift-register sequence random number generator. *Journal of Computational Physics* 40:517.

Lacy, R.C. 1993a. VORTEX: A computer simulation model for Population Viability Analysis. *Wildlife Research* 20:45-65.

Lacy, R.C. 1993b. Impacts of inbreeding in natural and captive populations of vertebrates: Implications for conservation. *Perspectives in Biology and Medicine*. 36:480-496.

Lacy, R.C. 1993/1994. What is Population (and Habitat) Viability Analysis? *Primate Conservation* 14/15:27-33.

Lacy, R.C. 1997. Importance of genetic variation to the viability of mammalian populations. *Journal of Mammalogy* 78:320-335.

Lacy, R.C., G. Alaks, and A. Walsh. 1996. Hierarchical analysis of inbreeding depression in *Peromyscus polionotus*. Evolution 50:2187-2200.

Lacy, R.C. and J.D. Ballou. 1998. Effectiveness of selection in reducing the genetic load in populations of *Peromyscus polionotus* during generations of inbreeding. *Evolution* 52:900-909.

Lacy, R.C. and T.W. Clark. 1990. Population viability assessment of the eastern barred bandicoot in Victoria. Pages 131-146 in: Clark, T.W. and J.H. Seebeck (eds.). *Management and Conservation of Small Populations.* Brookfield, IL: Chicago Zoological Society.

Lacy, R.C, N.R. Flesness and U.S. Seal (eds.). 1989. *Puerto Rican Parrot Population Viability Analysis. Report to the U.S. Fish and Wildlife Service.* Apple Valley, MN: Captive Breeding Specialist Group (SSC/IUCN).

Lacy, R.C. and D.B. Lindenmayer. 1995. A simulation study of the impacts of population sub-division on the mountain brushtail possum, *Trichosurus caninus* Ogilby (Phalangeridae: Marsupialia), in south-eastern Australia. II. Loss of genetic variation within and between sub-populations. *Biological Conservation* 73:131-142.

Lacy, R.C., Petric, A.M., and Warneke, M. 1993. Inbreeding and outbreeding depression in captive populations of wild species. Pages 352-374 in Thornhill, N.W. (ed.). *The Natural History of Inbreeding and Outbreeding*. Chicago: University of Chicago Press.

Lande, R. and G.F. Barrowclough. 1987. Effective population size, genetic variation, and their use in population management. Pages 87-123 in Soulé, M.E. (ed.). *Viable Populations for Conservation*. Cambridge: Cambridge University Press.

Lindenmayer, D.B. and R.C. Lacy. 1995a. Metapopulation viability of Leadbeater's Possum, *Gymnobelideus leadbeateri*, in fragmented old-growth forests. *Ecological Applications* 5:164-182.

Lindenmayer, D.B. and R.C. Lacy. 1995b. Metapopulation viability of arboreal marsupials in fragmented old-growth forests: Comparison among species. *Ecological Applications* 5:183-199.

Lindenmayer, D.B. and R.C. Lacy. 1995c. A simulation study of the impacts of population sub-division on the mountain brushtail possum, *Trichosurus caninus* Ogilby (Phalangeridae: Marsupialia), in south-eastern Australia. I. Demographic stability and population persistence. *Biological Conservation* 73:119-129.

Lindenmayer, D.B., T.W. Clark, R.C. Lacy and V.C. Thomas. 1993. Population viability analysis as a tool in wildlife conservation policy: A review with reference to Australia. *Environmental Management* 17:745-758.

Mace, G.M. and R. Lande. 1991. Assessing extinction threats: Toward a re-evaluation of IUCN threatened species categories. *Conservation Biology* 5:148-157.

Maier, W.L. (1991). A fast pseudo random number generator. *Dr. Dobb's Journal* (May 1991):152-7.

Manansang, J., A. MacDonald, D. Siswomartono, P.S. Miller, and U.S. Seal (eds.). 1996. *Population and Habitat Viability Assessment for the Babirusa* (Babyrousa babyrussa). Apple Valley, MN: Conservation Breeding Specialist Group (SSC/IUCN).

Mirande, C., R. Lacy, and U. Seal (eds.). 1991. *Whooping Crane* (Grus americana) *Conservation Viability Assessment Workshop Report*. Apple Valley, MN: Captive Breeding Specialist Group (SSC/IUCN).

