COMPREHENSIVE CONSERVATION MODELING: A SPATIALLY EXPLICIT INDIVIDUAL-BASED APPROACH USING GRIZZLY BEARS AS A CASE STUDY

by

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ABSTRACT

This dissertation illustrates how a mechanistic bottom-up approach to constructing a spatially explicit individual-based model (IBM) provides the proper theoretical and operational frameworks for constructing population viability analysis (PVA) models that avoid many of the substantive and theoretical criticism of the conventional demographic models used in PVA. Using Java™, such a model is developed for the grizzly bear population of the Cabinet-Yaak Ecosystem. This approach, coupled with spatially explicit landscape data, permits direct linkage of a population's viability with geographic attributes. This linkage extends the effectiveness of PVA as a tool to guide conservation and landscape management decisions. The individual-based perspective facilitates pedigree analysis and the direct calculation of individual kinship coefficients and other genetic measures. This permits the definition of viability to be expanded to include genetic criteria, and PVA to be used as a tool to predict the timing, scope, and intensity of population augmentation actions necessary to maintain a population's genetic integrity.

Spatially explicit IBMs as an approach to population genetics are explored in depth. Results suggest geography plays an important role in population genetic processes and raise questions about the adequacy of relying solely either on effective population size or heterozygosity for developing in situ conservation strategies. Technical tools for exploring population genetics from an individual-based theoretical framework are developed and discussed.

This research shows how the modern technologies of geographical information systems (GIS), remotely sensed imagery, and object-oriented programming, along with principles from complex adaptive systems can be integrated with more traditional ecology, wildlife biology, and genetics to create a comprehensive PVA model. The model is comprehensive in its inclusion of important aspects of species conservation: habitat protection, population genetics, and population demographics, along with the species' behavior and ecology, and is comprehensive in the type of conservation issues it can address.

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CHAPTER 1

INTRODUCTION

Our planet's biodiversity is in the midst of a deepening extinction crisis. Many experts agree that, unlike past extinctions that were driven by random catastrophes and major climate fluctuations, the current wave of extinctions is largely the result of human activities (IUCN 2000). While the extinction crisis affects taxa from throughout the animal kingdom, the impact is dramatic and acute on populations of large mammals (Herrero 1999). Large mammals, from rhinoceroses and elephants to bears, big cats, and wolves, are particularly vulnerable to human encroachments. Their large size equates to greater food demands and, thus, greater habitat needs. At times, these greater food and habitat needs put them in direct competition with humans for the same resources (Primm and Clark 1996). Unfortunately, their wide-ranging habits expose them to more risk while their large bodies make them easier to locate and kill than smaller species (Cardillo 2003). Human-caused mortality is, therefore, one of the leading factors contributing to the demise of large, highly mobile mammals.

Historically, nature reserves (e.g., wildlife refuges, parks) have played an important role in the survival of species in decline. Today, reserves remain an important tool for species conservation, but the designation of new protected areas is increasingly more difficult to achieve than a century ago (Soule and Terborgh 1999). The demands for land are exponentially greater, making it difficult to garner public support for reserve designation. Further, the protections offered to today's reserves are often graded rather than absolute. This results in making them less effective in conservation than in the past. For some widely ranging species, setting aside an adequate amount of land for protection is infeasible, since such a reserve would span millions of acres of private and public lands of multiple jurisdictions. To compound the problem, even existing refuges are not always large enough to sustain a population of sufficient size to withstand the effects of environmental and demographic stochasticity that may lead to extinction (Newmark 1987). For some species inhabiting refuges, their population numbers are too small to avoid potentially detrimental genetic change (Soule 1980; Shaffer and Sampson 1985; Simberloff 1988; Noss 1992).

Conservation strategies and decisions must be science-based if society is to address the problem in its full scope and with the most productive use of conservation resources. The imperative is to provide strong, science-based justifications for particular conservation actions (presuming stable, defined goals). Likewise, techniques need to be developed to monitor wildlife populations and the ecosystems that support them. This will allow the objective measurement of progress toward conservation goals (Beissinger and McCullough 2002). The science is largely biological, as genetics, demography, ecology, and animal behavior are the core concerns. Given global warming, increasing human demands, on ecosystem resources, and the geospatial aspects of conservation, the science must be climatological and geographic as well. In addition, the spatial complexity of the problems requires the use of geographic technologies, like geographical information systems (GIS).

Ecologists, biogeographers, wildlife biologists, and other scientists have worked for decades to develop and improve theoretical concepts and analytic tools and methods that would meet these needs. Most recently, these analytical tools and methods have been expanded to include GIS and remote sensing technologies. In the past 20 years, these efforts have prompted the creation of a new discipline, conservation biology. This discipline emerged largely to meet the challenge of the extinction crisis and to respond to demands by the Endangered Species Act (1973) and the National Forest Management Act (1976). This field shares many of the same concerns as other disciplines. The spatial distribution, abundance, and individual fitness of organisms, for example, are a shared concern with biogeography and wildlife biology.

As a young and evolving ‘crisis discipline’ (Soule 1985), conservation biology has adopted many analytical tools and concepts from other fields. Some of the first concepts proceeded along the lines of biogeography, for example, island biogeography (MacArthur and Wilson 1967; Diamond 1975) or the ‘rescue effect’ (Brown and Kodric-Brown 1977), and led to lengthy theoretical debates over such issues as what is the best landscape configuration for a reserve (Sarkar 2004).

Other early concepts took a more biology/ecology bent by considering population demography and genetics and led to discourse over such issues as the most important factor for species conservation, population numbers or genetic heterozygosity (Lande 1988), or the best formula for calculating effective population size. The spatial configuration of a population(s), its size and genetic heterozygosity, as well as, the contributions of these variables to preventing extinction of small populations continue to be central themes in conservation biology (Caughley 1994).

One of the first original ideas of conservation biology was the notion of a minimum viable population (MVP), which came from Mark Shaffer's (1978) computer simulation work on grizzly bears. A MVP was defined as the minimum population size necessary to prevent extinction within a certain time period, say 100 years. Though in some ways a useful concept, the method used to determine a MVP was very limited in its ability to include multiple factors affecting a population's decline. The more dynamic population viability analysis (PVA) of Gilpin and Soule (1986), thus, expanded upon the MVP idea and its method of calculation.

A PVA assesses a population's probability of persistence or extinction to a future time horizon based on a demographic model and may include up to four types of stochastic perturbations: demographic, environmental, catastrophic, and genetic. Initially, the models used in PVA were aspatial, but as the analysis technique evolved, spatially implicit (metapopulation) models, and finally, spatially explicit models connecting with GIS emerged. The demographic models used in a PVA can either be analytical, matrix, or individually based, but in all cases, the stochastic perturbations are realized through their effect on one or more demographic parameters. These effects and their magnitude and distribution must be known, assumed, or estimated for the analysis.

The popularity of PVA has been considerable, in part due to the advent of ready-to-use PVA software programs, such as VORTEX (Lacy 1993) and RAMAS (Applied Biomathematics®), designed to aid in performing the analysis. Also, stochastic simulation is a well-founded theoretical framework for dealing with complex problems that is easily understood, even by those without a strong modeling background. (The demographic models used do not have to be stochastic, but they are the most common [Beissinger and Westphal 1998].) They seem to have become particularly popular as support for government conservation policy decisions, and documentation of their development and use has at times been confined to the grey literature (Caughley 1994). Despite their popularity, many researchers have questioned their validity as an accurate, reliable, and scientific method to use for conservation management and planning (Caughley 1994; Beissinger and Westphal 1998; Brook et al. 2001; Coulson et al. 2001).

The most common criticisms of PVA models center around the data required for their parameterization and the difficulties surrounding their validation. PVA models being stochastic demographic models require estimates of vital rates and their variances. Oftentimes there is little, poor, or no data available for the species for which the model is being developed (Caughley 1994; Beissinger and Westphal 1998; Boyce 2001). Further, collecting data in order to estimate the variances in vital rates, especially as they relate to the stochastic perturbations, requires large sample sizes and long time periods, characteristics often in opposition with the fact a species is considered threatened or endangered. The data problem is exacerbated when the models take the form of a metapopulation and/or are spatially explicit. These types of models require additional information on how vital rates vary spatially or between habitat patches, the spatial configuration of the habitat patches, and dispersal behavior. Dispersal behavior and the data necessary to parameters associated with the behavior are some of the most difficult things to collect (Stacey and Taper 1992; Kareiva and Wennergren 1995; Beissinger and Westphal 1998), especially for highly mobile species.

Validation issues with PVA models arise from their predictive and stochastic nature and their structure. Validation issues with the structure of PVA models occur because of implicit and explicit assumptions that are made. Implicitly, because PVA models are based on empirical data, they necessarily make the assumption that vital rates and variances are stationary through time, and, thus, what has happened in the past is representative of the future (Karevia and Wennergren 1995; Beissinger and Westphal 1998; Boyce 2001). For all but the rare exception, this assumption is most likely incorrect given PVAs project population trends into the future 50+ years. Explicitly, because PVA models are population models, population-level assumptions must be made about the form of density dependency, carrying capacity, and Allee effects. Like vital rates and variance there may be little data to support the choice, and the choice can greatly influence calculation of persistence times (Stacey and Taper 1992; Mills et al. 1`996; Beissinger and Westphal 1998).

Issues with validating model results are inherent with long-term predictive, non-deterministic models, and, to some extent, are unjustified. Unlike deterministic models that produce a single result, stochastic models produce a sample of results whereby the average and distribution of the sample take on meaning. Even if a correct answer existed, comparison between the 'correct' result and a sample of results would be difficult. In long-term predictive models, however, there is not a single correct answer, because if there were, there would be no need to create a model to predict it. The best that can be done is to test and verify model assumptions and secondary results (Beissinger and Westhphal 1998).

In addition to the substantive weakness in PVA models mentioned above, there are also some theoretical shortcomings. First, is the model's inability to incorporate specific environmental changes directly. Current models handle environmental changes in an undifferentiated fashion subsumed under the category of environmental perturbation. It is deterministic factors, such as habitat modification, that are the primary causes of extinction today (Caughley 1994; Boyce et al. 2001). Second, along with the stationary assumptions of vital rates, the models usually assume a stationary environment (Beissinger and Westphal 1998), ignoring such things as vegetation succession and other land-use changes. (It should be noted that at least one PVA software, RAMAS/Landscape, does include a forest succession simulator, but it shares the same limitation as other spatially explicit PVA software which is discussed next). Third, though newer versions of popular PVA software have the ability to incorporate spatially explicit landscapes, they do so by simplifying the landscape attributes to a habitat suitability index (HSI) or something similar. HSI models are reviewed extensively in Chapter 2; suffice it here to say that these types of models have rarely been validated and when they have been, they have performed poorly (Minta and Kareiva 1994). Lastly, PVA models fail to incorporate individual animal behavior. Behavior is often the primary means by which an animal copes with an environmental challenge (Morrison 2001).

Despite the criticism of PVA, researchers usually agree the process may have value when used to predict the relative efficacy of alternative management actions or conservation strategies (Boyce 2001; Coulson et al. 2001; Allendorf and Ryman 2002) or, as Boyce (2001) argues, as part of an adaptive management program. I feel this optimism may be somewhat unwarranted at this time, unless the substantive and theoretical issues discussed above are addressed. Further, many of the issues arise because the models currently used are developed from a top -down perspective, as are the data collection efforts that support the models. In addition, the continued reliance on stochastic methods (perturbation) is at least in part due to the method's ability to deal with complex problems in a manner that is easily understood.

Specifically, this dissertation addresses some of the issues associated with PVA models by taking a look at the process of species extinction from a different theoretical framework:

- It uses concepts from the new field of complex adaptive systems (CAS) to apply a bottom-up approach to species conservation modeling.
- It develops the methods necessary to explore the mechanisms through which population dynamics, and hence its viability, arise from how individuals interact temporally and spatially with each other, their natural environment, and the human-dominated landscape.
- It develops a spatially explicit individual-based model (IBM) that directly links population viability with ecological factors so that the consequences of human-induced and natural landscape changes and management actions to persistence can be fully realized and elucidated.

The objective of this research is to develop a conceptual foundation and an analytic tool for designing science-based conservation programs for wild populations of large terrestrial mammals. This research is largely based on a species that has been and remains central to conservation decision making: the grizzly bear, *Ursus arctos*. The grizzly bear was chosen because it is a high profile species and, as such, has been the subject of much research. Every type of model and methodology used in conservation, wildlife biology, and management has been constructed for or implemented on one of the five grizzly bear populations in the United States. The grizzly bear provided an excellent focal point for an extensive literature review of conservation modeling practices, from which the ideas of this dissertation were formed.

The immense research interest in the grizzly bear has led to a great body of published literature of bear behavior. The set of behaviors modeled reflects information available on the

Rocky Mountain grizzly bears' foraging, denning, and mating behavior, their dietary needs and preferences, and their social organization. This information on behavior and ecology is integrated in the model using the CAS concepts of adaptation, fitness and strategy, state-based response, and prediction to produce realistic emergent population-level dynamics. These concepts facilitate the proper bottom-up approach to individual-based modeling that allows the model to overcome some of the inadequacies of conventional PVA models.

In order for the realistic population dynamics to emerge, spatial variation and temporal dynamics of the landscape must be modeled in conjunction with bear behavior. A large portion of this dissertation is devoted to the collection, processing, and/or derivation of spatial data to support the ecological factors in the model. Both raster and vector GIS data layers were used, and data were gathered primarily from city, county, and federal governmental agencies. Data for the model was centered on those aspects of the landscape that would influence grizzly bear movement, either attraction or avoidance, and their survival.

Grizzlies are attracted to locations that provide feeding, mating, or denning opportunities. Their foraging behavior and dietary needs and preferences require special modeling consideration. Grizzly bears have been documented to eat over 200 different food items including fish, ungulates, rodents, grasses, sedges, forbs, fruits, mushrooms, insects, and mast crops such as acorns and pine seeds. Even though a substantial portion of the grizzly's diet is vegetative foods, they are unable to digest plant fiber fully. This necessitates grizzlies to selectively consume plants at the phenologic stage that offers them the most nutrition (Rode et al. 2001). Any model then must account for the spatial and temporal distribution of important grizzly bear foods, and because phenological development of plant foods is a function of topographic position, a spatially explicit model must account for the spatial variation in plant development. Much of the model's spatial data information needs center around these two aspects of the model. As stated earlier, human-caused mortality poses a significant threat to the survival of large mammals like the grizzly bear. This human-associated mortality risk varies over the landscape as a function of likely presence of humans, for which trails, houses, and lodging facilities are a surrogate (Mattson et al. 1996; Johnson et al. 2005). The presence of roads also has been documented, at least seasonally, to affect grizzly movements (Mace et al. 1996). Spatial data layers representing human landscape features, therefore, make up the rest of the database.

1.1 Study area

This research used the western portion of the Cabinet Yaak Grizzly Bear Recovery Zone or Ecosystem (CYE) as a study area in which to develop the first iteration of a spatially explicit IBM that can be used as a grizzly bear conservation tool. The study area is between latitude 47 27' 32" to 49 00' 00" N and longitude 114 52' 52" to 116 32' 53" W. It is composed of national forest, state, and private lands, with the vast majority of acreage belonging to the federal government or the private company, Plum Creek Timber. The study area lies primarily within the boundaries of the Kootenai National Forest but also falls within parts of the Idaho Panhandle and Lolo National Forests. The area consists of two mountain ranges in the Rocky Mountains: Cabinet and Purcell, and is drained by two major rivers: the Clark Fork and Kootenai. The Pack River in Idaho, which flows into Lake Pend Oreille, also passes through part of the study area. Major water bodies include the Noxon and Cabinet Gorge Reservoirs, Bull Lake, and parts of Lake Koocanusa and Lake Pend Oreille. The study area can be seen in Figure 1.1.

The study area lies west of the Continental Divide and is greatly influenced by the Pacific maritime weather system, causing cool, wet weather in the winter and warm, dry summers (Kuennen and Nielsen-Gerhardt 1985). Some areas can receive over 100 inches of annual precipitation. Areas in the eastern and southern end of the study are much drier than those in the western portion. The entire study area falls within Bailey's Northern Rocky Mountain Forest-Steppe - Coniferous Forest - Alpine Meadow physiographic province (Bailey 1995). The abundant precipitation fosters productive and plentiful vegetation. Most of the study area is forested with Douglas-fir and cedar-hemlock-Douglas-fir forest types (Bailey 2001). Only a small portion of the landscape consists of grasslands and wet meadows (Kuennen and Nielsen-Gerhardt 1995).

This area is an excellent area to test the feasibility and usefulness of applying a spatially explicit IBM. Currently, the population in the CYE is estimated at between 30-40 grizzlies. Their small numbers and the fact that they inhabit a heterogeneous environment make them excellent candidates for such a model (Saarenmaa 1988; Metz and DeRoss 1992). In addition, many of the management concerns and decisions regarding grizzly bear conservation are relevant to the CYE.

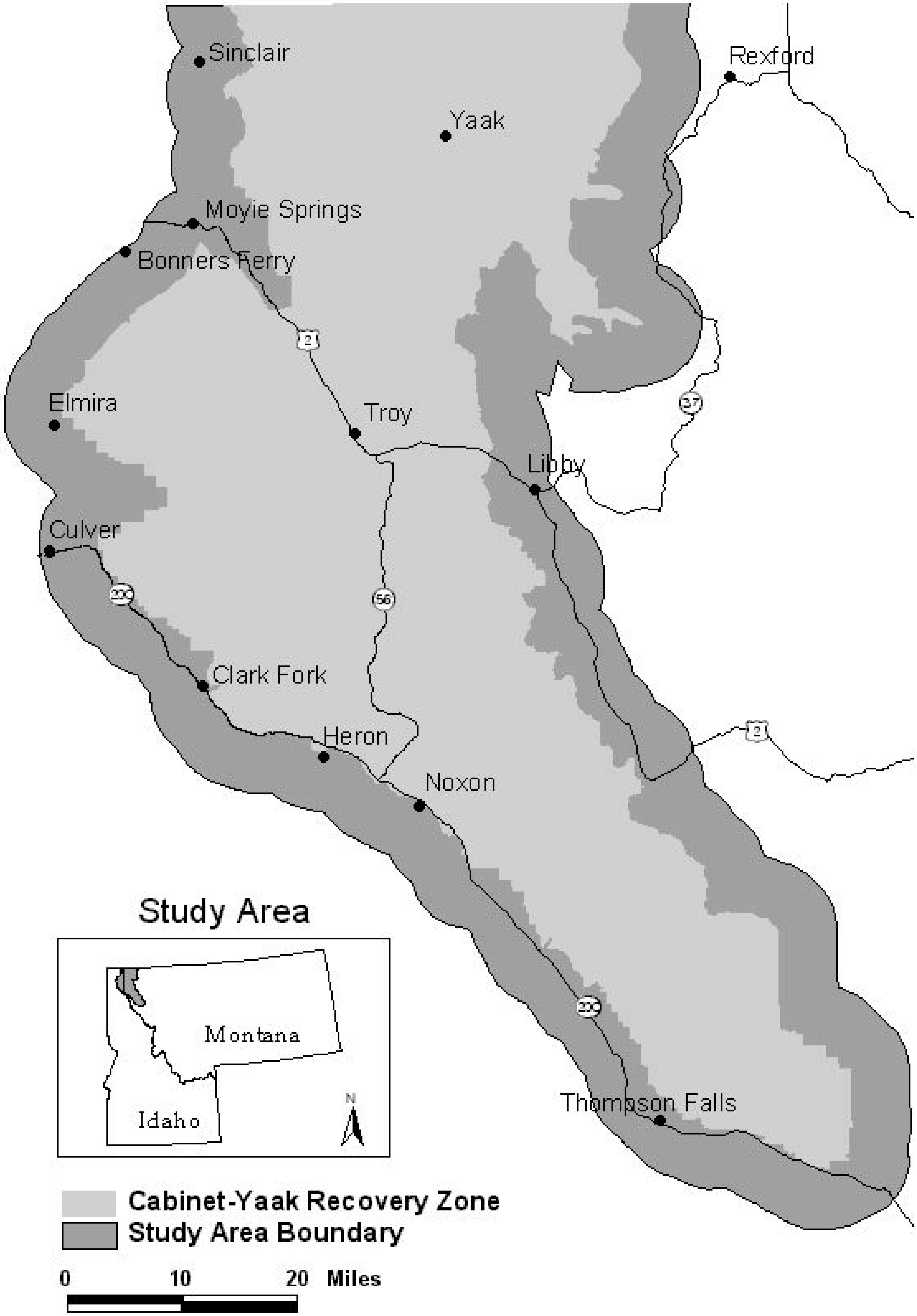

Figure 1.1. Study area boundary.

Due to their small numbers, population augmentation occurred in the early 1990s and a similar effort began in 2005. Though little attention is given to the genetic integrity of the population, concerns about inbreeding are relevant. In addition, the communities around the ecosystem have traditionally been heavily reliant on the natural resource extractive industries. Being west of the Continental Divide, the heavily productive forests may be subject to unsustainable timber harvest and associated road building. There are proposed mines on the border of the Cabinet Wilderness area. Realistic and accurate evaluation of the impacts of proposed timber harvests and mining is crucial to the survival of this small population. In addition, the increased human activity and alterations to the habitat associated with the proposed mines may act as a dispersal barrier to grizzlies, disrupting connectivity of the central part of the ecosystem with the southern tip. The connectedness of the Cabinets Mountains with the Yaak is already under question. In the United State Fish and Wildlife Service's (USFWS) Grizzly Bear Recovery Plan, it states: "Functional movement corridors for grizzly bears, with adequate cover, between the Cabinet Mountains population and population centers in the Yaak are undetermined currently, and no movement has been documented" (1993: 12). A similar comment appears more recently in an annual report prepared by the USFWS on the Cabinet-Yaak Ecosystem (Kasworm 2000).

The situation in the CYE is indicative of the types of threats posed to the persistence of grizzly bears in the lower 48 states: erosion of habitat brought about increased human encroachment and development and resource extraction pressure. On a smaller spatial scale, these issues of connectivity within the CYE are representative of the same issues involving connectivity between the various grizzly bear ecosystems. Finally, concerns over inbreeding depression, loss of heterozygosity, and population augmentation as a remedy to these genetic concerns pertain equally to the isolated Yellowstone Ecosystem population.

The spatially explicit IBM resulting from this research can be adapted to address conservation issues affecting grizzly bear population in other ecosystems. Modeling from the bottom up in a mechanistic manner allows population dynamics and hence its viability to arise from local interactions; these interactions between grizzlies themselves and grizzlies and the landscape are consistent across population boundaries. Behaviorally, grizzlies in the conterminous U.S. appear to be similar, though their diets vary with food availability. Also, the same human-associated risk of mortality applies to bears in all ecosystems. Model adaptation then becomes a function of developing the necessary spatial data layers. Not only could the model be adapted to other grizzly bear populations with the lower 48 states, but the conceptual foundation developed could also be used to develop similar analytic tools for other widely ranging large mammals around the world whose persistence is in question for the very same reasons as the grizzly bear.

1.2 Contributions

This dissertation provides the first in-depth treatment of the uses of spatially explicit individual-based modeling for grizzly bear conservation. It develops a conceptual understanding of how natural ecological systems and the human landscape interact with individual grizzly bear behavior to influence population viability. In this dissertation, viability refers to both population numbers and genetic variation, since the maintenance of these measures must be a central theme in plans for long-term population management (Lande and Barrowclough 1987). An IBM and a population viability model that interfaces with GIS-based habitat information have both been described as an urgent need by some leading grizzly bear researchers (Boyce et al. 2001). In addition to being the first spatially explicit IBM developed for grizzly bears, this model is the first PVA model that incorporates individual animal behavior. Lastly, the model developed in this dissertation goes beyond the current capabilities of prevailing PVA models, because it is designed as a tool for site-specific recovery management.

This research makes advances in understanding how the characteristics of individual agents, in this case grizzly bears and habitat cells, can lead to the emergence of population-level dynamics. Understanding the emergence of complex system-level properties has been described as the most important challenge for ecologists (Levin 1999). Emergence is one of the concepts from the field of complex adaptive systems identified by Railsback (2001) as having the potential to produce realistic system-level behavior in IBMs that implement them. This research extends the use of these concepts to modeling large mammals. Until now, application of these concepts has received little attention, especially for organisms other than salmonids (Railsback 2001).

This research also applies and extends the idea of having spatial units, in this case habitat grid cells, being equally as important dynamic components as the animal themselves. Box (2002) suggested this modeling scheme, but to this author's knowledge, it has not been implemented in spatially explicit population models. Instead, in conventional models the landscape is viewed as a supporting aspect of the model; that is, it is viewed only as a surface upon which individuals move around.

In addition to the theoretical contributions mentioned, this dissertation contributes technical tools that can be used by ecologists interested to explore population genetics from an individual-based theoretical framework. First, this dissertation develops an algorithm called the compressed kinship matrix algorithm that efficiently calculates the kinship coefficients on pedigrees that are large in number of individuals, or generations, or both. Using standard Java™ classes, the algorithm provides individual-based modelers a technique that is congruent with the individual-based modeling perspective. A full description of the algorithm appeared in the *Journal of Heredity* (Backus and Gilpin 2002). Second, this dissertation develops two Java ™ classes, Animal and Genetics, so that other individual-based modelers can easily incorporate genetics into their models. The Genetics class is a library class, like Java ™'s Math class that contains a library of methods. These methods calculate various population genetic measures and individual kinship and inbreeding coefficients. The Animal class has all the variables necessary to implement the compressed kinship matrix algorithm in conjunction with the Genetics class. A modeler only needs to make his or her specific animal class a subclass of the Animal class to be able to implement the algorithm and calculate various genetic measures.

This research develops a set of simulation models using the classes mentioned above to investigate how nongenetic forces influence a population's genetic processes. In particular, the models explore how variation in the geographic landscape, referred to in this thesis as a 'geographically explicit landscape', influences gene flow within the population. Besides the physical geographic features like rivers and mountain that can prevent movement or dispersal, more subtle variations in the landscape can influence the movement of individuals. Spatial variation in mortality risk associated with the amount of human development, for example, is a feature included in a geographically explicit landscape. Conventional population genetics models do not include subtle variations in the landscape and represent a yet unexplored area of research. Decisions regarding the necessity and intensity of population augmentation on genetic grounds rely on these conventional models. The inclusion of a geographically explicit landscape in population genetics models will aid managers in making better decisions.

1.3 Summary

The merging of empirical research, modeling, and management has the potential to dramatically enhance the future of many threatened and endangered species (Boyce 2001). This dissertation illustrates how using a mechanistic, bottom-up approach to construct a spatially explicit IBM provides the proper theoretical and operational frameworks for improved management of these species. This model is developed for the grizzly bears inhabiting the CYE. Ultimately, the significance of this research is its potential to be refined, extended, and applied to a broad array of wildlife species. Ideally, better understanding of the consequences of human actions and natural landscape changes on the survival of wildlife populations would lead to more effective and efficient conservation programs. In the following chapters, the merits of using a spatially explicit individual - based model as the theoretical modeling framework for predicting the long-term consequences of both human-induced and natural habitat changes to a population's viability are demonstrated.

In Chapter 2 an extensive literature review is presented. Topics covered include the conservation concepts and theory relevant to grizzly bear conservation, previous modeling used in grizzly bear-related research (demographic, genetic, and habitat suitability models), and spatially explicit and individual-based modeling. Object-oriented programming is discussed as well because it is conducive to individual-based modeling. The shortcomings of previous grizzly bear-related modeling efforts are highlighted, as are the benefits of individual-based modeling. The chapter concludes with a review of bear behavior gleaned from the literature.

Chapter 3 reviews the detrimental effects of inbreeding and the methods available for calculating inbreeding/kinship coefficients on pedigrees. The chapter also discusses reasons why those in charge of wildlife conservation and managements often ignore or underestimate the consequences of inbreeding depression to a population's viability. This is followed by a discussion of an algorithm developed that can be implemented in an IBM to calculate an individual animal's kinship coefficient. This chapter concludes by discussing how individual-based modeling may be used as an analytical tool to help understand the effect inbreeding depression has on a population's persistence, a poorly understood topic.

Genetic themes are explored further in Chapter 4. In the past, quantification of the genetic status and health of a species usually has taken one of two primary scientific approaches: empirical or (mathematical) theory. The key variable is the rate of loss of genetic variability, or equivalently, the rate of increase of average inbreeding in the population. There are problems, however, associated with the application of these two commonly used approaches. This chapter discusses how individual-based modeling provides a method for quantifying the genetic status of a population that avoids the problems and limitations of these more conventional methods. A series of IBMs were developed, using the algorithm in Chapter 3, to illustrate this point and to show such models provide a better understanding of the genetic processes and structure of small populations. In short, individual-based modeling offers insights and a more in-depth understanding of the nongenetic forces influencing a population's genetic processes not provided by either empirical or theoretical methodologies.

In Chapter 5, the development of a comprehensive, spatially explicit IBM for the CYE grizzly bear population is discussed. The model was designed to simulate a population of 40 grizzlies inhabiting the CYE. GIS was used extensively to develop several key spatial layers that can be divided into four thematic categories: vegetative and nonvegetative potential bear foods, human landscape features affecting bears or their movements, miscellaneous bear-related data layers, such as possible denning habitat, and plant phenology-related data layers. The potential grizzly bear vegetation foods layer was derived from remote sensing data combined with plant association descriptions. A full description of spatial data used, created or derived, can be found Section 5.3.

The spatially explicit IBM developed in Chapter 5 integrates the most important bear behavior, biological landscape elements, and human landscape elements relevant to grizzly bear movement and survival. In the model, these elements vary through time and/or space. The model uses the novel, but not original, idea of programming the habitat as individual habitat cell objects and not a single two-dimensional grid. It incorporates the kinship algorithm discussed in Chapter 3 and uses the same Genetics class developed for Chapter 4 to calculate important genetic measures for the population. Phenological events are incorporated into the model based on 25 different climate scenarios generated from historic climate data. Plant phenology is included by using the concept of growing degree days, in conjunction with a model that predicts temperature variation over rugged terrain. Mortality is directly linked to the landscape by means of multiplicative hazards model derived by Johnson and others (2005). A full description of the model is presented in Section 5.4

This dissertation concludes with Chapter 6. Areview of the significant contributions of the research and potential uses are given.

CHAPTER 2

REVIEW OF LITERATURE

This chapter reviews the principal literature on the theoretical and technical aspects of the research. This literature provides the foundation for the project's purpose, goals, and methods. The chapter consists of five sections; Theory, Previous modeling used in bear research, Modeling, Object-oriented design and programming, and Bear behavior.

2.1 Theory

2.1.1 Metapopulations

2.1.1.1 History

Ecologists have become increasingly aware of the role spatial distribution plays in population ecology (Begon, Mortimer, and Thompson 1996). They recognize the world is not spatially uniform, and at some scale, species are distributed 'patchily' over the habitat. This 'patchiness' can have unfavorable or favorable effects on local populations. Despite this recognition, field experiments continue to be carried out at temporal and spatial scales that put forth the appearance of spatial homogeneity, and modeling efforts continue to assume homogeneity. This is largely because researchers lack the proper tools or time to handle this spatial complexity (Begon, Mortimer, and Thompson 1996).

Elton (1948), Andrewartha and Birch (1954), Huffaker (1958), and MacArthur and Wilson (1967) were some of the first ecologists to demonstrate the treatment of populations as single and isolated was inadequate to capture the populations' true dynamics. Elton (1948), as well as Andewartha and Birch (1954), used field observations to conclude some species were able to persist only because of the their dispersal abilities, and other species were able to persist together only because of the spatial heterogeneity of their habitat. Huffaker (1958), constructing an experiment using mites and oranges, demonstrated that the spatial structure of populations could have an important effect on their persistence. MacArthur and Wilson (1967) used formulas to describe the relationship between the distance between islands and the diversity and abundance of species inhabiting the islands.

Later in the 1970s, Richard Levins developed a simple mathematical model to describe the dynamics of a single-species population in a temporally changing environment. He coined the term 'metapopulation' to define a population that was distributed as a series of subpopulations over a number of habitat patches, that is, to describe a population of populations (Hanski and Gilpin 1991). In any metapopulation model, populations inhabiting the individual patches are referred to as 'local populations.' Each local population has a finite lifetime, and within any local population, individuals move around and interact with others on a routine basis. These local populations then interact with each other through the processes of immigration and emigration to form the metapopulation (Hanski and Gilpin 1991).

A metapopulation also has a finite lifetime. The rates at which local populations go extinct, the rates that individuals can disperse from patch to patch, and the rates patches can become recolonized determine the dynamics and time to extinction of the metapopulation. It is worth noting that there is a difference between a metapopulation and a set of patchily distributed local populations. For species to conform to a metapopulation structure, there must be a tendency for local populations to become extinct, and the species should possess a relatively poor ability to disperse and colonize new habitats. If a population is patchily distributed, then individuals move routinely among the various patches perhaps on a daily basis. Metapopulation movement is infrequent, dispersal-type movement.

2.1.1.2 Relationship to other theory

The concept of a metapopulation shares some commonality with the theory of island biogeography (MacArthur and Wilson 1967), the population dynamics of species living in a patchy environment (Levin and Paine 1974; Fahrig 1988; Wu and Levins 1997), and landscape ecology (Minta and Kareiva 1994). The theory of island biogeography postulates a 'mainland' and a series of smaller islands. The mainland serves as an unlimited source of dispersers from many species to the smaller islands. The diversity and abundance of species on each of the smaller islands are directly related to their distance from the mainland. The key differences between the two concepts are as follows:

1. In the mainland scenario, the mainland population is not subject to extinction. The mainland is also treated as the only source of dispersers (colonists). In a metapopulation framework, all the islands have a nonzero probability of extinction and serve as sources for dispersers
2. In the mainland island scenario, it is assumed that all islands differ from the mainland only in size, not in habitat quality. This condition is not necessarily upheld in all metapopulation models.

Like metapopulation models, patchy distribution models investigate the dynamics of a population distributed unevenly across a heterogeneous environment. The difference, however, between the two modeling approaches is the interpatch movement allowed. In a metapopulation model, interpatch movement is characterized by dispersal. In a patchy distribution model, individuals routinely move between patches within their lifetime, not just during the dispersal phase.

Landscape ecology tries to answer many of the same questions as metapopulation studies: what influences the survival of species, communities, and ecosystems in fragmented habitats; what factors distinguish the matrix; what is the origin, size, and shape of habitat patches? Like the concept of metapopulations landscape ecology forms a bridge between the separate domains of population ecology (local populations) and biogeography (regional occurrence); however, their perspectives are different. The perspective of landscape ecology is holistic or top down, whereas metapopulations are developed from the perspective of the behaviors of local populations, or a bottom-up approach (Hanski and Gilpin 1991).

2.1.1.3 Progression of theory

Levins' model was very simple; since its introduction, many researchers have added complexity to the model or developed similar models with more realistic assumptions. Ray and others (1991), for example, looked at the effect conspecific attraction has on the recolonization scale. Verboom, Lankester, and Metz (1991) investigated the fragmented population of the

European badger using collected mortality, reproduction, and dispersal parameters and developed a stochastic, demographic Levins' model. Sjogren (1991) modified Levin's model to account for the effects of distance on colonization and population persistence of the pool frog. Gilpin (1991) explored the consequences of metapopulation structure on a population's genetic effective size.

Other researchers have relaxed the assumption that all local populations are equivalent in respect to habitat quality and demographic rates to create a model similar to Levins' known as a source/sink model (Pulliam 1988; Howe, Davis, and Mosca 1991; Pulliam and Danielson 1991; Doak 1995; Watkinson and Sutherland 1995). In a source/sink formulation, some of the local populations' birth rates are greater than their emigration rate, and other populations' birth rates are less than their emigration rates. In the first case, the populations serve as a 'source' in the metapopulation by producing an excess of the individuals that can feed the other local populations. In the second case, the populations serve as a 'sink' because these populations would eventually become extinct due to their negative growth, if not for the immigration from other source patches.

Today, the term metapopulation has become generalized to mean local populations of species that are geographically noncontiguous regardless of whether or not any of the populations go extinct periodically (Dobson et al. 1999). As summarized by Harrison (1994:117),

> It seems necessary to adopt a broader and vaguer view of metapopulations as sets of spatially distributed populations, among which dispersal and turnover are possible but do not necessarily occur….[we should ask], in each specific case, what is the relative importance of among-population process, versus within-population process, in the viability and conservation of this species?

2.1.1.4 Metapopulations and conservation

The concept of a metapopulation allows for a broadening of perspective from a single population to multipopulations of the same specie and from local to regional scales, making it particularly useful in the study of species persistence. More specifically, the paradigm of a metapopulation is of interest to conservation professionals because the expansion of human activities and development has fragmented the once continuous habitat of many species, for example, see Howe, Davis, and Mosca (1991); Wootton and Bell (1992); and Watkinson and Sutherland (1995). This habitat fragmentation has likewise caused the fragmentation of the species into many subpopulations that either may be patchily distributed over an area or totally isolated from each other. Even though they do not conform to Levins' strict original definition, the term metapopulation has become associated with the study of these subpopulations and the consequences of the connectivity between them (Watkinson and Sutherland 1995).

In addition, conservation professionals have realized that most existing nature refuges are too small to sustain a population of sufficient size to withstand the effects of environmental and demographic stochasticity. They are also too small to avoid potentially detrimental genetic change (Soule 1980; Shaffer and Sampson 1985; Simberloff 1988; Noss 1992). This is especially true for larger-bodied species. Consequently for some species, the only way they can persist in these small refuges is if connectivity to other populations and refuges exists, that is, if the combined, connected populations are allowed to act as a metapopulation (May and Southwood 1990; Noss 1992; Caroll, C. et al. 1999). For example, Stacey and Taper (1992), using data collected from a 10-year field study and a simulation model, were able to show that small, isolated populations of the Acorn Woodpecker (*Melanerpes formicivorus*) were prone to extinction, but with the inclusion of immigration, the birds were able to persist for well over 1000 years.

Even though from a theoretical perspective the concept of a metapopulation is well developed (see Gilpin and Hanski [1991] for a review), the theory is difficult to apply in practice. Obstacles to its application include determining the appropriate scale of the relevant habitat patchiness and quantifying the processes that govern local extinction and colonization (Minta and Kareiva 1994). Minta and Kareiva (1994) believe that in order to use the theory of metapopulations in conservation, studies that systematically measure patterns of movement among patches, both within and between generations, need to be emphasized.

2.1.2 Corridors

Janzen refers to national parks and wilderness areas as "islands of natural habitat in a sea of human development" (Janzen 1989: 109). This metaphor brings to mind a vivid picture of animals having to navigate through dangerous waters of human development features on their way to a safe island of secure habitat. These travel routes are known as 'corridors' and the islands of secure habitat as 'core areas.' Researchers have begun to refer to corridors as linkage zones instead, because corridors imply short-term travel areas only. For many species, either their movement rate or the distance they must travel makes it necessary for them to have to actually live for a time period in these areas before they reach another core area. Thus, the corridors need to be suitable habitat not just pathways (see Servheen and Sandstrom [1993] and Apps [1997]). McLellan and Hovey (2001) have empirically shown this to be true in the case of natal dispersal of grizzly bears.

Habitat fragmentation caused by human developments is one of the most challenging issues facing conservationists today (Soule 1987; Noss 1992; Dobson et al. 1999). It has the potential to reduce biological biodiversity, and, when unchecked, can lead to population isolation and its corresponding problems. Corridors have the potential to mitigate some of the effects of fragmentation, if they allow for the divided populations to act in a metapopulation structure. On a regional scale, these corridors or linkage zones have also been recognized as important to species persistence in the light of global warming (Hunter et al. 1988; Noss 1992). In addition to providing linkages for dispersal and 'tracking' of suitable habitat for a species, corridors are also important for linking seasonal and migratory areas (Noss 1992). Finally and most importantly, corridors have the potential to reduce the elevated extinction risk, probability of inbreeding depression,and loss of hetereozygosity due to genetic drift often experienced by small, isolated populations.

Corridors can be viewed as conduits of movement between the islands of secure habitat or core areas, i.e., as areas of 'connectivity.' Connectivity can refer either to allowing regular daily or seasonal movements (patchy) or allowing longer dispersal. The value of connectivity and consequentially animal dispersal and immigration to species persistence cannot be overemphasized. Even before the context of metapopulation, the importance of animal dispersal and immigration as a determinant in species extinction was recognized (see MacArthur and Wilson [1967] in regards to island biogeography), Simberloff and Abele [1982] in regards to reserve design, and Brown and Kodric-Brown [1977] for the 'rescue effect' of insular biogeography).

In terms of species conservation, efforts should focus on both the preservation and restoration of connectivity between populations. In order to halt the extinction of a species, researchers must strive to understand the role of connectivity between the various local populations and the factors contributing to the maintenance of such connectivity. Unfortunately, for some species, studies on dispersal and immigration can be costly, time consuming, or even impossible to conduct (Stacey and Taper 1992). Not to mention, given the current rates of fragmentation, critical habitat could be irreplaceably lost by the time more traditional studies conducted at the appropriate temporal and spatial scales were concluded.

2.1.3 Genetics

Founder effect, genetic drift, and inbreeding are the three mechanisms causing the reduced genetic variation experienced by some small populations (Frankel and Soule 1981; Schonewald-Cox et al. 1983; Shaffer 1986). The founder effect refers to when limited genetic raw material is available because a population was 'founded' by only a few individuals. Genetic drift, more prominent in small populations due to the decreased presence of rare alleles, refers to the loss of genetic variation due to random sampling of gametes in each successive generation. Inbreeding refers to the loss of heterozygosity due to the continual mating of closely related individuals. In the long run, loss of genetic variation poses a threat to a species' evolutionary potential, because species lose their ability to genetically adapt to a changing environment. In the shorter term, studies of domesticated animals have shown inbreeding can have harmful effects on development, reproduction, survival, and growth rate (Falconer 1981). Similar results have been shown for animals residing in zoos, and it is logical to assume the same effects would be manifested in wild populations of species (Ralls and Ballou 1983, 1986). More recently, decreased fitness has been documented in captive brown bears held in Nordic zoos (Laikre et al. 1996).

Genetic variation corresponds to heterozygosity. Heterozygosity is defined as $H = 1 - F$, where F is the inbreeding coefficient or pedigree. F is an exact measure of an individual's heterozygosity. What is of concern for conservation is the rate of loss of heterozygosity or rate of increase in inbreeding. Both F and H can be difficult to calculate directly and thus, a closely related concept, effective population size or N_e, is often used. If N is the census size, N_e is defined as the size of the 'genetically ideal' population that would experience the same loss of heterozygosity as the real population of size N (Wright 1931, 1969). An idealized population is one that has constant population size, N, over generations, genes that are not subject to mutation or select, random mating among members, no migration of members in or out, and discrete, nonoverlapping generations. Recent estimates of N_e consider populations characterized by, for example, overlapping generations, fluctuating population size, unequal sex ratios, geographic structure, or social structure (see Harris and Allendorf's [1989] work for a review of accuracy of several commonly used formulas). Heterozygosity loss is projected according the recursion formula:

$$H_{t+1} = H_t(1 - 1/(2^* N_e)). \qquad (1.1)$$

Another measure of a population's genetic health is the average inbreeding coefficient for a member of the population. The inbreeding coefficient of an individual is defined as the probability that the two gene copies present at a single locus are identical by descent, relative to a defined founding or base population. Two genes are said to be identical by descent if, and only if, they are descended from the same individual gene copy. Because continued mating between closely related individuals decreases hetereozygosity, the inbreeding coefficient is a direct measure of the level of hetereozygosity present. Its calculation depends on having available a population's pedigree. For wild populations, especially for long-lived species, the necessary data on the genetic relationships of individuals is usually unavailable and difficult or impossible to collect. Also, even though efficient methods have been developed for computing the coefficients (see Ballou [1983] and Boyce [1983]), computation is resource intensive and applicable only to pedigrees of limited size.

Gene flow between subpopulations is important in order to curb the genetic drift each subpopulation would undergo in isolation. The exact number of migrating individuals between populations necessary to balance the forces of genetic drift within and homogenization between subpopulations is a complex problem to answer. One theoretical result often applied in the management of insular or fragmented populations is the one-migrant-per-generation rule (Mills and Allendorf (1996). Mills and Allendorf (1996) thoroughly discuss the validity and applicability of the mathematically derived rule to natural populations and give some conditions in which more than one migrant per generation would be desirable. Newman and Tallmon (2001) empirically investigated the appropriateness of the one-migrant-per-generation rule to newly fragmented populations experiencing genetic nonequilibrium conditions and found 2.5 migrants were actually required for the mustard *Brassica campestris*.

2.2 Previous modeling used in bear research

This section reviews past modeling efforts used in grizzly bear management and addresses grizzly bear conservation issues. These efforts have primarily focused on four particular areas: population demography, genetic, or viability, and habitat. Population demography models are used to determine the growth and survival trends of a population. Population genetic models are concerned with determining effective population size or maintaining heterozygosity in a population. Models used for ascertaining population viability are concerned with extinction probabilities. Finally, habitat models are used to aid managers or conservation biologists in determining the effects proposed land-use changes will have on a population or in determining critical habitat areas necessary for the species persistence.

2.2.1 Demographic models

2.2.1.1 Population growth

Demographic models are used to estimate the growth or trend of a population using historic reproductive and survival rates. The vigor of a population is determined by the finite rate of increase λ, where $\lambda = e^r$ and e^r is defined as the exponential rate of population change given a stable age distribution and age-specific survival and fecundity rates. If $\lambda \geq 1$, the population is increasing and if $\lambda < 1$, then the population is assumed to be decreasing.

Many researchers have derived estimates of λ for various grizzly bear populations including the Yellowstone (Knight and Eberhardt 1985), Northern Continental Divide (McLellan 1989), and Selkirk (Wielgus et al. 1994) Ecosystems. In addition, estimates of λ, based on telemetry data, are calculated and presented every year in the annual management reports for the Selkirk and Cabinet-Yaak Ecosystems (Wakkinen and Johnson 2000; Kasworm et al. 2000). More recently, rather than calculating a single point estimate for λ, researchers have begun to additionally report estimates of uncertainty and standard error associated with derived values of λ, and to identify those demographic and environmental factors that most influence λ (see Eberhardt et al. [1994], Hovey and McLellan [1996], and Pease and Mattson [1999]). The most common models used are based are either a modified Lotka's equation or Leslie matrices.

2.2.1.2 Viability analysis

Viability analysis, usually referred to as population viability analysis or PVA, refers to an analysis performed to assess a population's probability of persistence or extinction to a future time horizon. It is a tool used by many in an attempt to improve management of endangered and rare species. Any model used in a PVA incorporates a population demographics model, as well as up to four types of stochastic perturbations that can affect population viability: demographic stochasticity, environmental stochasticity, natural catastrophes, and genetic stochasticity. As a practical analysis, it can be used to predict population responses to such things as habitat destruction, harvest, or reintroduction (Groom and Pascual 1998).

The analysis works by projecting the population into the future and, thus, determining its persistence. Two modeling approaches, mostly implemented as a simulation, are usually utilized; matrix (Caswell 1989) and stochastic (see Groom and Pascual [1998] for a list of models from 1987-1996). There are three general outputs of PVA: probability of extinction in a fixed number of years, probability of a population dropping below different thresholds (number considered extinct >0) in a fixed number of years, or the probability and distribution of times until a population reaches a fixed threshold. There are several generalized PVA software packages available. Mills et al. (1996) analyzed four of these packages: GAPPS, INMAT, RAMAS/AGE, and VORTEX, and found each package predicted different long-term fates for a hypothetical grizzly bear population, and the differences were mainly contributable to the way each model handles density-dependent growth. Because of these resultant differences and the fallacy of assuming what has happened in the past will continue to happen in the future, Boyce (2001) argues that the PVA models should not be used to determine definitive answers, but instead as tools of adaptive management.

PVA has been used on the giant panda, *Ailuropoda melanoleuca* (Wei et al. 1997). Wei et al. used a computer model called VORTEX that used the parameters of reproduction, age-specific mortality, and carrying capacity. Mark Shaffer performed the first PVA for the grizzly bear as dissertation research and later published his findings (Shaffer 1983). Shaffer's model was an age- and sex-structured simulation model that calculated the minimum population size that was needed for the population to persist for 100 years. Parameters included were survival and reproduction (varied to mimic chance events), mortality, age and sex structure, litter size, and percent reproducing. Mortality rates, percent reproducing, and litter size were varied to mimic environmental stochasticity. Most recently, Boyce et al. (2001) published a critical review of PVA for the grizzly bear. These researchers used spatially structured population models, RAMAS/GIS and ALEX software, to investigate the 100-year persistence of grizzlies mainly inhabiting the Greater Yellow Ecosystem. Though persistence probability was high, the inclusion of modest levels of dispersal between the various subpopulations increased overall population size and number of subpopulations containing bears. These researchers conclude linking habitat relationships and ecological factors to demographic models, in particular vital rates, would greatly aid understanding the effects of natural resource management decisions on grizzly bear persistence.

2.2.2 Genetic

Genetic drift is a serious problem for small populations. Since all but the Yellowstone and Northern Continental Divide Ecosystems have less than 90 grizzly bears, it has been recognized that the remaining populations are susceptible to genetic drift (Allendorf and Servheen 1986). It has been suggested that adequate levels of gene flow could be maintained with as little as one successfully breeding individual per generation, or for grizzlies in the Northern Rocky Mountains, one successfully breeding individual every 10 years (Allendorf and Servheen 1986). As discussed in Section 2.1.3, more current research shows the one-migrant-per-generation rule is not necessarily applicable to natural populations, and the calculation of the correct number must consider a variety of factors, both genetic and nongenetic in character (Mills and Allendorf 1996).

Allendorf and Harris (1989) estimated N_e for the number for grizzly bears in the Northern Rockies using several commonly published formulae. They found a critical component for the accurate estimation of N_e was the distribution of reproductive contribution among males; thus they tested three different mating systems in their simulation model. Their simulation was a 30 age-class, stable stationary (populations with similar numbers and age structures from year to year) model. After comparing the effective population size and variance by several formulas and comparing them to their simulation results, one conclusion on was as follows: “To estimate N_e for a wild population using a published formula, reasonably accurate demographic data are needed" (Allendorf and Harris 1989: 187). They suggest an alternative to trying to estimate these parameters would be to simulate the population dynamics and calculate the parameters directly from the results for input into the formulas.

Two shortcomings of the work by Harris and Allendorf (1989) are their commitment to the use of N_e as a measure of loss of heterozygosity and exclusion of spatial considerations. They used their simulation to estimate the necessary parameters for various formulas of N_e and then used N_e to estimate the loss of heterozygosity based on formula (1) instead of recognizing the simulation alone could give them reliable estimates of the loss. The lack of spatial consideration means their methods can only be used for a single, isolated population, not ones existing in a metapopulation context or ones that fall short of a panmictic assumption. In an unpublished report to The Wilderness Society, Gilpin, Billick and Debinski (1991) developed a spatial-structured model to calculate the genetic change in the Yellowstone grizzly bear population. They considered dispersal in a density-dependent sense and whenever a Bear Management Unit contained no males, a male was assumed to enter the population. The genetic relationships of the bears were calculated exactly using a recursive kinship function. Though their work added a spatial component, there were still several weaknesses, such as the assumption of stable age-structure, the use of general dispersal information, no inclusion of environmental stochasticity, and the lack of differentiated patterns of animal mortality.

Generally speaking, application of theoretical genetics to real-world problems will always be difficult. Reliance on mathematics necessitates simplifying assumptions for tractability and solvability purposes. These assumptions adversely affect real-world theoretical application for three reasons. First, outside of a controlled laboratory setting, the assumptions that constitute the ideal population are rarely met, bringing into question the validity of or the confidence in applying such methods. Second, earlier research into a population's viability pointed out the interaction among genetic, demographic, and environmental processes that exists (Gilpin and Soule 1986; Mills and Smouse 1994; Lacy 1997). Other researchers have shown the behavioral ecology of a species can have a profound influence on their gene dynamics, especially for highly colonial species like the black-tailed prairie dog (Sugg et al. 1996). Thus, simplification can overgeneralize a complex problem. Finally, the simplification can lead to parameters that are not usually collected or are difficult to collect from field research. The accuracy in the estimation of the needed parameters again can question the validity and confidence in the application of such methods. Unfortunately, the use of exact kinship relationships or recursive formulas can be computer resource intensive and so the technique is constrained to pedigree of limited size (Boyce 1983).

2.2.3 Habitat models

Habitat seems to be the number one limiting factor to grizzly bear recovery. As such, much time and money have been spent in developing models that study grizzly bear-habitat relationships. It is logical to think that in order to determine the effects of habitat alteration on wildlife species, one must understand and model the wildlife-habitat relationship. Thus, the model of choice among agencies in charge of wildlife and other natural resource management is a Habitat Suitability Index (HSI) model. The underlying assumption in a HSI is that individual habitat variables can be combined, primarily linearly, to produce a meaningful index that represents a habitat patch's suitability to a particular species (Laymon and Barrett 1984). The HSI used by those in charge of critical habitat for grizzly bears is referred to as the Cumulative Effects Analysis or Cumulative Effects Model.

Christensen and Madel in 1982 first developed Cumulative Effects Analysis to assess the cumulative effects of proposed projects on critical grizzly bear habitat in the Kootenai National Forest (Christensen and Madel 1982). It was developed as a tool to help make land management decisions. This original work used a paper, topographic base map of seasonal food and denning habitat components, and mylar overlays of existing or proposed alterations to the landscape. These maps presented a graphical display and a way to measure how known activities will affect grizzly habitat in terms of space, time, food, and denning habitat. Effects on habitat corresponding to activities could then be identified.

This process was later adopted by agencies in all four of the ecosystems containing grizzly bear populations, and a computerized version was developed named the Cumulative Effects Model (CEM) (Weaver et al. 1986). The CEM was designed to predict habitat effectiveness and mortality risk posed by various human activities using three subroutines: habitat, disturbance, and mortality. The habitat and disturbance subroutines produce a habitat effectiveness value, and the mortality subroutine determines mortality risk by integrating various variables, such as food, habitat diversity, seasonal equity, and denning suitability from the habitat subroutine (Weaver et al. 1985). Baseline habitat effectiveness and mortality risk values for an area then could be determined and the effects of various land-use decisions evaluated as the corresponding change in the these values.

Unfortunately, the popularity of HSI models, like the CEM, is due more to its general audience appeal and understanding than to its underlying scientific foundation or accuracy. HSI are practical, planning models designed to assess impacts of change. They are based on narrow definitions of carrying capacity and habitat; thus, they are not research models (Schamberger and O'Neil 1986). Laymon and Barrett (1986) report that the criticisms for HSI models are based on the legitimacy of the following assumptions: (1) there is a linear relationship among habitat parameters; (2) simple indices are as or more relevant than those based on multivariate analysis; (3) habitat use is invariable with regard to life stage or season; (4) species-observed density is a good indicator of habitat quality; and (5) there are minimal effects of interspecific interactions. Not all or any of these may be invalid for a particular species. Besides the legitimacy of the assumptions, another criticism is that species-habitat models have rarely been validated and when they have been, they have fared poorly (Minta and Kareiva 1994). For example, Laymon and Barrett (1986) present three specific cases involving the spotted owl, marten, and douglas squirrel, where HSIs failed to be good predictors. A final criticism, at least for CEMs used for grizzly bears, is that it is administered on isolated recovery zones and lacks an integrated regional approach necessary for grizzly bear conservation.

In addition to the criticisms mentioned by the researchers above, there are other epistemological problems with a HSI modeling approach that should be mentioned. First is the subjective fashion in which the habitat variables included in the final index are assigned and modified. Most of the assignment and modification is based on expert opinion, and though expert opinion may be defended on a theoretical basis, it cannot be tested by the rigors of mathematical methods. Another problem is it is an equilibrium, static model. The habitat variables are evaluated at a moment in time and assumed to be constant. This is not appropriate for a species that uses a variety of different habitat components throughout the year. The CEM accounts for this by increasing the habitat value if it contains foods that bears use in more than one season; however, it does not account for stochastic changes in food quality that could decrease the value in a particular year. A final criticism is the indices do not and cannot take into account the role individual bear behavior and bear interactions with other bears have in determining habitat use. Both individual behavior and interactions with other bears can influence habitat selection choice; for example McLellan and Shackleton (1988) reported females with cubs and weaned yearlings feeding in the vicinity of roads more often than adult males. Because adult males sometimes kill cubs and yearlings, they suggested the difference in use might be a consequence of females with cubs and yearlings trying to avoid contact with adult males.

A similar model to CEM is the Linkage Zone Prediction (LZP) model (Servheen and Sandstrom 1993; Apps 1997). Like the CEM, this model uses a raster representation of space, but where it differs from the CEM is in its intended use. It is used to evaluate habitat in terms of its potential as a linkage zone or corridor between two areas supporting bears. The model uses four factors: human features, linear disturbance elements, visibility cover, and riparian habitat. Its use as a predictor of potential linkage zones instead of habitat suitability makes it different from the CEM, but many of the same criticisms, like the use of subjectively derived parameters and linear combination of parameters into an index, are the same as for the CEM. The Linkage Zone Prediction model, however, is significant because it recognizes the need to look at grizzly bear habitat from a broad scale or regional-level approach and from a connectivity standpoint.

Carroll et al. (1999) question the appropriateness of the CEM and LZP model for regional scale analysis. Their main criticisms are as follows:

1. Lack of consideration given to the predictive power or contribution of individual factors to the final composite score. An exception is Apps (1997), who performed a sensitivity analysis on his LZP model and found human features and linear disturbance elements were more important than other variables.
2. Lack of integration of multiple habitat attributes in an explicit manner making it impossible to show the 'cumulative effects' of all the factors.

3. Lack of consideration given to the biological appropriateness of scale used to construct the model.
4. Lack of validation of modeling complex interaction based solely on expert opinion.
5. Failure to account for spatial and temporal lags in responses to disturbance. These lags are necessary to determine the long-term consequences of disturbance. For example, road development may trigger long-term development pressures that are not adequately addressed in the CEM.
6. Failure to account for population-related dispersal 'pressure' from the source habitat. This failure may prevent the identification of the most biologically important landscape linkages. For example, pressure from other individuals in the source habitat may force dispersal through degraded habitat with a high risk of human-caused mortality. Such habitat would not be identified in the CEM and LZP model because these areas would have been a priori assigned a low index value.

Recognizing the shortcomings in the current HSI models, researchers have recently begun to utilize more rigorous techniques to improve the model parameters or to create new models. Using logistic regression and resource selection functions, Mace et al. (1996) investigated the relationship among grizzly bears, roads, and habitat. They found bears' habitat selection tends to be most strongly influenced by elevation and cover-type and phenology. Also, they found within a bear's home range, road density did not strongly influence habitat use; but within seasonal ranges bears tended to avoid areas with a high density of roads or high vehicular traffic. Their findings show holding the influence of road density temporally constant in the CEM is not necessarily applicable. This technique was later extended to include the influence of all human activities on seasonal habitat use in the Northern Continental Divide Ecosystem. This methodology is an improvement over the CEM's qualitative static generalizations on species--habitat relationships derived from expert opinion and review of the literature. The CEM cannot show the relationship among variables, that is, cannot adequately show 'cumulative' effects because it is a series of univariate models combined into a single model.

More recently, Merrill et al. (1999) used empirical methods similar to Mace (1996) to produce a regional-scale model that investigated the best habitat for grizzlies in Idaho. The methodology involved first calculating indices for habitat productivity and the presence of humans derived from potential human activity and road and trail access. Next, this information was used in combination with grizzly bear observations to create an empirically based model of habitat suitability. Though the indices for habitat productivity and the final habitat suitability were calculated similar to those used in the CEMs, there are some notable differences between the two. First, the CEMs use simple road density. Merrill et al. (1999) derived an index for the presence of humans that used recreation visitor days, human population within 80 km of National Forests and Parks, and the inverse distance from town centers to National Forests and Parks. This parameter can be thought of as a surrogate for road use, a more realistic and relevant parameter than simple road density. Second, empirical methods were used to develop the relation between habitat suitability and bear observations yielding a probability of observation. The use of a rigorous mathematical approach over expert opinion and a regional perspective were improvements over the CEM.

Other researchers have also recognized the need for regional approaches to grizzly bear conservation; both Boone and Hunter (1996) and Walker and Craighead (1997) used simulation models to predict dispersal routes between populations of bears. Both simulations were implemented over a coarse grid 1 km^2 and derived a permeability value for each grid cell. Boone and Hunter subjectively assigned permeability values based on land ownership type, wilderness areas being most permeable and private lands being the least. The movement path of the bear in the model was simulated as a correlated random walk. Walker and Craighead (1997) assigned permeability values based on habitat quality, forest edge, and road density parameter values derived and combined in a fashion similar to those used in the CEM. The movement path of the bear was modeled as a least-cost path in Environmental Systems Research Institute Inc.'s ARC/INFO®. Both these models are an improvement over the LZP models discussed above because they include a risk of mortality, though this inclusion is indirect and implicit. The LZP model is a general spatial overlay operation in a GIS and can be thought of as yielding 'all' the area that has the potential to function as a habitat corridor. By including (indirectly) mortality risk, the dispersal route simulations of Boone and Hunter and Walker and Craighead determine areas with the 'highest probability' of successful dispersal, a more accurate assessment of connectivity potential.

It is worth noting the probability of success in these models is based on measures determined by the model developers. In the case of Boone and Hunter, a prior assignment of lowest permeability values to all private lands virtually precludes successful dispersal between wilderness areas in northern Montana and Yellowstone National Park. Undeveloped private land, however, may in fact provide high-quality bear habitat with low probability of mortality. Also, Boone and Hunter refer incorrectly to their correlated random walk diffusion model as an individual-based model. An individual-based approach is one in which the properties of an ecological system are modeled as the result of the properties, behaviors, and variations of the individuals making up the system and their relationship with each other. These individual properties, behaviors, and variation are considered in some level of detail (see section below for full discussion). The movement of only a single individual does not qualify a model as using an individual-based approach. Finally, no tests of validity or accuracy of either of these models have been conducted to date.

All the models discussed have contributed some advancement to grizzly bear habitat modeling:

- Christensen and Madel (1982) identified the need to quantify habitat effectiveness and mortality risk in order to facilitate the objective evaluation of land-use decisions in grizzly habitat.
- Apps (1997) and Servheen and Sandstrom (1993) recognized the need to investigate connectivity between ecosystems.
- Boone and Hunter (1996) and Walker and Craighead (1997) realized the importance of including mortality risk in a regional approach to connectivity.
- Mace et al. (1996) abandoned subjective, linear measures of habitat effectiveness for a more mathematical approach that more accurately reflected the 'cumulative effects' of various factors.
- Merrill et al. (1999), like Mace et al. (1996), not only used a more rigorous approach than the subjective indices of the CEM but also identified the need to

add a spatial component to mortality when using a landscape approach to investigate connectivity.

All the models, however, were behaviorally implicit and static. They fail to explicitly include mortality risk and ignore temporal variation and fail to incorporate bear-bear interaction and individual bear behavior. All of these factors have the potential to influence bear movement and, thus, connectivity between populations. The models also assume the best habitat present is likewise the best corridors available; thus, the areas identified as linkage zones are usually the 'most pristine' areas available. This can provide an unrealistically high estimate of the areal extent and the functionality of the connectivity areas present. A species can be severely habitat limited and, in fact, prone to extinction even if suitable but unoccupied habitat is still present. This is because the interactions with other individuals in the population can force them into areas other than the most favorable. These areas can be poorer or riskier habitat that actually decreases their survival probability.

2.3 Modeling

2.3.1 Spatially explicit population models

Spatially explicit population models (SEPMs) that keep track of the exact position of plants and animals, in order that any relationship with landscape geometries can be elucidated. In the models, a map showing the spatial distribution of landscape features and habitat patches is combined with a population-simulation model. In short, the models combine spatial representation with demographic models. In a very simple SEPM, an artificial landscape can be created where each grid cell is randomly assigned a few attributes and a hypothetical population can be created. This synthetic landscape-population model can be used to derive general landscape-population relations. An example of this type of investigation is the examination of Lamerson et al. (1994) of the relationship between patch size and spacing on the viability of the Northern Spotted Owl (*Strix occidentalis caurina*). Using GIS technology and actual demographic and life history data, more realistic models can be created (see the model designed for the endangered Red-Cockaded Woodpecker [*Picoides borealis*] by Letcher et al. [1998] for an example of a model containing actual demographic and life history data coupled with an artificial landscape), the generic large ungulate model of Turner et al. (1993) for an example of hypothesized behavior on an actual landscape, and the Bachman's sparrow (*Aimophila aestivalis*) model of Liu et al. (1995) for an example of a model using both actual landscape and demographic and life history data.

SEPMs can be developed from either an individual-based or population-based perspective. Population-based models are most useful when the species are abundant, such as rodents or insects (Dunning et al. 1995). For larger species whose numbers are not so plenteous, the individual-based approach is more applicable. This is exactly the case when dealing with large carnivores, especially those that are endangered.

With SEPMs, one is able to incorporate individual movements between patches, daily movements, and/or dispersal in the landscape and quantify how these movements affect the population's dynamics. Because it is difficult to design field experiments or control relevant parameters at the landscape scale, these types of models allow a 'virtual' experiment to take place at the appropriate scale (Dunning et al. 1995; Turner et al. 1995). The 'virtual' experiment nature of the models also allows statistical and sensitivity analysis to be performed. Statistically valid summarization is achieved through repetitions of the model. Each time the model is executed one or more parameters are stochastically varied, creating a statistical 'sample' that can be analyzed. Similarly, sensitivity analysis can be performed by repeatedly running the model while systematically varying the model parameters one at a time or in combination to see which ones have the greatest impact on the results. Sensitivity analysis is important to these types of models because they are sensitive to parameterization and are vulnerable to propagation of model uncertainty (Conroy et al. 1995, Dunning et al. 1995; Turner et al. 1995). Reasons why there may be problems with parameterization include lack of data availability for the scale or area of interest, outdated information, and the expense of compiling an accurate GIS database (Turner et al. 1995).

Ecologists recognize the intimate relationship among species, their habitat, and their movements (Lima and Zollner 1998; Carroll et al. 1999). Dunning and others state: "To project the impact of landscape change on wildlife populations, models must elate the demographics of the population explicitly to the landscape in which the organisms exist" (Dunning et al. 1995: 4). The utility of such models, thus, lies in the fact they can directly link landscape configurations with population dynamics and spatial distribution. Spatially explicit models are important tools for ecologists because they allow the ecologists to escape the bounds of spatial and temporal scales in which they typically have worked, that is to say, they form bridges between the fields of behavioral and population ecology, ecology and wildlife management, ecology and conservation biology, and landscape ecology and population genetics. They are particularly important to land managers who often have to make decisions concerning species at these larger scales. A typical example is when SEPM are used to explore the consequences of proposed management strategies or land-use changes to a population of a particular species. Specifically, SEPMs are of research interest because they provide a technique to (1) discern the effects ecological process acting on a global scale, such as climate change have on individuals; (2) discern the effects ecological process acting on a regional land-use have on individuals; (3) study the responses of species to changes in management strategies; and (4) study population dynamics more realistically across a complex landscape. Dunning et al. (1995) list three research problems that can be addressed by SEPMs:

1. Study of individual and population response to landscape change
2. Study of habitat selection and population regulation
3. Reserve design for threatened and endangered species

Spatially explicit models have become increasingly popular with researchers and land managers as tools of investigation or planning (Dunning et al. 1995; Pulliam 1995; Cramer 1999). The list of spatially explicit models is extensive; the following are just a sampling: Boone and Hunter 1996 and Walker and Craighead 1997 modeled grizzly bear dispersal; Mladenoff 1995 investigated favorable wolf habitat; Murphy and Noon 1992 and Lamerson et al. 1994 studied reserve design plans and dispersal, respectively, for the Northern Spotted Owl. The two main reasons for their increased popularity are (1) the invention and proliferation of GIS and computing power which simplifies the handling of complex, heterogeneous landscape information and (2) the realization of the corresponding loss in biodiversity generated by habitat loss and fragmentation. Other reasons include the realization that many times the prevention of a species' extinction requires an understanding of the effects human's activities have on the species, the realization that global warming may require preservation of migratory routes and habitat for species to move; and for endangered species, the fulfillment of the Endangered Species Act's mandate to protect their habitat.

2.3.2 Individual-based modeling

Mathematical models and individual-based models (IBMs) represent two extremes when choosing a modeling approach. Mathematical models utilize a top-down perspective where all individual particles in the system are considered identical, every particle may be affected by every other particle, and the particle's behaviors and the system's details are abstracted and generalized from known real-world examples. The individual-based models' perspective is from the bottom up, where each individual particle and its corresponding properties, behaviors, and variations are considered in some level of detail.

Formal mathematical models used to describe change in a system involve differential equations. When change in the system occurs with respect to both time and space, partial differential equations are used. Because they are generalized abstractions, they are considered to be conceptual, phenomenological, or strategic models (Murdoch et al. 1992; Metz and de Roos 1992; Turchin 1998). Relying on a solid foundation of mathematical theory, they can usually be solved analytically or by means of numerical analysis to obtain answers to broad questions about ecology.

IBMs are considered structural or tactical models (Murdoch et al. 1992; Metz and de Roos 1992). There is no formal theory associated with these models, and the answers to the questions being addressed are based on the analysis of output generated by repeated computer simulation. They are most appropriately used when the environment is heterogeneous, populations are small or patchy, and individual behavior is sensitive to local events (Saarenmaa 1988; Metz and DeRoss 1992). The underlying assumption of IBMs is that the properties of an ecological system can be derived from the properties of the individuals making up the system and their relationship with each other (Saarenmaa 1988; Huston et al. 1988; Lomnicki 1992; Palmer 1992). In this respect, IBMs resemble cellular automata models (for examples refer to, Conway's game 'life' [see Gardner 1970], Toffoli [1984], Hogweg [1988]), and artificial intelligence models (such as those developed by Taylor et al. [1988], Hogweg and Hesper [1990], Huth and Wissel [1994]).

Several theoretical reasons substantiate the individual approach. First, an individual plant or animal is more concretely defined than a population or ecosystem. Second, individuals are the units of selection; that is to say, natural selection works on the individual and does not operate or is not effective at higher levels. Third, it has been shown that for larger mammals, considering the members of a population as unique individuals yields better information of the population dynamics than the more classical ecological approach that considers individuals as identical molecules subject to mortality and natality. Fourth, whether by genetics, environment, experience, or all three, all individuals are different. Finally, interactions between individuals take place locally not globally. Lomnicki (1992) provides a thorough discussion of the first three reasons, and Judson (1994) comprehensively addresses the last two. Huston, DeAngelis, and Post (1988), earlier when the individual-based modeling approach began to gain popularity, discussed many of these same reasons.

Other researchers support the individual-based approach because it provides a method to bridge the research of behavioral ecologist who, on a fine scale, study the decision-making process of animal movement, dispersal, and habitat selection and landscape ecologists, who study, on a broad scale, the effect animal movement, dispersal, and habitat selection have on population dynamics and spatial distribution (Lima and Zollner 1996). In other words, IBMs provide a solution to the aggregation problem. Still others believe that biological organisms and systems are too complex, especially for all practical purposes, to be studied in generality. They contend species must be considered unique and models should incorporate their natural life histories and behaviors (Slobodkin 1988). More recently others have expressed a similar view. DeAngelis et al. (2001) reiterated the importance of considering individual variation. Using three examples, they explicitly addressed three sources of variation: ontogenetic change, genetics, environment (the experience with and accumulation of local interactions with the environment affect an organism's growth, risk of mortality, probability of finding mates, etc.) and showed how such variation strongly influenced population-level dynamics. They emphasized ignoring variance among individuals when applying simple mathematical models, like the Lotka-Volterra equations, can lead to management problems. Schmitz (2000) used an IBM to show how individual behavior and local interactions were important in determining community-level dynamics.

Finally, individual-based modeling offers advantages over empirical models. First, they can be used to predict outcomes to novel situations or those for situations which data have not yet been collected (Grimm 1999). Second, they can provide a more accurate prediction under conditions that may only affect part of the population or where there are gaps in the data. DeAngelis et al. (2001) point out the empirical, correlative approach, where data on population size and environmental conditions are collected over many years and then statistical models are derived, can be problematic because this methodology requires quality data over the whole time period which may be difficult to obtain or is nonexistent. Also, these statistical models cannot make accurate predictions under conditions that maybe only affect part of the population at any one time. Third, IBMs can be developed in less time than it takes to perform long-term data collection studies. For species with small populations numbers who are subject to demographic stochasticity, the population could face extinction before long-term studies can be completed. Fourth, IBMs can provide more accurate predictions for populations who have recently experienced some environmental change, such as habitat fragmentation. This is of particular importance for modeling many species of conservation concern because there is a strong possibility that (1) the data for empirical studies were collected when the species existed in an environment other than the current one in which they reside, and (2) if the data is being currently collected, the population may be in some state of disequilibrium (either genetic or environmental) and thus, the data will not be representative of the species in either the past or future. It is not appropriate to model such a population using equilibrium models or to assume equilibrium conditions (see Newman and Tallmon [2001] for an empirical example).

IBMs have gained popularity over the last decade; the following are but a few examples: Fleming et al. (1994) and Wolff (1994) used this approach to study wood storks in Florida, Letcher et al. (1998) the red-cockaded woodpecker in North Carolina, and Cramer (1999) the Florida panther. Their popularity has been partly due to advances in computing power, technology, and programming (Hiebeler 1994). One of the computing advances has been the development of object-oriented programming languages, discussed in detail below. These languages have made the formulation of IBMs easier and more structured. While the ease offered by object-oriented languages in the development of programs written for IBMs has encouraged their proliferation, it has also fueled some of the strongest criticisms of this technique. These criticisms stem from the problems associated with nonprofessional programmers writing complex programs. Oftentimes when attempted by nonprofessional programmers, these programs are inefficient and slow (Lorek and Sonnenschien 1998). In addition, poorly coded programs can lead to results that are falsely attributed to the ecological phenomenon being modeled when, in fact, they are a consequence of bugs in the software, implicit assumptions made by the programmer when writing the code, or errors in the code itself (Lorek and Sonnenschien 1998). Finally, these programs tend to be poorly documented by the developers and poorly described, if included at all, in publications (though developers often are willing to share code if asked) (DeAngelis and Rose 1992; Judson 1994; Hiebler 1994; Lorek and Sonnenschien 1998; Railsback 2001). This makes it impossible for replication of the model or comparison of results by other researchers (Minar, N. et al. 1996). It should be noted, however, part of the reason behind the lack of model documentation may stem from the impetus of the research. Grimm (1999) reflected on IBMs developed in the 1990s. He found the vast majority of models were pragmatically motivated and were developed as tools to answer questions about specific species. Not being necessarily concerned with contributing to theoretical ecology, individual-based modelers in the past may have likewise not been concerned about documentation.

The lack of adequate description and documentation also makes the model susceptible to the results being misinterpreted by others (Judson 1994). In order to overcome the 'novice programmer' problems and in an effort to facilitate the creation of error-free programs and to enhance the comparability of different models, several people have produced a general programming framework, consisting mainly of software class libraries that others can use to develop a particular model. For example, EcoSim was developed by Lorek and Sonnenschein (see Lorek and Sonnenschien 1998 for description) and Swarm was developed by scientists at the Santa Fe Institute (visit http://www.swarm.org for a description). Railsback (2001) discusses errors modelers typically make when developing an IBM and suggests several concepts, some from the field of Complex Adaptive Systems that might be useful. He also accentuates the utility of having a good user/model interface for model testability.

2.4 Object-oriented design and programming

The object-oriented design principle state complex systems or processes can be modeled as a set of individual, interacting objects that communicate with each other by sending messages. This principle allows realistic simulations to be built because it is congruent with the way researchers view and study complex systems as individual objects that interact with each other. Each object is a self-contained unit having both data and control structures. The object's data can be thought of as the object's current state, and the control structures can be thought of as the object's behavior or response rules. The object's behavior or response rules control the object's actions and are known as methods. An object performs an action (invokes a method) when it receives a message from another object. Messages can be thought of as procedures in traditional programming languages. Object-oriented design principles are easy to implement with object-oriented program languages, such as Java, Objective C++, or SmallTalk.

Several features of object-oriented programming languages, discussed by Saarenmaa et al. (1988), make them ideally suited for spatially explicit, individual-based population models. First, the containment of data and methods in each object allows two objects to respond differently to the same message. If one thinks of messages as being procedural calls, then if the object did not contain its methods, the message would have to specify the action or response the object was suppose to take. By letting the object contain its methods, it is allowed to respond to the message according to its current state or the current situation it is in. This makes it appear as though objects are acting and reacting in the modeled system, a perception compatible with our observation of the natural world in which individuals and objects interact and affect one another. Second, message passing between objects in the model is a clear analogy with signal perception in the natural world. Third, the support of hierarchy and multiple instances of classes allows for the accurate representation of a unique population consisting of individuals of different ages, sexes, life histories, and experiences.

All object-oriented programming languages share three concepts that make them useful in developing realistic animal movement simulation models: object, inheritance, and polymorphism. An object-oriented program (OOP) is written as a set of separate individual modules called *objects*.

Each object is a grouping of data and associated methods. This allows an animal to be realistically represented as an individual from a particular object in the simulation model. An animal's state, such as age, weight, and hunger level, and an animal's set of behavior rules correspondingly become the simulated object's data and methods. The containment of data and methods in objects allows the individual instances of the objects to respond and interact to messages according to their current state; for example, hungry bears move and forage differently and are more likely to take risks than satiated bears.

Objects that share common data and methods are created from a common *class*. Inheritance allows objects to share data and methods from a common *super-class* and, at the same time, to have their own data and methods gained from being members of a *subclass*. For example, all bears in a population (*super-class*) will share a common set of states and movement rules. However, male and female bears are in some ways unique, both characteristically and behaviorally, and could be thought of as being distinct subpopulations (*subclasses*). Inheritance allows the bear objects to have states and behaviors characteristic of all bears, as well as have unique states and behavior rules particular to their sex. Thus, inheritance makes it easy to accurately represent a bear population as a collection of individuals of different sexes (see Figure 2.1.).

Finally, many objects can exist in the model at one time. Each individual object is known as an *instance* of a particular class. For example, the model could start out with several juvenile and adult 'instances' of the female bear class and several juvenile and adult 'instances' of the male bear class. Polymorphism makes it possible for an OOP to easily keep track of numerous

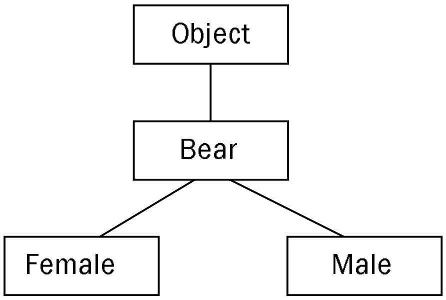

Figure 2.1. Class inheritance for a bear population.

objects because it allows the same message to be sent to different objects and then for each individual object to respond appropriately. Because it is easy for many objects to exist at any one time in the model, an entire population can be correctly represented in a simulation model in terms of population numbers and age structure. This frees the modeler from having to make any assumptions or conclusions about how individual behavior translates into population-level dynamics. Instead population-level dynamics emerge in the model as a consequence of the interaction between all the individual bear objects in the model. Thus, the simulation model outcome only reflects the effects of the known individual behavior of the bears and not extraneous modeling assumptions.

2.5 Bear behavior

There are reported cases of bears living in a social group (see Craighead et al. [1995]) and bear aggregations at ‘eco-centers’ or concentrations of high-quality food resources. High-quality food concentrations are seasonal sources including salmon or trout streams, berry shrub fields, moth aggregation sites, and artificial sources, such as garbage dumps. For the most part, however, grizzly bears are solitary animals, and a typical bear will spend the majority of its active season as an individual and will show little tolerance for other bears in close proximity (Nat’l Wild. Federation 1987). Two notable exceptions to these rules are when females are raising their cubs or when they are looking for a mating partner. In addition, mothers will often relinquish part of their home ranges to their female offspring

The age of first reproduction is between 3.5 and 8.5 years, and thereafter females will contribute young every 3.0 years (U.S. Fish and Wildlife Service 1993). A typical litter size is one to four cubs, with two being the norm (U.S. Fish and Wildlife Service 1993). Grizzly bear cubs are altricial, and have a dependent period of two years, occasionally one, and it ends abruptly when the mother begins estrous. The female bear makes it very clear by her actions it is time for her now ‘subadult’ young to leave her and begin independent life. Male subadults tend to disperse over much greater distances than females (Nat’l Wild. Federation 1987). This is probably due to two factors. First, female subadults are tolerated by their mothers and often establish ranges in proximity to or that encompass a part of their natal ranges. Second, subadult males are not tolerated by other bears. They are not tolerated by females with cubs, since they are male and pose a threat to dependent cubs, and they are not tolerated by adult males, since they are potential competitors for mating opportunities. They are thus forced by the aggressive behavi or of other bears to avoid existing home ranges. Since, these ranges can be up to 1000-1500 m^2, depending on habitat productivity. Subadult males frequently travel many miles before finding a place of their own. Bears move around in their home ranges foraging for food; with the exclusion of the first few weeks after den emergence, bears are constantly eating. How bears move and interact with the landscape depend largely on the spatial and temporal distribution of food resources. (Craighead and Mitchell 1982; Nat'l. Wildl. Federation 1987). They are omnivores whose foraging strategy can best be described as one of variation and opportunity. Their food habits vary with season corresponding with changes in plant phenology (Volsen 1994). Plants in early phenological stage development are high in soluble nutrients. In the spring, they eat grasses and forbs found at lower elevations and in avalanche chutes or slide paths, and take advantage of the carrion that is present in ungulate winter ranges. As summer approaches, they move back to midelevation meadows to forage on grasses, berries, insects, such as ants, bees, and wasps and ungulate neonates, if available. At higher elevations, berries, grasses, roots, and, where available, whitebark pine nuts and cutworm moths found in talus slopes are utilized in the fall. At the end of the fall season, they become lethargic as they prepare to enter their dens for winter hibernation. Movements on average are between 1.34 km/day and 4.0 km/day; however there are reports of extensive movements in short time periods (Nat'l. Wildl. Federation 1987).

Food is so important to a grizzly bear, because bears need to accumulate a large enough fat storage to carry them through hibernation. A bear that does not eat enough food or put on enough weight risks the possibility of not emerging from the den, or emerging in such a weakened state as to make it vulnerable to starvation the following spring. In females, the blastocysts will not implant in the uterine wall unless the bear has gained a sufficient amount of weight. Their quest for food often puts them in direct or indirect contact with humans, because they are attracted to human food sources. In bad food production years, they often travel outside the more secure, remote areas of their ranges and venture into areas with greater human presence. Unfortunately, contact with humans usually ends up as tragedy for the bear.

Humans are the primary source of mortality for the adult grizzly bear (Matteson et al. 1996; McLellan et al. 1999; Swartz et al. 2002). For a grizzly, human-caused mortality is a function of both the probability of encountering a human and the probability the encounter will result in death (Mattson et al. 1996; Mattson et al. 1996b). These two probabilities are directly influenced by the number and behavior of humans in or near bear habitat and the amount of access (roads, trails, and residential facilities) to the habitat (Mattson et al. 1996). The risk of mortality is not evenly distributed among a population but is dependent upon the sex and age class of the bear (Pease and Mattson 1999). Subadult males and females have some of the highest risks, because of their need to establish a home range. For males this is related to the distances they travel, often taking them out of secure areas and into the human-developed landscape, and for the females, because their ranges are on the periphery of the mother's range, they spend time foraging in less secure areas. Frequently foraging in less secure habitat is also documented for females with cubs and subordinate younger bears trying to avoid male bears (Mattson et al. 1987; McLellan and Shackleton 1988).

The human landscape features having the greatest effect on grizzly bears are roads, agricultural activities including livestock grazing, industrial and extractive activities, and private land development (Nat'l. Wildl. Federation 1987; Wakkinen 2000). The effects can be direct, as in mortality, or indirect, as in habitat modification or behavior adaptation. Roads have the greatest influence on grizzly bears. Besides their associated habitat loss and modification, roads increase the risk of mortality to bears because they increase human access to occupied habitat. They also cause avoidance and displacement behavior by grizzly bears. Mortalities associated with roads include those bears killed by vehicles and those legal or illegally killed. Dood et al.(1986) analyzed bear mortality data (known locations) in Montana and found 32% hunting and 48% nonhunting mortality occurred within 1.0 mile of a road.

Livestock grazing was the major cause of the grizzly bear extinction in California and the southwestern United States (Storer and Tevis 1955). In 1985 the leading cause of nonhunting mortality was mortality associated with livestock depredations (Nat'l. Wildl. Federation 1987). More recently, Schwartz et al. (2003) report as much as 90% of recorded mortalities are due to hunting, management removal, or defense of life and property by citizens (includes livestock depredation). Even in areas like Montana where grizzly bear hunting is illegal, bears are still killed by deer, elk and black bear hunters. Besides livestock, the most common agricultural attractants are apiaries and fruit orchards.

Industrial activities include hydrocarbon exploration and development, hydroelectric development, and timber extraction. The detrimental effects of these types of activities are mainly attributable to the associated additional construction of or improvement in existing roads (McLellan 1988) (see above for discussion of roads). In addition, there is increased human activity corresponding to project construction and maintenance and the possibility of increased availability of artificial attractants (especially garbage), both of which can lead to increased legal and illegal killing. Lastly, due to human activity, construction, use of equipment, or habitat modification, industrial activities can cause direct habitat loss, possible displacement from habitat, a disruption in normal behavioral patterns or physiological disturbances in bears (McLellan 1989). In contrast to an earlier study by other researchers, McLellan and Shackleton (1989) reported minimal displacement of bears in response to seismic activities but suggested the response by bears could be influenced by density and size of the grizzly population in an area or degree of habituation.

Human residences and developed areas affect grizzlies directly through habitat loss and an increase in mortality risk, especially if artificial foods and attractants (example, garbage dumps) are present. The more time bears spend in proximity to human facilities, the greater their risk of human encounter and thus, mortality (Knight et al. 1988; Mattson et al. 1996). In addition, there is the indirect effect of behavior modification. Bear responses to people in backcountry campsites is stronger than responses to people on trails. Gunther (1990) found that bears underused areas up to 1.0 km from campsites and Kasworm and Manly (1990) found that bears underused areas within 100 m next to trails in the Cabinet Mountains. McLellan and Shackleton (1989b) found bears more likely to respond to people on foot if they were in an open area. Elgmork (1978) in a 25-year study reported that bears tended to avoid, up to 2.0 km away, areas with concentrations of cabins or houses.

2.6 Summary

Because of human-caused habitat fragmentation, the only hope for the persistence of many of species is the protection of sufficient habitat to allow disjunct populations to act as a metapopulation. This is particular true for the grizzly bear, since five out of the six designated recovery zones are thought to be too small or too isolated to sustain a viable population of bears in the long term (Mattson et al. 1995). For the populations along the trans-boundary area, such as those inhabiting the Selkirks and the Cabinet-Yaak Ecosystems, similar conclusion were drawn by Allendorf and Servheen (1986), who found grizzly populations were too small to withstand the negative effects of environmental and demographic stochasticity, as well as to fend off the effects of genetic drift. Boyce et al. (2001), using RAMAS/GIS and ALEX metapopulation computer programs designed for conducting PVA, found that even moderate levels of dispersal between subpopulations in the United States, increased the probability of 100-year persistence for grizzly bears along the trans-boundary area.

If individual populations of bears are to act as subpopulations of a larger metapopulation, then geographic connectivity between the subpopulations must be maintained or restored. Developing methods for assessing the effectiveness of present connectivity to a population's viability, or methods for evaluating the consequences of management decisions that could influence connectivity and, thus, influence a population's viability would greatly improve grizzly bear conservation efforts. Because of the landscape scale involved, the solitary, low density of bears in the region, and the necessity of repeated collection of data to detect change, field methods could be inefficient, costly, and, most importantly, untimely (irreversible processes can be set into motion before detected). Another approach to answering these questions is with the use of modeling.

Models of grizzly bears in the past have independently focused on demography, habitat suitability, or genetic health. Demographic modeling has been concerned with calculating λ, population trend, or a population's persistence. With the exception of Boyce et al. (2001), who considered a spatial structure to the subpopulations, demographic models have solely concentrated on using vital parameters, for example, fecundity or survival, to predict future population numbers or viability and have lacked a spatial component or connections with habitat. Habitat or landscape ecology modeling, on the other hand, has solely concentrated on spatial explicit landscape aspects and has ignored demography. Genetic modeling, with the exception of unpublished reports, has been limited to using mathematical formulas for calculating N_e or determining the number of immigrants needed to stave off drift. Using a broader view of a metapopulation being a collection of spatially distributed subpopulations among which dispersal and turnover are possible but not necessarily occurring, Harrison (1994) contends both among-population process and within-population process play a role in the viability of a species. What would be of use then is a spatially explicit model of regional scale that elucidates how a population's demographic dynamics are linked to the landscape in which it inhabits and how bears move in regards to the landscape as well as to each other.

Since the early 1960s, the grizzly bear has been extensively studied in the field and there are numerous publications on bear behavior, bear interactions, and bear/habitat interactions. However, none of these studies have been conducted at a regional-scale, which is the scale most appropriate to investigate connectivity between bear populations. This can be accomplished using an individual-based simulation modeling approach. What is needed in order to conduct a regional-level assessment of the connectivity between populations is a method to use the information already collected, in a model of the appropriate scale. This need can be fulfilled by the development of an IBM using object-oriented design principles. The trans-boundary grizzly bear populations are ideally suited for IBMs because they are small in number, sensitive to local events and interactions, and inhabitants of a heterogeneous environment. Object-oriented design principles will allow the population dynamics to be modeled as a consequence of interacting 'bear objects' and 'habitat objects.' This ideology allows the model to be built using only known, documented behaviors of individual bears and prevents the need for making extraneous assumptions about bear/bear or bear/habitat interactions, or about how the individual behaviors scale to the population or regional level. It also allows the bears to become adaptive and makes the model truly dynamic because they are able to respond differently depending on the situation. This will be the first time a dynamic model is used to investigate the connectivity between and viability of grizzly bear populations.

The simulation developed in this research will extend the research previously done by adding an explicit spatial component to mortality, being a dynamic model, meaning all bears, bear - bear interactions, and bear-habitat interactions will be considered; adding a stochastic component to habitat productivity; and using exact pedigree information. This will produce a more accurate model of grizzly bear spatially dynamics and, hence, a better assessment of connectivity in the region and a better assessment of the populations' future viability. By being a more realistic representation, it will provide a more accurate assessment of the connectivity present in the area. Besides being able to determine the effectiveness of the current connectivity among bear populations, as is done in DNA field studies, modeling allows the exploration of what different levels of connectivity means to the populations viability. It can also aid in management decisions that might positively or negatively affect connectivity between the populations. Boyce at el. (2001) suggest a habitat PVA, using GIS, will do a lot towards advancing researchers ability in determining the consequences of natural resource management decisions on a grizzly bear population's long-term viability. This can be accomplished using an individual-based simulation modeling approach.

Grizzly bears are basically solitary animals whose movements, except during the mating season, are dictated by the need to find adequate food. They eat a variety of foods throughout the active season, and their choice depends on the phenological characteristics and abundance of foods available. Besides food considerations, human landscapes features, such as roads, also influence bear movement. These human landscape features likewise pose a risk of mortality to the bear. Bears only predator is man, and humans are the primary source of mortality for the bear. The search for food and the risk of human-caused mortality are the two most important factors that will need to be accounted for in the model.

CHAPTER 3

INDIVIDUAL-BASED MODELING AND INBREEDING

3.1 Introduction

Inbreeding depression refers to the loss of fitness caused by one or more generations of inbreeding. Avoiding inbreeding depression is a central genetic goal of species conservation programs. This concern has received a good deal of attention in captive breeding efforts for endangered species. For a variety of reasons, however, inbreeding depression has not been an urgent priority in most *in situ* efforts to conserve wild populations. (Lacy et al. 1995; Laikre 1999). Concerns, such as anthropogenic mortality, habitat destruction, and other demographic and environmental factors, are often viewed as being of immediate importance in wildlfe conservation (Lande 1988; Caro and Laurenson 1994; Caughley 1994). The role inbreeding depression plays in a population's extinction is poorly understood, and analytic tools for understanding the phenomenon are lacking. Individual-based modeling has the potential to illuminate the complex interactions between a population's genetic and demographic dynamics and its environment and, thus, to provide an understanding of the consequences of inbreeding to a population's long-term viability.

This chapter reviews the detrimental effects of inbreeding and the methods available for calculating inbreeding/kinship coefficients on pedigrees. Next, it discusses reasons why those in charge of wildlife conservation and managements often ignore or underestimate the consequences of inbreeding depression to a population's viability. Finally, it discusses how individual-based modeling may be used as an analytical tool to help understand the effect inbreeding depression has on a population's persistence.

3.2 Inbreeding and its consequences and measures

3.2.1 Inbreeding and inbreeding depression

Inbreeding is breeding among individuals that are more closely related to each other than mates selected at random (Crow and Kimura 1970). Inbreeding increases an individual's chance of inheriting two alleles descended directly from a common ancestor, and thus, it increases an individual's chance of having homozygous alleles at a locus. These homozygous alleles, having descended from a common ancestor, are exactly the same in function and nucleotide sequence (disregarding the possibility of mutation) and are referred to as being *identical by descent*. Homozygosity resulting from identical by descent alleles is called autozygosity. This is in contrast to allozygosity, the term used when a locus is homozygous with two *alike in state* (AIS) alleles, or alleles that have the same function but are not copies of a common ancestral allele. This distinction is important to keep in mind because inbreeding only relates to autozygosity.

Genetic drift is considered by many to be a form of inbreeding. Here all individuals of a small, finite population have lower fitness than ancestral members of the population due to the fixation of recessive alleles and loss of allelic diversity. Some consider this a form of inbreeding, (e.g. Hedrick and Kalinowski 2000; Keller and Waller 2002), because related individuals mate, even though mating may be random within the population. The mating between relatives is attributable solely to the population being small with a finite number of founders, and thus, eventually every member of the population will share a common ancestor, albeit the relatedness may be quite distant. Others, for instance, Gall (1987), refer to genetic drift as a closely related concept, rather than a specific form of inbreeding. The distinction is made here only to inform the reader of the ambivalent nature of the term (for a discussion of the various interpretations of inbreeding, see Jacquard [1975]). In this chapter, inbreeding will refer to the probability that two alleles are identical by descent regardless of the exact processes responsible for causing the homozygosity.

Offspring from the mating of closely related individuals are susceptible to inbreeding depression, a loss of fitness manifested as decreased vigor, survival rate, or fecundity. It is thought the homozygous expression of unfavorable recessive alleles is the major cause of inbreeding depression, though the exact mechanisms involved are still in question (Hedrick and Miller 1992). The loss of fitness due to inbreeding among individuals has long been acknowledged in humans and domesticated stocks. Documentation of inbreeding depression in endangered species did not occur until the late 1970s (Hedrick and Kalinowski 2000). Since that time, research has yielded no evidence of taxa that are immune to the harmful effects of inbreeding. Ralls et al. (1979) found increased juvenile mortality in various ungulate species due to inbreeding. Laikre (1999) reports examples of inbreeding depression in mammalian carnivore species. Keller and Waller (2002) summarize study results of inbreeding depression in plants as well as in animals. Similarly, Gall (1987) provides a summary of recorded inbreeding depression in various fish species.

Loss of fitness caused by inbreeding among individuals is more easily detected than a reduction in fitness attributable to within-population inbreeding. In a small, finite population, any decrease in individual fitness due to genetic drift can be difficult to detect because all individuals experience lower fitness. The only way this type of inbreeding depression may become obvious is by observing increases in fitness, heterosis, in outbred offspring (Hedrick and Kalinowski 2000, Keller and Waller 2002). Hedrick and Kalinowski (2000) give three examples of where introduction of new genes to small, remnant populations have led to increased fitness: Florida panther (*Felis concolor coryi*), Swedish adder (*Vipera berus*), and prairie chicken (*Tympanuchus cupido*).

3.2.2 Inbreeding and kinship coefficients

As discussed by Boyce (1983) the need for a coefficient to express the degree of inbreeding in individuals of a pedigree was recognized in the early 1900s by Pearl (1913) and Wright (1922). The coefficient of inbreeding, a probability value, measures the likelihood that an individual will have identical-by-descent alleles, or is autozygous, at a locus. It can also be interpreted as a measure of the increase in homozygosity, or correspondingly the decrease in hetereozygosity, due to inbreeding. This increase (decrease) is relative to a predetermined ancestral base population of individuals assumed to be totally unrelated. Cotterman (1940) later generalized Wright’s inbreeding coefficient to the coefficient of kinship (see Boyce 1983). Unlike the inbreeding coefficient, a probability measure concerning an individual, the kinship coefficient is a probability measure between two individuals. It is defined as the probability that two different individuals share alleles identical by descent. Another way to think about the kinship coefficient between two individuals is that it is equal to the inbreeding coefficient any hypothetical offspring of theirs would have regardless of whether the individuals have actually mated. The kinship coefficient is thus directly related to the inbreeding coefficient.

The genetic relatedness between individuals plays a central role in pedigree analysis; in fact, specifying the genetic relationship between all individuals in a population is the most complete and fundamental nonempirical analysis one can perform (Lacy et al. 1995). Pedigree analysis was developed originally for avoiding inbreeding depression or developing hybrids in domestic stocks and providing genetic counseling for humans. Today it is also utilized in the genetic management of wild animals to avoid inbreeding depression and maintain genetic diversity in captive populations.

Three computational approaches can be used for calculating inbreeding and kinship coefficients: ancestral lines comparison, path analysis, and algorithms of recursion (see Boyce [1983] for a review of these approaches). Calculating inbreeding coefficients using the ancestral lines comparison approach involves detecting all common ancestors between individuals and then summing up all the contributions of these common ancestors to the total level of inbreeding. The contribution to inbreeding is calculated using the following equation:

$$\text{inbreeding contribution} = (1 + f_A)*(1/2)^{m+n+1} \qquad (3.1)$$

In equation (3.1), m and n are numbers of generations between the common ancestor and the mother and father of the individual, respectively. The variable f_A is the inbreeding coefficient of the common ancestor. To calculate, for example, the inbreeding coefficient of an individual, A, one would first determine and store the maternal and paternal ancestral lines of A. Next, a systematic procedure would be used to detect common individuals between the two ancestral lines. Finally, for each individual detected, the inbreeding contribution of the common ancestor is determined and added to total inbreeding coefficient of individual A.

Ancestral lines comparison is computationally prohibitive for all but shallow pedigrees. Limiting pedigree analysis to shallow depths can lead to underestimation of the current level of inbreeding because remote inbreeding can substantially contribute to present relatedness (Boyce 1983). For extended pedigrees use of either path analysis or recursive algorithms is necessary.

Path analysis is similar to ancestral lines comparison in that it relies on the determination of all common ancestors and their individual contributions to the overall inbreeding coefficient. The difference between the two approaches is that path analysis uses algorithms to search the pedigree for paths between individuals and their common ancestors instead of storing and comparing maternal and paternal ancestral lines. Efficient algorithms for implementing such approaches have been developed. Path analysis algorithms, however, lend themselves to computational problems on extended pedigrees owing to the large number of paths that need to be generated, stored, and searched. For pedigrees of substantial depth, programming of recursive algorithms is more straightforward.

Ancestral lines comparison and path analysis calculate the inbreeding coefficient of individuals, whereas recursive algorithms focus on determining kinship coefficients. Recursive algorithms utilize the fact that the kinship between two individuals, x and y, can be expressed in terms of the kinship between one of them, the elder individual, and the mother and father of the other. That is to say, the kinship between two individuals x and y, denoted $\psi (x,y)$, can be defined by

$$\psi (x,y)= 0.5*(\psi (x,\varphi(y)) + \psi (x, \rho(y)) , \qquad (3.2)$$

where x is the same age or older than y, and $\varphi (y)$ and $\rho(y)$ are the mother and father of y, respectively. If x and y are the same individual, then (3.1) becomes

$$\psi (x,x)= 0.5*(1 + f_X) , \qquad (3.3)$$

where f_X is the inbreeding coefficient of x. Unless otherwise known, the initial individuals founding a pedigree are assumed to be noninbred and have coefficients of kinship equal to zero. This assumption along with formulas (3.2) and (3.3) allows a recursive calculation of $\psi (x,y)$ under any computer language that allows recursively defined functions. If $\psi(x,\varphi(y))$ and $\psi(x,\rho(y))$ are accessible as elements of a table or matrix, they can quickly be retrieved and thereby utilized to determine $\psi(x,y)$. Storing the kinship coefficients of all the older animals in a symmetric matrix permits a much faster calculation, and is the computationally time saving technique employed by the additive matrix method (Ballou 1983). The number of rows and columns of the matrix is equal to the number of animals in the pedigree, and a new row and column are added each time a new individual is added to the pedigree.

There is a practical issue regarding the use of kinship. The computer resources necessary to recursively compute $\psi(x,y)$ values depend on the depth of the pedigree and goes up roughly with the power of the size of the pedigree. The kinship relationships can also be stored in a symmetric square matrix, termed the additive matrix method (Ballou 1983). The number of rows and columns of the matrix is equal to the number of animals in the pedigree. The number of rows and columns scales exactly with pedigree size, but the size of the kinship matrix itself goes up with the square of the size of the pedigree. Both these issues can lead to storage or stack overflow problems inside digital computers.

3.3 Inbreeding and conservation

Frankham (1995) credits Sir Otto Frankel with bringing genetics into the conservation vocabulary and Michael Soulé with shaping conservation biology as a multidisciplinary field with genetics as a crucial component. Initially, relying on theoretical population genetics, researchers tried to provide general guidelines to conservation managers. Franklin (1980) proposed an effective population size, N_e, equal 50 as the minimum size to ward off inbreeding depression. This guideline was based in part on the experience of animal breeders who consider an increase in inbreeding coefficient, F, as high as 1% per generation acceptable. Franklin suggested N_e of 50 was also based on Wright's formula:

$$\Delta F = 1/2\, N_e, \qquad (3.4)$$

In addition, Franklin reasoned in the absence of natural selection forces and dominance or epistatic variance, the rate of additive variance would equal the rate of heterozygosity loss. Given that heterozygosity is related to inbreeding (see Section 2.1.3, formula (3.4) likewise equals the rate of change of heterozygosity per generation. Hence, using an additive variance rate of 10^{-3} per generation as measured for *Drosophila*, he proposed a minimum effective population size of 500 to preclude genetic drift.