Morton, N.E., Crow, J.F., and Muller, H.J. 1956. An estimate of the mutational damage in man from data on consanguineous marriages. *Proceedings of the National Academy of Sciences, USA* 42:855-863.

O'Brien, S.J. and Evermann, J.F. 1988. Interactive influence of infectious diseases and genetic diversity in natural populations. *Trends in Ecology and Evolution* 3:254-9.

Odum, A., et al (eds.). 1993. *Aruba Island Rattlesnake Population and Habitat Viability Assessment (PHVA) Workshop*. Apple Valley, MN: Captive Breeding Specialist Group (SSC/IUCN).

Ralls, K., Ballou, J.D., and Templeton. A.R. 1988. Estimates of lethal equivalents and the cost of inbreeding in mammals. *Conservation Biology* 2:185-93.

Robertson, A. (1960). A theory of limits in artificial selection. *Proceedings Royal Society of London* 153B:234-49.

Rohlf, F.J., and R.R. Sokal. 1981. *Statistical Tables*. 2nd ed. New York: W.H. Freeman and Company.

Ruggiero, L.F., G.D. Hayward and J.R. Squires. 1994. Viability analysis in biological evaluations: Concepts of population viability analysis, biological population, and ecological scale. *Conservation Bio*logy 8:364-372.

Rylands, A.B. 1993/1994. Population viability analyses and the conservation of the lion tamarins, *Leontopithecus*, of south-east Brazil. *Primate Conservation* 14/15: 34-42.

Samuels, A. and J. Altmann. 1991. Baboons of the Amboseli basin: Demographic stability and change. *International Journal of Primatology* 12:1-19.

Sapolsky, R.M. 1982. The endocrine stress-response and social status in the wild baboon. *Hormones and Behavior* 15:279-292.

Sapolsky, R.M. 1986. Endocrine and behavioral correlates of drought in the wild baboon. *American Journal of Primatology* 11:217-227.

Seal, U.S., J.D. Ballou and C.V. Padua (eds.). 1990. Leontopithecus *Population Viability Analysis Workshop Report*. Apple Valley, MN: Captive Breeding Specialist Group (SSC/IUCN).

Seal, U.S., R.C. Lacy, K. Medley, R. Seal and T.J. Foose (eds.). 1991. *Tana River Primate Reserve Conservation Assessment Workshop Report*. Apple Valley, MN: Captive Breeding Specialist Group (SSC/IUCN).

Selander, R.K. 1983. Evolutionary consequences of inbreeding. Pages 201-215 in: Schonewald-Cox, C.M, S.M. Chambers, B. MacBryde, and W.L. Thomas (eds.). *Genetics and Conservation: A Reference for Managing Wild Animal and Plant Populations*. Menlo Park, CA: Benjamin/Cummings.

Shaffer, M.L. 1981. Minimum population sizes for species conservation. *Bioscience* 1:131-134.

Shaffer, M.L. 1987. Minimum viable populations: Coping with uncertainty. Pages 69-86 in: Soulé, M.E. (ed.). *Viable Populations for Conservation*. Cambridge: Cambridge University Press.

Shaffer, M.L. 1990. Population viability analysis. *Conservation Biology* 4:39-40.

Simberloff, D.A. 1986. The proximate causes of extinction. Pages 259-276 in: Raup, D.M., and D. Jablonski (eds.). *Patterns and Processes in the History of Life*. Berlin: Springer-Verlag.

Simberloff, D.A. 1988. The contribution of population and community biology to conservation science. *Annual Review of Ecology and Systematics* 19:473-511.

Soulé, M.E. (ed). 1987. *Viable Populations for Conservation*. Cambridge: Cambridge University Press.

Soulé, M., M. Gilpin, W. Conway and T. Foose. 1986. The millenium ark: How long a voyage, how many staterooms, how many passengers? *Zoo Biology* 5:101-113.

Starfield, A.M. and A.L. Bleloch. 1986. *Building Models for Conservation and Wildlife Management.*, New York: Macmillan.

Thomas, C.D. 1990. What do real population dynamics tell us about minimum population sizes? *Conservation Biology* 4:324-327.

Walker, S. and S. Molur (eds.). 1994. *Population and Habitat Viability Analysis (PHVA) Workshop for Indian/Nepali Rhinoceros*. Zoo Outreach Organisation/CBSG India, Coimbatore.

Wright, S. 1977. *Evolution and the Genetics of Populations. Vol. 3. Experimental Results and Evolutionary Deductions*. Chicago: University of Chicago Press.