Wright's formula mentioned above is derived under the assumption of a genetically ideal population. Research involving genetically nonideal populations has focused on developing new formulas for estimating N_e, e.g., Lande and Barrowclough (1987) (see Harris and Allendorf [1989] for other examples). N_e is then used to estimate the rate of loss of heterozygosity per generation in a population. Using N_e to estimate the loss of genetic variation or applying the 50/500 rule is as far as genetic analysis has been taken in many recovery programs for endangered species (Lacy et al. 1995). Inbreeding and its effects are rarely considered outside captive breeding programs (Lacy et al. 1995; Laikre 1999). Groom and Pascual (1998) found for the population viability analyses they reviewed only 7% included genetics. There are several reasons for the casual attitude towards and lack of attention given to inbreeding in conservation management planning for wild populations, most of which seem to be based on either a lack of data or belief in misconceptions. Reasons commonly mentioned are discussed below.

3.3.1 Lack of data

In the management of captive populations, where pedigree information is available and managers can control mate choice, avoiding inbreeding depression is a major goal (Hedrick 2001). In natural settings, on the other hand, exact maternity and/or paternity are frequently unknown, making it impossible to implement pedigree analysis as a tool in wildlife conservation or management. Further, managers in charge of natural populations have little control of who mates with whom. In the future, though, in lieu of pedigree information, managers of natural populations may be able to use information derived from molecular genetics to monitor levels of inbreeding (Hedrick 2001). Ellegren (1999) used such techniques to determine the level of inbreeding in a captive population of gray wolves. Comparison with pedigree-derived inbreeding values showed good predictability between heterozygosity at microsatellite loci and the degree of inbreeding and microsatellite allele sharing and relatedness between pairs of individuals (Ellegren 1999). These techniques may be used to determine when critical levels of inbreeding are reached in a population, because managers of wild populations cannot control mating, translocation of individuals from other populations could be used as a management strategy.

Not only is pedigree information not available for wild populations, but data on the effects of inbreeding depression on members of natural populations are lacking. Most of the documented effects found in the literature (see Section 3.2.1 for sources) are from analysis of captive populations. Effects of inbreeding depression on natural populations could be quite different in kind and severity. Also, there is little empirical data available estimating the magnitude of the affects as a function of the values of inbreeding coefficients (Allendorf and Ryman 2002).

3.3.1 Misconceptions

There are many misconceptions about inbreeding. Two common misconceptions that prevail despite evidence to the contrary are as follows:

1. Consideration of inbreeding and its effects are not important because there are no proven cases of extinction in the wild caused by inbreeding, and because there are cases where species have gone through extreme bottlenecks and are doing fine (Frankham 1995; Keller and Waller 2002; Allendorf and Ryman 2002).
2. Certain species, particularly carnivores, are somehow adapted to close inbreeding (Laikre 1999; Allendorf and Ryman 2002).

It is somewhat understandable why misconception (1) prevails. In natural populations, deaths due to genetic defects are hard to detect as such. Oftentimes when a population goes extinct, there are other more observable factors contributing to their demise. The most striking example, discussed by Hedrick and Kalinowski (2000), is the song sparrow *Melospiza melodia*. In 1989, 89% of the adults in a population on Mandarte Island, British Columbia, died during a severe winter. Weather was definitely a factor. Closer examination, however, revealed all the birds that died had an average inbreeding coefficient about 5 times higher than the survivors, and 100% of the birds with a 10 times higher average inbreeding coefficient relative to the survivors died. Genetics, hence, seems to have been the real survival determinant. Keller and Waller (2001) discuss several similar examples of individuals more susceptible to environmentally inflicted mortality because of inbreeding depression. Examples of species surviving bottlenecks are used as evidence that a population can be 'purged' of its genetic load. The misconception of purging is discussed below.

Regarding misconception (2), as discussed by Laikre (1999), there are no strong arguments supporting this notion, yet it still prevails among managers of carnivore species. There is no basis for assuming any species is protected from inbreeding or its consequences. No one will refute the fact that some animals and monoecious plants have behavioral or physiological adaptations intended for discouraging inbreeding, for example, sex-biased dispersal in bears (McLellan and Hovey 2001), incest avoidance in prairie dogs (Dobson et al 1997), and heterostyly in plants (Lande and Schemske 1985). These adaptations, nevertheless, do not imply that specific organisms cannot experience or be affected by inbreeding. As all ready stated in Section 3.3.1, no species has been found to be immune to the negative effects of inbreeding. In particular for carnivores, Laikre (1999) found inbreeding depression in captive brown bear (*Ursus arctos*), wolf (*Canis lupus*), and lynx (*Lynx lynx*) populations, and summarizes hereditary defects in several other carnivore species. Out of the species Laikre analyzed or included in the summary, only two, Florida Panther and Lion (*Panthera leo*), were results from wild populations. This point is promoted by supporters of this misconception as implying that the effects of inbreeding in captive populations are not necessarily manifested in wild populations. There is a degree of truth to this statement, that the effects in wild populations might not be the same as those exhibited by captive populations (Laikre 1999). Still, 'different' effects are not the same as 'no effects,' and again, research has yet to uncover a species protected from inbreeding depression. Moreover, recent evidence shows inbreeding and inbreeding depression might even be more ubiquitous than previously thought (Keller and Waller 2002). Further if anything, inbreeding depression could be higher severe in natural populations due to the increased environmental stress (Allendorf and Ryman 2002), though Keller and Waller (2002) caution against making generalization about such increases. Finally, failure to detect inbreeding depression in a population does not necessarily mean it is not present. There are several possible reasons besides nonexistence to explain the failure, e.g., small sample size or testing wrong components of fitness (see Hedrick and Kalinowshi [2000]).

Another misconception is the belief that deleterious alleles are 'cleansed' or 'purged' from populations (Laikre 1999; Allendorf and Ryman 2002; Keller and Waller 2002). This is technically not a misconception. It is theoretically possible to reduce inbreeding depression by actually mating related relatives (Crow and Kimura 1970; Hedrick and Kalinowski 2000). The idea is that further inbreeding will expose recessive, deleterious alleles. These alleles will then be eliminated or 'purged' from the populations by the mechanism of natural selection. Supporters of this idea herald the Spekes gazelle (Templeton and Read 1983) or other species that have gone through a bottleneck as examples of purging leading to increased fitness (Hedrick and Kalinowski 2000; Allendorf and Ryman 2002). Additional research, though, appears to discount purging as an effective means of reducing inbreeding depression for natural populations, especially for species subject to further reductions in size or habitat (see discussion in Keller and Waller 2002 or Allendorf and Ryman 2002). Also, it is important to recognize that populations surviving bottlenecks could be the exception, not the rule. There is no way of determining how many populations have perished under similar circumstances.

Currently, minimizing inbreeding is the only acceptable method for minimizing inbreeding depression (Hedrick and Kalinowshi 2000). If inbreeding depression already exists, intr oduction of new genes into the population via outbreeding or restoration of natural gene flow between populations is the only proven method for alleviating inbreeding depression and restoring genetic health to an inbred population. In fact, there is evidence to suggest that even the migration of a single individual can be extremely beneficial (Ingvarsson 2001). It should be mentioned, however, gene flow may have some associated risks such as introduction of disease, manifestation of outbreeding depression, or loss of local adaptation (see Hedrick and Kalinowski 2000 for further discussion).

Finally, the most prevailing misconception is the belief that in the wild, demographic and environmental stochasticity and catastrophes are more important causes of wildlife extinction than inbreeding (Lande 1988; Mills and Smouse 1994; Frankham 1995; Allendorf and Ryman 2002). As stated by Mills and Smouse (1994), this dichotomy between genetic and ecological views of extinction was created as a backlash to earlier emphasis on genetics in conservation. Review of the literature reveals Lande (1988) most often is cited as supporting the notion that demographic and environmental factors are of more importance in determining a species' persistence. Reading Lande's paper, though, reveals he did not suggest demographic factors were more important than genetics, nor that management plans should consider one factor to the exclusion of the others. Rather, he states that they are equally important in the design of conservation management plans, with demographic factors being of more 'immediate importance.' Lande clearly recognizes the interactive roles demography and population genetics play in the process of small population extinction. Despite the fact Lande himself did not support a demography genetics dichotomy, his paper spurred such a diametrical perception of the two factors. This perception has repeatedly been denounced in the literature (Mills and Smouse 1994; Ballou et al. 1995; Lacy and Lindenmayer 1995; Keller and Waller 2001), and Allendorf and Ryman (2002) give two unpublished examples, tiger (*Panthera tigris*) in Nepal and brown bear (*Ursus arctos*) in the Rocky Mountains, where the probability of persistence differed depending on whether or not inbreeding depression was included in the models.

3.3.3 Other

These reasons are not as often referred to in the literature, nonetheless, they can be valid deterrents to including genetic analysis in conservation plans. First, hereditary disorders and diseases associated with inbreeding might not be well known because they are often not mentioned in the literature (Laikre 1999). If such disorders, therefore, are detected in a population they are not recognized as being genetically linked. Second, there is a reluctance of 'species experts' to acknowledge that someone without an expert's extensive knowledge of a particular species actually has something to contribute towards its conservation (Laikre 1999). Given the fact most 'species experts' are not likely to be trained as geneticists, failure to recognize the value of outside expertise can equate to negligence in genetic concerns for a species (Clark 1997). Lastly, the inclusion of genetics in conservation planning and management results in increased population sizes, which is not viewed as 'politically favorable' (Laikre 1999).

3.4 Inbreeding and individual-based modeling

In the last 7 years, inbreeding and conservation have been the topic of three separate review articles published in different journals: Frankham (1995), Hedrick and Kalinowski (2000), and Keller and Waller (2002). All three articles conclude research has established that inbreeding and inbreeding depression do occur in wild populations, and a better understanding of how inbreeding interacts with other factors, such as demography and environment, to affect a species' persistence is needed. As mentioned in the previous section, early emphasize on genetics in conservation management planning was followed by a demographic prominence. This caused a perceived dichotomy between the factors that has no ecological foundation. In truth, all three factors have the potential to contribute independently, as well as interactively, to a species' extinction (Gilpin and Soule 1986).

The mid-1990s saw a return to the multifactorial approach of addressing the subject of population viability, at least the congruent consideration of genetics and demography, e.g., Mills and Smouse (1994) and Lacy and LindenMayer (1995). Lacy and Lindenmayer used a metapopulation population configuration with a gene drop simulation provided with the software VORTEX. In addition, one allele in each of the founders was considered a recessive lethal. Their study demonstrated the influence of demographic instability on the loss of genetic variation and accumulation of lethal alleles in a metapopulation. Their methodology did not allow them to directly address population persistence. In contrast, Mills and Smouse showed explicitly how the inclusion of both genetics and demography and their interaction influenced population persistence. This was accomplished by using a Leslie matrix approach with inbreeding depression adjustments to fecundity and survival rates.

Individual-based modeling likewise permits the consideration of multiple factors in the assessment of a population's viability. Additionally, it offers several advantages over other approaches. First because all individuals are modeled, a pedigree can be created during the simulation. Having the pedigree allows the direct calculation of kinship or inbreeding coefficients; hence, one can avoid the estimation of N_e and calculate the loss of heterozygosity directly using inbreeding coefficients. The benefit of side-stepping the calculation of N_e and using inbreeding coefficients instead is discussed fully in the next chapter and will not be repeated here. Knowledge of an individual's inbreeding coefficient will allow illumination of how variance in the degree of inbreeding among individuals within a population affects the expression of inbreeding depression and subsequent population dynamics. This is an unexplored area of research (Keller and Waller 2002). Also, because a pedigree is created, the presence and distribution of founder alleles can be tracked. Allelic diversity is very important; for example, loci associated with disease resistance often have a large number of alleles (Allendorf and Ryman 2002) and increased susceptibility to pests and parasites is associated low genetic variation (Frankam 1995).

Second, individual-based models allow individual effects of inbreeding to be transformed into population-level effects. According to Keller and Waller (2002), the improvement in the understanding of how inbreeding affects individuals has not been matched by a general understanding of how inbreeding affects population dynamics. As new molecular techniques emerge, more and more information will become available on the effects of inbreeding on individual fitness. As researchers continue to learn more about how inbreeding affects individuals, individual-based modeling will allow this knowledge to be turned into testable hypothesis and insights about the effects of inbreeding on population dynamics. The link among levels of genetic variation, mean fitness, and population persistence is another unexplored area of theoretical modeling and empirical research (Ingvarsson 1999).

Third, individual-based models are ideally suited to be integrated with spatially explicit information. Metapopulations are a rudimentary way of considering spatial structure. The advent of GIS software precipitated the availability of spatially explicit landscape information. To date the use of such information in genetic modeling has been limited. There is lack of understanding about how landscape influences the spatial distribution within a population of allelic diversity loss or inbreeding level increase and what affects this distribution has on its dynamics and viability.

Finally, the Individual-based modeling approach allows for the inclusion of individual behavior. Like the spatial explicit genetic models, behaviorally explicit genetic models are also lacking. Individual behavior influences the social structure of a population and thereby influences its gene dynamics (Sugg et al. 1996). Without the inclusion of behavior, variation in inbreeding coefficients among individual members of a population and the accumulation of inbreeding through time cannot be accurately modeled. The importance of individual variation has already been mentioned. Accumulation of inbreeding is important when considering the time frame of 'viable'. A population could be viable for say 100 years, but during that time have loss so much variation that it is unlikely to survive for 115 years (Allendorf and Ryman 2002). Spatially and behaviorally explicit models will greatly improve our understanding of the spatial patterns of inbreeding within and between subpopulations and how inbreeding accumulates in a population due to the landscape and social behavior.

Two issues need to be resolved in order to use individual-based models (IBMs) to understand the effects of inbreeding depressions on a population's viability. First, there is a paucity of knowledge available on the affects of inbreeding on populations in the wild. Second, a method to compute kinship/inbreeding coefficients for large pedigrees needs to be developed. Several researchers offer possible solutions for the dearth of inbreeding information available for wild populations. Ralls and Ballou (1983) suggest important genetic information may be obtained from the analysis of pedigrees of threatened species held in zoos. More recently Laikre (1999) echoes this solution. Frankham (1995) suggests the genetic behavior of domestic and laboratory species could provide insight for species of which limited data is on hand.

Allendorf and Ryman (2002) point out several problems with using captive data, including differences in severity and even in vital rates affected by inbreeding depression between captive and wild individuals. Also, there are little empirical data available estimating the magnitude of the effects as a function of the values of inbreeding coefficients (Allendorf and Ryman 2002). Further, inbreeding depression seems to vary among taxa, environments, and even populations of the same species (Keller and Waller 2002) making generalizations difficult. There should, however, be little consequence of using captive, domestic, or laboratory data in place of natural species data, provided a range of values are used and different combinations of effects on vital rates used. One advantage of simulation modeling is that it is a method for handling uncertainty (Starfield et al. 1995). Because the simulation is run repeatedly with different values for those parameters characterized by uncertainty, a variance in the output or results is obtained. This at least gives some idea of the range of values that can be expected and for which variables the model results are the most sensitive.

As for the second issue, during the course of single simulation run of an individual-based model, thousands of individual animals will be created and a large pedigree generated. As discussed in Section 3.2.2, there is a practical issue regarding the use of kinship coefficients. Methods developed for their computational calculation have long execution times and excessive memory requirements on large pedigrees, making them impractical for IBMs. To overcome this obstacle, Backus and Gilpin (2002) have developed an efficient algorithm that can be easily incorporated into an IBM written in an object-oriented programming language. In this algorithm, each individual has as one of its data attributes a *Vector* object called kinshipWith. The kinshipWith stores all the kinship coefficients between that individual and all living members of the population. As new animals are born and other animals die, the kinshipWIth Vector objects of all the current living members get updated. Removing the kinship coefficients of the deceased animals helps keep memory storage to a minimum. The details of the algorithm can be found in their paper titled *An Efficient Algorithm for the Additive Kinship Matrix*.

CHAPTER 4

INDIVIDUAL-BASED MODELING AND CONSERVATION GENETICS

4.1 Introduction

Small, isolated populations are prone to the loss of genetic variation through the mechanism of genetic drift. Because loss of heterozygosity is detrimental to a population's viability (see Section 2.1.3), the maintenance of genetic variation is a primary conservation genetic goal (Hedrick and Miller 1992). Since heterozygosity loss is correlated with the increase of population-level inbreeding, the study of this phenomenon can be focused on either the rate of loss of genetic variation caused by random genetic drift or the increase in the level of inbreeding caused by limited mating opportunities.

In the past, quantification of the genetic status and health of a species usually has taken one of two primary scientific approaches: empirical or (mathematical) theory. The key variable is the rate of loss of genetic variability or, equivalently, the rate of increase of average inbreeding in the population. For reasons explored below, both of these rates can be approximated by the same variable, $1/N_e$, where N_e is called the genetic effective population size. The lower the value of N_e, the greater the rate of genetic decline.

The genetic management objective must be stated in relative terms, as the absolute amount of inbreeding depends on the measure chosen to assess it. Thus, a manager might strive to retain 80% of the baseline heterozygosity, or, if she or he focused on inbreeding, the goal might be to keep average inbreeding below 20%. In either case, this involves some particular lower limit on the variable N_e.

There are problems, however, associated with the application of the two commonly used approaches mentioned above. In particular, these approaches can be somewhat limiting in application for species of conservation concern. Individual-based modeling provides a method for quantifying the genetic status of a population that avoids the problems and limitations of these more conventional methods. In addition, individual-based modeling offers insights and a more in-depth understanding of the nongenetic forces influencing a population's genetic processes not provided by either empirical or theoretical methodologies.

After discussing some of the limitations and problems associated with the more popular methods, this chapter highlights the advantages of using individual-based modeling to estimate the key variables required for assessing and maintaining a population's genetic health. It also reviews some examples from previous individual-based simulation models. Finally, it closes with a discussion of an individual-based model (IBM) developed to show how such a model provides a better understanding of the genetic processes and structure of small populations than conventional methods.

4.2 Conventional approaches for analysis of genetic variation

4.2.1 Empiricism

Loss of heterozygosity can be studied by looking directly at the genes themselves. One empirically based method involves collecting samples of individual DNA and then using a particular class of enzyme to 'amplify' sections, or loci, on the DNA strand (Amos and Hoelzel 1992). The same sections are then amplified on samples from other individuals, allowing comparisons to assess genetic variation. Such snapshot information is fundamentally about the present, but inferences can often be made about past population structure. For example, the loss of heterozygosity between older and younger animals can give insight about the rates of heterozygosity loss, and the distribution of rare alleles can indicate something about animal movement between neighboring populations. Advances in molecular biology, the ease of gathering genetic information, and the detail of the information obtained have expanded rapidly, making these studies quite feasible.

Molecular genetic data have been the basis of a number of recent investigations. Andayani et al. (2001) examined the adequate number of conservation management units (Evolutionarily Significant Units) necessary to maintain genetic diversity in the silvery gibbon (*Hylobates moloch*). Beebee and Rowe (2001) identified recent population bottlenecks in the natterjack toad (*Bufo calamita*). Mech and Hallett (2001) estimated migration rates and corridor effectiveness for a closed canopy specialist species, the red-backed vole (*Clethrionomys gapperi*), and a habitat generalist species, the deer mouse (*Peromyscus maniculatus*). Gerlach and Kerstin (2000) determined population genetic subdivision caused by human-induced landscape fragmentation in the bank voles (*Clethrionomys glareolus*). Lu et al. (2001) assessed the current levels of genetic diversity and historic gene flow in the giant panda (*Ailuropoda melanoleuca*). Schwartz et al. (2002) determined the effects of dispersal on population dynamics in the Canadian lynx (*Lynx canadensis*).

For several reasons, empirically derived patterns of recent and current population genetic structure do not necessarily provide information about future genetic patterns. First, data collected over a short time interval in comparison to a species' generation time may not accurately reflect the rates of heterozygosity loss. To be able to legitimately extrapolate empirical rates of, say, heterozygosity loss, base data covering a long time period is required. If historical information were unavailable, it would take a minimum of two generation times before even an approximate assessment could be obtained. (A generation time is defined as the number of years necessary for an individual to reproduce and replace itself with sexual mature offspring): This could mean decades for many of the species of large-bodied individuals. Data collected during shorter time scales will not produce a valid sample to estimate heterozygosity loss.

Next, current assessments and inferences about past events do not necessarily yield accurate predictions of future events. This is because empirically based projections become unreliable for situations other than the one in which the data were collected. This shortcoming is important to keep in mind, especially for species of conservation concern. These species are most likely of concern due to rapid changes in their habitat, for example, loss or fragmentation. This habitat change means many aspects of the population's genetic and demographic structure could be out of equilibrium. (Here demographic nonequilibrium refers to a population experiencing continual decline or magnified oscillations in growth rates as a consequence of their altered habitat. Habitat fragmentation, for example, might make it more difficult to find mates. Genetic equilibrium is discussed below.) Finally, if data were collected under conditions that affect only part of the population for a period of time, extrapolation of these data to the whole population will not yield accurate predictions for the entire population (DeAngelis et al. 2001).

4.2.2 Population genetics theory

Theoretical modeling is an alternative to empirical approaches to predicting rates of inbreeding and heterozygosity loss in a population. Some theoretical models assume effectively an infinitely large population such that only selection, migration, and mutation are important forces. The relative temporal scale of these models is long, and equilibrium conditions can safely be assumed. For questions of conservation concern, however, the theory must address heterozygosity loss in populations of small, finite size subject to genetic drift, and possibly existing in various states of disequilibrium. In this section, the roles played by selection, migration, and mutation in shaping a population's genetics are ignored, and focus is placed on theoretical modeling as it pertains to a small population of finite size.

Often used in applications are theoretical models of heterozygosity loss based on the effective size of a population. The effective population size, N_e, is the theoretical geneticists' method of dealing with populations outside of the controlled laboratory setting. In natural settings, the criteria of being a genetically ideal population are rarely met. Deviations from the 'ideal' can be caused by a species' behavior, ecology, and spatial structure. The theoretical geneticist typically deals with the deviations by abstracting their effects into a single parameter, the genetic effective population size, N_e. Technically, N_e is defined as the size of the 'ideal population' (see Section 2.1.3 for exact definition of ideal population) that would experience the rate of heterozygosity loss, due to random drift, as measured or otherwise determined in a real population. More precisely, it is defined as the number N that when H_{t+1} and H_t are known, solves Wright's model of heterozygosity loss

$$H_{t+1} = H_t[1 - 1/(2N)], \tag{4.1}$$

where H_t and H_{t+1} are heterozygosities in the current and next generation.

The N_e concept can be used to determine directly the number of individuals needed to maintain enough genetic variation to ensure future adaptability to environmental change (Lande and Barrowclough 1987). It is most frequently used, however, indirectly to help determine the rate of heterozygosity loss experienced by a population. The rate of loss is obtained by recursively solving (4.1) back to t=0 to yield the equation:

$$H_t = H_0 (1 - 1/(2^* N_e))^t, \tag{4.2}$$

assuming $H_0 = 1$, equation (4.2) becomes

$$H_t = (1 - 1/(2^* N_e))^{t} \text{ or } N_e = 1/(-2e^m + 2), \tag{4.3}$$

where $m = 1/ H_t {}^*d H_t /dt = d\ln(H_t)/dt$. If one has an estimate of N_e, then (4.3) can be solved for m, which equals the rate of exponential decay in heterozygosity and has units 1/time.

There are several problems associated with using N_e to calculate heterozygosity loss in real-world populations. First, the method relies on knowing the value of N_e. N_e, because it is a concept, is not a directly measurable population variable. One is, therefore, forced to estimate N_e for a population. From equation (4.3), one sees that it can be estimated from $\Delta H = (H_t - H_{t-1})$. One must ask, however, is this really any different from a straightforward empirical extrapolation? In fact, it is not. N_e is only a comforting fiction related to slope of an empirical fit to the data and, hence, is subject to the same limitations discussed in Section 4.2.1. Specifically, one must be concerned that historical information is not guaranteed to be a good predictor of future loss. The current population could exist in a substantially different situation than in the past. For example, for a population whose habitat has only recently been significantly altered, the alteration could be limiting juvenile dispersal or increasing juvenile mortality, both of which could increase the rate of heterozygosity loss in the population. Estimates of ΔH based on data collected prior to or immediately after the habitat alteration would underestimate the rate of loss experienced by the population in the future.

To avoid calculating ΔH researchers have developed formulas to estimate N_e based on other variables. The problem with this approach is the value of N_e becomes dependent on the formula one chooses to use. Harris and Allendorf (1989) evaluated eight different theoretical formulas for N_e. Each one relied on various demographic measurements, such as number of breeding males and females and average lifetime number of successively breeding offspring. Each formula yielded a different approximation for N_e, and all approximations of the heterozygosity loss using N_e were somewhat inaccurate, the degree of inaccuracy varying between formulas. They also found that some of the formulas required variables difficult to collect or estimate from field studies. It should be noted, attempts to compute a meaningful N_e based on empirical features, other than the actual heterozygosity loss of a population, are in addition to the limitation inherent in the formula chosen to estimate N_e, also subject to the same problems discussed in the Section 4.2.1.

The second difficulty associated with using N_e to calculate population heterozygosity loss for real-world populations is that the method relies on equations like (4.2) that are derived using assumptions of equilibrium. The problem with the equilibrium assumption lies not in the assumption itself, but rather with assuming equilibrium conditions when they do not exist. Genetically, equilibrium can refer to many things depending on exactly what is being examined. For example, equilibrium can refer to individual gene frequencies being constant from generation to generation or to the rates of loss (selection) and increase (mutation) of genetic variability being in balance. Equilibrium can also refer to many things other than the genes themselves; for example, equilibrium may refer to demographics or the environment. Here demographic equilibrium can refer to births in balance with deaths (constant population size) or equal sex ratios, and environmental equilibrium can refer to stable or an unchanging world. These types of non-genetic equilibriums can have a marked effect on the genetic processes of a population and are therefore, an equally important consideration when assessing a population's genetic status.

Assuming equilibrium conditions is a powerful mathematically technique. When this assumption is made, it allows one unknown value to be solved for in terms of a known value. Also, it simplifies matters by eliminating variability and producing a single constant value. In essence, when one chooses to assume equilibrium, what is implied is there is very little change in the environment, population demographics, and gene frequencies, so, 'on average', for the population as a whole, the rate of loss of heterozygosity or increase inbreeding is some constant value. This assumption can lead to erroneous conclusions when not appropriately used.

For newly fragmented populations of conservation concern, the assumption of environmental and demographic equilibrium is certainly false because the population has become a matter of conservation concern most likely due to changes in its habitat (either anthropogenic or climate driven) and has not yet adjusted demographically to its new environment. Even if those two factors have stabilized, it is unlikely that genetically the population has reached any equilibrium, because a long time is required for a population to reach the equilibrium state (Varvio et al. 1986). Hence the application of theoretical results to newly fragmented populations should be undertaken with caution.

Beyond specific problems with N_e, in general, the standard approach of theoretical population genetics to real-world problems will always be problematic. Reliance on closed form mathematics necessitates the making of simplifying assumptions for tractability and solvability. Though no modeling exercise is free of assumptions, these assumptions and simplifications can limit their applicability, particularly to real phenomena. These assumptions adversely affect real-world theoretical application for the following reasons: (1) Unless inside a controlled laboratory setting, the assumptions are usually not met, bringing into question the validity or the confidence in the results of applying such methods. For example, application of formulas derived under an assumption of genetic equilibrium can lead to erroneous conclusions for populations in non-equilibrium conditions. (2) Simplifications, such as the use of N_e, can lead to model inputs not usually collected or that are difficult to collect from field research (Harris and Allendorf 1989). The accuracy in the estimation of the needed inputs can again question the validity and confidence in the application of such methods.

Further, theoretical population genetics is limited in its applicability to real-world problems because it only deals with the genetics aspect of the problem. It can, thus, overgeneralize a complex problem. The true population size needed to forestall inbreeding depression and retain enough genetic variation for future adaptability is based on a multitude of factors many of which interact with each other (Gilpin and Soule 1986; Mills and Smouse 1994; Lacy 1997).

Finally, real-world applicability is limited because it is difficult, if not impossible, to include geographically realistic data in theoretical models other than by gross abstraction of the landscape. Such landscape abstractions may include assuming the landscape is homogeneous or, if assumed to be heterogeneous, the heterogeneity can be categorized into two types of patches: suitable versus unsuitable patches or high versus low quality patches. Another technique is to only implicitly include the landscape. Good examples of this technique are island models of population genetics used for geographically structured populations, or metapopulation models. In these models, the population is divided into subpopulations, and exchange of individuals between subpopulations is some constant (or sometimes distance dependent) variable that is not a function of the actual landscape. The division of a population into subpopulations with the exchange of individuals 'implies' subpopulations distributed on the landscape with individuals moving between them, but neither the division into subpopulations nor movement of individuals is an explicit function of the landscape itself. The landscape can have a direct impact on a population gene dynamics by presenting impedances to movement either explicitly in the form of physical limitations (e.g., food availability) and barriers (e.g., rivers) or implicitly in the form of imposed limitations (e.g., increased human-caused mortality).

4.3 Individual-based modeling

4.3.1 Advantages of approach

The use of simulation is not new to population genetics research. What makes IBMs different from past simulations is their underlying premise. IBMs are based on the idea that the properties of an ecological system can be derived from the properties of the individuals making up the systems, the relationships between the individuals, and the interactions of the individuals with each other (Lomnicki 1992; Saarenmaa 1988; Huston et al. 1988; Palmer 1992). Because each individual organism is, in many important respects, unique, the effectiveness of individual-based modeling comes from their ability to simulate individual variation in physiology, behavior, and other key dimensions. (For further discussion of IBMs, see Section 2.3.2). Individual-based modeling has several benefits to offer the study of population genetic processes. These benefits are as follows:

1. Minimizes simplifying assumptions: Most populations in the wild do not adhere to the classical populations genetics 'ideal' view, and real populations may violate several

assumptions simultaneously. Unconstrained by the need to ensure solvability, IBMs keep simplifying assumptions to a minimum, hence providing an advantage over classical mathematics for real-world application. In addition, this increased level of complexity permits a more realistic representation of the actual population's genetic processes.

2. Permits the inclusion of behavioral aspects into the model because the individuals of a population are represented in the IBM: Frequently, animals possess behaviors that cause distinct patterns of mating and dispersal. For example, animals can exhibit sex-biased dispersal, inbreeding avoidance tactics, and dominant mating strategies (strategies where some individuals have an advantage in obtaining mates and contribution to the next generation). These patterns have genetic consequences for a population (see McLellan and Hovey [2001] and Dobson et al. [1997]). Likewise, social biology can have a profound influence on gene dynamics, especially for highly colonial species like the black-tailed prairie dog (Sugg, Chesser, Dobson, and Hoogland 1996). In classical population genetic models, behaviors for minimizing inbreeding are ignored. This can lead to an over- or underestimation of amount of inbreeding present in a population (Sugg et al. 1996). This is likewise true for the other behaviors mentioned.
3. Facilitates incorporation of the population's pedigree into the model: Knowledge of the pedigree is quite valuable when it comes to modeling population genetics for the following reasons:
    a. It allows inbreeding coefficients of population members to be calculated. Having access to the individual inbreeding coefficients allows one to directly estimate change in genetic diversity over time instead of relying on N_e or fixation indices. Difficulties with estimating loss of hetereozygosity by calculating N_e have already been discussed above.
    b. It allows the distribution and abundance of founder alleles to be tracked. Allelic diversity is very important; for example, loci associated with disease resistance often have a large number of alleles (Allendorf and Ryman 2002), and increased susceptibility to pests and parasites is associated with low genetic variation

    (Frankam 1995). Tracking allelic distribution and abundance, as well as calculating a population's heterozygosity loss, can be outputs of the same model.

   c. It allows individual variation in levels of inbreeding to be modeled. There has been very little theoretical or empirical research done on the role individual variation in inbreeding plays in determining a population's overall genetic health (Keller and Waller 2002). Similarly, knowledge of the pedigree means knowledge of coancestry is maintained. This is important when the model involves long time periods. Sugg et al. (1996) found that it was possible for coancestry to develop more quickly than inbreeding within social groups and that the effect on the inbreeding coefficient and total genetic variation did not appear until later generations.
   d. It provides a way inbreeding depression can be included in Principle Viability Analysis (PVA) studies because necessary information for the calculation of the inbreeding coefficients is available. Laikre (1999) notes that very few PVAs consider inbreeding depression, and when genetics are included at all, in threatened species recovery plans, it is done so rudimentarily (Mills and Allendorf 1996).

4. Allows for the inclusion of other considerations besides genetics, such as spread of disease and extremely low census numbers to be model as well: These other considerations can influence management decisions. The importance of including both demography and genetics is discussed more fully below. The spread of disease can be an important consideration when making decisions about the level of connectivity desired between populations, or whether or not to translocate individuals from one population to another. In individual-based modeling, many concerns that can influence the demographic as well as the genetic health, of a population can be concurrently addressed.
5. Easily accommodates the integration of demography, genetics, and their interactions into a single model: Research in population viability stresses the interaction between genetic, demographic and environmental processes (Gilpin and Soule 1986; Mills and Smouse 1994; Lacy 1997). Gilpin and Soule (1986) introduced the concept of the 'extinction

vortex' to emphasize that the demographic, environmental, and genetic factors impacting small populations do so synergistically and have the potential to drive a species to extinction. Despite this recognition of the synergistic effects of these factors, many studies on the extinction of small populations have focused on single factors, usually either genetics or demography. Early work focused on genetics (Soule and Wilcox 1980; Schonewald-Cox et al. 1983) and later work focused on demographic factors (see Chapter 3). Mills and Smouse (1994) denounced this dichotomy and showed the extinction probability of a population is not dependent on an either/or consideration of the factors, but rather both factors and the interaction between them. After completing a PVA on an Australian marsupial, Lacy and Lindenmayer (1995) likewise criticized the bifurcated view of genetics and demography. Population demography and genetics equate to the collective fates of the individual members of the population.

6. Facilitates linkage with geographically explicit data: In theoretical population genetics, geographical structure refers to a subdivided population. To a geographer, the geographical structure is much more complex. Besides the physical geographic features like rivers and mountains, that can prevent movement or dispersal, there are also more subtle variations in the geographical landscape that can influence the movement of individuals. An example of geographic variation is mortality risk. Individuals may experience different mortality risks as they move through the landscape in search of food and mates. Like demography and genetics, gene flow equates to the collective movements and mating of individual population members. IBMs, especially when they are developed using object-oriented design principles, can be integrated with spatially explicit geographic information using GIS. By keeping track of individuals and how they move on the landscape, geographic influences on the dynamics of a population's genetic processes can be modeled.
7. Provides a means for including more genetic complexity: With object-oriented programming languages, it is possible to create individuals with loci more complex than autosomal with two alleles, for example, linked, epistatic, or multiallelic loci could be given to each individual. This is very important, particularly in terms of modeling the

consequences of inbreeding, since the exact genetic mechanisms responsible for inbreeding depression are still not fully understood (see Chapter 3). Futuristically, as advances in molecular techniques lead to new understanding of genomes, a method for utilizing the new knowledge to aid management decisions concerning endangered or threaten species will be need. Individual-based modeling will prove to be such a method.

4.3.2 Advantages of approach for conservation

IBMs are particularly well suited for addressing the types of population genetic questions of interest to conservation biology. This is true for several reasons. First, in contrast to retrospective empirical methods, individual-based modeling is forward looking. As discussed in Section 4.2.1, current assessments and inferences about recent past events do not necessarily expose information about the processes involved. This is because empirically based projects become unreliable in situations other than the one in which the data were collected. This is an important limitation to keep in mind for species of conservation concern. These species are most likely of concern due to rapid changes in their habitat, for example, loss or fragmentation. The loss or fragmentation is often due to recent anthropogenic causes. These conditions produce a state of nonequilibrium in a population. As discussed in Section 4.2.2, analytical approaches often assume some form of genetic and/or demographic equilibrium and, therefore, are not applicable to populations in some state of disequilbrium: genetic, demographic, or environmental (Lande and Barrowclough 1987). IBMs, because they do not make any assumptions of equilibrium, are well suited to answer these population genetics questions because they are particularly robust with regard to nonequilibrium features of gene dynamics.

Next, individual-based modeling allows individual genetic parameters to be used. Three commonly utilized parameters for population genetic analysis are heterozygosity, inbreeding, and migration (symbolically: H, F, and m). These parameters characterize the whole population, and the individual members of the population share in these states in an undifferentiated manner. Other population genetic parameters are defined at the level of the individual, here indicated by the subscript i, such as h_i and f_i, where the former is the heterozygosity of the individual averaged over some set of loci, and the latter is its inbreeding coefficient (Note: $h_i = 1- f_i$). From a set of individual-level genetic measures, all of the population measures can be calculated. The individual information, however, offers a better assessment of a population's genetic health and elucidates the population's genetic processes. This deeper insight permits more precise management action.

In addition, representation of each individual organism in the model likewise means variation between individuals can be included. In fact, for an IBM to be effective, it must somehow simulate individual variation. Populations of conservation concern are frequently small in size. This smallness causes individuals and individual variation to have a greater impact on population-level dynamics, evidenced by the statistical property of smaller sample sizes having larger variances. The effect of individual variation on a population's genetic health has not been explored (Keller and Waller 2002), but the inclusion of individual variation has been shown to affect population persistence (DeAngelis et al. 2001). It is therefore reasonable to think the same would hold true for population genetic processes. As mentioned in the previous paragraph, having individual information provides a better assessment of a population's genetic health and permits more precise management action.

Inclusion of individual variation also means individuals can be linked to the landscape in which they inhabit. Unless held in captivity, individuals exist in a landscape. The landscape then becomes a source of variation among individuals, as each will occupy a single position. This is particularly important when individuals experience different vital rates depending on location; for example, with grizzly bears, mortality risk is dependent on the proximity to human landscape features (Mattson et al. 1996). Linking individuals to their landscape permits an individual's contribution to population-level processes, like population genetic processes, to be fully realized.

4.3.3 Previous genetic individual-based models

Using simulations is not a new technique in population genetic investigations. In fact, some of these simulations, by definition, could even be characterized as being individual based. The purpose of this section is not to provide an exhaustive list of all IBMs used in conservation population genetics. Rather it provides a selected sample of previous works illustrating some of the features discussed in the previous section. Specifically, this section considers for discussion the simulation models of Harris and Allendorf (1989), Starfield et al. (1995), and Katawa (1995, 1997).

Harris and Allendorf (1989) developed a simulation of grizzly bears in the Northern Rockies that could qualify as being a genetics individual-based model with no spatial representation. The researchers did not refer to their model as being individual based, but because they designed their computer program to follow the history of each individual bear from birth until death it very much was. Further, what really makes their model individual based is that mating success and mortality were not totally random events. Reproductive success and mortality were functions of an individual's age and/or sex and, therefore, changed throughout the life of the bear. Variation in rates between individuals and within an individual throughout its lifetime is what distinguishes IBMs from other stochastic simulations.

An interesting feature of Harris and Allendorf's research was their use of the average inbreeding coefficient in the calculation of the 'correct' value of heterozygosity loss. Their model, because it was individual based, gave individuals the necessary attributes to generate a pedigree and calculate the inbreeding coefficient of each new offspring. Knowledge of individual inbreeding coefficients permitted the average inbreeding coefficient of the population, F_t, to be computed each generation, t. The researchers determined the 'correct' value of heterozygosity loss using the relationship $H_t = 1 - F_t$. Surprisingly, despite their recognition of the ability of simulation to estimate heterozygosity loss and their findings that no published formula of N_e yielded the correct answer (see Section 4.2.2), they were resolute about the use of N_e by management. Their research conclusion, instead of suggesting the greater use of simulation to estimate heterozygosity loss, was to suggest a better way to compute N_e for a population with complex behavior is to use a process model to estimate the needed inputs to a selected N_e formula.

Even though Harris and Allendorf failed to recognize the value and potential of using an IBM to estimate loss of heterozygosity directly instead of indirectly using N_e, their research still illustrates a very important point: the use of the inbreeding coefficient as a direct measure of heterozygosity. In addition, their research provided an illustration of incorporating human affects. By including hunting strategies, Harris and Allendorf implicitly accounted for anthropogenic influences on population dynamics, which ultimately affects the population's genetic dynamics.

Starfield et al. (1995) simulated a small, wild population of lions in South Africa. Like Harris and Allendorf they did not specifically refer to their model as individual based despite the fact it possessed some characteristics that would qualify it as such. Unlike the previous example, however, these researchers recognized the value in generating a pedigree and using it to determine heterozygosity loss. Starting out with five founder individuals, each individual having 100 loci, and each locus having two distinct alleles, they simulated the population for 100 years. An aspect worth mentioning about the model of Starfield et al. is its inclusion of a behavioral dimension. Social biology can have a profound influence on a population's genetics. The behavioral aspect was accomplished by including in the model lion prides and territories within a reserve. The pride plays a key role in the breeding system of lions, as a female lion must be a member of a pride before she has the opportunity to mate. The use of distinct units and territories by Starfield et al. likewise implies a spatial structure to the overall population similar to the implicit spatial structure created when assuming a metapopulation structure. They also created an implicit spatial structure by having only the lions that wander out of the reserve experience a certain risk of human-induced mortality. The inclusion of a spatial dimension is another noteworthy aspect of their model. Finally, the last feature in their model warranting discussion was their simultaneous consideration of both loss of heterozygosity and allelic diversity. This was accomplished by including 100 loci as attributes of each lion. Each locus associated with each of the founders was assigned a unique allele value and existing of these alleles monitored throughout the simulation.

Kawata (1995, 1997) developed spatially explicit IBMs of nondistinct mobile organisms. Like Harris and Allendorf (1989), the purpose of Kawata's 1995 paper was to explore the accuracy of N_e, in this case, Sewell Wright's neighborhood effective population size, $N_e = 4\pi\rho\sigma^2$, where ρ equals the density of the population and σ equals the root mean dispersal distance. Kawata, because of the comparison with the neighborhood effective population size, developed the individual behavior in the model to mimic the assumptions used by Sewell Wright in the formulation: dispersal being random in direction with distance being normal distributed with mean zero, random mating and a closed population. In his 1997 paper, he uses a similar model to examine the loss of genetic variability in a fragmented, continuously distributed population.

Fragmentation is accomplished by placing barriers and corridors in the organisms' landscape. Individuals cannot disperse over a barrier and can only move through a corridor. Explicitly, he uses the model to examine the effects of population subdivision, dispersal distance of offspring, and migration rates on genetic variability as measured by H_I, H_S, and H_T. Though his studies seem to be predominantly concerned with matching the assumptions of mathematical formulations, Kawata does recognize the value of using individual-based modeling to estimate genetic variability and loss directly instead of the round about way discussed in Section 4.2.2, i.e., using N_e.

Kawata (1997: 236) also recognizes more complicated IBMs can be developed for conservation genetics stating,

> [An IBM] can incorporate more concrete geography and realistic data for wild animals, such as complex demography, social behavior and dispersal distance, and it can be used to estimate the effect of habitat destruction on genetic variability.

Of particular interest is his mention of concrete geography. The use of real geography can be referred to as being geographically explicit to distinguish it from the spatially explicit concept. Geographically explicit models are necessarily spatially explicit, but not vice versa. To date, I am not aware of any geographically explicit population genetics models that have been developed.

4.4 Illustrative examples

To illustrate the effectiveness of using individual-based modeling and geographically explicit information to quantify and assess the changes in a population's genetic status, an IBM for a hypothetical animal population that inhabits an imaginary landscape was developed. The IBM forms the basis for two series of simulation experiments. In the first series of experiments, the importance of including individual variation, animal behavior, explicit geographical information, and more complex genetic aspects (linked loci) is investigated. In the second series, the role geography plays in determining a population's genetic health is explored in greater depth by considering three different geographically explicit landscapes. This section discusses the IBM developed and the results of the simulation exercises.

4.4.1 The population

For the IBM a population of nonspecific, sexually reproducing diploid animals is considered. These animals become mature and capable of mating at age two and have a maximum live span of eight years. In accordance with having the sexual maturation age set at two, a generation equals four years. Juvenile survival is 5% lower than the adult survival of 80%, and there is no difference in survival between males and females.

Each individual animal in the population is given a chromosome pair made up of ten loci. Each locus has two alleles that can have either a plus one or minus one value. For linked loci, five pairs of loci are considered. The alleles in the first locus in a linked pair can have either a plus or minus one value, and the alleles in the second locus of the linked pair can have either a plus or minus two value. The adults in the initial population are considered founders and given unique alleles by using their ids in combination with the value of the allele. If a founder had an id equal to 12, for example, its possible alleles would be (12,1) or (12, -1); for linked loci, possible alleles in the first locus would be (12,1) or (12, -1) and possible alleles in the second locus would be (12,2) or (12, -2). Giving founder's unique alleles allows both loss of heterozygosity and change in allelic diversity to be recorded each generation simultaneously in the same model.

4.4.2 Explicit landscapes

The landscapes used are shown in Figure 4.1. The first landscape, landscape 1, represents a situation where the population's entire range has been set aside for conservation. No hunting or other sources of mortality are present. There is still, however, an increased risk of mortality in proximity to human features on the landscape, either roads or concentrations of people, such as might occur at lodging or other tourist/recreation facilities. Mortality risk is twice as high as natural mortality in these areas.

The landscapes 2 and 3 represent the case where only part of the animal's range has been set aside for conservation. In landscape 2, two thirds of the land is managed for conservation. In protected areas, mortality is the result of only natural causes. In unprotected areas, mortality risk is three times greater, due to hunting, poaching, or malicious intent. The risk associated with human features is the same as with landscape 1, that is, twice as high as natural

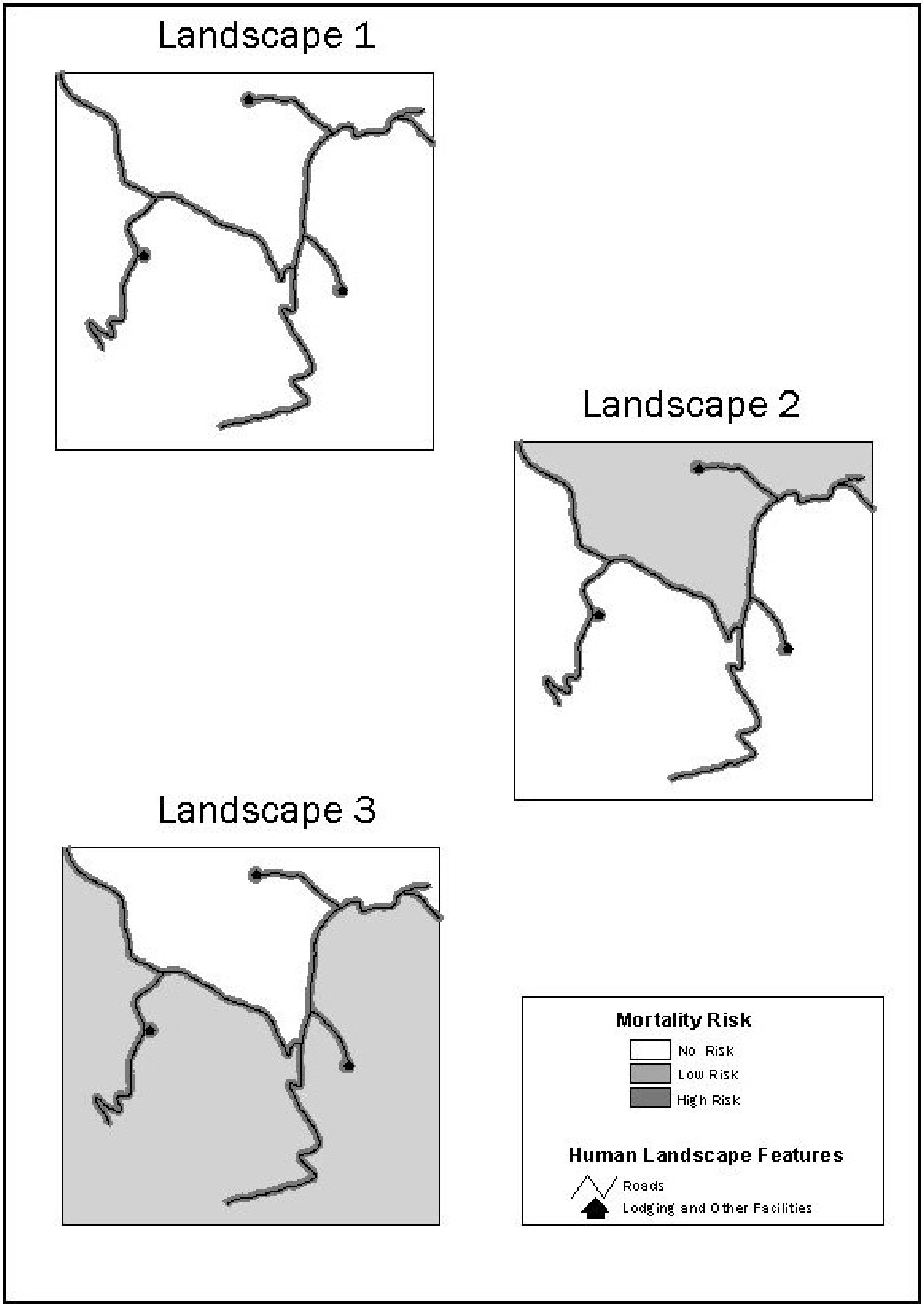

Figure 4.1. Geographically explicit landscapes used in simulations. Simulation exercises illustrate the affect of such landscapes in population genetic models.

mortality. The third landscape, landscape 3, is similar to landscape 2, except only one third, instead of two thirds, of the population's range is protected and set a side for conservation.

4.4.3 Model design

The IBM was created using the object-oriented programming language, Java™ 2 SDK, Standard Edition, Version 1.3. Object-oriented languages, such as Java, provide the architecture for creating simulations that are composed of independent objects that interact with each other. In this regard, they are ideally suited for the creation of IBMs because each individual in a population can be represented in the simulation (model) as an individual object in the program. The programmer, however, does not have to write a separate block of code for each object in the program. Each object, instead, gets created, or in technical terms 'instantiated', from a class. One can think of a class as a blueprint for describing the state of the object and the actions an object can perform. A class for an animal, for example, might contain the variable age as a state descriptor and the action of growing older as a method. Figure 4.2 shows the eight classes developed for this IBM and their relationship to each other. The classes created for the IBM can be broken down into three functional categories: utility, animal and animal management, and simulation control and display classes. The classes contained in each of these categories are discussed in detail below.

4.4.3.1 Utility classes

The two utility classes are *Demography* and *Genetics*. These classes can be viewed as library classes because they consist of a set or library of demographic and genetics methods that can be used in a population simulation model. They are similar to Java's *java.lang.Math* class that provides a set of mathematical methods. The two classes were created such that they are not specific to these particular modeling exercises and, therefore, can be used as part of other, future modeling efforts as well. All the methods in these classes were coded as static methods. This means the methods belong to the class and a class object does not have to be instantiated in order to make the methods accessible. To access static methods, one must type the class name followed by the method name, for example, Genetics.calcKinship() or Demography.calcStableAgeDist(). For conciseness, the class name will be dropped during the

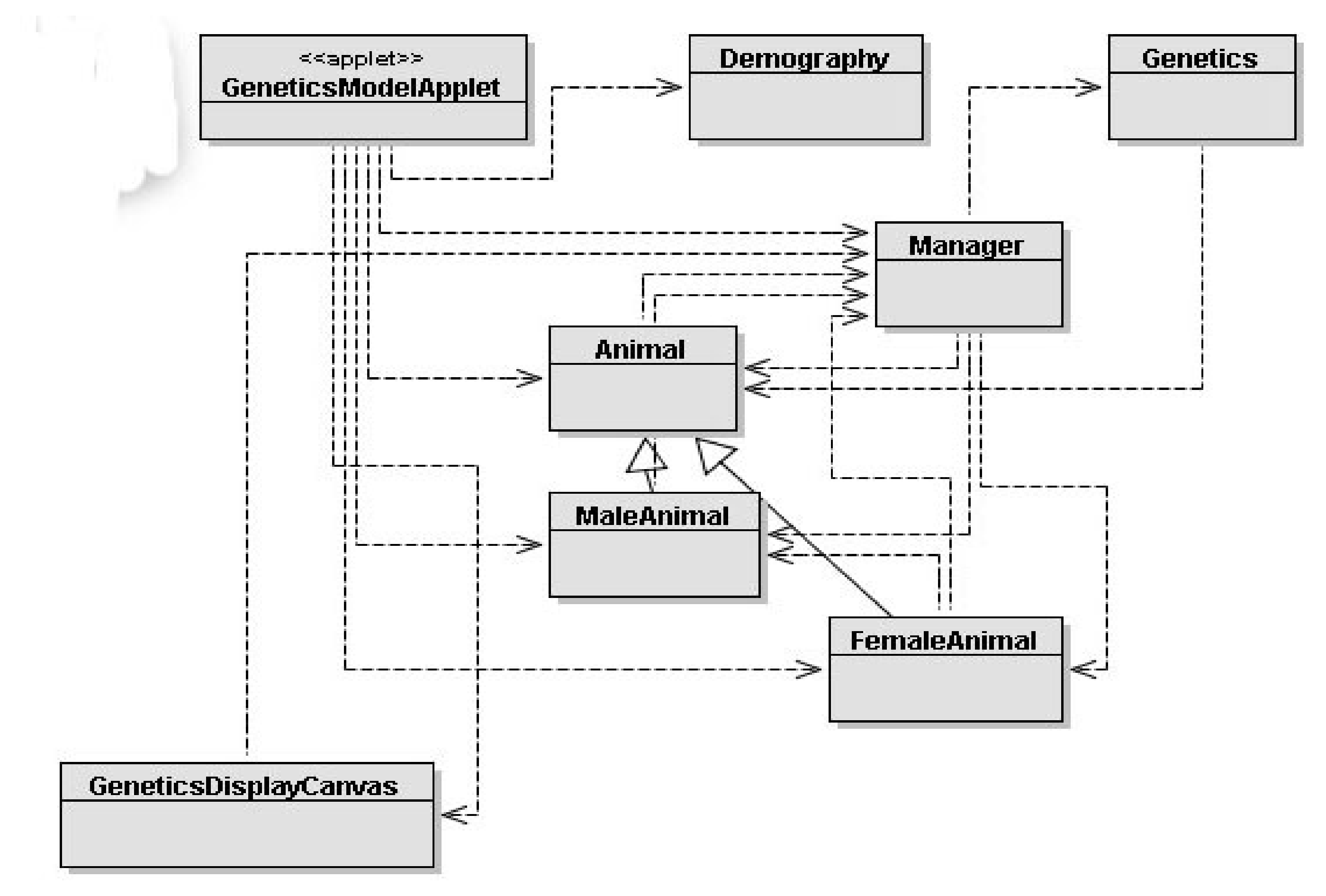

Figure 4.2. Diagram of individual-basedmodel. Dependency is shown with dashed lines and inheritance in solid lines.

discussion.

The *Demography* class contains methods for calculating various demographic parameters for a given population. Currently, it only has one method, calcStableAgeDist(), but more will be added in the future as needed. This method calculates the stable age distribution (number of individuals in each age category) for a population of a given size, with constant adult and juvenile mortality rates, and known maturation age and life expectancy.

The *Genetics* class provides a set of methods for calculating a variety of individual and population-level genetic measures. The methods for calculating kinship coefficients between individuals, calcKinship() and findKinship(), are part of the compressed kinship matrix algorithm of Backus and Gilpin (Backus and Gilpin 2002). The two methods are similar; they both calculate the kinship coefficient among members of the population. The difference in the methods is that calcKinship() calculates the kinship coefficients for an initial population where none of the kinship values are known for any of the individuals. (All adult founders are assumed to be unrelated.) The findKinship() method, on the other hand, determines the kinship coefficient values for all future offspring. (See Chapter 3 for a detailed description of the algorithm.)

The remaining methods provided by *Genetics* calculate population-level genetic measures for a current population. The following list provides a short description of the methods provided:

- meanKinship() – calculates the average kinship coefficient value for the members of the population
- meanHet() – calculates the average number of heterozygous loci for a member of the population
- aveHetVariane() – calculates the variance in individual heterozygosity present in the population
- likeInState() – calculates the average number of allozygous (two alleles are of the same type, but are not from a common ancestor) loci for an individual in the population
- likeInKind() – calculates the average number of autozygous (two alleles are identical by descent) loci per individual in the population
- calcFounderAllelles() – determines the set of unique alleles among the founders of a given population
- founderAlleles() - determines the number of founder alleles not present (lost) in the current population.

- alleleFrequency() – calculates the frequency of each of the founder alleles present in the current population

4.4.3.2 Animal and animal management classes

There are four classes related to the animals and their management: *Animal*, *FemaleAnimal*, *MaleAnimal,* and *Manager*. The *FemaleAnimal* and *MaleAnimal* classes are subclasses of the *Animal* class. Objects instantiated from a subclass, besides getting variables and methods associated with the subclass, also get all the variables and methods associated with the superclass. This reduces redundancy, because it allows those variables and methods common to both female and male animals to be written only once in the superclass *Animal*.

The variables and method for the animal classes can be seen in Figures 4.3 and 4.4. Most of variables and methods in *Animal*, such as the variables age and matSurvival and the methods growOld() and getAge(), are self-explanatory and would be commonly found in any population model. A few features of the classes are, however, worthy of further discussion. First, the access methods like getAge() and getId() return the values of the various variables associated with an animal object; and thus, allow other objects to obtain information about a particular animal object. Though this seems a bit laborious, it is good programming practice to allow only limited access to an object's state variables by other objects.

Second, there are two survival methods, surviveTick() and surviveTick(Object habitat), where habitat is a two-dimensional array representation of the landscape. At the end of each year (a simulation 'tick'), the animal is tested to see if it will survive into the next year. In the first survival method, survival is purely a random event dependent on the value of the survivorship variable, survival. In the second method, survival is a random event dependent on the value of survival and the individual's current location. This is an example of method overloading. With method overloading, a class can have two or more methods with the same name as long as the parameters required for the various methods are different. One advantage of overloading is a reduction in the number of if-then control statements necessary in the program. This is discussed further in the description of the *Manager* class.

Finally, the variables and methods forming the basis for modeling the population genetics call for additional elaboration. In this IBM, each animal has a Java *Vector* object of length ten

Animal

```
Data:
/*static variables for the Animal class*/
    static int count = -1;  //number of animal objects instantiated, is equivalent  to  an animal objects id
    static final int matAge = 2;                // age of maturation
    static final int maxAge = 8;                  // maximum age
    static final double juvSurvival = .8;      // jurvenile survival
    static final double matSurvival = .84;  // adult survival
    static final int numLoci = 10;              // number of loci on chromosome
 /*descriptive animal variables*/
    protected int age;                          // age of animal object
    private int mom;                            // mom's id
    private int dad;                            // dad's id
    public int id;                              // animal's id
   public double inbreeding;                  // animal's inbreeding coefficient
/*survival and genetic related variables */
    public double survival;                   // animal's current risk of death based on age
    public Vector chromosome;            // single chromosome that contains numLoci loci
    public Vector kinshipWith;             // stores the kinship of animal with all other living animals
 /*position and movement variables*/
    public int animal_i, animal_j;         // the i,j position coordinates of the animal on the landscape grid
     public int centerI, centerJ;            // the i,j posiion of animal's home range center on the landscape gri
    public Manager animalManager;   // manager that manages all activities for the animal

 Methods:
/* methods related to the static variable count*/
    static void resetCount()              // Resets static variable count for each new simulation run
    private static void addOne()        // Adds one to count without instantiation of a new Animal object
    static int getCount()                 // Returns the current value of count.
/*methods for accessing an animal'variables*/
    public void getMom()                 // Returns the id of the animal's mom.
    public void getDad()                 // Returns the id of the animal's dad.
    public void getId()                  // Returns the animal's id.
    public void getChromosome()       // Returns the animal's entire chromosome Vector object.
    public void getLocus(int i)         // Returns the locus at position i in the animal's chromosome.
    public void getGeneOne(int i)      // Returns the first gene in locus at position i in the animal's
                                          chromosome.
    public void getGenTwo(int i)       // Returns the second gene in locus at position i in the animal's
                                           chromosome.
    public void getAge()                 // Returns the animal's current age.
    public void getAnimalI()
/*methods for setting an animal's variables*/
    public void setInbreeding          // Sets the animal's inbreeding coefficient.
    public void setCenter()             // Sets the (i,j) landscape grid coordinates of the center of the animal's
                                          home range.
    public void setI$J()                 // Sets the (i,j) landscape grid coordinates of the animal's current
                                           position
    public void addManager            // Sets the current simulation's Manager object.
/*action methods*/
    public void growOld                // Ages the animal 1 year.
    public void changeSurvival         // Changes juvenile survival rate to adult when the animal matures
    public void surviveTick()          // Randomly determines whether animal dies, based only on age
    public void surviveTick(int[][]habitat) // Randomly determines whether animal dies, based on age
                                              and  animal's current position.
    public void randomMove()          // Empty method overwritten in subclasses.
    public void juvRandomMove()      // Empty method overwritten in subclasses.
    public void draw()                  // Empty method overwritten in subclasses.
```

Figure 4.3. Variables and methods for the *Animal* class.

MaleAnimal

```
Data:
/*static variables controlling movement */
    static int moveDist;                        // maximum move distance for a MaleAnimal object


 Methods:
/* action methods*/
    public void randomMove()                   // Moves adult animal randomly within their home
                                                  range.
    public void juvRandomMove()                // Moves a juvenile randomly from its current position
                                                   to a new position that is less than moveDist in either
                                                   the i or j direction on the landscape grid.
    public void draw()                         // Draws males as a blue circle on the landscape grid.
                                                  The size of the circle is a function of the male's level
                                                  of inbreeding.
```

FemaleAnimal

```
Data:
/*static variables controlling movement */
   static int moveDist;                 // maximum move distance for a FemaleAnimal object
   static int matDist;                  // maximum distance to attract a mate

 Methods:
/*action methods*/
   public void randomMove()// Moves adult animal randomly within their home range.
   public void juvRandomMove()          // Moves a juvenile randomly from its current position to a new
                                            position that is less than moveDist in either the i or j direction
                                            on the landscape grid.
   public void draw()                   // Draws females as  yellow circle on the landscape grid. The size
                                             of the circle is a function of the female's level of inbreeding.
  public void findRandomMate(boolean linked) // Chooses a mate randomly  from a list of mature male
   public void findClosestMate(boolean linked)  // Finds the closest mate within a rectangle centered a
                                                    the females current position with width 2 x matDist.
   public void findOldestMate(boolean linked)    // Finds the closest mate within a rectangle centered at
                                                     the females current position with width 2 x matDist.
   public void createOffspring(MaleAnimal mate) // Produces offspring from the female and her chosen
                                                   mate, parents and offspring do not have linked genes
   public void createLinkedOffspring(MaleAnimal mate) //Produces offspring from the female and her
                                                     chosen mate, parents and offspring have linked
                                                     genes
```

Figure 4.4. Variables and methods for the *MaleAnimal* and *FemaleAnimal* classes. As subclasses they also inherit variables and methods from the *Animal* class.

called a chromosome (short for chromosome pair) where each element in the chromosome represents one locus. Each locus is another Java *Vector* object of length two, where the first element is a maternal gene (allele) and the second element is a paternal gene. In addition, each animal keeps track of its mother and father by storing its mother's and father's ids in the variables mom and dad, respectively. Further, each animal stores all the kinship coefficients between itself and all current members of the population, including itself, in a Java *Vector* object called kinshipWith. The variables mom, dad, and kinshipWith are necessary to implement the compressed kinship matrix algorithm of Backus and Gilpin (2002). This algorithm facilitates the use of kinship coefficients in IBMs for genetic investigations such as this one, because it provides a means by which only the kinship coefficients of the existing population needs to be stored. This reduces the extensive computer memory resources that would be required to keep track of all ancestral and current kinship coefficients for the population over numerous generations. (See Chapter 3 for discussion of this algorithm.) Lastly, each animal stores its inbreeding coefficient in the variable inbreeding. This requires no additional computation because an individual's inbreeding coefficient is equivalent to the kinship coefficient between its parents and, therefore, has already been calculated and stored as an element of the Mom's kinshipWith *Vector*.

The *FemaleAnimal* and *MaleAnimal* classes, being subclasses of *Animal*, inherit all the variables and methods of *Animal* already discussed. In addition, *FemaleAnimal* and *MaleAnimal* contain one variable called moveDist, the maximum distance an indivdiual can move in any one direction in one year, and two methods for moving the animals over the landscape: randomMove() and juvRandomMove(). For this model, the two methods are exactly the same. They were written as separate methods in anticipation of using the model in future simulations of actually animal populations where juveniles might have different movements from adults. The moveDist in *FemaleAnimal* is set at one third that of males. This allows a male territory to possibly overlap several female territories. The draw() method overrides the similar method found in *Animal*. In the simulation display, males are drawn as blue circles. The size of the circle is an increasing function of its inbreeding coefficient, the higher the coefficient the larger the radius of the circle representing the individual. Analogous to members of the *MaleAnimal* class, in the simulation display, females are drawn as yellow circles whose size is an increasing function of the value of the female's inbreeding coefficient.

The methods that distinguish the *FemaleAnimal* class from *MaleAnimal* are the mate selection methods: findRandomMate(), findClosestMate() and findOldestMate(), and offspring creation methods: createOffspring() and createLinkedOffspring(). The selection methods allow for nonbehavioral, as well as different behavioral, mechanisms to be implemented. Nonmating behavior is exhibited with findRandomMate(). In this method, a female animal chooses a mate purely at random from a list of mature males. With findClosestMate() she chooses the male closest to her present location and within a defined area as a mate, and with findOldestMate() she chooses the oldest mate within a defined area centered around her current location. If no males are available, she is unable to mate.

Once a female animal object finds a mate, she invokes one of her two methods for creating offspring. The method chosen depends on the current simulation. The methods are similar in that they both randomly determine the sex of the offspring, and they both produce a chromosome object for the offspring. The offspring's chromosome has 10 loci, where each locus consists of one maternal gene and one paternal gene. For each parent, the probability of transmitting a gene at a locus is equal 0.5. The two methods are different only in the way the offspring chromosome gets determined. When linked loci are present, two consecutive loci get transferred to the offspring as a (linked) pair. The probability of a crossover event is set to be 0.3. Once the offspring's sex and chromosome have been determined, a new animal object is instantiated. If the simulation includes a spatial component, the offspring is given the (x,y) coordinates of its mother's location as a starting point. After two years of moving about randomly, the offspring sets up a territory or home range.

All animals are managed by an object instantiated from the *Manager* class. An instantiated object from the *Manager* class will be referred to as a manager. The manager 'manages' all simulation tasks associated with the entire population. Its first task is to create the initial population for the simulation run. Each simulation run starts with the exact same population, as described under the section Simulation control and display classes. If the simulation run is for a geographically explicit landscape, its next task is to create the landscape in which the animals move around on. It does this by reading in an ASCII file detailing the mortality rates associated with each (x,y) location and storing the rates in a two-dimensional array. It might seem odd that the class managing the population is also responsible for the landscape. For this model, however, the landscape is static in the sense that the increased mortality risk associated with a location is a spatially but not temporally varying variable. The landscape can be viewed, therefore, as variable associated with the population and does not need to be defined as class with its own variables and methods.

In this particular case, it also makes sense from a programming standpoint to have the landscape be a variable of *Manager* class. For every (simulation) year a manager invokes the survivorship methods of the animals in the current population, either surviveTick() or surviveTick(Object landscape). By having the landscape be a population-level variable maintained by a manager object, the manager object is able to check to see if a landscape exists and then invokes the appropriate method in each animal. This requires only one if-then statement in the code for the *Manager* class. If the landscape was an object or a variable in the *Animal* class, the surviveTick() method would have to include an if-then statement. This would mean, since each animal object has it own methods, when the manager invoked the surviveTick() method of an individual animal, the animal would have to check first to see if a landscape existed. This would result in n (size of the population) number of if-then statements as opposed to one in the *Manager* class.

Once the population and, if necessary, the landscape grid have been created, the manager takes care of a few other initial tasks. If the population exhibits anything but total random mating, a manger object will place the adult animals at random locations on the grid and the juveniles in the initial population at locations on the grid relative to their mother's position. Once the population is placed on the landscape, the manager object next instructs all the animals in the population to update their kinshipWith vectors, i.e., calculate their kinship coefficients to all the other members in the population. Finally, the manger object uses Genetics.calcFounderAllelles() to determine and store the founder alleles for the initial population.

After the preliminaries are accomplished, a manager object waits until it is instructed to implement its tick() method. Each (time) step of the simulation can be considered one 'tick' of the simulation clock; therefore, for these exercises, a manager object implements its tick() method

400 times (once a year for 400 years). In tick(), each animal is first directed to move and next to test its survival. The surviving animals are then made to grow a year older and, if mature, given an opportunity to mate. When individuals die or move off the landscape grid, they tell the manager to remove themselves from the population. When a female produces offspring she tells the manger to add a new member to the population. As a consequence of this, the manager object always knows the current population size and can control the number of births allowed each year. In these simulation exercises, the population size is held constant, so that fluctuating population size is not a contributing factor to changes in a population's genetic measures.

After every fourth year, the manager object is instructed by the controlling applet (the applet is discussed below) to update and store the population's genetic measures: average heterozygosity, mean kinship, variance in average heterozygosity, average autozygosity, and percentage of lost founder alleles. It stores the results calculated for each measure in a separate array. These arrays are then accessed by the controlling applet's graphing object to displayed on the screen as a line graph. The *Manager* class provides on additional summary function in its end-of-generation update method; it calculates the percentage of population members in each of ten inbreeding coefficient categories: [0,.1), [.1,.2), [.2,.3)……[.9, 1]. These percentages get displayed on the screen in the form of a bar chart.

4.4.3.3 Simulation control and display classes

The *GeneticsModelApplet* class, hereafter referred to as the applet, was developed to control a simulation and produce the simulation's graphical output. Either of the two series of simulation runs can be carried out from this applet by specifying in the applet's code the simulation series to execute. The applet continues to cycle through simulations 0-3, until the user closes the applet. Also, in the applet code, one can set the number of years in one run of the simulation, the number of years that makes up a generation (necessary because all genetic measures are calculated as functions of generation), and the number of individuals in a population. When the applet is instantiated, it creates a population of animals to be used in each of the simulation runs in a series. The population is created by randomly choosing the sex of the individual animal and the gene values for each of the individual's loci. Unlike other simulations where the entire founding population is considered to be unrelated, this simulation recognizes that the juveniles present in the population are most likely the offspring of the adults in the population. Members of the one-year-old age class are, therefore, created from members of the population older than age three. The two-year-olds would have been sexual immature during the mating season that produced the current one-year-olds; thus, they are not included as possible parents. The two-year-olds however are included as possible parents for the zero-year-age (newborns) class.

Information about the individuals of the population created, such as age, sex, and the value of the genes at each of loci in the individual's chromosome, are stored in a *Vector* object called initBios. This variable gets passed to a manager from the *Manager* class at the beginning of each simulation run in a series, so that each simulation run uses the exact same initial population. This is necessary because changes in genetic measures through time are influenced by the age, sex, and genetic structure of the initial population. This model was designed to look at the influence each of the factors: behavioral, genetic, and geographic, has on, say, heterozygosity; thus, it is necessary to negate this influence of changes in initial population. However, each instantiation of the applet produces a new initial population.

The applet makes use of three additional classes. These classes were developed for this particular simulation to display the simulation results in the form of line and bar graphs but were designed general enough to be used in future simulation models as well. The graphing classes developed are *GeneticsDisplayCanvas*, *BarGraph*, and *Graph*. The classes *BarGraph* and *Graph* are inner classes of *GeneticsModelApple*t, and *GeneticsDisplayCanvas* is a regular class. There is not much difference between the two types of classes, except that an inner class has full access to all the variables in the *GeneticsModelApplet* without having to have the variables explicitly passed to it. These graphing classes, because they are used for display only, will not be discussed in great detail. In short, the *GeneticsDisplayCanvas* provides methods to display the location of the animals on the landscape during the simulation; the *BarGraph* provides methods for creating a separate window to display data in the form of a bar graph; and the *Graph* provides methods for creating a separate window to display data in the form of a line graph. For these simulation exercises, a bar graph is used to show the percentage of the population in 1 of 10 inbreeding coefficient categories discussed previously. Line graphs are produced to show the change through (generation) time in the population's mean kinship value, mean heterozygosity, variance in mean heterozygosity, mean autozygosity, and percentage of founder alleles lost.

Once the applet creates all the necessary simulation objects, it proceeds to control the execution of the simulation. For each simulation run in the current selected series, the applet instructs the manager object to execute its tick() method once for every simulation time step (simulation tick). Every generation, the applet also instructs the manager object to update the population's genetic measures and instructs the graphing objects to update their information and redraw themselves. This updates the view on the screen. At the end of the current run, the user is queried to start a new simulation run. If selected to continue, the applet will advance the simulation number in the series and begin the next simulation run. The simulation series can be cycled through repeatedly. To create a new simulation with a different initial population, the applet must be closed and a new applet instantiated.

4.4.4 Model results

The IBM was designed to execute as a series of four different, individual simulations. For clarity, an individual simulation is herein referred to as a simulation run, and a series of four simulation runs is referred to as a simulation or series. The first series, or simulation, compares the change in genetic measures through time for a population of varying complexity. The second series explores the change in genetic measures through time for a population inhabiting various geographically explicit landscapes (see Figure 4.1). In both series, a constant population size is maintained by having, for each year, the number of required births equal the number of deaths that have occurred.

In order to generate a large enough data set for statistical evaluation, the *GeneticsModelApplet* discussed above was converted to a Java application designed to execute each series a fixed number of times consecutively and write the results to a file. All aspects of the applet, except for drawing graphics to the computer screen, were maintained. In each of the series, a population of 400 animals was modeled for 100 generations, or 400 years. The first simulation run of the first series, simulation number 0, is similar to Allendorf and Harris' model (Allendorf and Harris 1989). It includes individual variation by considering both females and males and having reproduction and mortality be functions of an individual's age. Individuals cannot reproduce until age two, and juveniles have a 5% higher mortality rate than adults. For every required birth, a random female and a random male are chosen from the current sexually mature segment of the population. Individuals can be chosen more than once in any given year, and thus, individual variation in reproductive success is also included in the model. There is no spatial component. Animals do not move around on a landscape grid, and therefore, neither mortality nor mate selection is dependent on an animal's location.

The second simulation run in the series, simulation number 1, is comparable to Starfield et al. (1995). The population moves about on a homogeneous landscape and exhibits social structure and selective mating behavior. Animals who disperse or otherwise move beyond the edge of the grid are permanently removed from the population, and their removal is treated as a mortality. As individuals move around on the landscape, they are constrained to a territory. Female territories are smaller than those of males'; therefore a single male territory may contain several different female territories. After two years of dispersal-type movements originating at the location of their birth, juveniles establish territories. These territories are somewhat relative to their mother's territory because they originate at the juveniles' birth locations. Mating between mothers and their male offspring is minimized, however, by having the maximum male move distance be three times larger than that of females. Like in the first simulation, mature females are chosen at random to mate, but this time, females choose the closest (distance) mate within a certain distance of their current location, as opposed to a male at random.

The third simulation run, simulation number 2, the social and behavior aspects of the population added to the previous simulation are maintained, and an explicit geographical landscape is added. Being geographically explicit makes this simulation run comparable to the model of Kawata (1997). The landscape represents a hypothetical situation where individuals experience increased mortality risk when they are in proximity to human features, such as roads and lodging facilities (see description of landscape 1 in Section 4.4.2).

In the final simulation run in the series, simulation number 3, the social, behavioral, and spatially explicit aspects from the second simulation run are again incorporated. This time, instead of a more explicit geography being added, however, more complex genetics (linked loci) are considered. During the creation of offspring, within each linked pair of loci in an individual's chromosome, the probability of a chromosomal crossover event is .3.

The second simulation series further investigates the effect of explicit geography on population genetics. The first simulation run in this series is exactly like simulation number 2 described above. It models a population that moves about on a homogeneous landscape and one that exhibits social structure and selective mating behavior. The second simulation then adds a heterogeneous landscape where mortality risk is increased in proximity to human features, like simulation run number 3 in the previous series. The third and forth runs in this series are exactly like simulation number 2 in this series, except they each use different landscapes. These landscapes have a varying amount of habitat set aside for protection. A description of these landscapes, landscape 2 and landscape 3, can be found in Section 4.4.2 and the landscapes can be seen in Figure 4.1.

It should be mentioned that the results of these simulations are somewhat of an artifact of the simulation itself. In particular, maintenance of a constant population size is not necessarily biologically realistic. IBMs are able to simulate a fluctuating population. Fluctuating population size, however, can have a strong effect on population-level heterozygosity and inbreeding. These simulation series were developed to illustrate the effect of social behavior, spatial structure, explicit geography, and linked loci on a population's level of heterozygosity and inbreeding. The effects of fluctuating population size was, thus, negated by holding size constant.

4.4.4.1 Results from simulation series 1

Results from one realization of a simulation run of the first series (including individual variation, animal behavior, explicit geographical information, and more complex genetic aspects [linked loci]) can be seen in Figure 4.5. Even though each simulation starts out with the same initial population, they all result in a different genetic outcome. In this particular realization, for example, the simulation incorporating linked loci (simulation 3) had the highest percentage of lost alleles, the lowest population average heterozygosity, and the highest variance in average heterozygosity. Including explicit geographical information, as well as behavioral aspects, led to a higher number of founder alleles being lost, but a higher average heterozygosity, than just

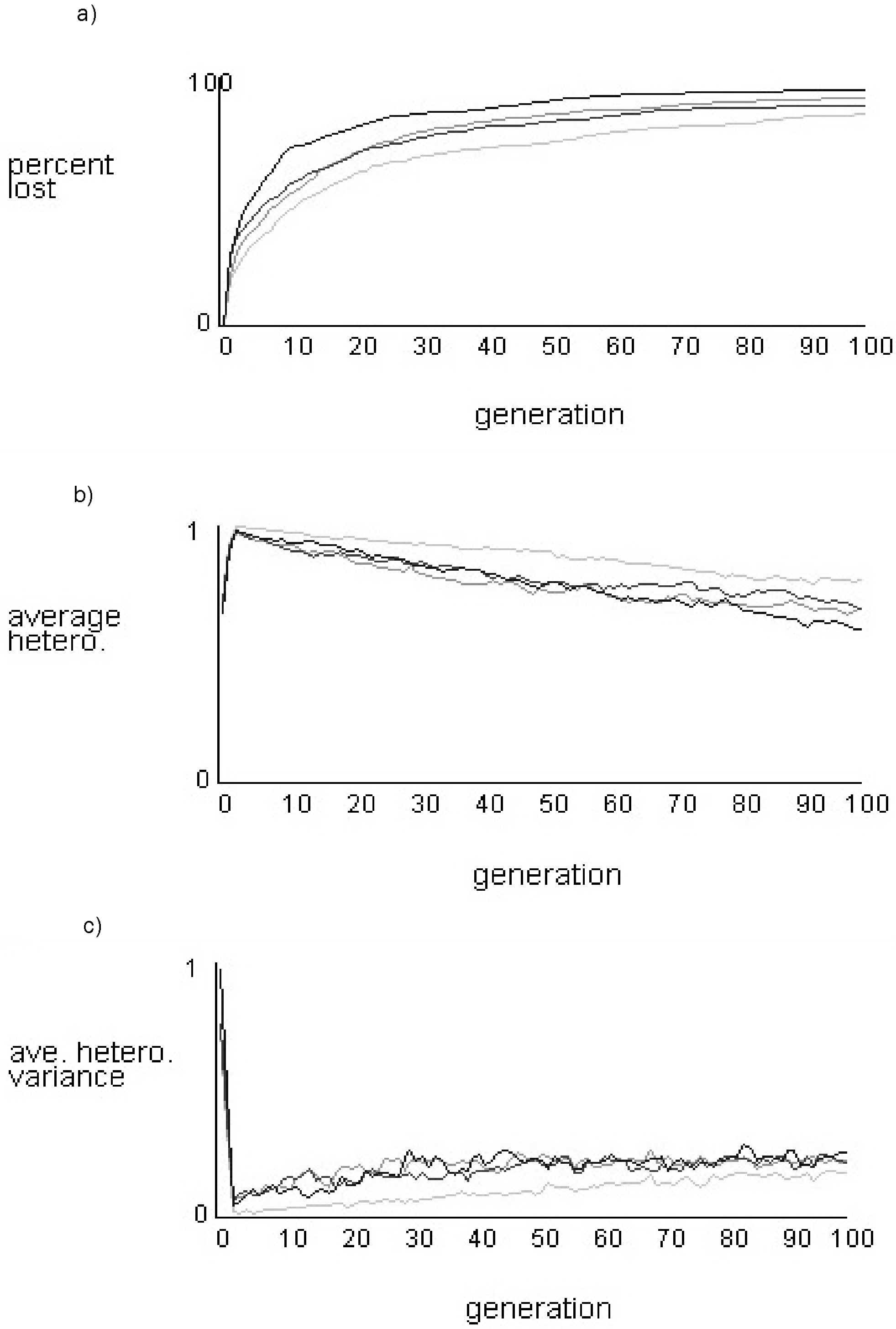

Figure 4.5. Series 1 model results. Shades of gray from lightest to darkest represent results from simulations exhibiting a population with randomly selected mating behavior (simulation 0); a population with social structure (territories) and nonrandom mating behavior (simulation 1); a population with social structure and mating behavior subjected to increased mortality associated with human landscape features (simulation 2); and a population with social structure and mating behavior that also has linked loci (simulation 3), respectively.

considering behavioral aspects alone. It would be imprudent to draw any conclusions from just one realization of the simulation; hence the Series 1 simulation was executed 100 times and genetic measures recorded at the end of the 100th generation. The measures recorded were (population) average heterozygosity, variance in average heterozygosity, mean kinship, and percentage of lost founder alleles. Descriptive statistics and an ANOVA were performed on the data collected for each genetic measure. Tables 4.1 – 4.4 display the descriptive statistics for the genetic measures, and Tables 4.5 – 4.8 show the results from the ANOVA. For all measures, significant differences with p = .01 were found between the means of the four simulations.

Examining the descriptive statistics yields the following observations. First, including geographically explicit information and behavioral aspects (simulation 2) produced the lowest mean value and the lowest maximum value of average heterozygosity of all the simulation runs. Mean average heterozygosity was reduced by another 2% when explicit geography was included in addition to behavioral aspects. Further, the maximum average heterozygosity value, when including explicit geography, was 6.5% lower than the maximum value for considering behavior alone. Likewise, including an explicit landscape led to the lowest mean value for the three largest values of average heterozygosity than any of the other simulation runs. The explicit geography, therefore, seems to reduce the maximum level of average heterozygosity that a population is able to maintain in 100 generations. On average, out of the four simulations, having linked loci generated the second lowest mean and maximum values of population average heterozygosity.

The second observation is that having linked loci leads to the highest variance in average heterozygosity at generation 100. Not surprisingly, have a randomly mating population leads to the lowest average heterozygosity variance. The mean values in this measure for simulations 1 and 2 were quite similar. It is interesting to note that despite the mean values of average heterozygosity variance being similar between simulations 1 and 2, the mean value of average heterozygosity for simulation 2 was 2% lower than the mean value for simulation 1. Since the difference between simulations 1 and 2 is the inclusion of explicit geography, it appears that the spatial distribution of variation in levels of individual heterozygosity, and not just the variation between individuals itself, plays a key role in determining the overall genetic status of a population.

Table 4.1. Descriptive statistics for population average heterozygosity (Series 1). Rounded to 1/1000th.

	Simulation 0	*Simulation 1*	*Simulation 2*	*Simulation 3*
Mean	0.778	0.641	0.626	0.636
Median	0.780	0.644	0.629	0.641
Standard Dev.	0.026	0.052	0.042	0.043
Sample Var.	0.001	0.003	0.002	0.002
Range	0.131	0.233	0.192	0.245
Minimum	0.703	0.517	0.510	0.472
Maximum	0.833	0.750	0.701	0.717
Ave. Largest(3)	0.825	0.728	0.694	0.698
Ave. Smallest(3)	0.719	0.523	0.530	0.536

Table 4.2. Descriptive statistics for population average heterozygosity variance (Series 1). Rounded to 1/1000th.

	Simulation 0	*Simulation 1*	*Simulation 2*	*Simulation 3*
Mean	0.172	0.238	0.238	0.244
Median	0.172	0.240	0.236	0.245
Standard Dev.	0.016	0.022	0.020	0.024
Sample Var.	0.000	0.000	0.000	0.000
Range	0.088	0.110	0.095	0.116
Minimum	0.134	0.189	0.195	0.195
Maximum	0.222	0.299	0.290	0.311
Ave. Largest(3)	0.203	0.278	0.283	0.306
Ave. Smallest(3)	0.143	0.196	0.201	0.200

Table 4.3. Descriptive statistics for the percentage of lost founder alleles (Series 1). Rounded to 1/1000th.

	Simulation 0	*Simulation 1*	*Simulation 2*	*Simulation 3*
Mean	0.855	0.902	0.910	0.945
Median	0.854	0.903	0.911	0.945
Standard Dev.	0.011	0.011	0.010	0.005
Sample Var.	0.000	0.000	9.34E-05	2.3E-05
Range	0.053	0.053	0.053	0.024
Minimum	0.830	0.873	0.881	0.933
Maximum	0.883	0.926	0.934	0.958
Ave. Largest(3)	0.879	0.924	0.928	0.954
Ave. Smallest(3)	0.837	0.877	0.892	0.935

Table 4.4. Descriptive statistics for the mean kinship (Series 1). Rounded to 1/1000th

	Simulation 0	*Simulation 1*	*Simulation 2*	*Simulation 3*
Mean	0.111	0.167	0.178	0.166
Median	0.111	0.165	0.176	0.166
Standard Dev.	0.001	0.009	0.010	0.008
Sample Var.	1.2E-06	8.203E-05	0.000	6.3E-05
Range	0.006	0.054	0.080	0.042
Minimum	0.109	0.149	0.160	0.152
Maximum	0.114	0.203	0.239	0.194
Ave. Largest(3)	0.113	0.188	0.200	0.188
Ave. Smallest(3)	0.109	0.153	0.165	0.154

Table 4.5. ANOVA average heterozygosity (Series 1). Rounded to 1/1000th.

Source of Variation	*Sum of Squares*	*df*	*Mean Square*	*F*
Simulation (Treatment)	1.551	3	0.517	293.539
Simulation Run (Block)	0.169	99	0.002	
Error	0.523	297	.002	
Total	2.242	399		

Table 4.6. ANOVA average heterozygosity variance (Series 1). Rounded to 1/1000th.

Source of Variation	*Sum of Squares*	*df*	*Mean Square*	*F*
Simulation (Treatment)	0.351	3	0.117	278.054
Simulation Run (Block)	0.045	99	0.002	
Error	0.125	297	0.000	
Total	0.520	399		

Table 4.7. ANOVA percentage of lost founder alleles (Series 1). Rounded to 1/1000 th.

Source of Variation	*Sum of Squares*	*df*	*Mean Square*	*F*
Simulation (Treatment)	0.414	3	0.138	1495.467
Simulation Run (Block)	0.008	99	7.97E-05	
Error	0.027	297	9.22E-05	
Total	0.449	399		

Table 4.8. ANOVA mean kinship (Series 1). Rounded to 1/1000 th.

Source of Variation	*Sum of Squares*	*df*	*Mean Square*	*F*
Simulation (Treatment)	0.270	3	0.090	1354.435
Simulation Run (Block)	0.005	99	5.3E-05	
Error	0.020	297	6.65E-05	
Total	0.295	399		

The third observation concerns the percentage of lost founder alleles. Again, having linked loci led to the highest mean percentage loss of founder alleles after 100 generations, followed by simulation 2 (explicit geography). These two simulations also had the lowest sample variance in this genetic measure. One can, thus, conclude that including either landscape or linked genes leads to greater lost in founder alleles through time and the lost are pretty consistent, ~91-94%, respectively.

The final observation involves mean kinship. For this genetic measure, the inclusion of explicit geography (simulation 2), as well as behavior, led to the highest average mean kinship value of ~.178 after 100 generations. This was 6.5% higher than the average value (~.167) of mean kinship when behavior was solely considered. The average value when considering linked genes was ~.166. The similarity in values between simulation 1 and 3 is not surprising since mean kinship is a measure of the relatedness between individuals. Having linked loci has no affect on this measure; therefore, because simulation 1 and simulation 3 are identical except for 3 having linked loci, their descriptive statistics for this measure should be similar. Simulation 2 also had the highest values for the median, sample variation, range, minimum, and maximum mean kinship. It is interesting to note that the inclusion of explicit geography, as well as behavior, has a greater influence on mean kinship than on average heterozygosity. In this generated data set, the inclusion of explicit geography in addition to behavioral aspects lowered average heterozygosity by 2%, but increased the mean kinship by 6.5%.

4.4.4.2 Results from simulation series 2

Results from one realization of a simulation run of the second (each simulation run incorporating a different landscape) can be seen in Figure 4.6. Similarly to Series 1, each simulation run starts out with the same initial population but results in a different genetic outcome,

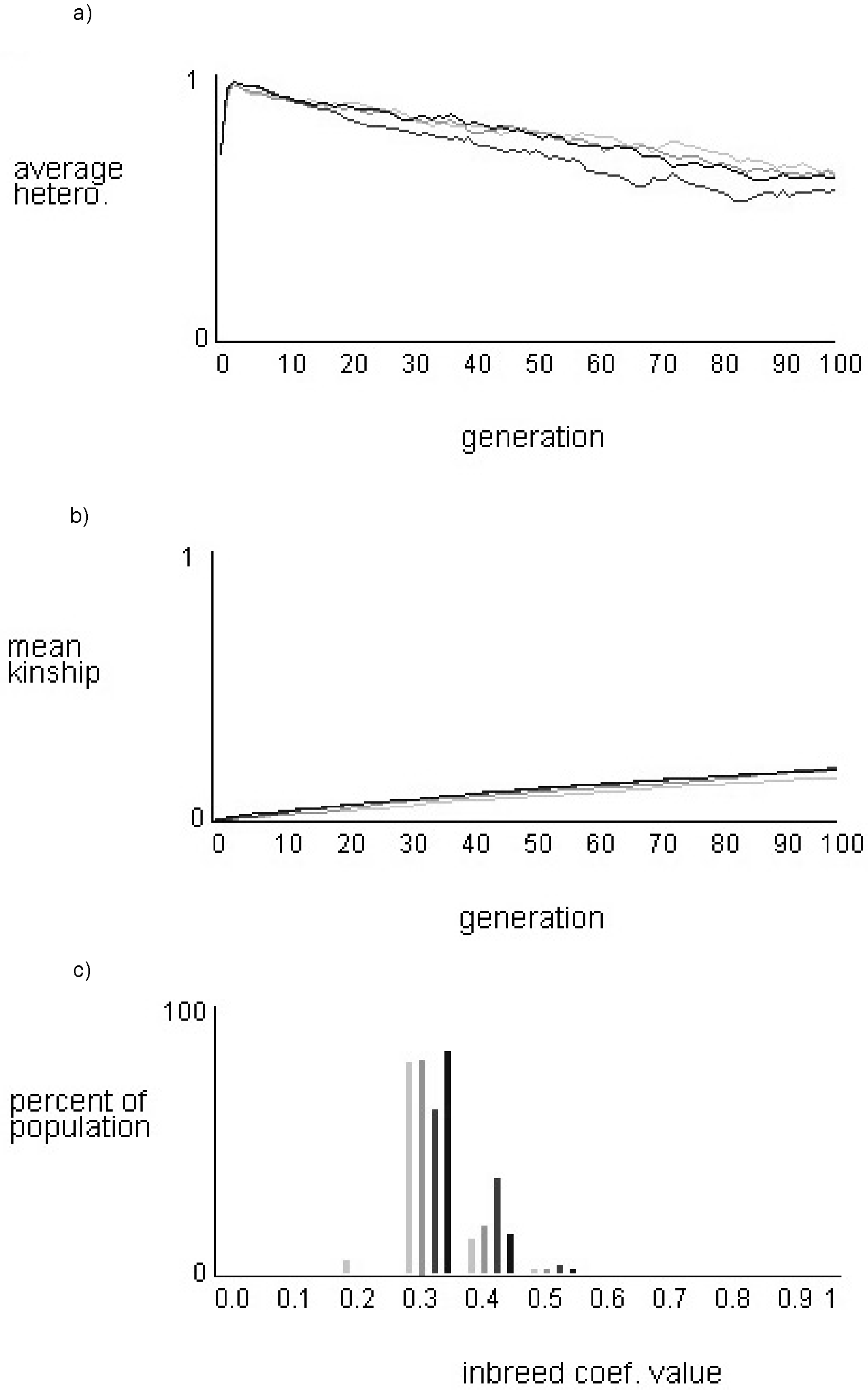

Figure 4.6. Series 2 model results. Shade s of gray from lightest to darkest represent results from simulations using a homogeneous landscape, landscape 1, landscape 2, and landscape 3, respectively.

though in some instances the differences are not as pronounced as in the first series. In this particular realization, for example, the simulation incorporating landscape 2 (2/3 of the lands held in protection) had, after 100 generations, the lowest value for average heterozygosity and the highest value for mean kinship out of the four simulations in the series. Also, any landscape other than one that is homogeneous (landscape 0) and poses no additional mortality risk to the individuals leads to higher proportions of the population being in the highest inbreeding coefficient categories.

Just like in Series 1, the simulation Series 2 was executed 100 times and genetic measures recorded at the end of the 100th generation. Descriptive statistics and an ANOVA were performed on the data collected for each of the genetic measures. Tables 4.9 – 4.12 display the descriptive statistics for the genetic measures, and Tables 4.13 – 4.16 show the results from the ANOVA. For all measures, except population average heterozygosity, significant differences with $p = .01$ were found between the means of the four simulations.

Examination of the descriptive statistics provides additional observations worth noting. First, not surprisingly, the percentage of lost alleles and average heterozygosity variance seems to correspond directly with the amount of land set asidefor protection. One can rank the landscapes by the amount of land protected in the following manner: landscape 0 (simulation 0), landscape 1 (simulation 1), landscape 2 (simulation 2), and landscape 3 (simulation 3). This ordering is from most area held in protection to the least. The simulation with the highest percentage of lost alleles after 100 generations is simulation 3, followed by simulation 2, simulation 1, and simulation 0. In short, the least amount of protected land leads to the largest number of lost founder alleles.

Listing the simulations from highest mean value of average heterozygosity variance to lowest value yields simulation 0, simulation 1, simulation 2, and simulation 3; i.e., the smallest area set aside for protections leads to the smallest amount of heterozygosity variation among individuals in the population. These results are not surprising when one views the area of protected lands in terms of restricted movement and mating opportunities. Smaller areas of land can restrict individual movement and mate selection; both these factors would act to homogenize heterozygosity among individuals and reduce the number of founder alleles present.

Table 4.9. Descriptive statistics for population average heterozygosity (Series 2).

	Simulation 0	*Simulation 1*	*Simulation 2*	*Simulation 3*
Mean	0.636	0.620	0.630	0.626
Median	0.637	0.623	0.632	0.623
Standard Dev.	0.043	0.046	0.044	0.040
Sample Var.	0.002	0.002	0.002	0.002
Range	0.290	0.199	0.233	0.196
Minimum	0.441	0.509	0.499	0.525
Maximum	0.731	0.707	0.732	0.721
Ave. Largest(3)	0.708	0.7005	0.71875	0.702
Ave. Smallest(3)	0.536	0.51875	0.5375	0.541

Table 4.10. Descriptive statistics for average heterozygosity variance (Series 2).

	Simulation 0	*Simulation 1*	*Simulation 2*	*Simulation 3*
Mean	0.242	0.237	0.230	0.225
Median	0.240	0.236	0.229	0.226
Standard Dev.	0.025	0.020	0.019	0.016
Sample Var.	0.001	0.000	0.000	0.000
Range	0.149	0.113	0.101	0.071
Minimum	0.191	0.177	0.180	0.181
Maximum	0.340	0.290	0.281	0.253
Ave. Largest(3)	0.293	0.274	0.276	0.253
Ave. Smallest(3)	0.197	0.189	0.195	0.191

Table 4.11. Descriptive statistics for percentage lost founder alleles (Series 2).

	Simulation 0	*Simulation 1*	*Simulation 2*	*Simulation 3*
Mean	0.903	0.909	0.913	0.924
Median	0.903	0.909	0.913	0.924
Standard Dev.	0.009	0.010	0.009	0.008
Sample Var.	8.94E-05	0.000	8.61E-05	6.33E-05
Range	0.061	0.047	0.053	0.044
Minimum	0.877	0.886	0.883	0.898
Maximum	0.939	0.932	0.936	0.943
Ave. Largest(3)	0.922	0.93	0.934	0.943
Ave. Smallest(3)	0.883	0.890	0.894	0.911

Table 4.12. Descriptive statistics for mean kinship (Series 2).

	Simulation 0	*Simulation 1*	*Simulation 2*	*Simulation 3*
Mean	0.167	0.177	0.176	0.182
Median	0.164	0.176	0.173	0.182
Standard Dev.	0.010	0.011	0.012	0.005
Sample Var.	9.26E-05	0.000	0.000	2.6E-05
Range	0.064	0.071	0.066	0.024
Minimum	0.153	0.156	0.158	0.172
Maximum	0.217	0.227	0.224	0.196
Ave. Largest(3)	0.186	0.201	0.211	0.195
Ave. Smallest(3)	0.154	0.160	0.163	0.173

Table 4.13. ANOVA population average heterozygosity (Series 2).

Source of Variation	*Sum of Squares*	*df*	*Mean Square*	*F*
Simulations(Treatments)	0.0131	3	0.004	2.308
Simulation Run (Block)	0.202	99	0.002	
Error	0.546	297	0.002	
Total	0.761	399		

Table 4.14. ANOVA average heterozygosity variance (Series 2).

Source of Variation	*Sum of Squares*	*df*	*Mean Square*	*F*
Simulations(Treatments)	0.017	3	0.006	12.695
Simulation Run (Block)	0.034	99	0.000	
Error	0.129	297	0.000	
Total	0.761	399		

Table 4.15. ANOVA percentage lost founder alleles (Series 2).

Source of Variation	*Sum of Squares*	*df*	*Mean Square*	*F*
Simulations(Treatments)	0.023	3	0.008	95.544
Simulation Run (Block)	0.010	99	09.9E-05	
Error	0.024	297	8.08E-05	
Total	0.570	399		

Table 4.16. ANOVA mean kinship (Series 2).

Source of Variation	*Sum of Squares*	*df*	*Mean Square*	*F*
Simulations(Treatments)	0.012	3	0.004	43.620
Simulation Run (Block)	0.008	99	8.56E-05	
Error	0.028	297	9.552E-05	
Total	0.049	399		

Second, though no conclusive observations could be made about average heterozygosity because the difference in means between simulations was not statistically significant; this fact itself leads to a noteworthy observation. If one considers that mean kinship was found to be significantly different, then the conclusion, as already mentioned in the analysis of Series 1, is that merely looking at a population's average heterozygosity does not necessarily provided the clearest picture of a population's genetic health. This point can be illustrated further by examining the proportion of individuals in each of the 10 inbreeding categories as described in Section 4.4.3.2. In Table 4.17, the highest, lowest, and mean values found in each category are summarized by simulation. By viewing this table one can see that even though simulation 3 has the highest mean kinship values, in none of the runs executed did this simulation produce individuals with inbreeding coefficients greater than or equal to .7. In contrast, both simulation 1 and 2 had on average lower values of mean kinship yet, during some executed runs, did produce individuals with these higher coefficients. The impact on the overall population's genetic health of such variation in kinship coefficients among members of a population is hard to surmise. This topic is an unexplored area of research (Keller and Waller 2002). Similarly, one can see from Figure 4.7, there exists a spatial component to the individual variation seen in inbreeding coefficients. The exact role geographically explicit landscapes play in maintaining a population's genetic health is likewise an unexplored area of research.

4.4.5 Conclusion

Three important conclusions for conservation population genetics can be drawn from the research presented here. First, geography plays an important role in determining a population's genetic status and health. The results from Series 1 demonstrate how a heterogeneous landscape may constrain a population's average heterozygosity; both the maximum and mean average heterozygosity values were lowest when the simulation was geographically explicit. Second, the spatial distribution of variation in levels of individual heterozygosity, and not just the variation between individuals themselves, seems to influence a population's mean average heterozygosity. Comparison between results from simulation 1 (inclusion of behavior) and simulation 2 (inclusion of behavior and explicit geography) in Series 1 shows the mean values of average heterozygosity

Table 4.17. Proportion of population in 10 inbreeding categories (Series 2). All numbers rounded to 1/1000th.

Simulation 0	*< .1*	*< .2*	*< .3*	*< .4*	*< .5*	*< .6*	*< .7*	*< .8*	*< .9*	*< 1*
Mean	0.000	0.000	0.0260	0.793	0.143	0.035	0.003	0.000	0.000	0.000
Mean +1std	0.000	0.000	-0.019	0.628	0.008	-0.004	-0.003	0.000	0.000	0.000
Mean -1std	0.000	0.000	0.071	0.959	0.279	0.073	0.008	0.000	0.000	0.000
High	0.000	0.003	0.273	0.938	0.900	0.350	0.030	0.003	0.000	0.000
Low	0.000	0.000	0.000	0.000	0.050	0.005	0.000	0.000	0.000	0.000
Simulation 1	*< .1*	*< .2*	*< .3*	*< .4*	*< .5*	*< .6*	*< .7*	*< .8*	*< .9*	*< 1*
Mean	0.000	0.000	0.002	0.793	0.167	0.035	0.003	0.000	0.000	0.000
Mean +1std	0.000	0.000	-0.009	0.628	0.017	0.016	-0.001	-0.001	0.000	0.000
Mean -1std	0.000	0.000	0.013	0.957	0.317	0.055	0.006	0.001	0.000	0.000
High	0.000	0.000	0.093	0.968	0.870	0.120	0.018	0.010	0.000	0.000
Low	0.000	0.000	0.000	0.000	0.033	0.000	0.000	0.000	0.000	0.000
Simulation 2	*< .1*	*< .2*	*< .3*	*< .4*	*< .5*	*< .6*	*< .7*	*< .8*	*< .9*	*< 1*
Mean	0.000	0.000	0.002	0.806	0.157	0.033	0.002	0.000	0.000	0.000
Mean +1std	0.000	0.000	-0.007	0.595	-0.036	0.011	-0.008	-0.000	-0.000	0.000
Mean -1std	0.000	0.000	0.012	1.016	0.349	0.055	0.012	0.000	0.000	0.000
High	0.000	0.000	0.073	0.953	0.943	0.145	0.100	0.003	0.003	0.000
Low	0.000	0.000	0.000	0.000	0.028	0.003	0.000	0.000	0.000	0.000
Simulation 3	*< .1*	*< .2*	*< .3*	*< .4*	*< .5*	*< .6*	*< .7*	*< .8*	*< .9*	*< 1*
Mean	0.000	0.000	0.000	0.903	0.077	0.020	0.000	0.000	0.000	0.000
Mean +1std	0.000	0.000	0.000	0.861	0.037	0.012	-0.000	0.000	0.000	0.000
Mean -1std	0.000	0.000	0.000	0.945	0.116	0.029	0.001	0.000	0.000	0.000
High	0.000	0.000	0.000	0.965	0.243	0.048	0.003	0.000	0.000	0.000
Low	0.000	0.000	0.000	0.735	0.030	0.003	0.000	0.000	0.000	0.000

Figure 4.7. Spatial distribution of modeled population after 100 generations. This represents the graphic results of a simulation run using landscape 3. Open and closed circles signify juveniles and sexual mature adults, respectively. The dark gray color circles represent females and the light gray circles represent males in the population. The larger the radius of an open or closed circle, the greater the value of an individual's inbreeding coefficient. Note: the landscape shown here is the discrete raster version of the landscape 3 shown in Figure 4.1 used in the simulation.

variance were similar, yet the mean value of average heterozygosity for simulation 2 was lower.

Third, merely looking at a population's average heterozygosity does not necessarily provide the clearest picture of the population's genetic status and health. Results from Series 2 illustrate the complexity of the situation when explicit landscapes are included. Further, kinship and inbreeding coefficients provide a clearer assessment of a population's genetics than does heterozygosity. Though an apparent inverse relationship was observed between the amount of protected area and the amount of variation in heterozygosity among individuals in the population and, likewise, the amount of protected area and the percentage of lost alleles, no obvious relationship between average heterozygosity and the amount of protected land was detected. Indeed, there was no statistically significant difference in population average heterozygosity among the various landscapes. Yet, there was a statistically significant difference in the mean kinship of the populations. Additionally, there were dissimilarities in the proportion of individuals in each of the 10 inbreeding categories among the landscapes. These dissimilarities are especially noteworthy because of the lack of correlation between high population-level values of mean kinship and the presence of individuals with the highest level of inbreeding. The landscape with the least amount of land in protection had the highest mean kinship values yet did not have individuals in the highest inbreeding categories.

The intricate relationship between geography and mean kinship (or inbreeding) and heterozygosity holds many challenges for species conservation. Most in situ conservation strategies, if concerned about genetics at all, focus either on N_e or heterozygosity. The simulations presented here raise questions about the adequacy of these approaches.

For the case of establishing a reserve, if keeping the level of population average heterozygosity above a certain level is the only genetics criterion used to evaluate different potential reserves, then as the simulations in Series 2 showed, all reserves may look comparable. If, however, population mean kinship was used as a measure, one or two possible reserves might stand out as being better because they have the lowest mean kinship or the lowest percentage of the population with high inbreeding coefficients. As discussed in Chapter 3, high levels of inbreeding can have deleterious consequences for a population's persistence.

Another example would be the case where the managers in charge of a species' conservation relied solely on an estimation of average heterozygosity to judge the genetic health of the current population or to predict when management action, such as tanslocation of individuals from another population, would be necessary. Results from these simulations show this reliance could have dire consequences. First, a certain level of heterozygosity does not necessarily equate to a certain level of mean kinship. If population average heterozygosity was fine but mean kinship was high, the population may survive in the short term only to face irreparable levels of inbreeding in the long term. Second, the problem could be compounded if the managers were basing their decisions entirely on models lacking explicit geography. As discussed earlier, geography appears to constrain the level of heterozygosity a population is able to achieve and maintain, when compared to a population modeled on a homogeneous landscape. The managers therefore may overestimate the species ability to rebound and return to an acceptable level of heterozygosity.

In closing, this research suggests looking at a population's mean kinship and inbreeding instead of average heterozygosity may provide a more realistic view of its genetic status and future genetic health. It further suggests that geography, at least for some species, plays a central role in determining population genetics. It should be noted that the inclusion of explicit geography in models of real-world populations should have an even greater effect than seen in the simulation exercises performed here. Variation in mortality rates over the landscape can lead to fluctuating population size, which would in turn influence population genetics. Likewise, simulating a constant population size could have covered up the fact that geography can play a role in the ability of individuals to find mates. Difficulty in finding mates would undoubtedly influence the overall genetic health of the population. Finally, this work suggests that both individual and spatial variation has some yet-to-be explored contribution to a population's overall genetic well being. In the future, IBMs will prove to be excellent tools by which to investigate these aspects in greater depth. These models focus on the individual, can easily incorporate geographically explicit landscapes, and can provide calculations of mean kinship and inbreeding, as well as heterozygosity. Furthermore, it should be mentioned, these exercises considered a population size of 400 (quite large in comparison to some species of conservation concern). The effects of the factors considered would most likely be greater in populations of smaller size.

CHAPTER 5

INDIVIDUAL-BASED MODELING: A MODELING FRAMEWORK FOR GRIZZLY BEAR CONSERVATION

5.1 Introduction

In 1975, the grizzly bear, *Ursus arctos*, was given federal protection status as a threatened species under the Endangered Species Act (ESA). At that time, the once abundant and contiguous population in the United States had been reduced to less than 1000 grizzly bears existing in five disjunct ecosystems in the northwest portion of the United States (USFWS 1993). Modeling the population dynamics of one of these ecosystems, the Cabinet-Yaak in the northwest corner of Montana, is the focus of this chapter.

As a threatened species and with its popularity as a symbolic image of the American west, the grizzly has been the focus of much conservation effort and scientific research (Primm and Murray 2005). From the pioneering telemetry research of Frank and John Craighead (1965) until the GPS technology of today, wildlife biologists have been conducting empirically based field studies of grizzly bear behavior, such as food selection, habitat use, and road avoidance. Field data have been used in efforts to predict population size and growth rate or to estimate population trend and long-term viability (see, for example, McLellan 1989; Eberhardt et al. 1994; Hovey and McLellan 1996; Pease and Mattson 1999; Wakkinen and Johnson 2000; Kasworm et al. 2000; Boyce et al. 2001).

One of the most extensive research efforts to utilize empirical studies, along with expert opinion, was the cumulative effects analysis process (Christensen and Madel 1982, Weaver et al. 1986). This process was adopted by all agencies with jurisdiction in one of the grizzly bear recovery zones. The process tries to predict the indirect and direct consequences of individual natural resource management decisions, along with the cumulative effect of all such decisions, on grizzly bear viability. The process is comprehensive in its attempt to discern important grizzly bear habitat. It recognizes, for example, grizzlies utilize different foods throughout their active season and may avoid areas with human landscape features. Yet, because the process uses a map-based approach, it fails to link habitat directly with population demography or genetics in any meaningful way, both of which are accepted as core factors in viability analysis (Soule 1987).

The cumulative effects analysis process is not alone in its disregard for population genetics. In comparison to other aspects of conservation, habitat protection and demography, population genetics has received the least attention. Laikre (1999) suggests genetics are often excluded in conservation planning and management because doing so results in increased population sizes, which is not viewed as 'politically favorable.' As reviewed in Chapter 2, there has been some theoretical research done on this aspect of grizzly bear conservation. In short, the research has mainly focused on using an analytical approach to predict effective population size, N_e, or calculating the number of effect migrants needed to stave off genetic drift and inbreeding. In more recent times, empirically based methods involving molecular DNA have been used to assess historic or current levels of gene exchange between various grizzly populations (Proctor et al. [2005]; Miller and Waits [2003]).

These latest genetic DNA studies mentioned reflect a trend in research perspective from single population or ecosystem to multiple populations or ecosystems. Under the right circumstances, these multiple (sub) populations may function as a single population. This perspective has followed naturally from conservation biology principles that note in isolation, small populations are subject to genetic drift, inbreeding depression, and stochastic demographic events. Experts speculate that bears in all but one of the recovery zones, the Northern Continental Divide Ecosystem, are at elevated risks of extinction due to the zone's small size and isolation from other zones (Mattson et al. 1995). In the four zones along the northern U.S. border, the survival of the populations is dependent upon connectivity with Canadian grizzly populations (Servheen, Waller, and Kasworm 1998). Genetically this is called 'gene flow', and demographically this is called a 'rescue effect.' Modeling efforts for the Greater Yellowstone Ecosystem found inclusion of even modest levels of dispersal between the various recovery zones increased overall population size and number of subpopulations containing bears (Boyce et al. 2001).

Having dispersal between populations has become known as 'connectivity.' Maintaining connectivity or, in a generalized sense of the concept of metapopulation, allowing the various grizzly bear ecosystems to function as a metapopulation seems to be an important objective for successful grizzly bear conservation. In this context, GIS has been used frequently as a tool to determine areas between grizzly bear ecosystems that would result in a high probability of successful individual dispersers. As important as determining connectivity may be in and of itself, it may also be framed as just one manifestation of the overall challenge of trying to predict the consequences of natural or human-induced landscape changes to a population's long-term viability. Here viability refers to both population numbers and genetic variation, since the maintenance of these measures must be a central theme in plans for long-term population management (Lande and Barrowclough 1987).

Predicting the consequences of natural or human-induced landscape changes to a population's long-term viability is known as a population viability analysis. Central to any such analysis is a model. For any model to be able to predict the consequences of landscape changes to a population's persistence, it must be able to explicitly link habitat relationships and ecological attributes directly to the population's demographics and genetics. This direct connection between landscape attributes and population demographics and genetics is where most methods and models used in grizzly bear management and research fall short in their ability to be used in a consequential predictive manner. They independently focus on population demographics or genetics or habitat (see Chapters 3 and 4 for full discussion). This is especially true in population genetics in which no research to date has included a geographically explicit landscape. Chapter 4 shows geography does play a role in population genetic processes. Commonly used stochastic simulation software packages designed to perform principle viability analysis also fail to explicitly link habitat attributes with relevant population attributes.

A promising technique for linking habitat relationships and ecological factors directly to the populations' demographics and genetics is spatially explicit, individual-based models (IBMs). A spatially explicit model is important for grizzly bears, because human landscape features, such as roads and centers of development, can influence their movements and mortality risk. Grizzly bear movements can also be influenced by the presence of other bears, making the individual-based contribution significant. Further, focus on modeling the individual allows the additive kinship matrix algorithm discussed in Chapter 3 to be implemented and pedigree analysis to be performed in place of calculations of indiscriminate, summative measures like N_e. Finally, being individual based means the model can be behaviorally explicit as well, thereby utilizing the numerous, empirical-based observations of grizzly behavior collected by field biologists.

This chapter reviews the development of a spatially explicit IBM that can be used as a grizzly bear conservation tool. The model developed is comprehensive in that it integrates all important aspects of bear biology and behavior and the area's geographic features in a spatially varying and temporally dynamic way, while simultaneously keeping track of the genetic and demographic changes central to effective conservation analysis. After discussing preliminary design issues, the chapter turns to a more in-depth treatment of the model features and design. The data collected in support of the spatially explicit aspects of the model are discussed in the context of the modeling features to which they pertain. Model outputs are discussed in the chapter's final section.

5.2 Preliminary model development

5.2.1 Problem statement

Determination of the affect of natural and human landscape changes have on the viability of grizzly bear populations is difficult. In order to do this, habitat relationships and ecological factors must be directly linked to the populations' demographics and genetics. Despite the recognition that linking habitat relationships and ecological factors to a population's demographic and genetic processes would improve grizzly bear conservation, there are currently no models that do so in a spatially explicit fashion. The matter is further complicated by the fact the dietary preference of grizzly bears changes throughout their active season, creating a need for a model to be temporally dynamics, as well as spatially explicit. The problem is therefore to see if such a temporally dynamic, spatially explicit model that links grizzly bear population dynamics directly with the landscape they inhabit is possible.

5.2.2 Model objectives

The objectives of the study are to create an IBM that replicates grizzly bear movement using landscape variables, spatially explicit habitat information, and accepted bear behavior. Longer term, the consequences of this response will be realized genetically and demographically; that is, the viability of the modeled population will be revealed. This model will do the following:

1. Assess the direct effects (mortality) of the human landscape on the population's viability.
2. Assess the indirect effects of the human landscape on dispersion and mating success and consequently on fecundity.
3. Assess the frequency of successful dispersal between the two populations.
4. Using (3), determine the number of population segments in the study area 1 or 2
5. Determine the presence of any landscape barriers to dispersal, as represented by mortality hot spots.
6. Assess the long-term demographic and genetic viability of the population segment(s).

5.2.3 Scope

The model is designed to simulate the grizzly bear population inhabiting an area within a 5.0 mi buffer around the western portion of the Cabinet-Yaak Grizzly Bear Recovery Zone. This buffer distance captured 96% of the grizzly bear sightings documented between 1980-99. Based on an average daily move distance of between 1.34 and 4.0 km/day (Nat'l. Wildl. Federation 1987), the buffer allows a bear to spend a few days outside the recovery zone. Most of the study area is forested with Douglas-fir and cedar-hemlock-Douglas-fir forest types (Bailey 2001). Only a small portion of the landscape consists of grasslands and wet meadows (Kuennen and Nielsen-Gerhardt 1985). In this ecosystem, the grizzly bear's diet consists mostly of vegetation (grasses, sedges, and the leaves, roots or corms, and flowers of various forbs) and the fruits of numerous shrubs and trees, with a smaller percentage of their diet consisting of protein (carrion, small mammals, and some insects.)

There are approximately 30-40 bears in the Cabinet-Yaak (Kasworm et al. 2000). For this study, it is assumed that the grizzly population is divided between two local subpopulations referred to as Yaak and Cabinet populations (see Figure 5.1 for hypothesized boundaries between populations). The areal extents of these local populations were derived from verbal descriptions of the grizzly population inhabiting the recovery zone (USFWS 1993; Kasworm 2000).

5.2.4 Data collection and subject matter experts

The areal extent of the study area spans multiple administrative jurisdictions: two states, four counties, and three national forests. This made data collection a challenge, since all organizations did not have (1) the same data sets or (2) the different attributes in similar data sets could not be merged. Land parcel GIS data, for example, were only available in three out of the four counties. The data collected is broken down into three thematic groups: human landscape,

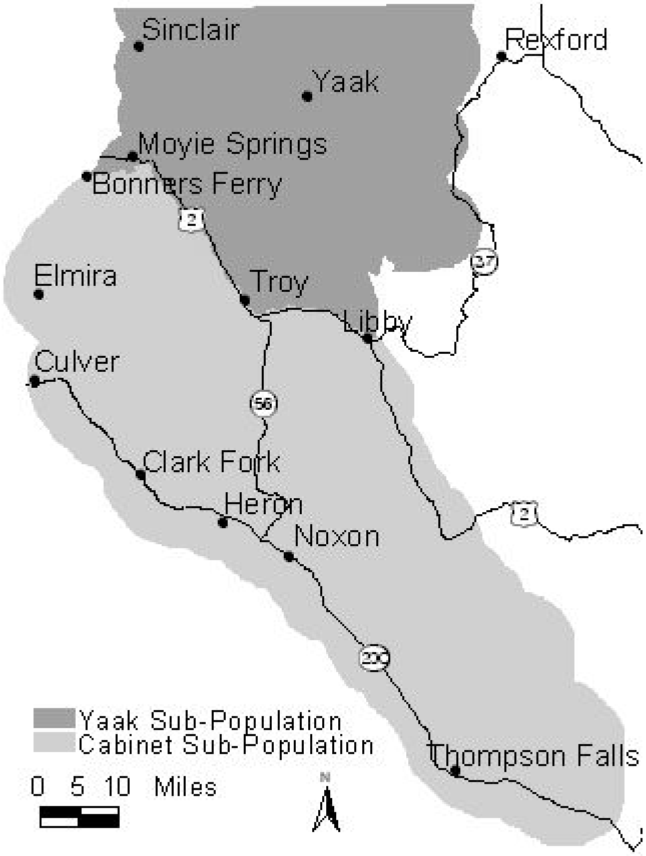

Figure 5.1. Hypothesized boundary between grizzlies inhabiting the Yaak and Cabinet portions of the study area.

vegetative and nonvegetative bear foods, and bear-related. All data is described in detail in Section 5.4.

Subject-matter experts are people acknowledged as being an authority in their chosen fields. The validity and credibility of a simulation model rely heavily on the appropriateness of the data used and the assumptions made while developing the model. Therefore, this research utilized over 50 subject-matter experts for data collection. These experts were from the forest service, state fish and game departments, county agencies, state agencies, U.S. Fish and Wildlife Service, Geological Survey and Natural Resource Conservation Service, and academics. Information and insights from these individuals, in combination with data availability and limitations, yielded an iterative, inter-related modeling process.

5.3 Model design

As discussed in the literature review section, there can be several problems associated with the development and use of IBMs stemming from nonprofessional programmers writing complex programs. In order to overcome these problems and to facilitate the creation of error-free programs that could enhance comparability between different models, several general simulation programming frameworks or libraries have been developed. In the model design phase, several of these frameworks were considered for use: EcoSim Lorek and Sonnenschein (see Lorek and Sonnenschien 1998 for description), Swarm developed by scientists at the Santa Fe Institute (visit http://www.swarm.org for a description), and Gecko (see Booth 1997 for description).

After review of these general frameworks, all three were determined to have limitations affecting their applicability to this project. EcoSim's documentation is available only in German, it is coded in objective C, a pseudo-object-oriented language not commonly used and whose executable program files are not multiplatform executable. At the start of this project, Swarm was still largely objective C as well, though it has become more Java™ oriented since then. The focus of Gecko's development was a simulation to investigate community interactions and formations, not single species population viability. Given these previous limitations, it was determined it would be best to build, independently of existing simulation libraries, a spatially explicitly, individual-based grizzly bear population model, here in referred to as the model.

The model integrates important aspects of grizzly bear biology and behavior and the area's geographic features in a spatially varying and temporally dynamic way. Simultaneously, the model tracks the genetic and demographic changes central to effective conservation analysis. The model is designed using a discrete-event simulation approach and is programmed entirely in the object-oriented language Java^{TM} 2 SDK, Standard Edition, Version 1.4.2. Object-oriented languages, such as Java^{TM}, provide the architecture for developing simulations that are composed of independent objects that interact with each other. Each object gets generated, or in technical terms 'instantiated', from a class. The class is the entity the individual-based modeler creates. One can think of a class as a blueprint for describing the state of the object, called a variable, and the actions an object can perform, usually in response to some event, called methods. A class for an animal, for example, might contain the variable age as a state descriptor and the action of growing older as a method that occurs in response to an end-of- year event.

Through the selection of events and then execution of series of events, the modeler replicates real-world time. The modeler replicates real-world objects and their behaviors and interactions through the design and creation of classes. The events selected and the classes developed for this project are described in full in the next sections.

The goal in the model design was to create a set of classes that would allow bears to act as bears and the habitat to be dynamic with minimal global control; that is to say, the bears and the habitat should be able to make decisions. Instead of the model telling each bear to move once a day, for example, the bears would decide for themselves how many they were going to move that day, and instead of the model telling each cell to change its food availability from spring food to summer food to fall food, the cell would control what, if any food, it had available on any particular day. In addition to minimal global control, the following other aims guided the model design:

1. To incorporate data produced by or available to natural resource managers.
2. To incorporate empirical data and information gathered by field researchers as much as possible.
3. To include both the direct and indirect effects of the human landscape.
4. To include climate variability.

By designing a model with minimum global control, the population dynamics will emerge from modeling the local interactions of key elements of the system. For grizzly bears, herein referred to as just bears, the main interactions are between bears and other bears, bears and the natural landscape, and bears and the human landscape. In addition to emergence, the CAS concepts of adaptation, fitness and strategy, state-based response, and prediction are used to create realistic bear movement and behavior.

Time must be included in the model design as well, because the dietary preference of bears change throughout their active season, and the model is concerned with the long-term viability of the population. The things that needed to be represented in the model are time, the landscape, and the bear population. The thesis of this dissertation, however, is that individual variation and mechanisms are the driving forces behind population dynamics. The bear population therefore is modeled as a group of individual bears and similarly the landscape as a group of individual habitat cells and time as a group of individual calendar years. Classes representing a bear, habitat cell, and calendar year, therefore, are the three primary ones developed.

At the same time the model recognizes the importance of the individual bear and habitat cell, it is as an aggregated group that information pertaining to the individuals is input or output to the model. Data to attribute the habitat cells are derived from GIS layers of the entire landscape and are input as ASCII files. Information about the population as a whole is what is relevant as output, for example, mean kinship and population size. In addition, even though individual bear and habitat objects act independently of each other, many of the events that occur affect all the objects simultaneously. A year-end event, for example, would affect all bear objects by making them age one year. For these reasons, two more classes were developed: *AnimalManager* and *GridManager.* (Note: it is the convention throughout this chapter to italicize class names.) These classes help manage events and modeling tasks that affect the entire landscape or population.

There is a class developed to manage the calendar object. This class, *TimeManager*, however does a lot more in the model. This class is the one that actually runs the model by initiating various events. The events in the model can be broken down into events that happen on an annual basis, a daily basis, and irregular events that occur during the day. These events are listed Table 5.1.

Table 5.1. Model events.

Class	Annual Events	Daily Events	Irregular Events**
Bears	- Enter the den - Emerge from den - Choose a den location - Give Birth - Grow Old - Mate - Record demographic data - Calculate and record population genetic measures*	- Move to find food, find mates or find a den	- Test survival - Encounter another bear (results in another move, mating event, or no action)
Habitat Cells	- Set the starting availability dates for grasses, forbs and berries		- Record mortality - Adjust food availability
Calendar	- Choose a climate scenario		

*only happens every generation
**events occurring as the result of object interaction

Classes representing individual calendar years, bears, habitat cells, and their associated management classes are some of the primary classes developed for the model. All in all there were 33 classes and interfaces involved in developing the model, 14 of which compose the core of the model. The other 19 were graphics classes that played an integral part of model development, most of which aided in 'visual error detection' and allowed presentation of the model to others who may not be familiar with programming and/or modeling. The 14 classes making up the core of the model and their relationship to each other are shown in Figure 5.2.

5.4 Model implementation

It is typical for the discussion of an IBM to include only concepts rather than the implementation details. In this case, the matter is further complicated by the spatially explicit nature of the model, where the reader may or may not be familiar with spatial data tools like remote sensing and GIS. In order to meet the needs of a diverse audience, the following subsections are all written in a format that is both general and specific. Each section will start out with a general overview, next will be a rather detailed discussion of the data and any other supporting model or concepts used, and finally a similarly detailed discussion of program implementation will be presented. This format should facilitate understanding of important model

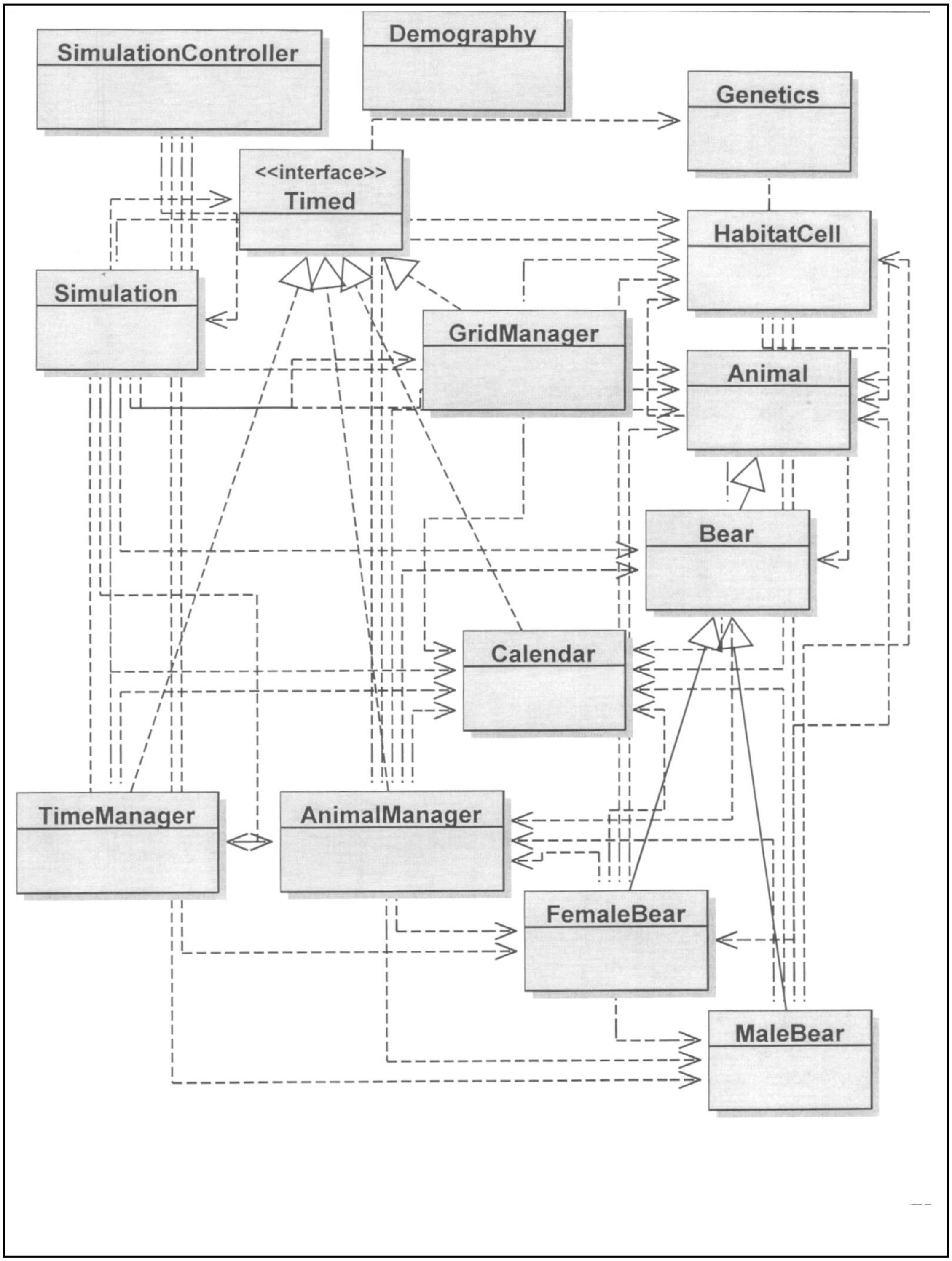

Figure 5.2 Model diagram.

features and details without an extensive knowledge of Java™, GIS or remote sensing.

Classes created for the model can be broken down into five functional categories: utility, animal and animal management, habitat and habitat management, time and time management, and simulation control and display classes. The classes contained in each of these categories are discussed in the sections below. In addition to having Java™ class names appear in italics, the following stylistic format will be used throughout the chapter; class methods will be shown by name followed by (), the name of GIS data layers will be italicized and bolded, and GIS commands will be bolded. All data layer processing was done in either Environmental Systems Research Incorporated, ArcInfo™ version 7.2 or ArcView™ version 3.2 GIS software, herein referred to as ArcInfo or ArcView.

5.4.1 Utility classes

5.4.1.1 Overview

The two utility classes, *Demography* and *Genetics*, are a set of equations that calculate various demographic parameters and genetic measures for a population, respectively. The genetic measures are used to track the population's genetic processes, detect changes in the population's genetic status, and assess its viability. These classes are designed to be stand-alone (static) classes that can be readily used in similar modeling projects.

5.4.1.2 Data

No spatially explicit data are required.

5.4.1.3 Implementation

These classes can be viewed as library classes because they consist of a set, or library, of demographic and genetics methods that can be used in a population simulation model. They are similar to Java's *java.lang.Math* class that provides a set of mathematical methods. The two classes were created in conjunction with the simulations in Chapter 4, but slight modifications and additional methods are added. The classes and additional methods are discussed here to aid comprehension. All the methods in these classes were coded as static methods. To access static methods, one must type the class name followed by the method name, for example, Genetics.calcKinship() or Demography.calcStableAgeDist(). For conciseness, the class name will be dropped during the discussion.

The *Demography* class contains methods for calculating various demographic parameters for a given population. Currently, it only has one method, calcStableAgeDist(), that calculates the stable age distribution (number of individuals in each age category) for a population of a given size, with constant age class morality rates, and known maturation age and life expectancy. (This is a generalization of the previous calcStableAgeDist() method that only used juvenile and adult mortality rates.) The method assumes a population growth rate equal to 1.

The *Genetics* class provides a series of methods for calculating a variety of individual and population-level genetic measures. The methods for calculating kinship coefficients between individuals, calcKinship() and findKinship(), are part of the compressed kinship matrix algorithm of Backus and Gilpin (2002). The two methods are similar in that they both calculate the kinship coefficient between two members of the population. The difference in the methods is that calcKinship() calculates the kinship coefficients for an initial population where none of the kinship values are known for any of the individuals. (All adult founders are assumed to be unrelated.) The findKinship() method, on the other hand, determines the kinship coefficient values for all future offspring (see Chapter 3 for a detailed description of the algorithm).

The remaining methods provided by *Genetics* class calculate population-level genetic measures for a current population. The following list provides a short description of the methods provided:

- meanKinship() – calculates the average kinship coefficient value for the members of the population
- meanHet() – calculates the average number of heterozygous loci for a member of the population
- aveHetVariane() – calculates the variance in individual heterozygosity present in the population
- likeInState() – calculates the average number of allozygous (two alleles are of the same type, but are not from a common ancestor) loci for an individual in the population
- likeInKind() – calculates the average number of autozygous (two alleles are identical by descent) loci per individual in the population

- calcFounderAllelles() – determines the set of unique alleles among the founders of a given population
- founderAlleles() - determines the number of founder alleles not present (lost) in the current population.
- alleleFrequency() – calculates the frequency of each of the founder alleles present in the current population.
- Fst – determines the genetic distances between subpopulations using a simple weighted average.

The method F_{st} is an additional method created after the simulations in Chapter 4 in order to address questions of connectivity between seemingly disjunct populations. It should be noted there are several methods for calculating the genetic distance, F_{st}, and the best method for its calculation is an area of discussion among population geneticists. The weighted average method was chosen for its simplicity. It also should be noted the author recognizes the long duration of separation necessary for increases in genetic distances between populations to become significant (speciation). A duration that is longer than the practical application of the model, it nonetheless is included, because in a relative sense (comparisons between two or more proposed changes in the landscape), the measure could be used as an indicator of the connectivity.

5.4.2 Bear and bear management classes

5.4.2.1 Overview

The bear-related classes developed for the model have the necessary characteristic attributes and methods to respond to events that allow bear objects instantiated from them to biologically and behaviorally function in the model-like real bears. These classes are designed such that each bear object, herein referred to as bear, would be born, move around on the landscape, grow old, mate, produce and rear young (female only), and die. Their movements are not orchestrated by the model itself, but rather are motivated by their biological needs and responses to external events. Their biological needs are food, mates, safety, and a place to hibernate. The external events are encounters with other bears, which may precipitate additional moves or mating between individuals. While they move around on the landscape, bears are subject to a spatial-varying mortality rate. The spatial mortality rate reflects the relationship between the human landscape features and bear mortalities reflected in the literature (Merrill et al. 1999 and Johnson et al. 2005) and is discussed in Section 5.4.3.

In order to make the bears' movements over the landscape realistic, their movement rules and parameter values vary with age, sex, and reproductive status. The number of daily moves a bear makes, for example, is drawn from an empirically derived distribution of daily move distances that varies with these individual bear characteristics. Also, the bears' movement motivations vary temporally throughout the active season, switching from finding food, mates, food again, and then finding a place to hibernate. The active season is defined as the period of time from a bear's den emergence until its den entrance. In the model, the length of the active season varies stochastically from year to year with the variance in length being based on actual historic climate data, as explained in Section 5.4.3. Likewise, the length of the active season varies among individual bears, with adult males having the longest active season and females with cubs the shortest, as suggested by the literature (Werner and Jonkel 1977; Nat'l Wild. Federation 1987; Kasworm and Manley 1988; Kasworm et al. 2000).

Additional realism in the bears' movement patterns is achieved by giving the bears a high caloric food preference. This preference, in conjunction with having the habitat cells be phenologically dynamic (details are discussed in Section 5.4.3), lets bears forage for high caloric foods, while allowing their diet to change throughout the active season based on availability. High caloric food preferences and seasonal changes in food item selection are both suggested in the literature (Husby and McMurray 1978; Sizemore 1980; Kendall 1986; Craighead et al. 1995). Modeling plant phenology is important to attaining realistic bear movements, because bears, unlike ruminants, cannot fully digest fiber. They are forced to eat different plants at different times of the year in response to the plant's nutritional value, a function of its fiber content. Finally, bears are given a preference for areas with low open road and motorized trail densities and an aversion to areas with high densities. Their aversion is modeled as a multivariable function that includes variables for food; thus areas with higher road densities may, in fact, get utilized, at least seasonally, if there are abundant high caloric foods available. Mace et al. (1996) have documented the seasonal use of areas with high road densities.

The model realizes a true picture of the population's genetic processes by, in addition to modeling the lifelike movement of individual bears, allowing multiple paternity and sex-biased dispersal. Individual bears store the identity of their mother and father and their kinship relationship with other members of the population. This facilitates an accurate assessment of the population's genetic status, because in essence what this accomplishes is storing the population's pedigree. Finally, the model makes no special considerations to track the population's demographics because in an IBM, since all members of the population are known, all births and deaths are easily observed and recorded.

5.4.2.2 Data

Only three spatially explicit data layers are related to the bears themselves. A data layer of grizzly bear sightings was created and used to help determine a boundary for the study area. A denning habitat layer was developed from descriptive information found the literature. Finally, a layer of home ranges was digitized and used to help guide model development and in the validation of the denning habitat layer. All GIS work was done in either the ArcView or ArcInfo software packages of Environmental Research Systems Incorporated (ESRI).

5.4.2.2.1 Bear home range

This layer represents the annual home ranges of grizzlies in the Cabinet and Yaak local populations. It was based on the home range maps provided in the 1999 Cabinet-Yaak annual research report (Kasworm et al. 2000). These included the life ranges of grizzlies tracked with telemetry in the recovery zone. The maps were scanned in and then on-screen digitized in ArcView from the resultant images. The ranges served only as approximate areas of use in the model verification process, because the scale and accuracy of the maps could not be determined.

5.4.2.2.2 Denning

This grid layer was developed using empirical information describing the location of known grizzly bear dens. This information indicates some den preference by bears for higher elevations on slightly to moderately steep slopes (Werner and Jonkel 1977; Nat'l Wild. Federation 1987). Dens located were beneath either beargrass or whortleberry patches or at the base of subalpine fir trees with < 30 cm dbh (Werner and Jonkel 1977). The annual research report for the CYE (Kasworm et al. 2000) shows there is some variation in the preference of den locations between those bears in the Yaak portion of the study area and other bears. The mean den elevation is 1,911 m for bears in the Cabinet Mountains, and a majority of bears locate dens on southern aspects of the mountains. Dens found in the Yaak have a mean elevation of 1,689 m and are located on southern aspects the least. The selection criterion used to create a layer of possible den locations was kept to a minimum, because denning habitat is not viewed as a limiting habitat component in any of the grizzly bear ecosystems. The criteria used were based on elevation, slope and aspect only. The distinction between den locations in the Yaak and the remaining ecosystem was incorporated in the layer. For the area south of the Kootenai River, the criteria are elevation between 1,800 - 2,300 m, slope between 26-35 degrees, and all aspects except north. For the Yaak portion of the study area, the criteria are elevation between 1,600 – 2,100 m, slope between 26-35 degrees, and all aspects, except south, were considered.

ArcInfo's GRID module was used to generate slope and aspect grids from 30 m digital elevation model (DEM) data. The module was then used to generate the final potential denning habitat grid using the criteria mentioned above. For validation, using ArcInfo, the life ranges coverage described above was spatially overlayed onto the potential denning habitat grid to make sure all the life ranges contained some denning habitat. All life ranges contained some potential den sites selected by the criterion, suggesting the criterion was not too restrictive and did at an adequate job of representing potential den locations. Original data layer development used 30 m DEM data.

5.4.2.2.3 Grizzly sightings

This layer is created from importing the x,y UTM coordinates of known grizzly bear sightings from a table obtained from Wayne Kasworm of the United States Fish and Wildlife Service (USFWS). This layer was used to delineate the final study area boundary. The final boundary incorporated 95% of all grizzly bear sightings recorded.

5.4.2.3 Implementation

There are four Java^{TM} classes pertaining to bears themselves and one class in charge of managing all activities and events involving the bears. A hierarchy of classes (see Figure 5.3) is created using the inheritance property of object oriented programming languages. A class one level above another class is referred to as a superclass, and a class one level below another classis referred to as a subclass. At the top of the hierarchy (ignoring the *Object* class that all classes in Java^{TM} are extended from) is the *Animal* class. The variables and methods in this class are necessary for any animal to be able to utilize the methods found in the *Genetics* and *Demography* classes described in Section 5.4.1, such as calculating its kinship coefficient with another member of the population. Each individual animal in the population (*Animal* object) is given 1 chromosome pair made up of 10 loci. Each locus has 2 alleles that can have either a

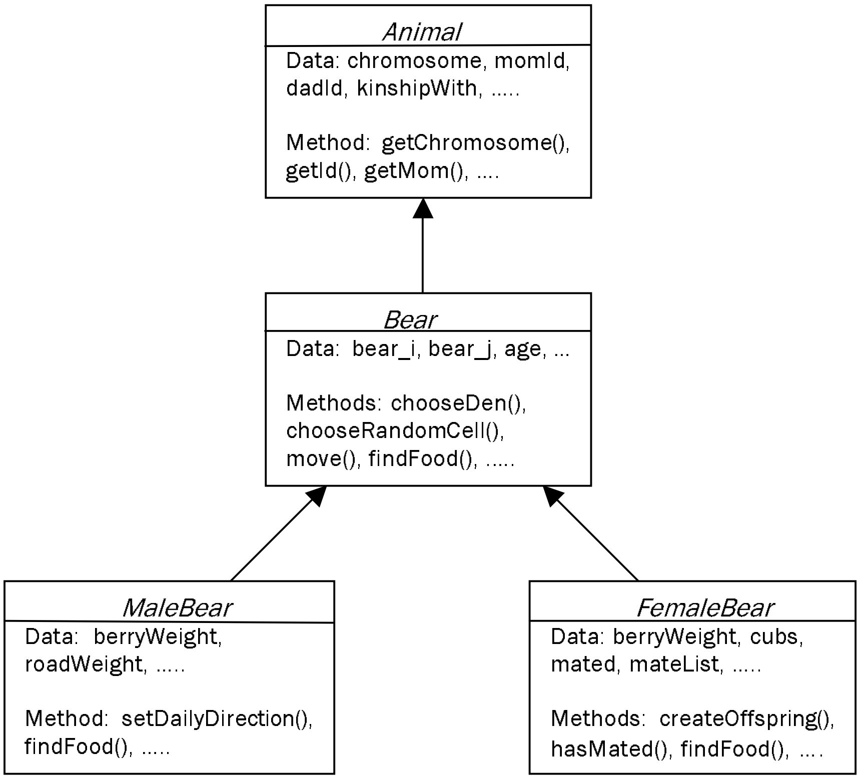

Figure 5.3. Inheritance relationships of the bear-related classes. Subclasses can have their own unique data variables and methods in addition to those inherited from all superclasses. Subclasses can also overwrite data variables and methods found in a superclass.

plus one or minus one value. The adults in the initial population are considered founders and given unique alleles by using their ids in combination with the value of the allele. If a founder had an id equal to 12, for example, its possible alleles would be (12,1) or (12, -1). Giving founder's unique alleles allows both loss of heterozygosity and change in allelic diversity to be recorded each generation simultaneously in the same model. Each individual animal in the population stores its kinship coefficient with every other member of the population in a *Vector* object called kinshipWith. Finally, each *Animal* object stores the identity of its mother and father and inbreeding coefficient for use in population genetics analysis.

Next in the hierarchy is the *Bear* class. Being a subclass of *Animal* means objects instantiated from *Bear* also inherit all the variables and methods associated with being an *Animal* as well. In addition, they inherit the variables and methods associated with being a *Bear*. The variables and methods in the *Bear* class are those that are independent of the bear's sex, such as its current position (i,j) or choosing a den location. The location of the den varies from year to year, and in the chooseDen() method, the current year's den location is chosen within a 5 km radius of the previous years den location, as suggested by the literature (Nat'l Wild. Federation 1987). (Note: This method worked for this study area because there were clear breaks [> 5 km] in the potential denning habitat between the two subregions. The method would, therefore, not artificially cause bears to move between the ecosystems just because of the random selection of a den location. In other ecosystems, with more continuous potential denning habitat, another method would have to be devised or this one slightly modified so as not to artificially produce connectedness between subpopulations.)

Last in the hierarchy, shown in Figure 5.3, are the *FemaleBear* and *MaleBear* classes. These classes inherit all the variables from the *Animal* and the *Bear* classes, but because they are subclasses, they will have additional variables and methods specific to a bear of that particular sex; for example, only females need methods for producing offspring. The methods in the *FemaleBear* relating to reproduction simulate delay embryonic implantation and allow multiple paternities. Females are allowed to produce one or two cubs with a 49:51 female to male ratio. (A slightly skewed sex ratio has been documented [Craighead et al. 1974]). The ratio of 1 cub to 2 cubs born was 40:60. The 10% increase was arbitrarily chosen for the model to improve the probability of persistence for such a small population of bears. The *FemaleBear* class also has methods responsible for, at the start of mating season, sending their cubs dispersing when the cubs are two and a half years old. To simulate sex-biased dispersal, female offspring choose den locations within a minimum 5 km radius of their mother's current location at the time. Male offspring, on the other hand, choose a den location at the end of the active season based on their current location at that time.

Another property of subclasses is they can overwrite the methods found in their superclass. In this particular case, the feature allows males and females to act differently when appropriate. Females with cubs, for example, emerge from their dens last and enter their dens first, and adult male behavior is just the opposite. Males in general emerge from their dens earlier than females and enter their dens later. This behavior was replicated in the model by having the setDenEmergence() and setDenEntrance() methods be specific to the *FemaleBear* and *MaleBear* classes. The two methods basically functioned the same as a stochastic process centered at the date set by the *Calendar* object (*Calendar* class is discussed in Section 5.5) for den emergence and entrance; however, the range of possible values differs between the sexes. Females without cubs can emerge from the den 0-7 days after the *Calendar* object's den emergence date and females with cubs 7-14 days after. For den entrance, females with cubs can enter 0-7 days earlier and females without cubs 0-7 days later. Similarly for males, emergence can be 14-21 days earlier than the *Calendar* object's den emergence date and 0-14 days later than the *Calendar* object's den entrance date.

Other methods that differ slightly between the sexes are the ones that may change if the female has cubs. When a female mates and produces cubs, the cubs stay with her until age two and a half. This is accomplished in the model is by making the mother grizzly in charge of all the activities regarding her cubs; i.e., the cubs do not move or otherwise function independently. In the growOld() method that ages bears a year; for example, the mother first ages herself a year and then sends a message to each of her cubs for them to age. A more elaborate example is in the testSurvival() method that represents a random death process. If a female has cubs, like in growOld(), she tests her own survival and sends messages to each of the cubs to test their survival. The matter, however, is further complicated if the mother bear or all of the cubs die. If all of the cubs die and it is mating season, the female immediately goes into estrus. If anyof the cubs survive, but the mother grizzly does not, then the cubs are sent on their own way and are given a decreased chance of survival. Cubs of the year are given a zero chance of survival and the survival of one-year-olds is decreased by 75%.

The remainder of the methods are either perfunctory in nature or relate to bears moving over the landscape. The perfunctory methods will not be discussed, but the movement methods will be discussed in some detail. Some movement rules are found in the *Bear* class, and others, though similar in implementation, vary between the sexes and are found in the *FemaleBear* and *MaleBear* class. The bear classes have five different movement methods that mimic the three different types of movements bears are thought to make.

The first type of movement is a move made under stress or duress. It is meant to mimic a flight response, such as a female with cubs or a juvenile male fleeing from an adult male. In this type of move, the bear is not concerned with finding food or avoiding areas with high road densities; it only wants to move away from the situation responsible for the stress. This can be thought of as a purely random move. The bear simple chooses one of the eight neighboring cells at random and moves there. The duress method is exactly the same for both sexes.

The second type of movement is a random move. This is similar to the duress type of move in that finding food is not a priority and the eight neighboring cells are the ones under consideration, but it is different in regards to road avoidance. When choosing a random cell to move into, preference is given to neighboring cells with road densities less than .0625 km/km^2. If none of the surrounding cells meet this criterion, then preference is give to neighboring cells with road densities less than .125 km/km^2. If no such cells exist, then the bear is located in an area with high road densities, and this is assumed to be a high-stress situation. Hence, it resorts to making a move under duress as described in the previous paragraph. The road density cutoff values were taken from the literature (Kasworm and Wakkinen 1997). The random movement method is exactly the same for both sexes.

The third type of movement is a directed move. It has been suggested in the literature bears make directed moves to desirable locations. Directed moves are made in a predetermined direction based on a goal. The goal can either be food (findFood()), a possible mate (findMate()), or the end-of-the-year den site (findDen()). In the findDen(), bears start making directed types of moves two weeks before their set den entrance date. The length of the move is a function of the distance between the bear's current location and the den location. The length is adjusted each day so that the bear will reach the den site no later than den emergence date. The two-week duration was arbitrary but was found to be sufficient when looking at the move distances this method generated in model verification runs. The method is the same for both sexes.

Another directed movement goal is finding the greatest abundance of food. Males and females both move in the direction of greatest food quality and abundance. Preference is given to cells with lower road densities and cells that have not been visited recently. This method was designed to act in conjunction with the methods of the *HabitatCell* objects to simulate moving in accordance with plant phenology. Several researchers have found bears' habitat and vegetative food selection tend to be strongly influenced by phenology (Husby and McMurray 1978; Sizemore 1980; Kendall 1986; Craighead et al. 1995; Nielsen et al. 2003). The temporal and spatial aspects of plant phenology are described in Section 5.4.3.

Bears move in the direction (north, south, east, or west) of highest food abundance and quality. Food quality is determined by nutritional and caloric values to bears. Different food items get weighted differently, with the higher caloric foods having higher weights. Ants, meats, and preferred berries, therefore, get the highest weights. Road density is given a negative weight. The negative weight for the road density is multiplied by the factor (road density/.125). This creates a preference for areas with lower road densities. The combination of weights for the various food items and road density allows areas with slightly high road densities (.63 km/km^2< road density < .125 km/km^2) to still be utilized, if there are abundant food resources in the same location. The nutritional value of vegetative food items is synonymous with plant phenology and is controlled by the *HabitatCell* objects as described in Section 5.4.3. In short, the *HabitatCell* object only has vegetative food items available when they are most nutritious for bears.

Highest food abundance is found by using the weights for the individual food items times their availability (presence = 1 or absence = 0) in a particular *HabitatCell* object to calculate a ‘score’ for each cell. Scores from all the cells in each direction get summed and divided by the number of cells in that direction, and then the direction with the highest average score is chosen. The average food score, not the total score, had to be used because when a bear is close to the study area boundary, fewer cells are available in one or more directions. Directions with the most cells might therefore be chosen even though they really have less food available. If a tied score occurs, preference is given to the previous direction. This move direction is set at the start of everyday and only applies when bears are looking for food, i.e., not mating or finding a den.

Bear objects from the *MaleBear* and *FemaleBear* each have their own set direction methods. This is because individual food items are weighted differently for each class, and the number of cells used in calculating a score for each direction differs (the number of cells used by males is smaller to reflect a less cautious nature than females). For females, no weight is given to meat items: guts or carrion. This is not because females do not eat these food items, but because the literature indicates more males than females look for carrion in the spring and gut piles in the fall. This should, therefore, be interpreted as females do not seek out meat food items, but they will eat them if found. Additionally, males show slightly less aversion to roads than females.

Once the direction is set for the day, all the moves associated with finding food will be in that direction. For every direction, the bears can move to one of three cells; for example, if the daily direction is north, the bear could move northeast, true north, or northest. They choose the cell with the highest overall score using the same weights as explained above for setting the daily direction. A tie score between cells is settled randomly. The number of moves a bear makes in a day is set at the beginning of that day. The number of moves (1-5 cells) is drawn from an empirically derived move distance distribution (Sizemore 1980). The distributions vary by sex, age, and reproductive status; i.e., young males will draw their number of daily moves from a distribution that is different from a female with cubs. The distribution also varies by season. The seasons are spring-summer and summer-fall, where the summer-fall season indicates the availability of berries.

The last type of goal is finding a mate. Male bears have this goal during the mating season, but not females. Mating season was a fixed length of 26 days. During this time, the move direction is set in the direction of the most females and the move distance is doubled. The search radius used to detect females is 50 cells or about 10 mi. This is 10 times the radius used in the find-food method and was arbitrarily chosen because no estimate for the maximum distance males are able to detect estrus females was found in the literature. In the model, having females not seek out males during mating season facilitated a sex-biased difference in home range size, with males having the larger range sizes. The methods in the model mimic what has been suggested in the literature as the reason behind this phenomenon (males seeking females during mating season).

Each time a bear moves regardless of its goal, its survival is tested at the current location before it moves to the next cell. If it does not survive, it is immediately removed from the population. The mortality rate a bear experiences at a particular location is dependent upon the open, motorized road and nonmotorized trail densities at that location and how far away it is to a center of human development, as explained in Section 5.4.3.2.2. All bears record their move in a location *ArrayList*. These locations are written out to a file, so they can be imported to GIS or software programs for later analysis. They are also used to calculate home range size by generating a convex hull. This is done at the end of the year when graphics are used to aid in visualization of the model and was done for model validation purposes during model development. If the model is executed as an application, this calculation is not performed. The ranges sizes produced by the model fell within ranges reported by the BC Parsnip project. (Male ranges were probably smaller than reality, as they did not consistently fall within the two to four times larger than female ranges reported in the literature.)

All animals are managed by an object instantiated from the *AnimalManager* class. An instantiated object from the *AnimalManager* class will be referred to as an animal manager. The animal manager handles all functions that involve the entire population, including recording data on demography and genetics. Its first task is to instantiate the initial population of bears for the simulation run. Once the population has been created, the animal manager places the bears randomly at a den location (half of the bears are placed in each subregion). Once the population is placed on the landscape, the animal manager next instructs all the animals in the population to update their kinshipWith vectors, i.e., calculate their kinship coefficients to all the other members in the population. Finally, the manger object uses *Genetics*.calcFounderAllelles() to determine and store the founder alleles for the initial population. As the model runs, bears will die and new bears will be born. When individuals die, they tell the animal manager to remove themselves from the population. When a female produces offspring, she tells the animal manger to add a new member to the population. As a consequence of this, the animal manager always knows the current population size. When births and deaths occur, the animal manager instructs all the bears in the current population to update their kinshipWith *Vectors* that store all the kinship coefficients with other members. These births and deaths are also recorded, so that they can be printed out to files at the end of the model run.

For the initial population (generation equal to 0) and after the end of every subsequent generation, the animal manager updates and stores the population's genetic measures: average heterozygosity, mean kinship, variance in average heterozygosity, average autozygosity, percentage of lost founder alleles, and F_{st}. It stores the results calculated for each measure in separate arrays for exportation to files at the end of the model, or if graphics are being used, to display the measures as a line graph. The animal manager class provides one more summary function in its end-of-generation update method. The function calculates the percentage of population members in each of ten inbreeding coefficient categories: [0, .1), [.1, .2), [.2, .3), ...[.9, 1]. If there are graphics with the model, the percentages are drawn to the screen as a bar graph; otherwise the breakdown is written to a file at the end of the model run.

At the start of the year, in response the model's clock (discussed in Section 5.4), the animal manager instructs the females who have mated in the previous year to give birth and sends messages to all the adult bears to choose their den emergence and entrance dates and choose a den location for the end of the active season. Once the start of the year events have been completed, the animal manager, in response to the model's clock, tells the bears to set their daily directions and number of daily moves and to adjust their visitation list every day of the active season. If it is the start or end of mating season, the animal manager sends a message to the adult bears to alter their behavior, i.e., females to be receptive to males and males to seek females. Once this is done the bears move the requisite number of times in search of foods, or for males during mating season in search of females. Any conflicts resulting in additional moves are handled immediately as described in the description of *HabitatCell* objects below. All of this is done as part of the animal manager's pretick() and tick() methods.

At the end of the year, in response to the model's clock, the animal manager sends a message to the bears to age a year, and then it records the demographics (number of births, deaths, and population size) in an *ArrayList* to be written out at the end of model run. If there are graphics involved, the home range sizes of all the subadult and adult bears are calculated, after which the bears are sent messages to clear their locations *ArrayList* object for the following year. (When model is executed for model validation purposes, the size of the home range can be recorded and written out to a file as well.)

5.4.3 Habitat and habitat management classes

5.4.3.1 Overview

The landscape is represented in the model as a two-dimensional array referred to as a grid. Each element in the array, indexed by row i and column j, is referred to as a cell. In the real landscape each cell represents .1089 km^2 or 26.9 acres, and in the model, eachcell in the grid is represented as a dynamic individual *HabitatCell* object. The *HabitatCell* objects, here in referred to as habitat cells, are instantiated from the *HabitatCell* class. The characteristic attributes and methods chosen and developed for this class were those deemed most important in influencing the movements of a bear. In this regard, the attributes and methods were chosen to support four purposes of the habitat cells in the model. These purposes for each habitat cell are, if applicable, to provide food for the bears, to serve as denning habitat, to reflect the direct and indirect effects on bears of human landscape features, and lastly, to observe bear occupancy and resolve potential conflicts between bears.

The first purpose, for habitat cells to provide food for bears, is complicated by the vast array of suggested food resources for bears and by the temporally dynamic availability of these resources. For the model the wide range of food resources is simplified to include only those regarded as important food items for bears in the CYE or similar ecosystems, that is, those documented as being a high percentage of the bear's diet during some part of the active season. These important food items are considered as being either present or absentin the habitat cell, as was denning habitat. The temporally dynamic aspect of the food resources is implemented by providing the habitat cells with methods to (1) adjust their food resource availability after visitation by a bear and (2) imitate plant phenology. The model incorporated plant phenology by using the concept of growing-degree-days in conjunction with a statistical model by Rich and Fu (2002) that predicts temperature variation over rugged terrain. Annual stochasticity in phenological events was likewise included into the model by deriving 25 different climate scenarios using historic climate data obtained from the Utah Climate Center at Utah State University.

The third purpose, to reflect the direct and indirect effects on the population of human landscape features, was straightforward, since unlike the food resources, the effects are temporally constant. To reflect the indirect effects, each habitat cell was given a road density attribute. As mentioned in the previous section discussing the bear-related classes, bears considered open road density in their decisions of what direction and which cell to move to. To reflect the direct effects, each cell was given a mortality risk factor. The magnitude of the risk factor is dependent on the habitat cell's open, motorized road and trail density, nonmotorized trail density, and distance to the closest human development center and was calculated using a modification of the multiplicative hazards model derived by Johnson et al. (2005). To help a nalyze the direct effects of the human landscape, each habitat cell recorded actually mortalities occurring in its location. The location and number of mortalities are written to a file at the end of the model for importation into a GIS.

Finally, the last purpose of the habitat cells, to observe bear occupancy, allowed the model to have irregular events occur immediately (see Table 5.1 for list of irregular events). These irregular events occur when a bear either enters or leaves a habitat cell. When a bear visits a habitat cell and then leaves, the cell's food availability is immediately adjusted. If a bear visits a cell that is already occupied, then based on the published social hierarchy found in bears, one of the bears may be forced to leave. If it is mating season and one of the bears is a responsive female, however, then mating would occur. In either case, the event occurs immediately, as it would in real life.

5.4.3.2 Data

The spatially explicit data related to the *HabitatCell* objects for the creation of realistic, spatially varying and temporally dynamic habitat cells are extensive. Except for the elk winter range data that went directly into the habitat cells as carrion, the other data layers had to be generated using supporting data layers and models. Figure 5.4 shows the relationship of the data layers generated for the *HabitatCell* class. The following sections discuss supporting data layers, models, and concepts used in the development of each of the final layers seen in the figure.

5.4.3.2.1 Human landscape

Data in this category consist of various human landscape features considered as attractants or repellants to bears and/or whose presence contributes to an increased risk of mortality to bears. Garbage dumpster locations represent a potential attractant to a bear. Household garbage cans, as well as miscellaneous foods associated with humans, such as birdfeeders, improperly stored dog food and grains, and orchards also pose as attractants to bears. They were not included because these attractants are associated with homes, and the availability of spatial data for land parcels was limited to three of the four counties. Factors contributing to an elevated risk of mortality were based on a multiplicative hazards model developed by Johnson et al. (2005), hereafter referred to as the mortality model. Each layer created and used as a variable in the mortality model is described here, and a discussion of the mortality model used can be found in the next section.

5.4.3.2.1.1 Garbage. Garbage dumpster locations throughout each of the counties and campgrounds with garbage dumpsters maintained by the National Forest Service were considered as attractants. Neither of the counties in Idaho used bear-resistant containers. Though the counties in Montana used bear-resistant containers, one cannot be guaranteed they are used properly. Edwards (2003) investigated two factors that can reduce the effectiveness of bear resistant containers: lack of regular and consistent maintenance and user misuse. In Lincoln county, Montana, she found upon inspection that 50% of the 24 garbage sites reported to be using bear-resistant containers had a least one container in poor physical condition. The *garbage* layer depicts the garbage disposal locations in the study area. Sources were county sanitation

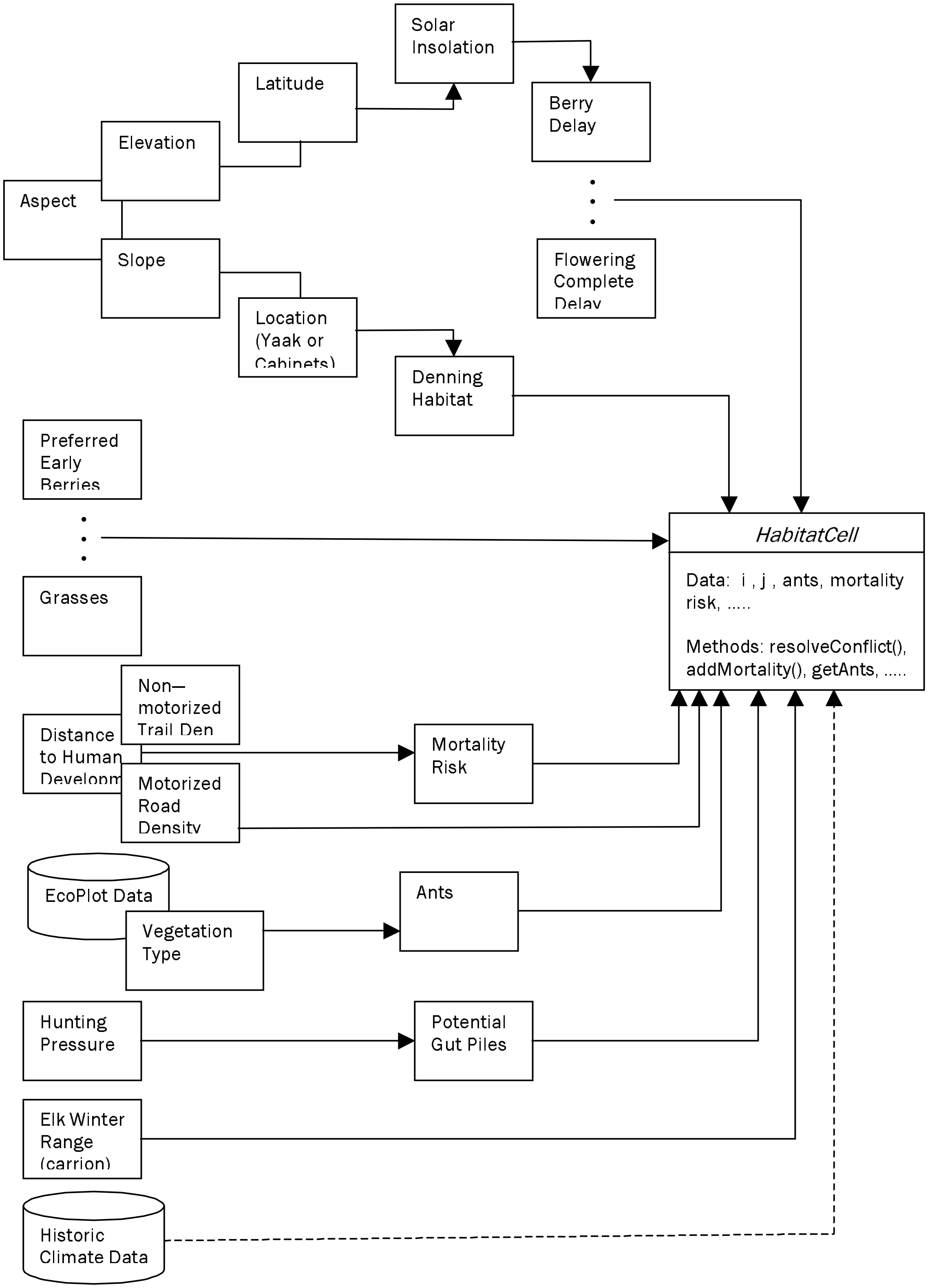

Figure 5.4. Relationship of spatially explicit data layers to *HabitatCell* class. Dots indicate additional, similar data layers as described in the text. Solid lines indicate static relationships. Dashed lines indicate dynamic relationships.

departments. Workers from the sanitation departments provided maps of various scales marked with the location of garbage disposal sites. This data layer was developed but not used in the grizzly bear model because the final grid resolution was too large to make these single point locations meaningful.

5.4.3.2.1.2 Campgrounds. The *campgrounds* layer represents available overnight camping sites and picnic areas within the study area. Location data were obtained from the three forest services. This layer included all campgrounds regardless of number of sites available. These sites were considered as bear attractants because of the possible garbage and human foods available. Even though some of these campgrounds have bear-resistant garbage dumpsters available, as discussed above, this does not equate to proper use. Also, within this study area there is no food storage order in place; therefore, it is conceivable that campers will leave food out or otherwise available for bears. There were 34 campgrounds included in this layer. Small individual campsites were not included in the grizzly bear model because the final grid cell resolution was too large to make their location meaningful. Large campgrounds served as supplementary data for the mortality model. They were added to the *bigcamps* layer discussed below and seen in Figure 5.5.

5.4.3.2.1.3 Trails. The *trails* layer represents nonmotorized trails in the study area. It was compiled from GIS trails coverages received from each of the national forests in the study area. Attributing was not consistent between each of the forests; therefore, it was necessary to consider motorized use as a binary attribute: motorized or nonmotorized. This would tend to overestimate the amount of motorized trail use because (1) if a trail is designated as motorized, it does not necessarily mean the trail actually gets motorized use (trail maybe too steep or not sufficiently maintained to facilitate motorized use), and (2) the potential for motorized use does not necessarily equate to greater than one vehicle per day of use (the definition of motorized trail in the mortality model). All nonmotorized trails were maintained in this layer and used in the calculation of trail density in the mortality model. All motorized trails were added to the roads layer discussed below. It is important to note that the trails coverages from all the forests are not 100% accurate. They are constantly being updated and improved as additional information becomes available. If the trails coverage was digitized from aerial photos, for example, there is no way of

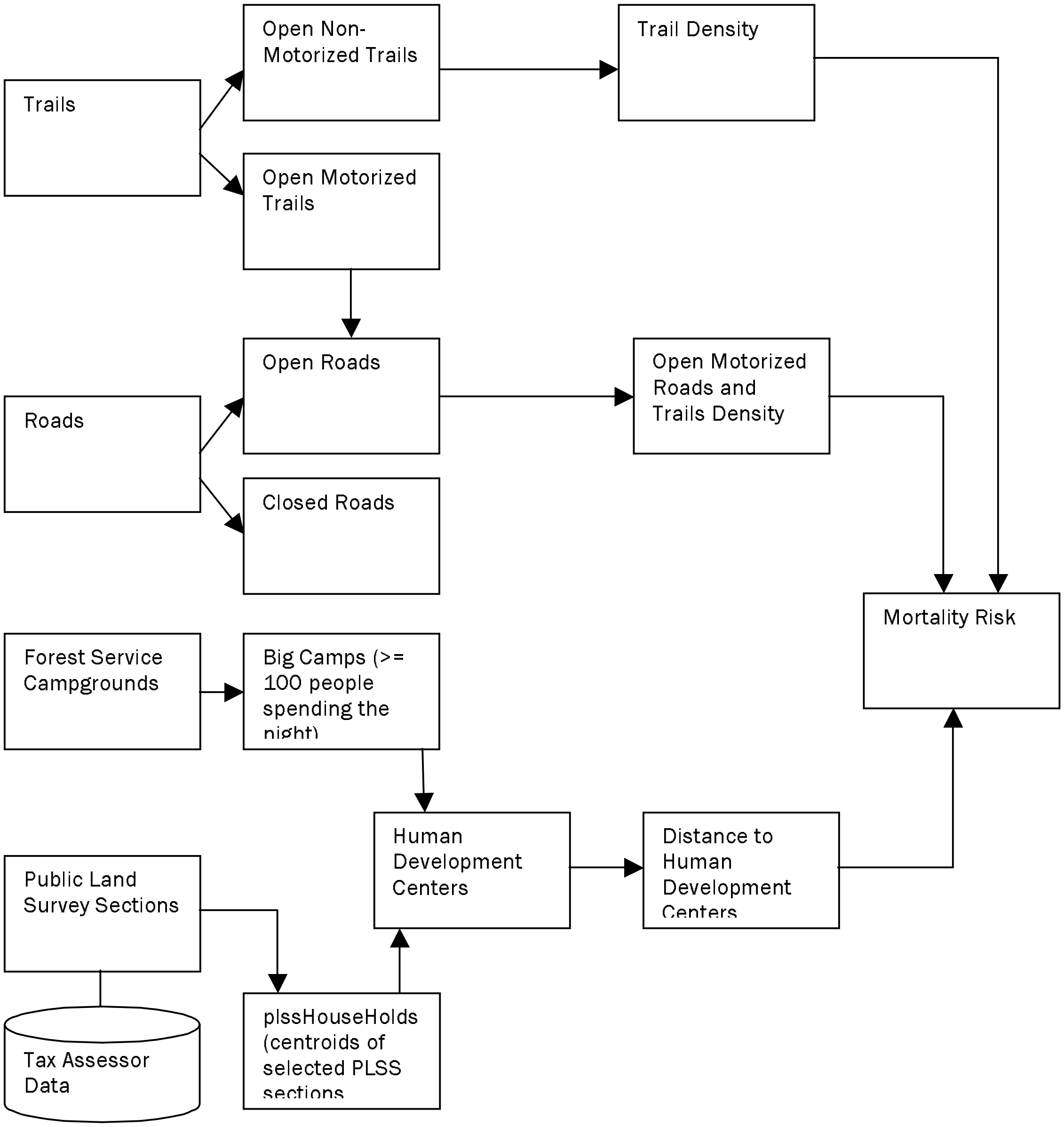

Figure 5.5. Relationship of spatially explicit data to mortality risk grid.

discerning from the photo whether or not it really is a hiking trail or just a heavily used game trail. The coverages received from the forests, however, represent the most complete and accurate information available at the time of model development. Motorized trails that were open during the bear active season were considered motorized and added to the motorized roads coverage. If a motorized trail was coded as being closed during the active season, it was assumed the closure was effective and no motorized travel occurred; thus, the trail was considered a nonmotorized trail and kept in the *trails* coverage.

The *trails* coverage was converted to a grid coverage using ArcInfo's linegrid command. ArcInfo's grid linedensity function was then used on this grid to calculate the density of trails in units km/km^2. This grid of line nonmotorized trail density is used in conjunction with the mortality model discussed in Section 5.4.3.2.2 to derive a final mortality risk grid to use in the model.

5.4.3.2.1.4 Roads. The *roads* coverage is a summation of selected roads and motorized trails. Motorized trails are discussed above. Roads open and receiving relatively high use during thebear active season were taken from GIS roads coverages obtained from the three national forests. High-use roads, as defined in the mortality model, are roads with greater than one vehicle per day traffic. The roads data from the forests were used 'as is', i.e., no changes to the spatial or descriptive information received were made.

There are some important things to note regarding the *roads* coverage. First, the coverages are not 100% accurate. They are constantly being updated and improved as additional information becomes available. If the coverage was created by digitizing aerial photos, for example, there is no way of determining from the photo whether or not a road is open or closed. This is especially the case for roads on land owned by Plum Creek Timber, where all roads had to be assumed open, because additional information was not available. Also, in the case of roads on private lands, from aerial photos one cannot distinguish whether it truly is a road or just someone's driveway. Second, some of the roads have seasonal or yearlong closures. It has been documented that road closures, all except reclamation of the road/trail, are ineffective (Havlick 2002). Information regarding the type of device or method used to close a road was not available for all forests. The design of this study, also, did not include assessing the effectiveness of road (trail) closures on each of the forests. The following assumptions, therefore, were made: (1) Roads (trails) with yearlong closures, despite closure device used, were considered closed. (2) Roads (trails) that were closed throughout the bear active season were considered closed to motorized use, i.e., assumed the closure was effective. (3) Roads that were only seasonally closed during hunting season were considered open. This last assumption was made because if the roads were only closed during hunting season, the closure device used was probably not a barrier (barriers are thought to be the most effective method of closure) and local expectation would be that the road was open. This could lead to failure by users to observe the seasonal closure.

The (open) *roads* coverage was converted to a grid coverage using ArcInfo's linegrid command. ArcInfo's grid linedensity function was then used on this grid to calculate the density of roads in units km/km^2. Researchers have found areas of high road densities (> = 1.242 km/km^2) are avoided by bears (Kasworm and Wakkinen 1997). This grid of motorized road density was used in conjunction with the mortality model discussed in Section 5.4.3.2.2 to derive a final mortality risk grid used in the model.

5.4.3.2.1.5 PLSS households. The *plssHouseholds* layer is a point coverage derived from the centroids of selected PLSS sections. Tax assessor data were used to determine the PLSS sections that met a requisite number of households that were equivalentto 100 persons spending the night within a 1 km radius, the definition of a human development center in the mortality model. The tax assessor database for each of the four counties in the study area: Boundary and Bonner, Idaho, and Lincoln and Sanders, Montana, was obtained from either the counties themselves (Idaho) or the state GIS library (Montana). From each record in the tax assessor database, the type of property and the township/range/section it was in could be discerned either directly or indirectly using additional information. A series of small Java^{TM} programs were written to summate the total number of households for each township/range/section. For Montana, household was defined as a house, mobile home, single apartment, condo, or townhouse. Multifamily residential structures were counted as the appropriate number of households, such as two for a duplex or three for a triplex. For Idaho, commercial residential data were not available; hence, household was defined as mobile homes, single-family dwellings, and condos.

The county assessor data for Montana had the necessary information to determine the location of hotels/motels in Montana. There were 14 sections within the study area that contained one or more hotels/motels. Of these, 7 sections were already listed as developed because of the number of households present, and 1 was disregarded as a labeling error. Three of the 14 sections were left as undeveloped because they were adjacent to sections that were already labeled as developed; i.e., they were considered as a 'cluster' of developed sections with the center of the cluster lying within another cell (another way of saying this is that they were thought to be within the radius of a neighboring section). Only three sections containing one or more hotels/motels were added to the development coverage because of the combinations of households and hotels/motels present equated to the required number.

For Idaho, the county assessor database did not contain the required information for hotels/motels. No hotel/motel lodging facilities, therefore, were included for the Idaho portion of the study area. It was determined this was not a significant deficit. Based on the results from Montana, most hotels/motels would be located close to cities and would most likely be accounted for in the sections selected based on the number of residential dwellings. Reading the verbal descriptions of lodging facilities available in the Idaho Panhandle found at travel/tourism websites confirmed this view.

This layer resulted in 102 development points being included in the *humandev* coverage (discussed below). There were 56 sections meeting the criterion for the two counties in Idaho and 46 residential sections meeting this criterion for the two counties in Montana within the study area. The selection of the appropriate sections within each county was complicated by the fact that all sections are not 1 mi^2 in area. This was handled by converting the density from homes/mi^2 to homes/m^2, as described below.

From the U.S. Census Bureau quick facts (http://quickfacts.census.gov), the average number of persons per household was as follows for the four counties;

Bonner, Idaho	2.49
Boundary, Idaho	2.61
Lincoln, Montana	2.40
Sanders, Montana	2.35

The average for each of the two counties was 2.55 and 2.375 persons for Idaho and Montana, respectively. Using the two county averages, one gets 39 households for Idaho and 42 for Montana being equivalent to 100 persons being able to spend the night. Given the area of a circle of radius 1 km is equal to 3,140,000 m^2, the potential for 100 persons to spend the night could be restated as .00001242 homes/m^2 for Idaho and .0000134 homes/m^2 for Montana. (Note this conversion is necessary because not all PLSS sections are equal in area.)

The sections with the required density were labeled 'developed.' Next, each section that had the required density but was less than 1 mi^2 in area was examined individually. If the section being examined had at least 39 households (42 for Montana), then it was kept as a developed polygon. Otherwise it was labeled as nondeveloped. However, if the examined section had the requisite density but was shy of the 39 (42 for Montana) households necessary to meet the definition, the surrounding sections were examined. If the surrounding sections had, in total, enough homes to meet the deficit between the required homes stated in the definition and the number of households in the examined section, the section under examination was maintained as developed. (Enough homes to meet the deficit was met if the sections surrounding were candidate section, were not labeled developed, and had homes, or if the sections were labeled as developed but had more homes than 39 (42 for Montana). I attempted to find the center of the development when there was a cluster of sections.)

The labels for all the section polygons were then centered, and the labels corresponding to developed sections were exported to a point coverage. This point coverage was then clipped to the study area boundary. (Note: Three labels slightly outside the study area boundary were moved in order to ensure their inclusion in the clipping operation). Within the study area, there were 56 sections meeting this criterion for the two counties in Idaho and 46 sections meeting this criterion for the two counties in Montana, for 100. The points in this layer were incorporated into the human development layer, *humandev* (discussed below).

<u>5.4.3.22.1.6 Big camps</u>. The *bigcamps* point coverage represents the locations of forest service campsites having 20 or more campsites available. Twenty campsites were assumed to be equivalent to the capacity to sleep 100 persons overnight, the definition used in the mortality model for a human development center. This estimate assumes five people per site, as suggested by Bill Fansler, recreation forester for the Kootenai National Forest. These points became part of the human development layer, *humandev* (discussed below). Location and number of sites at each campground were taken from the recreation point coverages of the Lolo and Kootenai National Forests. The recreational campground locations and number of sites per campground for

the IPNF were converted into a GIS coverage from lat/long coordinates and description information provided by the *National Forest Campground and Recreation Directory*. There were five campgrounds meeting this criteria, none of which fell within a developed sections, as described above, so they were all included in the human development layer.

An attempt was made also to include large, private RV Parks and campgrounds. There were a few large private RV Parks and campgrounds found at various travel/tourism websites or by examining *Woodall's Western America Campground Directory*, however, only verbal descriptions were provided. Private RV Parks and campgrounds were not included in this layer, because without coordinate locations, it was impossible to locate the facilities on a map. The points in this the layer were incorporated into the human development layer discussed next.

<u>5.4.3.2.1.7 Human development</u>. The *humandev* coverage contained 107 points representing centers of human development as defined in the mortality model (discussed in the next section) as having, within a 1 km radius, either 30 facilities or the potential for 100 people to spend the night. This definition was used to define human development as seen on the landscape for the Yellowstone Ecosystem, an ecosystem consisting almost entirely of national parks or forests. For the study area, where private lands are profusely intermingled within the recovery zone, this definition needed to be slightly adapted. The human development layer for the model consisted of two point features: campsites having the capacity for 100 people to spend the night (*bigcamps*) and the centroids of all PLSS sections having the capacity for 100 people to spend the night (*plssHouseholds*). The largest PLSS sections are 1 mi^2 in area; therefore, one section can contain a circle of radius .80465 km. Using sections instead of circles of radius 1 km, hence, had the potential to overestimate the number of development points in the study area. ArcInfo's euclidean grid function was used to create a grid representing the distance to the nearest human development, after the *humandev* coverage was converted to a grid using ArcInfo's pointgrid function. The grid representing distances to the human development points was used in conjunction with the mortality model discussed in Section 5.4.3.2.2 to derive a final mortality risk grid used in the model.

5.4.3.2.2 Spatial mortality

Mortality was based on a statistical, multiplicative hazards model developed by Johnson and others (2005) for the Yellowstone grizzly bear population. The model was chosen because it included spatial, human disturbance variables as risk factors, and thus, the equation ties the risk of mortality experience by a bear to its spatial location. The original multiplicative hazard model equation, h(t), was

$$h(t) = h_o(t) * (1.44*road + -.124*road^2 + .302* man\# + -.410* inPark + -.02*humanDist + .001*humanDist^2 +.159*trail + .606*sex + -.026*age + .009*age^2), \qquad (5.1)$$

where,

$h_o(t)$ = inherent risk of death to all individuals in the population

road = road density of high use roads (>1 vehicle/day) per square km (km/km^2),

man# = number of management actions against a bear,

inPark = binary variable, 1 in a National Park, 0 else,

humanDist = distance (km) to closest permanent, major human development,

trail = nonmotorized trail density per square km (km/km^2),

sex = binary variable, 1 for male and 0 for female, and

age = age of the bear.

In the CYE, no grizzlies live within a National Park, and their low number in the ecosystem means there are not a noteworthy number of management actions against grizzlies. The variables ‘inPark’ and ‘man#,’ therefore, can be set equal to 0, simplifying equation (5.1) to

$$h(t) = h_o(t) *exp(1.44*road + -.124*road^2 + -.02*humanDist +.001*humanDist^2 + .159*trail + .606*sex + -.026*age + .009*age^2) \qquad (5.2)$$

There were some problems with trying to use equation (5.2) as a spatially explicit mortality function for the CYE. First, the natural vegetation differs between the two ecosystems with the CYE vegetation providing more cover for grizzlies; therefore, the mortality risk associated with human landscape features is most likely less in the CYE than in and around Yellowstone. Second, using GIS to create the spatial variables used in equation (5.2) and then calculating the risk ratios over the range of values found in the GIS layers, such as road density, some of the resultant risk ratios were rather large. These large risk ratios would equate to mortality risk being larger than 100. The reason for this is Johnson and others truncated values for road densities and other variables in their model to the highest values utilized by bears In Yellowstone National Park. None of the variables were truncated in the application of (2) to the study area. Finally, what was truly desirous for this model was a rate that is purely spatial, i.e., is a function of the landscape variables alone, not a bear's age and sex. If a bear spent most of its times close to human developed areas, its mortality risk would be higher than that of a bear that spent most of its time in more remote locations regardless of its sex or age. Developing a similar hazards model for the CYE based on only landscape features, however, was beyond the scope of this project.

Several measures were taken to better fit equation (5.2) to the CYE and the needs of the overall model. First, to make the mortality risk only a function of landscape variables, equation (5.2) was rewritten as follows;

$$h(t) = h_o(t) *\exp(1.44*road + -.124*road^2 + -.02*humanDist +.001*humanDist^2 +.159*trail)* \exp(.606*sex) *\exp(-.026*age + .009*age^2) \quad (5.3)$$

This formulation divides the equation into a baseline hazard, landscape-related risk factors (road density, distance to closest human development, and trail density), and bear-related risk factors (sex and age). The formulation allowed the baseline hazard and the bear-related risk factors to be incorporated into the *Bear* class and the risk factors pertaining to the landscape-related features to be incorporated into the *HabitatCell* class. It was next decided to ignore age and sex and to solely concentrate on the risk posed by the landscape features. This was done because the spatial variation is what was deemed most important to the model. Second, to make sure mortality risk did not exceed 100, one constraint was made. The constraint limited the maximum risk of any cell. When multiplied by the baseline hazard, none of the mortality rates for any of the cells could exceed 0.30. This worse case scenario rate was arbitrary but was believed to be reasonable. To insure no individual cell would exceed the limit, the mortality risk was truncated at the appropriate maximum value based on the baseline mortality rate.

The mortality rates calculated in the 1999 Research and Monitoring report (Kasworm et al. 2000) for CYE females were used as a starting point for the mortality rates incorporated in the model. These were .235 for cubs, .113 for yearlings, .156 for subadults, and .081 for adults. For simplicity, yearling mortality was set equal to cub mortality. The baseline hazard rate was then found by repetitive iteration of the model. A baseline hazard rate was chosen such that at the end of the model, annual rates generated by the model would be close to those obtained from the annual report. Finding a baseline hazard rate that is different from the average rates found in the annual reports may seem odd at first but is necessary when going from a nonspatial to a spatially explicit modeling framework and moving from an annual rate to a daily rate. A nonspatial rate is an overall summation of the rate that occurred at each location visited throughout the active season. If a bear visited n-number of cells over the course of the year, then the risk it faced at each cell would be the 1/nth power of the risk associated with that cell. If the landscape is homogeneous and, consequently, mortality risk constant, then space is irrelevant, as the n-th power of the 1/nth root of the rate is equal to the rate itself. If this is not the case, however, then the initial hazard rate must be adjusted to reflect the fact a bear, throughout the active season, may spend some time in a combination of areas of relatively safe and relatively not-so-safe habitat.

5.4.3.2.3 Nonvegetative bear foods

5.4.3.2.3.1 Elk carrion. The *elkCarrion* polygon layer was obtained from the Rocky Mountain Elk Foundation. Important to bears are elk winter and calving habitat. Elk winter habitat represents potential carrion for bears when they emerge from their dens in the spring. Elk calving habitat represents a potential for elk calves as a food source. Bears in this geographic area do not seem to utilize calves as much as the bears in the Yellowstone Ecosystem; thus only elk winter habitat was consider as a potential food source. The original polygon layer had a scale of 1:250,000. Using ArcInfo's polygrid function, it was converted to a 330 m grid.

5.4.3.2.3.2 Elk gut piles. The *elkGutPiles* layer was derived from the coverage *huntlevel*. This layer depicts three levels of elk hunting pressure in the study area: low, medium, and high, as delineated by expert opinion. Level is a relative measure based on road access, terrain, and animal population numbers and not actual hunter numbers. Following a process suggested by Bill Fansler (recreation specialist) and Wayne Johnson (biologist) on the Kootenai National Forest, the recreation management specialist on the national forest (Montana forests) or fish and game personnel (Idaho) were asked, based on their experience, to draw on a map zones of hunting pressure. The two criteria used were access and animal populations. Access considered the distance from open roads, steepness of the terrain around the road, and density of vegetation. It was assumed that areas with steeper terrain and dense vegetation received less hunting pressure because people do not like to hike the steeper terrain and the dense vegetation is noisy and hunters cannot see the animals. Access also considered trails and closed roads and proximity to towns. Areas with trails and closed roads were assumed to receive more pressure because they facilitate hiking. It was also assumed, areas closer to town would be hunted more heavily than those further away. Animal populations included the elk population distribution only. Moose, sheep, goats, or other animals that are hunted with a limited number of permits were not considered. The fairly uniform distribution of the deer population precluded its consideration. Only large land units (25,000+acres) were delineated as areas having low or high hunting pressure. Everything else was labeled moderated. This could potentially exclude smaller areas receiving a substantial number of hunters. Areas of high hunting pressure were assumed to be equivalent to areas with possible elk gut piles, a possible food source for grizzlies during hunting season. Source of the maps were the Kootenai, Lolo, and Idaho Panhandle National forests. The scale of the maps were 1:24,000 and 1:126,720 on the Kootenai and the Lolo and Idaho Panhandle, respectively. Road closure information pertained to 2001. Polygons attributed with high hunting pressure were selected and put in a new polygon layer. This new layer was converted to a 330 m grid using ArcInfo's polygongrid function.

5.4.3.2.3.3 Ants. An important food source for grizzly bears is ants and their larvae (Matteson 2001; Swenson et al. 1999; Wayne Kasworm, personal communication, 2000). Bears search for ants in old logs and under stones. For this model, ants refer to log-dwelling ants, which include carpenter ants, *Camponotus* spp., and some *Formica* spp. (personal communication with entomologist Torlof Torgerson, 2004). These ants prefer downed logs of at least 15 cm at the large end (personal communication with entomologist Torlof Torgerson, 2004). Tons/acre of course woody debris (CDW), a measurement associated with fire fuels estimates, was used as a surrogate for downed tree diameter. CWD loads of 25+ tons/acre indicate significant amounts of larger materials (personal communication with research forester Mic Harrington at the USFS Fire Science Lab [FSL], 2004).

The *ants* grid was derived from data received from the FSL. Don Long, GIS analyst at the lab, provided a vegetation-type grid (30 m cell size) and a file relating those vegetation types to the proportion of field data plots for that vegetation type that contained fuel loads of over 30 tons/acre. These files were linked together and the cells with a proportion of plots greater than or equal to 35 % were chosen. This is a more liberal criterion than that suggested by Long (proportion >=45) and, therefore, may have overestimated the distribution of heavy fuel loads across the landscape. This more liberal criterion was chosen in light of the fact that this approach has never been field tested; hence it was decided to error on the side of overabundance. Aspen and other broadleaf stands are also potential locations for ants (personal communication with entomologist Torlof Torgerson, 2004). Broadleaf plant associations from the vegetation grid discussed below were added to this heavy fuels grid to produce the final *ants* grid.

5.4.3.2.4 Vegetative bear foods

This layer was the most difficult to derive. The main problem was finding a method that was both feasible and consistent over a large areal extent, while at the same time producing enough detailed information about vegetation to be useful in the model. Before making a final decision several avenues were pursued, including using remotely sensed data, the forest service's TSRMS database, and grizzly bear habitat component mapping.

The TSRMS database provided a feasible option, because it was available for all three national forests, but it lacks consist information about understory vegetation and information for non-timbered stands. Similarly, data produced from remote sensing lacked information about understory vegetation. It does, however, provide a feasible and consist option. Field sampling and mapping from aerial photos, when done well, rates high on accuracy and vegetation specificity but is often infeasible to carry out over a large area due to monetary and time constraints. Data produced by this method was available because this method was used to produce the grizzly bear habitat components for the cumulative effects model discussed in Chapter 2. These components would have been well suited for this project, but unfortunately, the mapping was not available over the entire study area. Combining the TSRMS or remotely sensed data with the habitat component mapping was also considered but was dismissed in favor of consistency across the study area and future feasibility. Finally, it was decided to improve the applicability of remotely sensed data to this research.

The remotely sensed data was obtained from the USDA Forest Service Region 1 Cohesive Strategy Team (CST). These data were a slightly modified version of the data generated from the Satellite Imagery Land Cover Classification Project 1 (SILC 1) carried out by the Wildlife Spatial Analysis Lab. Improvements to the data's generalized, cover-type classification scheme was implemented by using a rule-based process to translate site characteristics and general cover-type classes and information to a more specific vegetation community type known as a plant association. The narrative description and/or cover-constancy tables of the specific community types or plant associations were then used to assess the presence of particular bear foods. The site characteristics used were slope, aspect, and elevation (determined from the USGS DEM 30 m data), annual average precipitation (obtained from PRISM climate mapping system [http://www.ocs.orst.edu/prism/)], potential natural vegetation type (produced by and obtained from the CST), and potential solar radiation (derived using a potential solar radiation program developed by Mark Wilson).

The plant associations used were mainly taken from Leavell (2000), but because his work focused on upland terrestrial community types older than 10 years, other sources had to be consulted as well. As seen in the discussions below, 11 different sources were consulted. A rule set, consisting of approximately 500 individual rules, was derived to assign a plant association to a particular combination of cover type, site characteristics, size class (applies only to forest cover types), canopy closure class (applies only to forest cover types), and when necessary, potential natural vegetation. Discussion of the plant associations used for each cover type and their sources is contained under the broad vegetation categories conifer – nonriparian, mixed broadleaf forest, nonriparian shrubland, grassland, montane parklands/subalpine meadows, conifer riparian and mixed broadleaf/conifer riparian, broadleaf riparian, mixed riparian, shrub riparian, grass/forb riparian, burns, and other. The rules were applied on a cell-to-cell basis in ArcInfo's Grid using programs written in Arc Macro Language. For each category, such as conifer riparian or mixed broadleaf forest, after all rules had been applied, any remaining grid cells not yet classified with a specific plant association were determined using the ArcInfo's nibble grid function. This function assigns a value to a cell based on the value of its closest neighbor. Once the plant associations were assigned to each cell, the association's corresponding cover/constancy tables were used to determine the presence of certain grizzly bear foods. How this is done is discussed in Section 5.4.3.2.6.

5.4.3.2.4.1 Conifer – nonriparian cover types. There have been several attempts to classify forests based on potential climax communities (habitat types) (see Pfistner et al. [1977]; Cooper et al. [1991]; Steele et al. [1983]). These classification schemes are useful more as a site descriptor than as a predictor of the current or existing vegetation on the landscape. In order to capture the current, as opposed to potential, variability in the presence of known grizzly bear foods in conifer – nonriparian cover types, the plant associations developed by Leavell (2000) for the Kootenai National Forest were used. These plant associations, though developed using sample plot data only from the Kootenai National Forest, were believed to be likewise applicable to the other parts of the study area (Dan Leavell, personal communication, 2003). Below is a description of the process used to develop the rule set for assigning plant associations to each of the cover types within this category. There were nine single tree species, along with mixed xeric, mesic, whitebark pine, and conifer/broadleaf cover types in this category.

The first step in the assignment process was to determine the most likely plant association(s) for a particular conifer cover type, such as western red cedar (*Thuja plicata*) or mixed whitebark (*Pinus albicaulus*), regardless of tree size or canopy closure. The decision whether or not to consider an association as a candidate for a cover type was based on the detailed description of the associations provided by Leavell (2000) in his Appendix 4. The values found in the association's cover/constancy table were mainly used in the assessment, but information found in their vertical diversity profiles, height and age distribution of dominant species graphs, and narrative description were also utilized. An association was considered a candidate for a single species cover type class, if it appeared with at least 89% constancy and/or if it was considered an indicator species for that particular association, and it occurred with an average canopy cover of at least 20%. (Note: [1] the Psemen/Pincon associations were associations in which both Douglass fir [*Pseudotsuga menziesii*] and lodgepole [*Pinus contorta*] occurred at least 89% of the time, and [2] Leavell's plant association PA3 – Sitka Alder – Mountain Lover [Thimbleberry]/Fireweed/Northwestern Sedge/Juniper Moss [*Alnus sinuate – Pachystima myrsinites (Rubus parviflorus)/Epilobium angustifolium/Carex concinnoides/Polytrichum juniperinum*] was used for a variety of seedling sampling classes as it represented an early seral plant association whose corresponding cover/constancy table showed the presence of several tree species.)

Once the possible candidates were chosen for each cover type, the second step in the process was to place the candidate plant associations for a particular cover type into size and canopy cover combinations, such as seedling/sapling with 20-40% cover. This was done based on the descriptive information of the sample plots collected for each association found in Leavell's Appendix 4. The information used was found in the distribution of the sample plots by structure class graph and the narrative description and the vertical diversity profile graph of the association. The CST project used size classes (seedling/sapling, pole, medium/large, very large) whereas Leavell used the structure classes suggested by O'Hara and others (1996); therefore, the crosswalk between the two schemes found in Tables 5.2 and 5.3 were used. In addition, all cells

Table 5.2. Crosswalk between SILC-1 size classes and structural classes for single tree species cover types.

SILC-1 Size Class	O'Hara and Latham's Structural Class
seedling/sapling	A or B
Pole	B, C or D
medium/large	C, D, or G
very large	F or G

Table 5.3. Crosswalk between SILC-1 size classes and structural classes for mixed tree species cover types. The ( ) represent classes that were only used if sample plots from the other structure classes were not available, because from their descriptions, they are more single species dominant.

SILC-1 Size Class	O'Hara and Latham's Structural Class
seedling/sapling	E (A)
Pole	C or D (B)
medium/large	C, D, E, or F
very large	F (G)

with canopy cover = 13 (no info.) were assumed to be 40-70% cover.

The third step in the assignment process was only used if there was more than one possible plant association for a given combination of cover type, size class, and canopy cover. If this was the case, then differences in the site specific characteristics and/or potential natural vegetation among the possible associations were used to develop rules that would assign the most probable plant association. Information found in the site attributes table, and the distribution of habitat types for the sample plots (Leavell's Appendix 4) was used in this step. After all rules had been applied, any remaining conifer-nonriparian cells not yet classified were determined using the ArcInfo's nibble function. When all the cover types had been converted to a plant association, they were joined into one grid titled *conifer*.

Regardless of the plant association assigned to a conifer-nonriparian cell, one rule applied to all cells; for all size classes, the understory was assumed to be depauperate and void of important bear foods or important bear foods available in a quantity that would be attractive to bears, if canopy cover is > 70%. This criterion is less restrictive than the 50% shade tolerance cutoff for berry production suggested by Bob Gough (Montana State University professor of horticulture) for huckleberries. It is assumed all berries would be similar to huckleberries in that respect, which is, again, probably a more lenient restriction than warranted given that most berry species are not as shade tolerant as huckleberries. A similar cutoff of 60% canopy cover was used in the cumulative effects analysis (Madel 1982).

Finally, in an attempt to capture this variability in terms of important bear foods, a general fact regarding berry production and a specific fact regarding *Vaccinium membranaceum* and *globulare* were used. According to Bob Gough (Montana State University professor of horticulture), one can expect decreased berry production starting with 50% canopy closure because the lack of sunlight inhibits flower development and fruit set. Martin (1979) found production of huckleberries decreasing when canopy cover increased beyond 30%. It was therefore assumed no berry production for shrubs in both conifer and conifer/broadleaf cells whose canopy cover was greater than 70%.

5.4.3.2.4.2 Mixed broadleaf. There are three broadleaf species in the study area: aspen (*Populus tremuloides*), black cottonwood (*Populus trichocarpa*), and paper birch (*Betula papyrifera*). As pioneers after a disturbance, these broadleaf trees are found quite often concurrently with conifers. They however can, appear in pure stands under the right conditions (Burns and Honkala 1990) or as mixed broadleaf forests before replacement by conifer. All three species can be associated with riparian areas in northwest Montana (Hansen et al. 1995). On the Kootenai National Forest, aspen communities are commonly found on drier nonriparian sites (personal communication Dr. Dan Leavell, 2003). It was, therefore, assumed the mixed , broadleaf cover type referred primarily to drier, upland broadleaf stands composed mainly of aspen. The other two species will assume to be found in the riparian cover types.

In the northern Rockies, aspen is found only in scattered groves and small st ands; thus, a floristic classification of aspen communities for the study area could not be found. A generalized characterization of such stands had to be utilized. This characterization was formulated from the following information:

- Common shrubs found in the aspen undergrowth east of Glacier National Park include *Amelanchier alnifolia, Purnus virginiana, Rosa acicularis, Symphoricarpos albus*, with common grasses including *Bromus* and *Carex*, and possible important forbs including *Heraceum lanatum* and *Osmorhiza occidentalis*. (DeByle and Winokeru 1985). It should be noted, however, not all stands necessarily have a tall shrub layer; in fact, Mueggler (1988) estimated in the Intermountain region, only about 17% of the stand had such a layer.
- Aspen stands have luxuriant undergrowth when compared to coniferous forests.

- The British Columbia Ministry of Water, Land and Air Protection's Columbia River basin website (http://habitat.cbt.org/habitat_types/08.html, last visited 10/29/04) listed snowberry (*Symphoricarpos oreophilus*) as the most common dominant shrub, with the possibility of Scouler's willow (*Salix scouleriana*) and serviceberry (*Amelanchier alnifolia*) also abundant. Common grasses may include pinegrass (*Calamagrostis rubescens*), Idaho fescue (*Festuca idahoensis*), California brome (*Bromus carinatus*), or blue wildrye (*Elymus glaucus*). Characteristic forbs are horsemint (*Agastache* spp.), aster (*Aster* spp.), senecio (*Senecio* spp.), coneflower (*Rudbeckia* spp.), meadowrue (*Thalictrum* spp.), bedstraw (*Galium* spp.), sweet cicely (*Osmorhiza* spp.), and valerian (*Valeriana* spp.).
- Review of Leavell's (2000) plant associations with a broadleaf component showed the above mentioned species are indeed commonly associated with mixed conifer/broadleaf stands on the KNF. Leavell also found the important bear food, buffalo berry (*Sherperdia Canadensis*), present in these associations. The USDA Forest Fire Effects (FEIS) database confirmed the typical presence of this shrub in aspen stands.
- Entomologist Torlof Torgerson (personal communication, 2004) acknowledged the likely presence of ants in this cover type, as well.

Combining these descriptions, the following bear foods were assumed to be present in sufficient abundance in the (upland) mixed broadleaf class; *Amelanchier alnifolia, Purnus virginiana, Rosa acicularis, Sherperdia canadensis, Symphoricarpos albus, Bromus sp. and Carex sp., Osmorhiza occidentalis*, other miscellaneous edible forbs, and ants. All canopy classes will be considered the same because unlike conifer forests, herbage production does not seem to decrease with increased canopy cover. Since only a single generalized plant association was used, it was not necessary to use the nibble function to replace missing values. The grid was joined with the nonriparian shrubland cover types to produce a single grid called, *vegetation_other*.

5.4.3.2.3 Nonriparian shrubland cover types. There were less than 1100 cells with a nonriparian, mesic shrubland cover type. It was decided, because of the low numbers, not to attempt to reclassify these cells into associations or alliances but, instead, just to use the indicative species list used by the SILC-1 project in the original classification. The classification used by the SILC-1 researchers considered two broad classes of nonriparian shrublands: mesic and xeric. The mesic class was further broken down into warm and cold mesic shrublands. For cold mesic shrublands, the important bear food shrubs considered indicative were *Vaccinium membranaceum* and *globulare.* For warm mesic shrublands, western serviceberry, devil's club, and Canada buffaloberry were considered indicative. The lower limit of *Vacc. mem.* is 3000 ft or 914 m. Using this as a cut-off, all cells with a mesic shrubland cover type and elevation > 914 m were assumed to have *Vacc. glob or mem.* All other cells were assumed to have serviceberry, devil's club, and Canada buffaloberry.

The description found in the SILC1 report for xeric shrublands suggests these cells most likely represent a bitterbrush community. Examination of the site characteristics of these cells showed they are mostly gently sloped, but some are steeply sloped, with the majority having a southerly aspect. These characteristics match those listed for the *Purshia tridentate* associations (Cooper 2003). Only one of these associations, *Purshia tridentate/Festuca campestris,* may have appreciable amounts (5-10%) of shrubs species which bears utilize, for example, kinnikinnick, service berry, or wild rose, along with grasses and forbs. The other two association, *Purshia tridentate/Hesperostip comata* and *Purshia tridentate/Pseudoroegneria spicata,* contain only trace amounts of edible shrubs, grasses, and forbs. It was impossible to distinguish among these associations with the available data; thus it was assumed cells classified as xeric shrubland did not contain enough edible vegetation to attract bears.

Like the mixed broadleaf cover type, because only a single generalized plant association was used (not ones based on a multitude of site specific characteristics), it was not necessary to use the nibble function to replace missing values. Each of these grids, xeric and mesic shurbland, was joined with the mixed broadleaf cover type to produce a single grid called *vegetation_other*.

<u>5.4.3.2.4.4 Grassland cover types</u>. There were six grassland cover types within in this category: very low cover, low/moderate cover, and moderate/high cover grasslands, grassland, montane parklands/subalpine meadows, and altered herbaceous. An area may have a grass cover type for two different reasons. First, site characteristics could be prohibitive for forest growth. These are 'true' grasslands. Second, the area could actually support trees but is currently grass due to disturbance, such as fire or harvest. Whether or not a particular cell was a 'true'

grassland was determined by its potential natural vegetation type (PNV). Cells with PNVs equal to a grass type were considered true grasslands and those with PNVs equal to a forest habitat type were considered transitional grasslands. The PNV information (grid) for the study area was produced by and obtained from the CST.

A list of existing grassland plant associations, alliances, and forest habitat types used for assignment to the true grassland cells, came from the following sources; *Assessment of Kootenai National Forest Vegetation Types with Potential for Silene spaldingii in the Tobacco Plains, Rexford Bench and Salish Range Foothills* (Cooper 2003), *Grassland and Shrubland Habitat Types of Western Montana* (Mueggler and Stewart 1980), and Montana Natural Heritage Program Community Ecology Field Guide (http://nhp.nris.state.mt.us/community/guide.asp). Assignment of the most appropriate community type for 'true' grasslands was based on cover type and annual precipitation. (Note: For this category, climax habitat types and alliances had to be used in addition to associations because suitable associations did not exist for the study area.)

For transitional grasslands cells, it was assumed the graminoids and forbs present would be the same as those corresponding to a forested stand with the same PNV and a seed/sapling structure with 20-40% canopy cover. The PNV type was used to determine the appropriate alliance found in Leavell (2000). The alliance level was used because of the difficulty in determining what the current vegetation would be based solely on the PNV categories assigned by the CST. If the PNV was abgr1 (Abies grandis 1), for example, rather than find all the plant associations corresponding to a specific habitat type within the abgr1 category, such as 505-8 (see Cooper et al. 1991 for descriptions), it was assumed the grasses and forb species present would be the same as those found in the *Abies grandis* alliance. When there were two or more possible alliances, the alliance with the most grasses listed in the cover/constancy table was chosen. If there were more than one association within the chosen alliance, the ones with the most dominate foliar cover in grass were selected, and then the listof possibilities was shortened to the ones that best represented the range of site characteristics associated with that alliance, for example, low to midelevation or mesic and xeric moisture. Assignment of the most appropriate association to a cell was then based on a cell's PNV and site characteristics (see Table 5.4).

Tables 5.5 through 5.7 summarize the plant alliances or associations and additional

Table 5.4. Plant associations corresponding to PNV used for transitional grassland cells.

PNV Category	Additional Site Characteristics*	Plant Association or Sub-Association
abgr1 or abgr2	-	PA12_32
abla1, abla2, abla3 or picea	mid to upper elevation in VRU2 & VRU7	PA5
abla1, abla2, abla3 or picea	upper elevation in VRU9 & VRU10	PA9_ES
psme2 or psme3	Mesic	PA18_23
psme2 or psme3	Xeric	PA20_16
thpl1, thpl2 or tshe	-	PA3

*VRU stands for Vegetation Response Unit. See USDA, Forest Service, Kootenai National Forest, 1999.

Table 5.5. Very low cover grasslands.

Additional Criteria	Association or Alliance
none	*Achnatherum nelsonii/Eriogonum flavum* Herbaceous Association

criteria, if any, used for each grassland cover type: very low, low/moderate, and moderate/high cover grasslands, grasslands, montane parkland/subalpine meadows altered herbaceous. In general, these grass cover types have both edible grasses and forbs available for bears. After each cover type was assigned a specific or generalized plant association or alliance, they were all joined into one grid titled *vegetation_grass*.

5.4.3.2.4.5 Very low cover grasslands. All the cells classified with this grassland cover type had dry grass for its PNV. All cells were below 800 m in elevation and received 50-75 cm of precipitation. In totality, this group made up << 1% of all grassland cells. Representative species were taken from the *Achnatherum nelsonii/Eriogonum flavum* Herbaceous Vegetation Plant Association (Cooper 2003). This association contains both grass and forbs bear biologist have found grizzlies eat, including biscuit root and blue bunch wheatgrass. This association was described for the Tobacoo Valley and, thus, may be more xeric than is characterized by some of the cells within the study area.

5.4.3.2.4.6 Low/moderate cover grasslands. The majority (70%) of grassland cover-type cells fell within this category. The *Festuca Campestris* Herbaceous Alliance is described as having

Table 5.6. Grassland and low/moderate cover grassland.

Additional Criteria	Association or Alliance
PNV = 1 or 2	PA12_32
PNV = 3, 4, 5 or 10 and mid to upper elevation in VRU2 & VRU7[1]	PA5
PNV = 3, 4, 5 or 10 and upper elevation in VRU9 & VRU10[1]	PA9_ES
PNV = 16 or 17 and VRU3, VRU5 or VRU7[2]	PA18_23
PNV = 16 or 17 and VRU2[2]	PA20_16
PNV = 18, 19 or 20	PA3
PNV = 25, 26 or 27 and precipitation <=60 cm	Festuca Altaica – Pseudoroegneria spictata (=Festuca scabrella/Agropyron spictum h.t.)
PNV = 25, 26 or 27 and 60 < precipitation <=75 cm	Festuca Campestris-Festuca idahoensis (=Festuca scabrella/Festuca idahoensis h.t)
PNV = 25, 26 or 27 and 75 < precipitation <= 150 cm	Festuca Idahoensis herbaceous alliance
PNV = 25, 26 or 27 and precipitation > 150 cm[3]	Deschampsia caespitosa/Carex spp. h.t.

[1] Elevation and precipitation were used as a surrogate for Vegetation Response Units (VRUs). Reading the descriptions of the VRU 2,7,9 and 10, it was decided elevation greater 5400 and precipitation levels greater than 55 would a good cut-off between VRUs 9 and 10 and VRUS 2 and 7.

[2] Elevation and precipitation were used as a surrogate for Vegetation Response Units (VRUs). Reading the descriptions of the VRU 2,3,5 and 7, it was decided elevation greater 5800 or precipitation levels greater than 30" would a good cut-off s between VRUs 3, 5 and 7 and VRU 2.

[3] The FEID/DECA and DECA/CARE are moderate to high cover types and it was a stretch to used these, however, given the sources used, these were the best choices.

Table 5.7. Moderate/high cover grasslands.

Additional Criteria	Association or Alliance
PNV = 1 or 2	PA12_32
PNV = 16	PA18_23 or PA20_16*
PNV = 18, 19 or 20	PA3
PNV = 25, 26 or 27	*Festuca Idahoensis* herbaceous alliance

a moderate dense graminoid layer of cool-season grasses with a sparse to moderately dense forb layer. It is a common alliance in the foothills and mountain parklands in the study area; however, its annual precipitation range is only 40-60 cm. This range is inclusive of only 11% ofthe cells with this cover type. Mueggler et al. (1980) states, however, that one of the associations in this alliance, *Festuca campestris - Festuca idahoensis*, can be found in the annual precipitation range of 50-75 cm. In order to cover the wide range of precipitation values, a combination of associations or alliances and habitat types were used.

5.4.3.2.4.7 Moderate/high cover grasslands. This cover type makes up 9% of the grassland cells. The *Festuca idahoensis* herbaceous alliance will be used to estimate representative species for these cells. This alliance is characterized by a moderate to dense cover of graminoids and is robust in regards to its site characteristics (see Montane parklands/subalpine meadows). This alliance will be used for all 'true' grassland cells in this category, 98% of which have annual precipitation levels <= 105 cm. The *Pseudoroegneria spicata* herbaceous alliance was also considered. This alliance is almost as robust as *Festuca idahoensis*, but only pertains to montane forests and is usually found only on southerly and westerly aspects. It has a sparse to moderate cover of graminoids and forbs and does not contain *Festuca spp*. It can, however, have *Poa spp*., especially, *Poa pratensis* on disturbed sites, another grass eaten by bears. These two alliances would appear similar in the vegetation layer, because only presence/absence of bear foods and not abundance was considered. As a matter of practicality, it was thought not worth the effort to divide cells among these two alliances. Should at a future date, however, a sparse to moderate cover of grass and forbs be considered not likely to attract bears, this would need to be changed.

5.4.3.2.4.8 Grassland. This 'true' grassland cover type represented 14% of grassland cells. The same logic as that used for the low/moderate cover grasslands was used for cells with this cover type (see above).

5.4.3.2.4.9 Montane parklands/subalpine meadows. Cells with this cover type made up less than 1% of the grassland cover types found in the study area. The criteria used to assign plant associations or alliances to cells with this cover type can be seen in Table 5.8. For the cells classified as being true grasslands, the *Festuca idahoensis herbaceous* alliance was chosen. This alliance spans a wide variety of site characteristics. Stands can be found on undulating prairie, valley bottoms, expansive park meadows openings in both montane and subalpine forests, on ridges above subalpine forest, and glacial outwashes. They can be found from 20-3500 m and in places that receive from 33-60 cm of precipitation. In a more maritime climate, however, precipitation may reach over 100 cm. They can be found on nearly level to steep slopes and all aspects. Looking at the species list for these associations and alliances, one can conclude these

Table 5.8. Montane parklands/subalpine meadows.

Additional Criteria	Association or Alliance
PNV = 1	PA12_32
PNV = 20	PA3
PNV = 25 or 27	*Festuca idahoensis* herbaceous alliance*

cells would provide bears with some edible grasses and forbs.

5.4.3.2.4.10 Altered herbaceous. According to the SILC-1 report, this cover type must include >= 30% relative to total cover of at least one of following species: cheatgrass, Japanese brome, knapweed, black medic, yellow sweet-clover, spurge, St. John's-wort, common dandelion, field pennycress, hound's-tongue, or bull thistle. No alliance or association was thought to be appropriate for this cover type. Given its infrequency (cells classified as altered herbaceous made up only 1 1/2% of all grassland cells), it was decided to just use the report definition. Grizzlies are known to eat some of these plants, even though they are non-native, invasive species. These cells, therefore, were considered to have cool season grasses and forbs present.

5.4.3.2.4.11 Riparian cover types. Riparian vegetation had both nonforested and forested cover types. For the forest cover types there were three categories: conifer dominated, broadleaf dominated, and mixed conifer-broadleaf. For nonforested cover types, there were two categories: shrubs and grass/forbs (this included wetland areas as well). Additionally, there was also a mixed riparian category representing a cover type that was definitely riparian in nature but was not distinguishable spectrally as any one particular lifeform. It represented some mix of broadleaf trees, forbs, and grasses.

Like the nonriparian conifer forest, there has been an attempt to classify riparian vegetation based on potential climax (see Hansen et al. 1995). These classification schemes, like the forest habitat types, are useful more as a site descriptor than as a predictor of the current, existing vegetation on the landscape. An effort was made to use the *Aquatic Response Units (ARUs) Classification of the Kootenai National Forest* (Kootenai National Forest), in order to capture the current, as opposed to potential, vegetation and the variability in the riparian vegetation in the study area. This classification delineates riparian vegetation based on hydroclimatic (elevation and stream size) and geomorphic criteria (slope, sinuosity and geology). Unfortunately, as the SILC1 researchers and CST efforts were not coordinated with those of the KNF it was not always possible to utilize the level of detail present in the ARU report. Most ARUs, also, seemed to best describe a stand with a conifer tree component; thus in some cases, a more general description of the probable plant species present had to be formulated from supplementary sources (Hansen et al. 1995; Leavell 2000; British Columbia Ministry of Water, Land and Air Protection's Columbia River basin website [http://habitat.cbt.org/habitat.html]).

Ignoring abundance, there are certain trees, shrubs, grasses, and forbs one would expect to find in riparian areas. Generally speaking, riparian areas contain many foods eaten by bears and are considered good bear habitat. In terms of specific bear foods, however, all riparian areas are not the same. For example, looking at two important berry producers, only half of the ARUs contain *Vaccinium membranaceum* or *globulare* and 80% of the ARU contain *Cornus stolonifera* at least 10% of the time (see Table 5.9).

In an effort to capture the variability of important bear foods present, the general rules regarding berry production discussed previously were used. These rules are (1) no berry production for shrubs in both conifer and conifer/broadleaf cells whose canopy cover was greater

Table 5.9 Percent cover of important bear foods occurring with a constancy of at least 10% by Aquatic Response Units (ARU).

ARU	*Amelanchier alnifolia*	*Cornus stolonifera*	*Lonicera involucrata or utah.*	*Oploplanax horridus*	*Sherpherdia canadensis*	*Vaccinium mem. or glob.*	*Equisetum arvense*	*Heracleum lanatum*
1A	6		2			2	*1*	
1AB	3	16	*2*	9		24		
3AB	3		1	1				
1B	4		3	9		11	2	4
3B	3		4	8		8	3	
1C	1		3	*3*	*5*		1	1
3C	3	11	*2+*	15		*22*	*5*	2
4C	5	14	3+	10			1	3
5C	11	15	11				*5*	5
6C	10							

than 70%, and (2) no *Vacc.* below 3000 ft. From the descriptions of the ARUs, these rules appeared to apply to riparian cover types as well. The first rule could explain the lack of *Vacc.* found in ARU 3AB (though drier site conditions are also a plausible explanation), and the second rule could explain the lack of huckleberries found in the lower gradient streams (1C- BC), which tended to be found at lower elevations. Review of the ARU descriptions yielded four additional suppositions. First, no shrubs other than *Amelanchier alnifolia* exist and produce fruit below 2000 ft (600 m). In addition, there is no or very little cover of grasses, *Equisetum arvense*, *Heracleum lanatum*, *Athyrium filix-femina* and *Carex spp.* Second, no *Oploplanax horridus* exists on very steep slopes (> 20%). Finally, on slopes greater than 20%, no *Heracleum lanatum* exists, and on these slopes at elevations greater than 5,000 ft, no *Equisetum arvense* exists as well. The combination of these rules yielded six different broad riparian vegetation classes, in addition to one plant association described by Leavell (2000), that were applied to the conifer and mixed broadleaf/conifer cells.

5.4.3.2.4.12 Conifer riparian and mixed broadleaf/conifer riparian. Analysis of cells classified as conifer or broadleaf/conifer showed by far the vast majority of cells fell within the medium-size class. All size classes except the largest were found mainly on moderate to steep slopes between 700 and 1800 m. The largest size class was found primarily on steep to very steep slopes between 800 and 1300 m. This analysis concurs with the information provided in the ARU descriptions. These descriptions noted the presence of cedar-hemlock. These species are indicative of late succession implying larger trees. Many of the sample plots were also located on steep to very steep slopes. It would be safe to assume on these slopes many trees would be medium to very large in size due to the absence of harvest disturbance.

For all sizes classes larger than pole and with canopy cover less than 70%, it was assumed that all riparian conifer cells would have cool season grasses and forbs available for bears. The variability in important fruit-bearing shrubs seen in Table 5.9 was achieved by implementing the rules discussed above.

For the smaller size classes, inference of bear food availability based on the rules generated from review of the ARU report would have been inappropriately applied. It was therefore decided to use the Dan Leavell's plant association PA12_33 – *Abies grandis-Pseudotsuga* *menziesii (Thuja plicata)/Pachistima myrsinites* because many of the associated sample plots were located within stream bottoms. This association can be found from 1900-5000 ft and has habitat type similar to those mentioned in the ARU descriptions. Half the plots sampled for this plant association were considered to be in structure class A, B, or C (seedling-pole), this, along with the fact that grand and Douglass fir can be early seral for both western cedar and hemlock, suggests this plant association would be a good representation of current vegetation found in riparian conifer seedling/sapling cells. Also, the presence of *Betula papyrifera* suggests a somewhat recent disturbance, again applying the presence of younger conifers.

5.4.3.2.4.13 Broadleaf riparian. Within riparian areas in the study area, the broadleaf species one would expect to find are black cottonwood (*Populus trichocarpa*), paper birch (*Betula papyrifera*), and in some cases, perhaps aspen (*Populus tremuloides*). Though many of the ARUs contain a broadleaf component, these habitat types were not covered separately in the ARU report, probably due to their limited presence. Broadleaf forests, because they allow a significant amount of sunlight through their canopy (even with a high canopy cover percentage) tend to be richer in forbs than conifer stands. This fact, along with the fact that broadleaf stands are known to be attractive to ants (Torgerson, pers. comm.), makes it safe to assume cells in this class contain likely bear foods. For this cover-type class, two community types from Hansen et al. (1995) were utilized: *Populus trichocarpa/*Recent Alluvial Bar and *Populus trichocarpa/Cornus stoloniferal.* The *Populus trichocarpa/*Recent Alluvial Bar community type represents an early seral (pioneer) stage dominated or at least co-dominated by seedlings or saplings of black cottonwoods. The *Populus trichocarpa/Cornus stoloniferal* community type is a midseral stage readily found throughout Montana. Besides ants, the following list of probably important bear foods was formulated from the cover/constancy tables provided with the two riparian community types (constancy was at 10%):

- Seedling/sapling: Sitka alder (*Alnus sinuata*), serviceberry (*Amelanchier alnifolia*), red-osier dogwood (*Cornus stolonifera*), chokecherry (*Prunus virginiana*), horsetail (*Equisetum arvense*), cow parsnip (*Heracleum lanatum*), graminoids (*Agropyron spicatum* [bluebunch wheatgrass], *Calamagrostis Canadensis* [bluejoint reedgrass], *Carex prionophylla* [saw-leaved sedge], *Phleum pratense* [common timothy] and *Poa spp.*], miscellaneous other bear edible forbs.

- Pole, medium/large or very large: red-osier dogwood (*Cornus stolonifera*), woods rose (), serviceberry (*Amelanchier alnifolia*), chokecherry (*Prunus virginiana*), snowberry (*Symphoricarpos albus*), black hawthorn (*Crataegus douglassii*), alder buckthorn (*Rhamnus alnifolia*), black currant (*Ribes americanum*), cow parsnip (*Heracleum lanatum*), along with a variety of other edible forbs and gramonoids (includes *Carex bebbii*).

5.4.3.2.4.14 Mixed riparian. This cover type represented a cell definitively riparian in nature but not spectrally distinguishable as a particular lifeform. Ground truth plots collected during data processing were divided equally between shrub or grass-forb riparian/wetland and broadleaf-dominated riparian communities. It was decided to treat these cells as 'shrub riparian' cover types (see below for discussion) due to the lack of additional information available.

5.4.3.2.4.15 Shrub riparian. Shrub communities were broken down into two categories: willow and nonwillow. For nonwillow, one plant associations from Leavell's (2000) work was appropriate: PA13 – *Alnus incana (Cornus Canadensis) – Symphoricapos albus/Calamagrostis Canadensis-Elymus glaucus* . The sample plots for this association were located primarily within the A structure classes and within similar habitat types (PIEN/CLIN, PIEN/EQAR, THSE/CLUN), as those listed in the ARU descriptions (*Draft Aquatic Response Units reports from the Kootenai National Forest*). Common snowberry, mountain alder, and field horsetail are indicative of this plant association. *Amelanchier alnifolia* appears with 1% cover and black cottonwood appears with 20% cover 33% of the time. The association is characterized by streamside, riparian, and wet meadows habitat types within Vegetation Response Unit 7 – Cool and Moist and is most appropriately applied to areas between 2000 and 4300 ft elevation with a low to moderate gradient.

Willow communities have a wide elevational extent and can be found on steep gradients (Hansen et al. 1995). Willow shrublands were, therefore, assumed for all shrub riparian cells below 2000 ft, higher than 4300 ft, and/or with a gradient greater than 6 %. These basic rules provide a level of landscape variability among shrub riparian cells, despite the fact they likely oversimplify a more complex set of variables that determine the shrub community type.

The *Salix drummondiana/Calamagrostis canadensis or Salix drummondian/ Carex rostrata* habitat types of Hansen and others (1995) were two likely candidates for this cover type. These habitat types were similar in the types of bear foods they provided, differing mainly in the frequency and/or amount of these possible foods. The cover/constancy table associated the *Salix drummondiana/Calamagrostis canadensis* was used to provide a list of likely (>=10% constancy) species found in a willow shrubland. These species, besides willows, include *Lonicera involucrata, Carex spp., Epilobium angustifolium, Heracleum lanatum* and *Equisetum arvense*.

5.4.3.2.4.14 Grass/forb riparian. Review of the cover/constancy tables in the KNF's ARU report, Hansen et al. (1995), and the herbaceous wetlands description found at the British Columbia Ministry of Water, Land and Air Protection's Columbia River basin website (http://habitat.cbt.org/habitat_types/22.html) shows riparian areas can contain a variety of bears foods, such as cow parsnip, carex spp., queen's cup beadlily, and mountain sweet cicely. The number and abundance of grasses and forbs present in riparian areas vary, but it is safe to assume all cells classified with this cover type contain edible cool season grasses and/or forbs for bears. The following generalized species list was used: *Equisetum arvense*, *Heracleum lanatum*, *Athyrium filix-femina*, *Carex spp.*, and other various bear edible grasses and forbs. Applying the suppositions discussed previous (*Equisetum arvense*, *Heracleum lanatum*, *Athyrium filix-femina* and *Carex spp.* absent below 2,000 ft, *Heracleum lanatum* absent on steep slopes greater than 20%, and *Equisetum arvense* absent on steep slopes at elevations greater than 5,500 ft) led to four grass/forb riparian categories being considered.

Wetlands would contain various grasses and grass-like plants, such as tufted hair grass (*Deschampsia caespitosa*), bluejoint reedgrass (*Calamagrostis canadensis*), sedges, and rushes. Montane meadows occasionally are forb-dominated with plants such as arrowleaf groundsel (*Senecio triangularis*) or ladyfern (*Athyrium filix-femina*). Field horsetail (*Equisetum arvense*) and common willow-herb (*Epilobium ciliatum*) were presently in all phases of the *Carex rostrata* sedge habitat type, a common, widely distributed type throughout Montana between the elevations of 671 m and 2,256 m (Hansen et al. 1995). The *Carex scopulorum* habitat type occurs at mid to high elevations (1,983 – 2,532 m). In addition to the plants found commonly in the *Carex rostrata* habitat type, whortleberry (*Vaccinium scoparium*) and Utah honeysuckle (*Lonicera utahensis*) might also be present. (*Arctostaphylos uva-ursi* (kinnikinnick) was found in another midelevation to high elevation h.t.). Perusal of nonsedge habitat types found in Hansen et al. (1995) confirmed the likely presence of the aforementioned species, with the occasional inclusion of cow parsnip or exclusion of field horsetail. Those at lower elevations were found to have sedges, grasses (bromes, poa sp. tufted hair), and dandelions. Those associated with recently deposited alluvial bars may have sparse vegetation.

After assigning a specific or generalized plant association to each of the six riparian cover types: conifer, mixed broadleaf/conifer, broadleaf, mixed, shrubland, and grass/forb riparian, the individual grids were joined into a single grid titled *vegetation_riparian*.

5.4.3.2.4.15 Burns. To assume that cells listed as burns contain no bear foods would have been overly restrictive. Depending on the severity of the disturbance, fire may actually increase the presence of foods eaten by bears. It was decided, because it was impossible to determine the severity of the fires, to replace cells coded as burns with their original SILC1 classification. They were then assigned plant community types as describe previously.

5.4.3.2.4.16 Other. There were seven different cover types in this category: urban and developed, agricultural dry and irrigated, water, rock/barren, clouds and cloud shadows. Out of these seven cover types, only agricultural dry and irrigated were considered to have any potential bear foods. They were assumed to have grasses (hay for irrigated and rangeland pasture grasses for dry agricultural) suggested eaten by bears. The remaining five cover types were assumed to have no food. These cover types were joined into one grid titled *vegetation_non*.

5.4.3.2.5 Final plant association grid

In the end, there were 64 different plant community types (specific plant associations or alliances or generalized description of a particular plant community) used to recategorize the broad vegetation types used by the CST: conifer – nonriparian , mixed broadleaf forest, nonriparian shrubland, grassland/altered herbaceous/montane parklands – subalpine meadow, conifer riparian, broadleaf riparian, mixed broadleaf – conifer riparian, mixed riparian, shrub riparian, grass - forb riparian, and other, into more meaningful vegetation types for the model. Each grid generated during the assignment process: *conifer*, *vegetation_other*, *vegetation_riparian*, *vegetation_grass* and *vegetation_non*, was combined into a single grid called *plant_associations* (see Figure 5.6). How these plant community types were then converted to specific bear foods is described in the next section.

5.4.3.2.6 Plant community types to bear food items

Once the plant community types were assigned to each cell, the association's corresponding cover/constancy tables were used to determine the presence of certain grizzly bear foods. For generalized plant community types, their descriptions were used. From here on, all community types will be referred to as plant associations. It should be understood that when reference is made to a plant association's corresponding cover/constancy table, in certain instances, this reference is to the generalized description found in Section 5.4.3.2.4.

A list of potential bear foods was compiled from several sources (Craighead 1982; Madel 1982; Ciarniello et al. 2003) (see Appendix A). The final list suggested bears have been documented to eat over 200 food items. It was conceivable that every cell would be considered a 'good food' cell, if all 200 food items were considered. This would be the same as assuming a homogeneous landscape. In some regards, for areas in the Pacific Maritime Climate influence, this wide availability of food sources is relatively true in comparison to areas under a more xeric, continental climatic influence. The assumption, however, greatly minimizes the importance of high caloric foods, in this case berries, that bears are known to seek out. It would also prevent annual variability to be considered; i.e., every year would be the same.

In order to avoid implicitly making the homogenous landscape assumption, it was decided to consider three broad categories of bear foods: berries, animal, and herbaceous items (grass and forbs). Within the berries and herbaceous categories, individual food items were further broken down into the subcategories preferred and other. Preferred items are those highly used, preferred, or sought after versus those that are eaten when the preferred foods are unavailable. In the model, it is assumed bears seek out preferred or highly used foods first, turning to other foods when the preferred foods are not available. Whether a food item was considered in the preferred or other subcategory was determined from the literature. If a food item was reported as highly used by grizzlies during some season in either northwest Montana or southeast British Columbia, it was

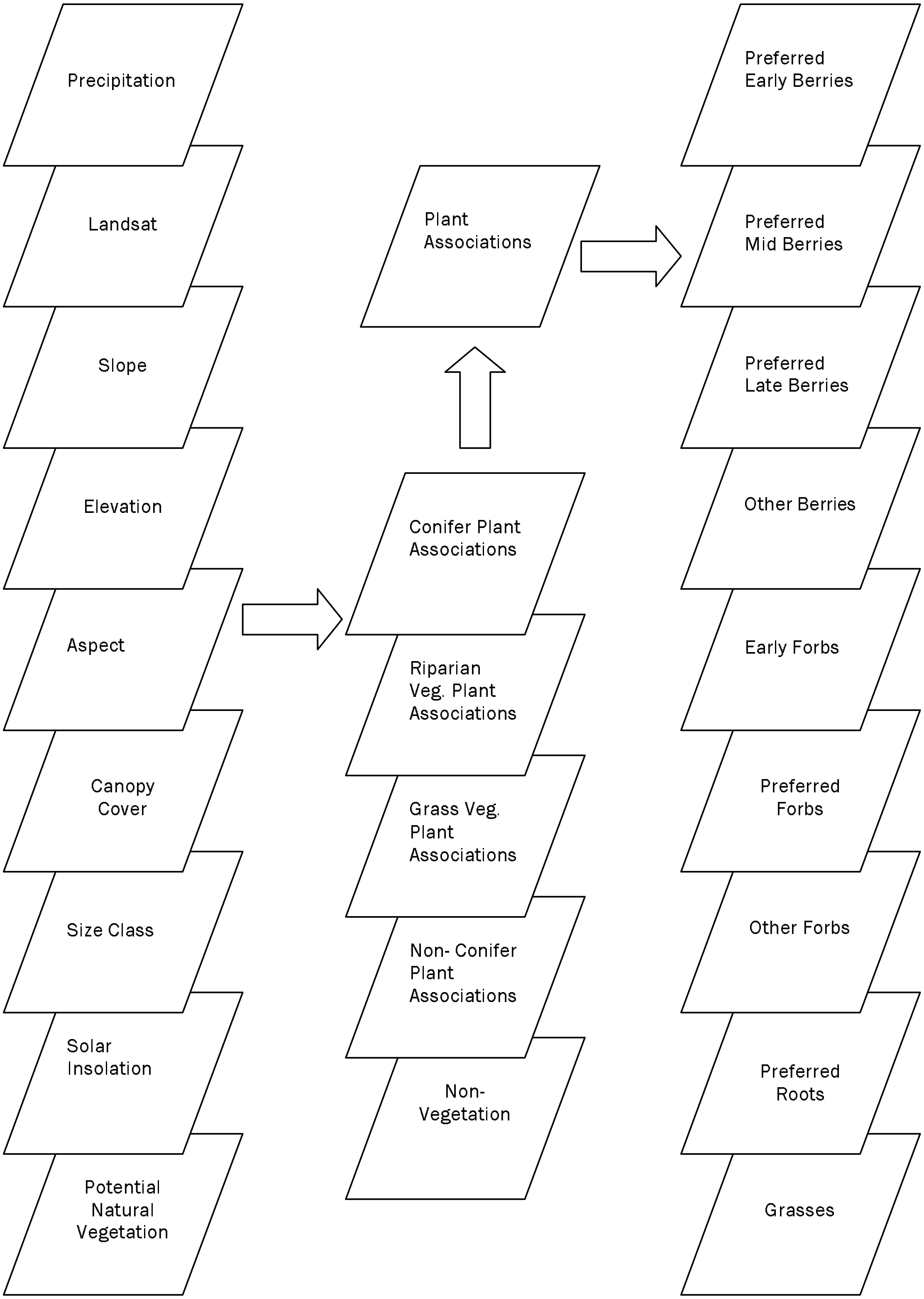

Figure 5.6. Process used to translate a remote sensing classification scheme into individual bear food category layers.

considered as an important food source (Husby and McMurray 1978; Kendall 1986; Kasworm and Manley 1988; Ciarniello et al. 2003). Ants, elk carrion, and gut piles are the important food items in the animal category. The important or preferred vegetation food items in the other categories can be seen in Table 5.10. All species not listed in Table 5.10, but found in Appendix A are considered other items in the corresponding food categories.

In addition, food items were divided into early, mid and late season food categories. The forbs were broken down into those utilized by bears early in the season and those utilized later. Berries were divided into categories based on when they typically ripen: early, mid and late. Grasses were considered available during every season, and the ants and meats divided into early season carrion, mid season ants, and late season gut piles. These divisions coupled with phenology (discussed in Section 5.4.3.2.7) would facilitate more realistic movements by allowing bears to direct their movements to important berry sources in the summer and fall and other preferred food items when seasonally appropriate.

Table 5.10. Preferred bear food items as suggested by the literature. The asterisks indicate forbs available in the early spring.

Berries & Fruits	Forbs	Ferns	Roots & Corms
Amelanchier alnifolia	_Angelica arguta_	_Equisetum arvense*_	_Claytonia lanceolata_
Lonicera utahensis	_Angelica dawsonii_	_Athryrium filix-femina_	_Erythronium grandiflorum_
Vacc. mem , globulare	_Epilobium angustifolium_		_Hedysarum alpinum_
Vaccinium scoparium	_Heracleum lanatum_		_Hedysarum boreale_
	Osmorhiza chilensis		_Hedysarum sulphurescens_
Lonicera involucrata	_Osmorhiza depauperate_		_Lomatium cous_
Oplopanax horridum	_Osmorhiza occidentalis_		_Lomatium dissectum_
Shepherdia Canadensis	_Pedicularis bracteosa_		_Lomatium dissectum_
	Taraxacum officinale*		_Lomatium macrocarpum_
Crataegus douglassii	_Trifolium repens*_		_Lomatium sandbergii_
Cornus stolonifera	_Trifolium pratense*_		_Lomatium triternatum_
Sorbus scopulina	_Valeriana sitchensis_		_Polygonum bistortoides_
	Ligusticum canbyi		_Osmorhiza occidentalis_
			Perideridia gairdneri
			Melica bulbosa
			Melica subulata

Applying the food item categories and seasonal divisions produced nine separate vegetative food item categories: grasses, early forbs, preferred forbs, other forbs, early ripening berries, mid season ripening berries, late ripening berries, other berries, and preferred roots. To convert the plant association grid, plant_associations, discussed in the previous section, into nine separate food category grids a Java$^{\text{TM}}$ program was written. A plant association was included in a particular food category, if it contained at least one qualifying food item (species) seen in Table 5.10 and, as a whole, met a relative cover percentage for the lifeform of that food category (grass, forb, or shrub). A species qualified if, as determined by its corres ponding cover/constancy table, it occurred with a certain cover, constancy, and relative cover. For all vegetative food categories, a species in that category was required to have 10% constancy. In addition to meeting the constancy threshold to qualify, a species had to have a certain cover percentage. To be apreferred forb or berry, the species had to have at least a 5% cover. If it was a nonpreferred forb or berry, it had to have a cover of at least 10%, the 10% benchmark pertained to grasses as well. Finally, for preferred roots, the cover only had to be at least 1%. The rational behind these percent cover benchmarks was that bears would seek out preferred foods with less cover, but to seek non-preferred foods (usually less nutritious or requiring more effort to obtain), they would need to be rewarded with a higher abundance. The exception was roots, which only required a 1% cover. This was chosen because it was known that bears use roots, especially if berries are not plentiful (Mace 1980), yet the plant associations used in the preparation of the potential foods layer rarely listed roots used by bears with cover greater than 5%. To get any associations listed with edible roots the constancy had to be reduced. This was not viewed as a problem because roots are not above ground and therefore maybe the above-ground cover does not reflect abundance very well.

The relative cover criterion for the plant association as a whole was 40% relative cover of total bear-edible species cover, in a particular life form, such as grass, forb, or shrub, to the total cover in that association of the in life form. A similar criterion, minus the 10% constancy, was used by the forest service during the grizzly bear habitat component mapping project for mapping shrub components. In order for a shrub component to be mapped, there had to a 40% relative cover of fruiting shrubs to the total cover of all shrubs. There was no reason given for this particular percentage. The relative cover criterion, was extended in this project to pertain to all vegetation food categories; for example, for a plant association to be added to list of associations with edible forbs, the association would have to contain forb(s) that bears ate, each occurring with a 10% constancy, with a relative cover to total cover of all forbs of at least 40% (did not account for difference in height of forbs so total cover could have been >100%).

Once all lists of relevant plant associations were created for all nine vegetative food categories, GIS was used to produce the individual grids. For each particular food item category grid, the cells were coded as 1 if it contained that food item category, such as early forbs, and 0 otherwise. This binary coding scheme was likewise used for the individual food items making up the animal category.

5.4.3.2.7 Phenological events

Phenology is the study of when biological events occur in relation to the environment. Flower dates and plant height vary with number of frost-free days, exposure, and elevation. Hopkins' bioclimatic law states weather-related events such as bloom time, occurs four days later for every 400 ft increase in elevation, one degree north in latitude, or 5 degrees west in longitude (Hopkins 1938). This law quantifies in general terms the relationship between temperature and phenological development. Hopkins' law is a good guide and may be appropriately used at small scales to map generalize broad patterns; however, what was required for this project was a method to capture delay in phenological events in rough terrain. This would allow vegetation located in ravines, for example, to green up later than vegetation located at the same elevation but on less shaded sights, such as concave ridge or vegetation on south-facing aspects to green up earlier than on north facing slopes.

In order to take into account topographic complexity the concept of a growing degree-day (GDD) can be used. GDD values quantify 'temperature' or 'heat' unit accumulation on each day. The accumulation of heat units or degree-days provides a measure of the developmental or growth rate because the growth or phenological development rate (1/time to develop) of plants increases approximately linearly from a lower to an upper threshold temperature. Temperatures below or above the thresholds are not considered favorable for growth or development.

The phenological event occurs when the GDDs equal the accumulation threshold. The number of GDDs is dependent on the choice of lower and upper thresholds. These thresholds are determined by the organism's physiology and are independent of the method used to calculate degree-days. Lower thresholds vary with different organisms, but for cool season crops grown in Montana, 0 ^{o}C (32 ^{o}F) is often the best base temperature for predicting development (Miller et al. 2001). The upper developmental threshold is the temperature above which the rate of growth or development begins to decrease or stop. Determining a consistent upper threshold is more difficult. Often, such thresholds are unavailable for use in phenology models and may occur at higher temperatures than typically seen in Montana (Miller et al. 2001). The number of GDDs is likewise dependent on the start date, such as January 1 or March 1. In addition to the lower and upper thresholds, one also needs an accumulation threshold for the phenological event to be predicted, such as first true leaves appearing, 50% flowering completion, or fruit ripening. Such threshold data for native species is extremely limited but is widely available for domesticated agricultural plants. Table 5.11 shows the start dates, lower and upper thresholds temperatures, accumulation thresholds, and the agricultural crop used to determine the accumulation threshold for the events chosen. Grass was assumed to always be available, i.e., a dependable food source, from den emergence to entry; thus, its emergence and senescence were not modeled using the GDDs concept.

GDDs can be calculated by a variety of methods. One simple method uses the maximum and minimum daily temperatures in the formula;

$$\text{GDDs} = (\min(t) + \max(t)) / 2 - \text{lower threshold}, \tag{5.4}$$

where

min(t) = minimum daily temperature for minimum daily temperature is >= lower threshold, lower threshold for minimum daily temperature < lower threshold.

max(t) = maximum daily temperature for maximum daily temperature is <= upper threshold, upper threshold, if maximum daily temperature > upper threshold.

Using equation 5.4, modeling of phenological response over a complex landscape then reduces to the modeling of the maximum and minimum temperature variation across the landscape. To model temperature spatial variation an equation developed by Fu and Rich (2002)

Table 5.11. Lower, upper, and accumulation thresholds used for GDD model. Thresholds taken from the following sources for the agricultural crops listed: Miller, Lanier and Brandt (2001), Friesen and Stushnnoff (in manuscript) and Carlson and Hancock (1991). Note: All accumulation thresholds were for ^{O}C.

Event	Lower Threshold	Upper Threshold	Accumulation Threshold	Accumulation Start Day	Agricultural Crop
Forb Emergence	32	70	506	January 1	Flax-1st pair of true leaves
Early-Season Berry Ripening	41	74	1081	April 1	Serviceberry
Mid-Season Berry Ripening	39	70	1514	March 1	Early Highbush Blueberry
Late-Season Berry Ripening	19	90	5099	March 1	Late HighBush Blueberry
Forb Flowering 50% Complete	32	70	1643	January 1	flax

to predict maximum and minimum soil temperatures over rugged terrain was used. They found the change in daily soil temperature (maximum – minimum ^{O}C) near Gunnison Colorado could be reasonably approximated using the equation

$$\text{Temperature}_{\text{max}} - \text{Temperature}_{\text{min}} = (.003629 * \text{solar insolation}) - 15{:}01. \quad (5.5)$$

In order to capture both the temporal and spatial variation in phenological events, a two-pronged approach was implemented. First, temporal variation was accounted for by using the historic climate data from a single location or base. The base was the Heron, Montana, weather station (48.05 latitude; -116.00 longitude; 692.07 m elevation), because it had the most consistent and complete data sets in comparison to other weather stations within the study area. Historic climate data for the base from 1968-93 and 2001 were obtained from the Utah Climate Center. A Java program was written to calculate, using daily minimum and maximum temperature climate data, the GDDs formula (equation 5.4), and the thresholds listed in Table 5.11, for each year from 1968-93 and 2001, the number of calendar days needed for the GDDS to equal the accumulation threshold for the phenological events listed in the table. Second, topographic or spatial variation was accounted for by using equation 5.5 to calculate for each location other than the base the maximum temperature to be used in theGDDs formula, as explained next. The GDDs for the base for a phenological event in Table 5.11 was then subtracted from the GDDs calculated for every other location to obtain the delay or advance, in days, of the event at the location relative to the base.

The calculation of GDDs using equation 5.4 is straightforward. The methods used to calculate the maximum and minimum temperatures at locations other than the base, however, is deserving of more explanation. The direct application of equation 5.5 to the study area is limited due to the statistical formulation of the equations and the fact that the researchers measured soil temperature; however, it was beyond the scope of this project to derive such equations for this study. For this project, it was assumed the spatial variation in air temperature would be similar to variation in soil temperature. In addition, an effort was made to modify the equation to better fit the study area by adjusting the coefficient and constant. Using the maximum and minimum monthly temperatures from the Heron, Montana, weather station (data downloaded from the Western Regional Climate Center), the average minimum and maximum monthly temperature from 1968- 1999 was calculated and then compared repeatedly to equation 5.5 after adjusting the coefficient and constant. A 38% reduction in the coefficient and dropping the constant brought equation 5.5 to within 1 ^{o}F or better of the actually average. It was assumed that the modified equation, though not exact, nonetheless would capture the monthly variation in temperature over the landscape adequately, once the solar insolation over the landscape was calculated.

In equation 5.5, solar insolation refers to the amount of daily solar radiation (Wh/m^{2}) received at a location. In order to use equation 5.5, daily solar insolation values are needed in units Wh/m^{2}. To be consistent with other aspects of the project, the annual solar radiation values calculated for the assignment of plant associations (see Section 5.4.3.2.3), were appropriately adjusted to approximate daily values in correct units (Wh/m^{2}/day). This was done by first converting to the correct units (Wh/m^{2}/year); second, allocating a percentage of annual radiation to each of the months (based on the average daily solar radiation data for each month found at Watson Solar Trackers (http://www.wattsun.com/resources/insolation_data); and finally, dividing that amount by 28-31 days, depending on the month (Wh/m^{2}/day). The average monthly minimum temperature at Heron weather station was used as the daily minimum temperature at all locations. In short, for the spatial variation, it was assumed that for each day of a particular month the daily minimum and daily maximum temperatures were the same. Though this is not correct, it was believed this method would consistently and satisfactorily approximate the variation seen in phenological events across the landscape due to changes in topographic position. Using only the minimum daily temperature from Heron weather station probably introduced some error, since minimum temperature varies over a complex landscape just like maximum daily temperature. Originally the delay or advance calculated by these means was going to be further adjusted by applying Hopkins bioclimatic law to account for elevation changes; however, because the program used to calculate the solar radiation accounts for elevation change, it was thought this would be redundant. In addition, further refinement was believed unnecessary, since realistic and plausible results, as discussed next, were obtained.

The solar radiation level at the base location was 2,006,488 Wh/m^2/day. At this level, the GDD calculation produces a ripe fruit date for early ripening berries, such as serviceberry (*Amel. aln.*) of July 9 (190 days). At the maximum solar radiation level found in the study area, the ripening date is 20 days earlier (June 19), and at the lowest solar radiation level found in the study area, berries would not ripen until November 30 (334 days). The earlier ripening dates are consistent with dates found in the USDA FEIS. Dates after October 15 would indicate that the shrubs would not produce fruit in most years. Similar comparisons were made for other events listed in Table 5.11 and were found to be equally reflective of corresponding documented dates. As an additional check to the methods, a comparison was made between the average number of days for berries to ripen when restricted to one of four compass directions while controlling for elevation within 100 m. In all 100 m elevation categories chosen, berries were predicted, on average, to ripen first on south slopes and last on north slopes, as expected. Further, the same comparison was performed for 50% completion of flowering. At the lower elevations, <= 700 m, delay between south and north facing directions were 5-6 days, a result consistent with the work by Jackson (1966). (Note: Only lower elevations were thought to be comparable to Jackson's study site that occurred at much lower elevations than the majority of the CYE.) At higher elevations, an average delay between south and north aspects was still observed, but the difference was greater.

This project recognizes the difficulty associated with modeling plant phenology and the many factors that are involved. It acknowledges that the methods used do not account for the effects of snow cover or melt, wind, precipitation, or the microclimate formed by surrounding vegetation that greatly influences green up, ripening and flowering dates as well. Overall, however, the aforementioned performance assessments provide confidence that the dynamics of phenological events in relation to a complex topography were encapsulated to some degree by these methods and sufficiently met the objectives of the project.

In addition to plant phenological dates, also several events occur during the bear's active season without a fixed date: den emergence, availability of hunter left gut piles, and den entrance. The exact mechanisms that signal den emergence and entrance are unknown. One reasonable explanation depends on food availability. Keeping this in mind, it was decided to use first lilac leaf date as a surrogate for den emergence (Schwartz and Caprio 2003) and seven consecutive days below 30 ^{O}F (historical climate data, Utah Climate Center) as the surrogate for den entrance. The location of both data sets was the base station: Heron, Montana. First lilac leaf was assumed to correlate well with the dates when vegetation foods would first become available, and consecutive freezing days with the dates when vegetation foods would no longer be available. The criterion of several consecutive days was chosen over a single day, because most plants can stand a single night that drops below freezing, but not several such nights in a row. Acomparison of these dates with data on denning habits of grizzlies (Nat'l Wild. Federation 1987; Kasworm and Manley 1988) confirmed the applicability of these phenomena as good predictors of den emergence and entrance. The elk hunting season dates for Montana were used for the start and stop dates of gut pile availability. Generally speaking, the season ends the Sunday of Thanksgiving week and lasts for five weeks. Idaho's hunting season is slightly different, but was assumed to be the same for convenience.

This rounds out the calendar events used in the model. Table 5.12 shows the climate scenarios used for the model. Four other important food sources for bears were not considered as having annual variation for modeling purposes: grasses, preferred roots, ants, and elk carrion. Bears utilize grasses throughout the season, but with varying intensity depending on the availability

Table 5.12. Climate scenarios used in the model.

Climate Scenario	Year	Den emergence (Lilac First Leave)	Forb Emergence	June Start-Berries (GDD-Serviceberry)	July Start-Berries (GDD-Early Highbush Blueberry)	August Start-Berries(GDD-Late Highbush Blueberry)	50% Flowering Complete	Fall Carrion (Elk Season, MT - Rifle)	Den Entrance (7 Consecutive days <=30)	Length of Active Season
1	1968	30-Apr	Mar 26	Jun 28	Jul 10	Aug 5	Jun 10	Oct 27 - Dec 1	Nov 23 - 29	208
2	1969	1-May	Apr 13	Jun 20	Jul 10	Aug 5	Jun 10	Oct 26 - Nov 30	Oct 13 -19	166
3	1970	2-May	Apr 10	Jun 28	Jul 14	Aug 5	Jun 16	Oct 25 - Nov 29	Oct 26 - Nov 1	178
4	1971	22-Apr	Apr 13	Jun 25	Jul 15	Aug 6	Jun 15	Oct 24 - Nov 28	Oct 27 Nov 2	189
5	1973	26-Apr	Apr 5	Jun 24	Jul 9	Aug 5	Jun 12	Oct 21 - Nov 25	Nov 1 - 7	190
6	1975	11-May	Apr 25	Jul 3	Jul 19	Aug 11	Jun 24	Oct 26 - Nov 30	Nov 8 - 14	182
7	1976	29-Apr	Apr 14	Jun 30	Jul 18	Aug 11	Jun 19	Oct 24 - Nov 28	Oct 14 - 20	169
8	1977	20-Apr	Apr 7	Jun 23	Jul 12	Aug 5	Jun 11	Oct 23 - Nov 27	Nov 15 - 21	210
9	1978	22-Apr	Apr 8	Jun 30	Jul 10	Aug 4	Jun 14	Oct 22 - Nov 26	Nov 9 -15	202
10	1979	20-Apr	Apr 11	Jun 25	Jul 10	Aug 4	Jun 12	Oct 21 - Nov 25	Nov 7-13	202
11	1980	25-Apr	Apr 13	Jun 20	Jul 7	Aug 2	Jun 9	Oct 26 - Nov 30	Nov 11-17	201
12	1981	4-Apr	Mar 27	Jul 2	Jul 10	Aug 6	Jun 7	Oct 25 - Nov 29	Oct 12-18	192
13	1982	22-Apr	Apr 17	Jun 27	Jul 13	Aug 8	Jun 19	Oct 24 - Nov 28	Nov 7-13	200
14	1983	13-Apr	Mar 30	Jun 26	Jul 9	Aug 4	Jun 7	Oct 23 - Nov 27	Nov 28 - Dec 4	230
15	1984	14-Apr	Apr 4	Jul 5	Jul 20	Aug 7	Jun 17	Oct 21 - Nov 25	Oct 17 - 23	187
16	1985	16-Apr	Apr 11	Jun 24	Jul 12	Aug 4	Jun 14	Oct 20 - Nov 24	Nov 9 - 15	208
17	1986	3-Apr	Apr 1	Jun 23	Jul 4	Aug 1	Jun 7	Oct 26- Nov 30	Nov 8 - 14	220
18	1987	3-Apr	Apr 3	Jun 15	Jun 30	Jul 27	Jun 3	Oct 25- Nov 29	Oct 16 - 22	197
19	1988	9-Apr	Apr 3	Jun 22	Jul 7	Aug 1	Jun 7	Oct 23 - Nov 27	Nov 24 - 30	230
20	1989	13-Apr	Apr 16	Jun 22	Jul 9	Aug 2	Jun 13	Oct 22 - Nov 26	Nov 27 - Dec 3	229
21	1990	1-Apr	Apr 5	Jun 27	Jul 8	Aug 2	Jun 13	Oct 21 - Nov 25	Nov 27 - Dec 3	241
22	1991	16-Apr	Apr 5	Jun 30	Jul 13	Aug 7	Jun 12	Oct 27 - Dec 1	Oct 27 - Nov 2	195
23	1992	27-Mar	Mar 19	Jun 17	Jun 23	Jul 25	May 26	Oct 25 - Nov 29	Nov 23 -29	242
24	1993	19-Apr	Apr 12	Jun 25	Jul 10	Aug 5	Jun 10	Oct 24 - Nov 28	Nov 4 -10	200
25	2001	17-Apr	Apr 16	Jul 1	Jul 15	Aug 7	Jun 18	Oct 21 - Nov 25	Dec 4 - 10	232

of other more nutritious foods. Edible grasses, therefore, were assumed to always be available (dependable food source) from den emergence to entry. Insects, especially ants, are a significant food source (Husby 1978; Kendall 1986; Kasworm and Manley 1988). They were assumed to be available every year during the months of June through July, as were preferred roots. Similarly, elk carrion can form a significant food source for at least some bears in the spring. They were assumed to be available from den emergence until the end of May.

5.4.3.2.8 Final grid processing

All GIS processing to this point occurred using a 30 m cell resolution. These grids were resampled to a 330 m cell size. To prevent homogenization of the food resources across the landscape, the 40% relative cover criterion, discussed in the previous section, was applied again; that is, a 330 m cell was considered to have a particular food category if 40% or more of the 30 m cells making up the larger cell contained the food category. A comparison of the percentage of t he landscape in each food category before and after the resampling was performed. The 40% threshold was adjusted up or down to maintain as close as possible the original percentages. The final relative percent thresholds for the 30 to 330 m resampling step for each food category can be seen in Table 5.13.

In addition, there was spatial mortality risk and phenology delay grids that need to be resampled. For the mortality risk grid, the average mortality risk over a 11 x 11 cell neighborhood was calculated using ArcInfo's focalmean, and then this average mortality risk grid was resampled. For phenology, it was assumed food would be available from the minimum delay (or advance) to the maximum delay (or advance). ArcInfo's focalmax and focalmin , therefore, were used to calculate the maximum and minimum delay of each phenological event over a 11 x 11 cell neighborhood, respectively. These minimum and maximum grids for each phenological event were then resampled.

5.4.3.3 Implementation

Two classes fall under this category: *GridManager* and *HabitatCell*. The *GridManager* is responsible for all functions involving the spatially explicit parts of the model, i.e., the functions involving the GIS grids described in Section 5.4.3.2. The class was called *GridManager* instead of

Table 5.13. Relative percentages used when resampling to larger grid size.

Food Category	Relative % used in resampling
Ants	48
Elk Carrion	N/A
Elk Gut Piles	N/A
Early forbs, preferred forbs, preferred roots	40
Other forbs, other berries	55
Grasses	60
Early Berry	47
Mid Berry	40
Late Berry	30
Denning	36

HabitatManager, because it involves the GIS grids developed and the *HabitatCell* objects represent one cell in these grids. It manages or controls events or actions that occur in all the *HabitatCell* objects or the entire study area. Its primary functions are as follows:

1. Read in each of the grid layers used in the model and instantiate *HabitatCell* objects for every cell. The *HabitatCell* objects are initialized with the values read in from the individual grid layers.
2. Send messages to the *HabitatCell* objects to set their start dates for forbs, berries, and carrion availability at the beginning of every year. This should not be confused with what takes place in the *Calendar* regarding phenological events. What the *Calendar* does is set the dates based on the selected climate scenario at a single location, the base location, described in Section 5.4.4.2.6. From this base location, all other cells in the study area must set its minimum and maximum start dates relative to the base location as described in Section 5.4.3.2.6 and Section 5.4.3.2.7. The *GridManager* tells every cell to do this at the start of the year. (This is a start-of-the-year event as described in the *TimeManager* section.)
3. Send messages to the *HabitatCell* objects to adjust their display color and to draw themselves on the screen every day, if graphics are used. (This is a condition pretick event as described in the *TimeManager* section.)
4. Write out in ASCII grid format the number of mortalities occurred in each *HabitatCell* object, at the end of the model run.

As mentioned above, the *HabitatCell* objects (habitat cells) get instantiated by the

GridManager object, and there is one such object for every cell in the GIS grid covering the study area. The most relevant variables and methods of each habitat cell include those necessary to keep track of what food categories it has available to the bears every day, what mortality risk it poses to a bear, whether or not it is a possible den site, what bears and what females bears, if any, are currently occupying the habitat cell, and what road density it has. It also contains methods for communicating this information with the *Bear* objects; for example, what food it has available on a particular day, if any females are occupying the cell, what is the road density in the cell, and what is the mortality risk associated with occupying the habitat cell.

Changes in food availability can either be natural, a function of time, or bear induced, a function of bear visitation. Food availability changes daily naturally due to the growing and maturing process, and it varies annually due to climate. Based on the dates set by the *Calendar* object at the start of every year, every cell adjusts its own minimum and maximum start date for each food item category it might contain (early forbs, grasses, preferred forbs, preferred early, mid, and late berries, other berries, and possible gut piles). The adjustment made is relative to base location as describe in phenology (Section 5.4.3.2.6), and is a function of the cells topographic position. As stated in the phenology section, carrion, ants, and preferred roots start at a fixed time every year, so their start dates are not dependent on the dates of the current calendar.

The duration of availability of particular food item categories either depends on plant phenology or is set at a fixed number of days. The duration intervals for the various food item categories were chosen to mimic the temporal food item preference shown by bears (Husby and McMurray 1978; Mace 1980; Kendall 1986; Ciarniello 2003). The duration of food item categories dependent on phenological events were early and preferred forbs. Early forbs are available from first leaf emergence until preferred forbs begin to leaf; then bears are assumed to switch to preferred forbs. Preferred and other forbs are then available until 50% flower completion, at which time the forbs are assumed to have become too fibrous and least nutritious for bears. At that time, bears begin to focus mostly on berries. Time to seed drop for all berries was taken to be 3.5 weeks (corresponding to the duration of several preferred species found in the USFS FEIS), and dried berries were assumed not to be available the following spring for simplicity. In the model, ants and preferred roots are available for a fixed period of time from June 1to July 31, and carrion is available until May 31; after that decomposition is assumed to have advanced to a stage where it no longer provides food for bears.

Food availability varies from day to day within a year based on visitation to the cells by bears. After a bear visits a cell the food items available at the specific time are assumed depleted. If more than one bear is in the cell, the food availability is not adjusted until the last bear leaves. The assumption behind this is if a bear leaves a cell when another bear enters, then this event happened before the first bear had a chance to eat any food or it ate very little food. In the case of carrion, bears are assumed to eat all that is available before moving on to the next location.

For vegetative food items, bears are assumed to eat all that is present, but for non-root items, the depletion is only temporary. After a certain time period, the particular item category is available again to bears. All vegetative food items, except roots, can replenish by regrowth or in the case of berries, additional berries becoming ripe. Ants are similar in that they can replenish as well. When a bear tears open a log, the ant colony is destroyed. The bear eats all the ants it can before the ants disperse. The surviving ants then build a new colony. For the model, ant recolonization was assumed to be seven days (bears have to forage where there are concentrations of ants, because the calories/ant are small and only become significant to the bear when they are concentrated. Regrowth for forbs and grasses was set at nine days and additional ripening at five. The nine days falls within the seven to nine days used from grasses in pasture management (Matt Ricketts NRCS, personal communication, 2005), and the five days was an estimate based on document reports that all berries ripen within a short time period (Martin 1979). Unlike the other food items categories already discussed, gut piles are not reduced by visitation because hunting is a reoccurring event that may produce gut piles at a future day; therefore, bears can potentially revisit the site in anticipation of gut piles during the entire hunting season.

Besides being a container of food the habitat cells also have the important tasks of keeping track of mortalities that have occurred there and resolving conflicts between two or more bears. Conflicts arise when a new bear enters the cell and is resolved immediately. A juvenile male, for example, will be forced to leave a cell when an adult male enters. Which bear(s) leaves, if any, is based on the social behavior documented in the literature. The conflict-resolving methods in the habitat cells use the follow rules:

- Juvenile males yield to adult males
- Juvenile males may or may not yield to adult females (decided by a coin toss)
- Juvenile males do not yield to other juvenile males or juvenile females
- Females with cubs yield to juvenile and adult males.
- Females with cubs do not yield to other females.
- Females without cubs and juvenile females are tolerated by males.

During the mating season, dual occupancy of an estrus female and adult male bear triggers a mating event. This event is handled immediately. To keep track of mortalities, each habitat cell keeps a record of the accumulated number of mortalities that occurred at its location. This number is recorded in an ASCII grid file that gets printed out at the end of the simulation run. If graphics are being used, the mortalities accumulated, up to the current day, can be drawn to the screen in a separate window.

5.4.4 Time and time management classes

5.4.4.1 Overview

The classes in this category work together to represent and advance time in the model. The *Calendar* class is designed to represent one calendar year, but more importantly than representing 365 days, the calendar year in the model represents one of the 25 climate scenarios in Table 5.12. As described in the previous sections, the *HabitatCell* objects use the dates in climate scenarios to determine their food availability and the *Bear* objects use the dates to determine their den emergence and entrance dates. The *TimeManager* object functions as the model's clock, ticking off each day and communicating with the other model objects to carry out their daily or annual event actions at the appropriate regular interval. The combination of having regular events initiated by the *TimeManager* class and irregular event initiated by the *HabitatCell* class allows the model to function in an event-driven framework. Using the *TimeManager* and *Timed* interface allows an event-driven framework to be implemented without having to worry about synchronizing multiply threads.

5.4.4.2 Data

No spatially explicit data are required.

5.4.4.3 Implementation

There are five classes and one interface found in this category*: Calendar, TimeManager, ImmutableList, ImmutableListEnumerator*, and *Timed*. All classes except the *Calendar* are modifications to the classes provided by Lea (2000). The *Calendar* is literally a calendar, and the other four classes work together to form a simulation clock. All objects with events that must be executed on a regular basis: daily or annually, must register with the *TimeManager* object, herein referred to as the time manager. Objects that register with the time manager must implement the *Timed* interface. An interface is Java's way of allowing classes to inherit variables and methods from more than one superclass. The *Timed* interface has four methods: pretick(), tick(), startOfYear(), and endOfYear(). The pretick() and tick() methods occur on a daily time scale and the other two on an annual scale, but otherwise function in the same regard. The pretick() and startOfYear() methods can be thought of as preconditions for the events that will take place during the day or year, respectively. They usually change the current state of an object and prepare the objects for whatever might take place during the tick() method. The tick() method is responsible for executing the events. The method is named tick because it represents the advancement of daily clock or one 'tick' of a real calendar, starting from March 1 until December 21 (days are represented by an integer starting with January 1 being equal to 1).

All objects that register with the time manger will have the opportunity to perform at least one action on any given day. The endOfYear() works similarly except on an annual time scale. The actions the objects perform each day or year are discussed under the individual manager classes that register with the time manager: *TimeManager*, *AnimalManager* and *GridManager*. The *ImmutableList* and *ImmutableListEnumerator* are used within the *TimeManger* itself, where they function in a utilitarian role. For this model, the time manager does not perform any action in response to the methods pretick(), tick(), startOfYear(), and endOfYear().

The *Calendar* object has 295 days, which, based on the dates found in the literature, is the longest active season possible of any grizzly. The *Calendar* object is responsible for annual or climate variation in the model. It registers with the *TimeManager*. Everyday it advances one day (action in the pretick()). Once a year it chooses a particular climate scenario from the 25 scenarios based on historic climate data, as described in Section 5.3. The chooseScenario() sets the calendar date for the following events: den emergence, leaf emergence, 50% flower completion day, start of the early, mid and late berry ripening day, availability of elk and deer gut piles, and den entrance; that is, it controls the phenological events. Individual bear and habitat cell objects then have methods for using these *Calendar* dates to set their individual phenological dates based on their sex, age, and reproductive status or location and topographic position, respectively.

5.4.5 Simulation control and graphics

5.4.4.1 Overview

In nontechnical terms, the *Simulation* class is what initiates the creation of all the objects in the model and starts the model running, i.e., starts the simulation model clock. For analysis purposes, it is necessary to run the model or simulate the ecosystem numerous times starting with the same initial data. This is the purpose of *SimulationController* class. It controls the number of *Simulation* objects that gets created and makes sure all the Simulation objects get created with the same initial data.

For reasons that will not be explain, it is possible to initiate the creation of all the objects in the model using the standard Java class *Applet*. One of the advantages of using the *Applet* class is that it allows the model to be executed in an internet browser. A subclass of *Applet* and supporting graphic classes were created to allow the model and its features to be viewed by other interested parties. This class was also used in the model development and verification process for the visual detection of errors.

5.4.4.2 Data

No spatially explicit data are required.

5.4.4.3 Implementation

There are two classes involved in controlling the simulation: *Simulation* and *Simulation Controller*, and 13 are involved in displaying the model graphically. The *Simulation* objects run the model for n-number of years, and the *SimulationController* runs the simulation for x-number of times or runs. When the simulation model is executed for n-number of years it is referred to as a model run. When an x-number of model runs of the simulation model are executed, it is referred to as a batch. The role of the *SimulationControlle*r is as a 'batch controller.' It creates an initial population of 40 grizzlies with an age distribution that is close to a stable age distribution with lambda equal to one and with an equal sex ratio. (Note: The small number of bears prevented the exact stable age distribution to be used, while at the same time dividing the population between the subregions.) Half of the bears are then assigned an initial den location in the Yaak portion of the study area and the other half a den location in the Cabinets portion. (Note: Fewer grizzlies are reported to exist in the Cabinets than in the Yaak portion, but for this project the population was equally divided between the two areas.)

After creating the initial population, the *SimulationController* then instantiates a *Simulation* object for each number of simulation runs in the batch. Each *Simulation* object is given the same initial population and the directory where the input data are located. This dualistic style is necessary because when performing analysis, each simulation should start out with the same initial population and input grids. After the *Simulation* objects are instantiated they are executed one at a time. Each *Simulation* object instantiates an *Animalmanager*, *GridManager*, and *TimeManager* object. It then sends a message to the *Timemanager* object to start the simulation clock. When the model is finished running, the *Simulation* objects send a message to the *AnimalManager* and *GridManager* objects to write out the results (demographic and population genetic information) of the simulation.

When graphics are desired, the *SimulationController* is not needed and an *Applet* class takes the place of both the *SimulationController* and *Simulation* objects. Instead of writing out the simulation results, the results are displayed on the screen. The display for the *Applet* is an object instantiated from the *DisplayCanvas* class. This class, developed for this project, is a subclass of Java's *Canvas* class and is herein referred to as the display. The display registers with the *TimeManager* and its daily action is to tell all the *Bear* and *HabitatCell* objects to draw themselves (via the *AnimalManager* and *GridManager*) to the display. This creates the illusion of movement and time advancement; in other words, it produces an animation of the model.

In the upper right-hand corner of the display the current model year and current model day are drawn. The landscape is represented by a collection of *HabitatCell* objects. These objects draw themselves on the display based on a RGB-color model schema. Red values represent meat and ants, blue values represent berries, and green values represent grasses and forbs. Brighter cells represent a greater variety of food items. A cell that contains both ants and some berries would, for example, appear on the landscape as a purplish-colored cell. A cell that contains both preferred forbs and roots would appear as a brighter green than cells containing one or the other. Possible den locations and areas with high road densities are also indicted.

Male and female grizzlies draw themselves on the display as blue and pink circles, respectively. Cubs move with their mothers until family breakup, so they are not displayed as individuals on the landscape until they begin dispersing. At the beginning of mating season, eligible bears will change colors. Mature males will turn yellow and mature receptive females will turn red. Subadult males and females will remain blue and pink, respectively, and females with cubs turn magenta.

At the end of the year, the model calculates the individual home ranges of the still living adult bears in the population using a minimum convex polygon algorithm and displays the results on the grid. All classes for calculating minimum convex polygon were taken from Goodman and O'Rourke (2004) and modified slightly. Female home ranges are displayed in pink and male home ranges are displayed in blue. The sizes (km^2) are likewise displayed underneath the calendar day and year string in the upper right-hand corner

Each of the genetic measures and the percentage of population members in each of 10 inbreeding coefficient categories: [0,.1), [.1,.2), [.2,.3)……[.9, 1], calculated in the *AnimalManager* object using the methods in the *Genetics* class, are displayed in separate windows as a line or bar graphs. These graphs are updated every generation. In another window, mortality locations appear in red. The intensity of the color is dependent on the number of mortalities at that location relative to the maximum number of mortalities occurring in any cell. The brighter red the cell appears the greater the number of mortalities accumulated in that cell. For example, if 10 mortalities have occurred in a particular model run at four different cell locations. Five of these mortalities occurred in one cell, two at another, and one mortality each at the remaining three cells. In this case, all four cells would appear in red on the mortality grid. The cell with the five mortalities would appear the brightest (five out of five), the three cells with a single mortality the least bright (one out of five), and the remaining cell with two mortalities a brightness between these extremes (two out of five).

5.5 Model outputs and conclusion

This section discusses the model's outputs in the context of two conservation-related problems. First, assessing the current viability of a population: Given the current vegetation and human development features on the landscape, the model can predict the population's viability to a predetermined horizon. The horizon was chosen as 100 year, acommon time frame for such an assessment. Second, in the same context, the model can also be used to assess the current level of connectivity between disjunct population segments and identify any areas of excessive mortalities that may be preventing inter-subpopulation segment movement or acting as a demographic sink.

As the model is executed during one simulation run, pertinent information regarding the population's viability and the location of mortalities are recorded. The most significant Information regarding the population's viability includes demographic and population genetic parameters. The demographic parameters include the annual number of births, deaths, and population sizes. Also, recorded were the number of individuals in each subpopulation, as determined by their year-end den location, the number of individuals in each age class, and the annual survival rates for each age class. The population genetic parameters recorded were (population) average heterozygosity, variance in average heterozygosity, average autozygosity, mean kinship, percentage of lost founder alleles, and F_{st}. In another file, the distribution of percentage of the population in each of the 10 inbreeding categories (discussed in Section 5.4.2.3) is recorded.

Mortalities and their locations and births are recorded as they occur. The number of births and deaths is also summed at the end of the year, and these sums along with the resultant population size are recorded annually. The population genetic parameters are recorded when they are calculated (every generation). All demographic and population genetic parameters recorded during the model run are then written out to text files at the end of the run. The locations of all the mortalities are written out to a text file at the end of the run as well. The format for the mortality locations text file allows importation into a GIS. Samples of these output files can be seen in Appendix B.

The files in Appendix B are results from one simulation execution or running the model for 100 years. The simulation was executed 20 times; each time files like the ones in seen in Appendix B were created and written to storage. Table 5. 14 shows a summary of extinction times derived from the demographics data for each simulation. The table shows three criterion for being classified extinct: population size less than three, population size equal to zero, and year of last reproduction success. Depending on the criterion, 70% (zero bears) or 80% (less than three bears) of the populations went extinct before 100 years. In run 15, there were only three bears left at year 100; if this run is included, then 84% of populations went extinct before 100 years. The average time to extinction was 65.6 and 74 years, for less than three bears remaining or zero bears remaining, respectively. Similarly, the minimum time to extinction was 44 and 58 years,

Table 5.14. Summary of extinction times for each model run. Last three columns indicate which subpopulation had bears remaining.

Run #	Year-< 3 Bear	Year-0 Bears	Year of last offspring*	Yaak	Cabinet	Both
1	61	67	54	1		
2	57	69	48		1	
3	58	66	49	1		
4	76	97	80	1		
5	53	76	57	1		
6				1		
7	86		76	1		
8	55	64	39		1	
9					1	
10	68	75	61		1	
11						1
12	74	89	64	1		
13	44	60	35	1		
14	66	87	62	1		
15			92		1	
16	63	74	49		1	
17	70	82	62		1	
18	73	77	64	1		
19	52	55			1	
20	93		90		1	
ave.	65.56	74.14	61.38			
min	44	58	35			

respectively. Probably a better estimate of extinction is when reproduction ceases, a situation that will be termed functional extinction. Functional extinction occurred as early as 35 years and on average at around 61 years.

The mortality locations ascii file contains the location of all the bear mortalities over the course of the run. These are only the locations of bears that died before the maximum age (25 years). The file is written out in a raster grid format for importation into a GIS. The resultant layer has the potential to highlight any areas of excessive mortalities that may be preventing inter-population segment movement or acting as a demographic sink. Viewing each layer individually showed most cells had no mortality. Cells that did have a bear mortality usually had at most one over the course of the 100 year period. Seven was the most mortalities accumulated by any one cell. Each layer was combined into a single grid to see if a consistent pattern emerged (this layer can be viewed in Figure 5.7). One can see there seems to be two clusters: one in the northwest and another in the southern portion, though not extreme southern tip, of the study area. These areas both may represent demographic sinks for the population. The southern cluster is concentrated in the center of a group of nine mortalities occurring prior to 1971. Given the low number of bears reported in the Cabinets, it is not surprising there are not more recent mortalities recorded there. This area may pose a substantial risk to bears moving south or west through the lower portion of the CYE. The northern clusters occur right on theIdaho-Montana border, with the cells with the highest recorded mortalities occurring on the Idaho side. Historically, mortalities have not been reported in this area; however, this may just indicate this is an area where mortalities go undetected.

Figure 5.7 does not indicate conclusively any areas acting as barriers to disperal. There are a string of mortalities between the towns of Troy and Libby on either side of Highway 2. This may very well be a place where bears are trying to disperse between the Yaak and Cabinet subpopulations, and are not making it. Review of the demographic data found that in simulation run 11, there were bears moving into and denning in the Cabinet Mountain portion of the study area from the Yaak portion. This happened on two, maybe three separate occasions, between years 94 and 98. At this time, the concentration of bears in the Yaak had reached 121 bears and the Cabinet population had gone extinct in year 65. It is undeterminable from the model's output

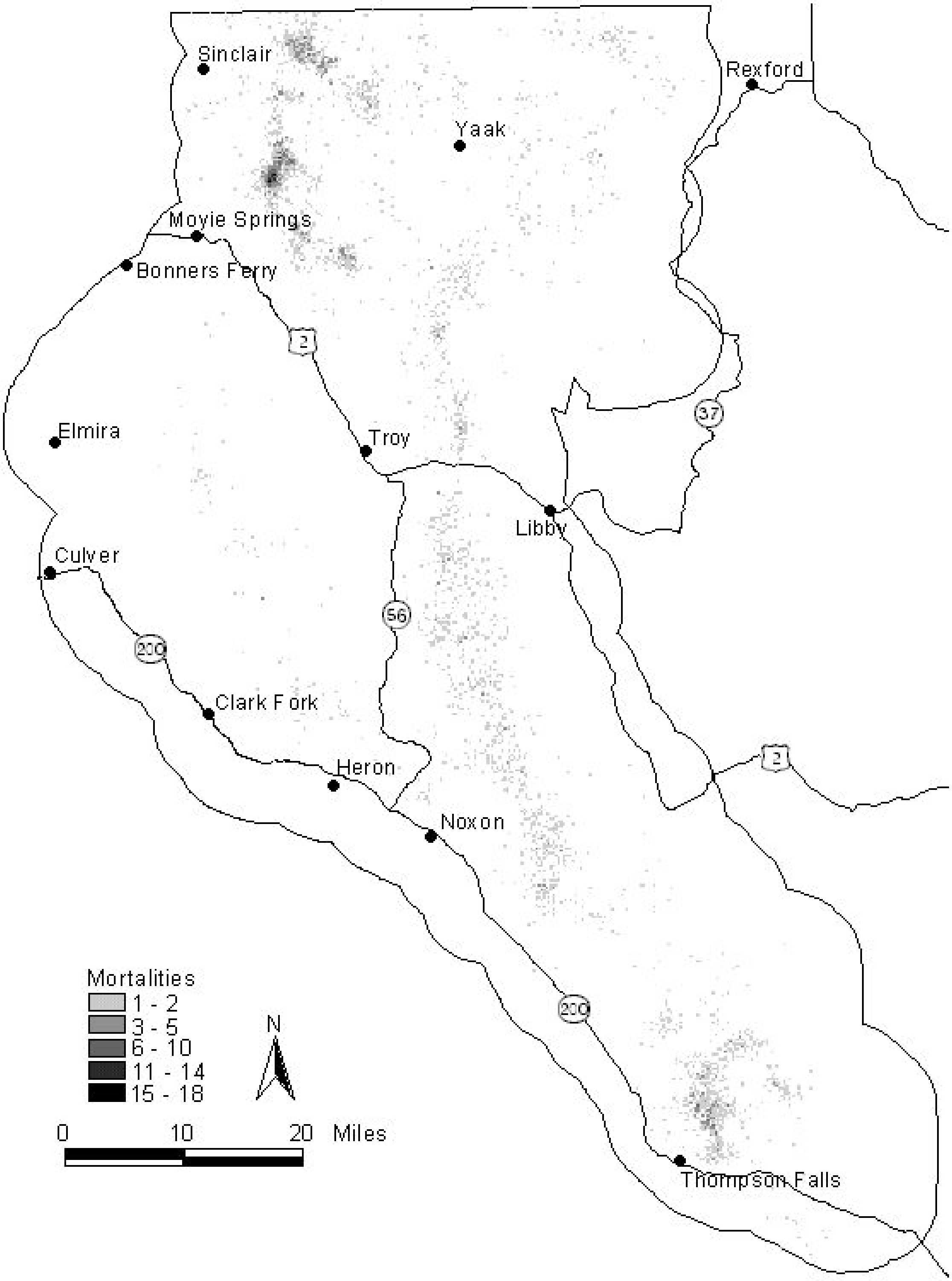

Figure 5.7. Mortality locations for all model runs.

whether these bears moved across Highway 2 between Troy and Libby, indicating dispersal is possible, or another area, which may indicate the area between Troy and Libby is a type of barrier. In the future, it may be worthwhile to write the individual bear's home ranges to files for later analysis. This would facilitate answering these suppositions.

Table 5.15 shows the genetic parameters for the last generation that had more than one individual in the population. Table 5.16 shows the descriptive summary statistics pertaining to Table 5.15. In general, it is difficult to conclude a lot from these data. First, the initial population is assumed to be unrelated to each other, except for the cubs whose parents are from the initial population of adults. Second, bears have a generation time of 10 years; hence, for 100 years, at most 10 generations of data will be recorded (less if population goes extinct before 100 years). This is not a lot of generations where population genetic processes are concerned. Finally, in all but one simulation run (15) where a couple of dispersers recolonized the Cabinets, one of the subpopulations always went extinct before the other. This affects the calculation of F_{st}, because

Table 5.15. Population-level genetic measures calculated at last generation with > 1 bear in population. Rounded to the 1/1000th.

Run	Average Heterozygoisty	Average Heterozygosity Variance	Average Autozygosity	% Lost Founder Alleles	Average Mean Kinship
1	0.767	0.089	0.233	0.783	0.276
2	0.783	0.281	0.217	0.667	0.118
3	0.750	0.025	0.250	0.750	0.300
4	0.600	0.100	0.400	0.867	0.454
5	0.400	0.100	0.600	0.917	0.555
6	0.797	0.205	0.200	0.600	0.119
7	0.700	0.000	0.300	0.867	0.707
8	0.367	0.022	0.633	0.900	0.426
9	0.648	0.313	0.352	0.683	0.165
10	0.600	0.100	0.400	0.817	0.340
11	0.747	0.218	0.253	0.700	0.103
12	0.867	0.156	0.133	0.867	0.328
13	0.960	0.064	0.040	0.783	0.161
14	0.800	0.320	0.200	0.567	0.141
15	0.900	0.000	0.100	0.650	0.196
16	0.900	0.080	0.100	0.733	0.194
17	0.800	0.400	0.200	0.800	0.395
18	0.633	0.089	0.367	0.750	0.297
19	1.000	0.000	0.000	0.650	0.175
20	0.678	0.506	0.322	0.650	0.163

Table 5.16. Descriptive summary statistics for the population genetic measures in Table 5.15. Rounded to the 1/1000th.

Statistic	Average Heterozygoisty	Average Heterozygosity Variance	Average Autozygosity	% Lost Founder Alleles	Average Mean Kinship
Mean	0.735	0.153	0.265	0.750	0.281
Standard Error	0.037	0.032	0.037	0.023	0.036
Median	0.758	0.100	0.242	0.750	0.236
Standard Deviation	0.165	0.144	0.165	0.103	0.162
Sample Variance	0.027	0.021	0.027	0.011	0.026
Range	0.633	0.506	0.633	0.350	0.603
Minimum	0.367	0.000	0.000	0.567	0.103
Maximum	1.000	0.506	0.633	0.917	0.707

this parameter is based on a comparison between within subpopulation and between subpopulation heterozyosity.

The original intent was to have F_{st} be a measure of connectivity between the two subpopulations; that is, a value of 0 would indicate a panmictic population and a value of 1 would indicate migration was not high enough to distinguish the two populations as anything but distinct. As mentioned in the previous paragraph, this was not possible because one of the subpopulations always went extinct. Not much can be gleaned from the population average heterozygosity as well. In all simulation runs, population average heterozygosity increases. This is model artifact due to having the initial population be unrelated and the short number of generations considered. The same thing can be observed in the simulations presented in Chapter 4, because the same assumptions about the founding population were made. Also, the results from Chapter 4 show under these assumptions heterozygosity does not start to decline until around the 10th generation.

Some observations can be made from the data. First is the large percentage of lost founder alleles, between 57- 92%. This may put the population at risk of an epidemic, since allelic diversity is important for disease resistance (Allendorf and Ryman 2002). Second the average population mean kinship is 0.28. Despite the idea by some who argue mammalian carnivores are somehow adapted to close inbreeding (Laikre and Ryman 1991), Laikre and others (1996) found a 6.3% relative reduction in litter size following a 10% increase in inbreeding coefficient. What this means is the reduction in litter size of some offspring produced from a population with mean kinship of 0.28 could be as high 17.4 %. Lastly, Allendorf and Ryman (2002) suggest defining a viable population as one with no more than 5-10% overaccumulation of inbreeding over 100-200 years. Just looking at the simulation runs where there were more than three bears remaining at 100 years yielded inbreeding accumulations of 8, 10, and 16%, nearly two to three times as much suggested for a viable population.

Absent management action, the preliminary quantitative outputs of the model identify serious challenges to the persistence of the small, isolated population of grizzly bears in the northwest corner of Montana. This result corroborates what many have suspected about the prognosis for grizzly bears in the Cabinet Mountains. In addition, the model shows the grizzly bears in Yaak are also at risk of extinction. The population, however, was modeled as a closed population. Movement between bears in Canada and the Yaak has been documented. This study highlights the need for maintaining connectivity with Canadian bear populations. At this time, these results should not be treated as conclusive as the proper parameterization of the model developed herein demands the full participation of relevant natural resource managers and bear experts. The results nonetheless suggest the model adequately captures the population's dynamics.

CHAPTER 6

CONCLUSION

6.1 Research summary

This study develops a conceptual foundation and an analytic tool for designing science-based conservation programs for wild populations of large terrestrial mammals. The conceptual foundation integrates principles from conservation biology, ecology, geography, object-oriented programming, and complex adaptive systems. The tool is a spatially explicit IBM constructed using a mechanistic, bottom-up approach along with georeferenced, real-world data.

Predicting the consequences of alternative planned management action or landscape changes to the long-term viability of a population is a common challenge in wildlife conservation. It has been suggested this challenge can be met by carrying out the process called PVA (Gilpin and Soule 1986; Boyce 1992; Coulson et al. 2001; Allendorf and Ryman 2002). This process has come under criticism (Caughley 1994; Beissinger and Westphal 1998; Brook et al. 2000; Coulson et al. 2001) due to both the difficulties associated with data requirements and the flaws in the theoretical underpinnings of the demographic models upon which the process is based. A central premise of this dissertation is that many of these issues arise because the models currently used in PVA are developed from a top-down perspective, as are the data collection efforts that support the models. In addition, this dissertation contends the form of the currently used PVA models prohibits them from being used effectively to guide conservation and management action.

This study takes a different approach to designing a population model for PVA and conservation planning. Relying on concepts from complex adaptive systems, this study develops the methods necessary to explore the mechanisms through which population dynamics – and hence population viability – arise from the spatial and temporal interactions between individuals, their natural environment, and the human-dominated landscape. The approach is illustrated by developing such a population model for the CYE grizzly bear population, discussed in Chapter 5. GIS and remote sensing data are utilized to produce spatially explicit data layers for the model. Remotely sensed data, along with other georeferenced data detailing site characteristics, are used to derive a spatially explicit grizzly bear foods data layer. Georeferenced data are also used, in conjunction with historic climate data, to make the availability of these foods temporally dynamic, that is, phenologically explicit. Finally, georeferenced data are used to incorporate the direct and indirect effects to grizzly bears of human landscape features into the model. Indirectly, human landscape features can affect grizzly bears by potentially influencing their movements, and directly, all of the human landscape features affect grizzly bears by contributing to their mortality risk. Java™ is used to create grizzly bear classes that allow each grizzly bear in the CYE to be represented as an individual grizzly bear object in the model. These grizzly bear objects move over the landscape, making decisions that will affect their potential fitness. Their decisions are based on simple rules of habitat and mate selection and their current state. This decision-making behavior by individual grizzly bears, coupled with temporally dynamic and spatially explicit landscape data, allows population-level dynamics to emerge as a function of the interaction of the individual grizzlies with other grizzlies and the landscape they inhabit.

It is the bottom-up, mechanistic perspective of individual-based modeling, when implemented and joined with spatially explicit real-world data, that allows this model to avoid many of the criticism of conventional PVA models and produces an effective management tool. Conventional PVA models require estimates of vital rates and their variances. Often there is little, poor, or no data available for the species for which the model is being developed (Caughley 1994; Beissinger and Westphal 1998; Boyce 2001). In addition, collecting data in order to estimate the variances in vital rates, especially as they relate to the stochastic perturbations, requires large sample sizes and long time periods. These conditions are often unattainable in cases of small populations whose survival is highly uncertain in the near term. Current forms of PVA models that address metapopulation structures also require data on dispersal, some of the most difficult data to collect (Kareiva and Wennergren 1995; Stacey and Taper 1992; Beissinger and Westphal 1998), and dispersal behavior information, likewise difficult to acquire (Kareiva and Wennergren 1995; Stacey and Taper 1992; Beissinger and Westphal 1998). For widely ranging species, collecting dispersal data at the appropriate spatial scales is a challenge. For endangered or threatened species, data collection at appropriate time scales that may permit beneficial conservation action, e.g., protection of lands used for dispersal, is equally challenging. Finally, typical PVA models require assumptions about population-level dynamics besides dispersal, such as density dependence, carrying capacity, and Allee effects. Assumptions regarding population-level dynamics can greatly influence model outcome (Stacey and Taper 1992; Mills et al. 1996; Beissinger and Westphal 1998).

Though an IBM also has data needs, some of the problems associated with PVA can be avoided because population dynamics emerge as a function of individual interactions with other individuals and the landscape. No assumptions about the correct form of population-level responses, such as density dependency and Allee effects need to be made, nor do data have to be collected on long-distance dispersal. The population-level-observed phenomenon of density dependence and Allee effect will emerge as a natural response to high and low numbers of individuals in the current population, respectively. Allowing dispersal behavior to emerge from local movement negates having to make assumptions and collect data about dispersal at the population level. Data on localized behavior and movement are oftentimes available and, if not, are easier to collect than long distance dispersal information.

On theoretical grounds, conventional PVAs underestimate the importance of each individual in small populations and rely on historical data that may not be representative of future conditions. Commonly used forms of PVA models rely on historical averages and associated variances of vital rates and stochastic perturbations that require large sample sizes. This implies the fate of the population is governed by the law of averages. For small populations, it is the fate of individuals that is almost synonymous with the fate of the population as a whole. Further, these values are assumed to apply in an undifferentiated manner to all individuals. The inclusion of individual variation has been shown to affect population persistence (DeAngelis et al. 2001). The grizzly bear model being individual based realizes the full impact of each individual on the overall population dynamics. Further, its bottom-up, mechanistic approach is forward looking and obviates assumptions that the past is representative of the future.

Conventional PVA models lack the ability to incorporate specific environmental changes directly, yet it is deterministic factors or processes, such as habitat modification and loss and human mortality, that are the primary causes of extinction (Caughley 1994; Holsinger 1995; Boyce et al. 2001). This inability stems from their failure to directly link ecological landscape attributes with a species' viability. This acontextuality limits their use as an effective management tool for predicting the consequences of any proposed landscape change. This is especially true for the more popular PVA models that represent the extinction process as driven exclusively by stochasticity (environmental, demographic, catastrophic, and genetic) in the system (Beissinger and Westphal 1998). Typical PVA models, in order to predict changes in a population's viability caused by proposed management action, require a priori knowledge or estimation of how the action will affect vital rates or how the action will affect one of the four perturbations and their associated variances. In spatially structured populations, a priori knowledge or estimation of how the action would affect dispersal behavior and rates and, in terms of population genetics, a priori knowledge or estimation of how the action would affect gene flow is needed. Unless the same management action had occurred previously and data collected at that time, the required information would not be available.

What is known or can be reasonable forecasted about management actions, however, is how they will modify the landscape. The grizzly bear model presented in Chapter 5 directly links ecological attributes of the landscape to the population's genetics and demographics via individual local interactions between grizzlies and other grizzlies and grizzlies and the landscape. Individual grizzly bear fitness and survival are modeled as outcomes of these interactions, and population-level dynamics result. Landscape attributes, hence, are directly linked to a population's genetic integrity and demographics (i.e., a population's viability). The resultant effects of any, or multiple, landscape changes proposed by management on a population's viability can therefore clearly and explicitly be realized.

Besides the direct linkage of landscape attributes to a population's viability, the grizzly bear model in Chapter 5 is an effective management tool for several of other reasons. First, the model incorporates individual animal behavior, something typical PVA models fail to do. Including individual animal behavior allows the model to incorporate both the direct and indirect effects of the human landscape: directly human landscape features affect grizzlies by increasing their mortality risk, and indirectly they can influence grizzly bear movement. Though conventional PVA models may be able to include anticipated changes in mortality risk, they are limited in their ability to include indirect effects. This exclusion may fail to accurately predict changes to the population's viability. Wildlife biologists have reported that grizzlies (though maybe only seasonally [Mace et al. 1996]) avoid areas of high road density (Kasworm and Manley 1990; Kasworm and Wakkinen 1997). The avoidance of certain areas of the landscape could influence the ability of some individuals to find mates, thereby contributing to a decrease in population size. Without the inclusion of grizzly bear behavior, commonly used forms of PVA models may not be able to predict this decline.

Second, the model in Chapter 5 includes a complete pedigree of the simulated population. Having the pedigree allows the calculation of kinship or inbreeding coefficients, and this permits a direct calculation of the loss of heterozygosity, thus avoiding having to estimate it using N_e. (Chapter 4 discusses the problems associated with using either empirically or analytically based estimates of N_e to calculate heterozygosity loss in real-world populations.) In addition to providing a better estimate of heterozygosity loss, the grizzly bear model calculates a variety of other population genetic measures. This allows the word <u>viability</u> to be defined in a more meaningful and comprehensive way than just time to or probability of extinction, the single output of most PVA models. Allendorf and Ryman (2002) question the utility of using only persistence over a certain time period as the sole indicator of a population's viability. If over that time period the demographic and genetic characteristics of the population have changes such that it is unlike they will persist much longer, is that maintaining a viable population? As an example Allendorf and Ryman cite the research of Shaffer and Samson (1985) who showed where PVA results indicated a high probability of extinction for a small population of grizzly bears (50 individuals) within 114 years, even though the probability of extinction to 100 years was low. Allendorf and Ryman suggest defining viable populations as one with an accumulation of inbreeding of no more than 5-10% over 100-200 years. Mean kinship is one of the genetic measures calculated in the grizzly bear model, and therefore accumulation of inbreeding can be assessed. Further, the other genetic measures calculated by the grizzly bear model have the potential to help wildlife managers set more specific goals to maintain a population's genetic integrity. Another criterion of viability, for example, might include maintaining a certain percentage of individuals in the population below a certain level of inbreeding or a certain percentage of founder alleles. Increased susceptibility to pests and parasites is associated low genetic variation (Frankam 1995), and loci associated with disease resistance often have a large number of alleles or allelic diversity (Allendorf and Ryman 2002).

Third, the model developed in Chapter 5 uses F_{st} as a means of assessing the level of dispersal, if any, between subpopulations. In metapopulation models, dispersal frequency and characteristics (sex specific, distance dependent, etc.) are defined as input parameters of the model by the user. Evaluation consists of determining whether or not the level of dispersal increases the persistence of any or all of the subpopulations. In the grizzly bear model in Chapter 5, dispersal is not assumed but rather emerges (if it does indeed occur); hence the model evaluates whether or not dispersal between subpopulations actually occurs. This knowledge coupled with the map showing mortality locations may indicate areas acting as dispersal barriers. Areas of high mortality between subpopulations, for example, may indicate areas where possible dispersers are attracted but are frequently killed. This information would be important when evaluating proposed management actions that affect the landscape as well. One can evaluate if the proposed action improves or reduces dispersal between populations. (The advantages of the model over habitat suitability models are described in Chapter 2.)

Finally, the model developed in Chapter 5 is an effective management tool because, unlike conventional PVA models, wildlife managers can use it to predict the timing, scope, and intensity of population augmentation actions necessary to improve grizzly bear persistence. Augmentation can be done for demographic or genetic improvement to a population. Though the grizzly bear model can be used to guide demographic augmentation action, its real value is in being able to guide genetic augmentation decisions. Current guidelines for such action focus either on N_e or heterozygosity as derived from traditional scientific approaches: empiricism and analytic (mathematical) theory. The results from Chapter 4 indicate reliance on these traditional approaches to judge the genetic health of a population or to predict when management action, such as translocation of individuals from one population to another, would be necessary could have dire consequences for a couple of reasons. First, a certain level of heterozygosity does not necessarily equate to a certain level of mean kinship. If population average heterozygosity was acceptable but mean kinship was high, the population may survive in the short term only to face irreparable levels of inbreeding in the long term. Second, the problem could be compounded if the managers were basing their decisions entirely on models lacking explicit geography; neither traditional scientific approaches includes a geographical component. As discussed in Chapter 4, geography appears to constrain the level of heterozygosity a population is able to achieve and maintain, when compared to a population modeled on a homogeneous landscape. Managers relying on only traditional methods may therefore overestimate the species ability to rebound and return to an acceptable level of heterozygosity.

6.2 Potential uses

This dissertation shows how all important aspects of species conservation: habitat protection, population genetics, and population demographics can be integrated along with the species' behavior and ecology, to form a single comprehensive model. The inclusiveness of the model makes it versatile in its application as a practical conservation tool. Its application as a tool to assess a population's current long-term viability or evaluate current landscape conditions was described at the end of Chapter 5.

In addition to its use as conservation tool to evaluate the viability of the current population or the effectiveness of connectivity between populations under existing landscape conditions, the model can be used predictively to determine the consequence of foreseeable landscape changes to these two conservation concerns. These changes can either be management planned or naturally occurring. Building and reclaiming roads, permitting mines, and conducting timber harvests are examples of planned landscape modifications. The previous section discussed the reasons why the grizzly bear model in Chapter 5 will provide a better evaluation of proposed landscape changes than more conventional PVA models. To evaluate the consequences of various alternatives, new data layers would need to be generated reflecting the landscape changes and then a comparison of model outputs performed. Given the mechanistic design of the model, the cumulative effects of multiple concurrent changes can be evaluated simultaneously.

A key reason why the grizzly bear model presented in this dissertation provides a better management tool than more typical PVA models is because the model's mechanistic, bottom-up approach facilitates the direct linkage of landscape attributes with population viability. This linkage allows the model to predict the consequences of naturally occurring alterations to the landscape as well. Natural alterations could occur because of fire or disease, for example, the loss of mature whitebark pine (*Pinus albicaulis*) due to mountain pine beetle (*Dendroctonus ponderosae*) or loss of huckleberries due to severe fire. Natural changes to the landscape can be assessed in the same manner as planned management alterations.

The grizzly bear model's mechanistic bottom-up approach also facilitates linkage with other models. One of the most powerful uses of the grizzly bear model could be as part of a meta-model. A meta-model has the potential to become a better conservation planning tool than a stand-alone PVA model. To date, conservation work is usual focused on evaluating the current landscape and/or the consequences of proposed human-induced changes in the landscape. The evaluation usually assumes the landscape is stationary with respect to time that is other than the possible proposed change. Even without human-induced changes, the landscape is temporally dynamic. For example huckleberries: are an important grizzly bear food source that may experience increases in berry production after a fire, if the fire is not hot enough to kill the plant's rhizomes. The increase in production does not occur, however, until 815+ years after the fire (Martin 1979). At some point further in the future, production will decline with increased canopy closure. Whitebark pine in the Yellowstone Ecosystem is another example. Without fire, the climax species subalpine fir will eventually replace whitebark pine. This dynamic nature of huckleberries and other vegetative grizzly bear food sources is seldom considered when making conservation decisions and plans. In Chapter 5, to derive the spatial distribution of key vegetative grizzly bear food categories, a rule-based method was used to assign plant associations to timber stand types. This translation from timber stand to grizzly bear food may be a way to facilitate linkage of the model with vegetation succession models. A place that provides good habitat for grizzly bears today may not necessarily be good habitat for them in the future, and a meta-model that includes natural vegetation succession could guide proactive measures to improve or restore habitat.

Land-use planning models could be connected to the grizzly bear model to form a different metamodel. Land-use planning models predict the location and density of human landscape features, e.g., houses. The current distribution of grizzly bears is found primarily on public lands. Those in charge of managing public lands are the ones usually evaluating the consequences of their actions on the lands under their jurisdiction. There is little, if any, consideration given to the surrounding private lands. Continued human development around public lands has the potential to create islands of public lands that would be the sole refugia for threatened species like the grizzly bear. Additionally, lands surrounding the public areas can act as buffers to changes within public lands (for example, buffers to loss of key food sources within public areas). Either scenario could have long-term effects on the health of a population, since small isolated populations have a greater risk of extinction. Only if society understands the human dimension outside the public lands, will we be able to anticipate habitat change, fragmentation, and loss to its greatest extend. Even if not connected in a temporally dynamic fashion, a metamodel that combines planned landscape modifications on public, as well as surrounding private lands, with the grizzly bear population model would provide a comprehensive assessment of the population's viability.

In addition, the grizzly bear model could be used to formulate genetic objectives for in situ conservation strategies. Chapter 3 discusses the reasons why those in charge of wildlife management often ignore population genetics. One reason often stated is the lack of data available on the effects of inbreeding on populations in the wild. Several researchers offer possible solutions for the dearth of inbreeding information available for wild population, such as using information obtained from threatened species held in zoos (Ralls and Ballou 1986; Laikre 1999) or domestic, and laboratory species (Frankham 1995). Though there are some problems associated with using captive data (Allendorf and Ryman 2002), there should be little consequence of using captive, domestic, or laboratory data in place of natural species data, provided a range of values are used, and different combinations of effects on vital rates used. One advantage of simulation modeling is that it is a method for handling uncertainty (Starfield et al. 1995). Because the simulation is run repeatedly with different values for those parameters characterized by uncertainty, a variance in the output or results is obtained. This at least gives some idea of the range of values that can be expected and for which variables the model results are the most sensitive. Chapter 4 discusses how spatially explicit IBMs, like the grizzly bear model, offer many advantages over the more traditional empirical or theoretical-based approaches to population genetics. Results from the simulations presented in the chapter also raise questions about the adequacy of these approaches for informing most in situ conservation strategies.

Lastly, the inclusion of phenology in both the landscape and bear behavior in the grizzly bear model may provide a means to investigate the consequences of climate change to a population's viability. There has been a renewed interest in plant phenology due to the increased interest and research into climate change. No research has been done specifically in evaluating the consequences of climate change to grizzly bear persistence. The model provides the framework for perhaps incorporating some of the climate change research results into a future version of the model.

6.3 Future research

6.3.1 Population genetics

As discussed in Chapter 4, IBMs are particularly well suited for addressing the types of population genetic questions of interest to conservation biology. Using IBMs offers several advantages and avoids some of the problems associated with empirical and analytical-based methods (see Chapters 3 and 4 for full discussion). This research contributes technical tools, the compressed kinship matrix algorithm, and the *Animal* and *Genetics* Java™ classes, that can be used to explore population genetics from an individual-based theoretical framework.

Inbreeding and inbreeding depression do occur in wild populations, yet a clear understanding of how inbreeding interacts with other factors, such as demography and environment, to affect a species' persistence is lacking (Frankham 1995; Hedrick and Kalinowski 2000; Keller and Waller 2002). Also, needed is theoretical modeling that links levels of genetic variation, mean fitness, and population persistence (Ingvarsson 2001). The grizzly bear model, or a similar IBM designed using the technical tools mentioned above, could be used to pursue such investigations. The IBMs developed in this research consider multiple factors simultaneously in the assessment of population viability, and they allow individual effects of inbreeding and mean kinship to be transformed into population effects. In addition, because the technical tools facilitate the calculation and storage of the inbreeding coefficients of individual members of the population, simulation-based studies using IBMs that incorporate these tools will allow an illumination of how variance in the degree of inbreeding among individuals within a population affects the expression of inbreeding depression and subsequent population dynamics. This is an unexplored area of research (Keller and Waller 2002). The inclusion of individual variation has been shown to affect population persistence (DeAngelis et al. 2001). It is therefore reasonable to think the same would hold true for population genetic processes, but this is yet to be thoroughly investigated.

Not only are the effects of variance in the degree of inbreeding among individuals within a population an unexplored area of research, but the spatial distribution of this variation is as well. In fact, results from Chapter 4 suggest the spatial distribution of variation in levels of individual heterozygosity, not just the variation between individuals themselves, appears to influence a population's mean average heterozygosity. Further, results from Chapter 4 indict the need for more research into how the geographic landscape features influence the spatial distribution of a population's variation in heterozygosity. The model presented in Chapter 4 shows how spatially explicit IBMs can be coupled with real-world geographic information to produce a geographically explicit model. To date the use of such information in genetic modeling has been limited. There is a lack of understanding, therefore, of how the landscape influences the spatial distribution of within-population allelic diversity loss or inbreeding level increases, and what effects this distribution has on the population's overall dynamics and viability.

6.3.2 Grizzly bear conservation and management

The merging of empirical research, modeling, and management has the potential to dramatically enhance the future of many threatened and endangered species (Boyce 2001). This research demonstrates the usefulness of spatially explicit IBMs (as presented in this dissertation) as the proper modeling framework for this merger. This dissertation is meant to guide further grizzly bear research by encouraging wildlife biologists to move beyond site/time specific studies that do not further the understanding of the mechanisms that drive population dynamics. It is also meant to encourage reexamination of the use of habitat as a surrogate for population fitness and well-being and implementation of empirical studies that go beyond mere descriptive, observational assessments. Empirical studies were the focus of a reflective article by Morrison (2001). Morrison asks the question, "Are we asking habitat to do too much?" He suggests the endless array of site and time specific studies, fatuous null hypothesis testing (i.e., null hypotheses that are wholly improbable and can be rejected prior to analysis), and the reliance on using habitat as a predictor of animal fitness and abundance as factors prohibiting advancement in the field of wildife biology and ecology. These suggestions can be extended to conservation biology and wildlife management as well.

6.4 Conclusion

IBMs have been considered a mechanistic bottom-up approach to population modeling. Railsback (2001), however, argues the typical way individual-based models are designed, by imposing behaviors and population dynamics on the model as top-down empirical relations, makes them really nothing more than re-creations of empirical models. This dissertation illustrates how modern technologies -- GIS, remotely sensed imagery, and object-oriented program, and principles from complex adaptive systems -- can be used along with the more traditional ecology, wildlife biology, and genetics to facilitate a new approach to spatially explicit individual-based modeling. The approach is mechanistic and bottom-up and lets population dynamics emerge as a function of landscape attributes and local interactions among individuals and between individuals and the landscape. Throughout this dissertation, the advantages of this approach over more conventional forms of modeling have been discussed and/or demonstrated.

This dissertation also illustrates the need for an integrated multidisciplinary approach to species conservation. Phenology, vegetation mapping, habitat classification, GIS, remote sensing, animal behavior, population demographics and genetics, and PVA are the subject matter of several academic disciplines. One of this dissertation's most important contributions is the integration of the work in these fields into a single comprehensive model. It is this integrated, multidisciplinary approach with a focus on the individual that I believe will lead to the greatest improvements in conservation biology and the conservation of threatened and endangered species.

APPENDIX A

GRIZZLY BEAR VEGETATIVE FOODS

The following list was taken from several sources. When a family name was given, all species listed in the plant association's cover/constancy table were included. Similarly, if the species was not identified, for example, *Rosa spp.*, all species listed in the plant association's cover/constancy were included, unless known not to be eaten by or be poisonous to grizzlies.

Latin Name	Common Name
Forb	
Achillia millefolium	common yarrow
Aconitum colubianum	coumbia monkshood
Anaphalis margariticae	common pearleverlasting
+Angelica arguta	sharptooth angelica
Angelica dawsonii	dawson angelica
Antennaria racemosa	raceme pussytoes
Apocynum androsaemifolium	spreading dogbane
Aquilegia flavescens	yellow columbine
Aralia nudicaulis	wild sarsaparilla
Arenaria congesta	ballhead sandwort
Arnica cordifolia	heartleaf arnica
Arnica latifolia	broadleaf arnica
Aster spp.	aster
Aster chilensis	long-leaved aster
Aster ciliolatus	
Aster conspicuus	showy aster
Aster engelmannii	Engelmann's aster
Aster foliaceus	
Aster integrifolius	
Aster laevis	smooth aster
Aster modestus	
Aster stenomeres	Rocky Mountain aster
Aster occidentalis	
Astragalus spp.	milk vetch
Astragalus adsurgens	standing milk-vetch
Astragalus atropubescens	Kelsey's milk-vetch
Astragalus inflexus	bent milk-vetch
Astragalus miser	weedy milk-vetch
Balsamorhiza sagittata	arrowleaf balsamroot
Caltha leptosepala	alpine white marsh marigold
Campanula rotundifolia	harebell
Castilleja spp.	paintbrushes
Cirsium spp.	thistles
Claytonia lanceolata	spring beauty
Clintonia uniflora	queencup beadlily
Collinsia parviflora	littleflower collinsia
Cryptogramma crispa	american rockbrake
Delphinium spp.	larkspur
Delphinium bicolor	little larkspur
Disporum trachycarpum	wartberry fairybells
Dodecatheon pauciflorum	
*Epilobium angustifolium	firewood
Epilobium latifolium	
Epilobium ciliatum	purple-leaved willowherb
Equisetum spp.	
Erigeron spp.	
Erigeron caespitosus	
Erigeron corymbosus	long-leaved fleabane
Erigeron divergens	spreading fleabane

Latin Name	Common Name
Erigeron filifolius	thread-leaf fleabane
Erigeron gracilis	slender fleabane
Erigeron philadelphicus	Philadelphia fleabane
Erigeron pumilus	shaggy fleabane
Erigeron speciosus	showy fleabane
Eriogonum flavum	
Eriogonum heracleodes	
*Erythronium grandiflorum	glacier lily
Fragaria spp.	
Fragaria vesca	bracted strawberry
Fragaria virginiana	wild strawberry
Galium boreale	northern bedstraw
Galium triflorum	sweet scented bedstraw
Geum macrophyllum	largeleaf avens
Gymocarpium dryopteris	oakfern
Habenaria dilatata	white bogorchid
+*Hedysarum alpinum4	alpine hedysarum
Hedysarum boreale4	sweet vetch
+Hedysarum sulphurenscens	
Heuchera cylindrica	roundleaf alumroot
+*Heracleum lanatum	cow parsnip
Hieracium spp.	
Hieracium albertinum	western hawkweed
Hieracium albiflorum	white-flowered hawkweed
Hieracium aurantiacum	orange hawkweed
Hieracium canadense	Canada hawkweed
Hieracium cynoglossoides	houndstongue hawkweed
Hieracium umbellatum	narrow-leaved hawkweed
Hypericum formosum	southwestern st. johnswort
Lathyrus ochroleucus	creamy pea vine
Ligusticum spp.	
Ligusticum canbyi	canby lovage
Ligusticum verticillatum	
+Lomatium spp.	biscuit root
Lomatium cous	Cous biscuit-root
Lomatium dissectum	fern-leaved desert-parsely*
Lomatium macrocarpum	bigseed desert-parsely
Lomatium sandbergii	Sandberg's desert-parsely
Lomatium triternatum	nine-leaf lomatium
Lupinus spp.	
Lupinus argenteus	silvery lupine
Lupinus caudatus	tailcup lupine
Lupinus laxiflorus	spurred lupine
Lupinus leucophyllus	velvet lupine
Lupinus sericeus	silky lupine
Lupinus wyethii	Wyeth's lupine
Lysichiton americanum	skunk cabbage
Maianthemum stellatum	
Menyanthes trifoliate	buckbean
Mertensia longiflora	small bluebells
Mitella spp.	
Mitella breweri	Brewer's mitrewort
Mitella nuda	bare-stemmed mitrewort
Mitella pentandra	five-stamened mitrewort
Mitella stauropetala	side-flowered mitrewort
Montia spp.	

Latin Name	Common Name
Montia arenicola	sand montia
Montia cordifolia	broad-leaved montia
Montia parvifolia	little-leaved montia
Montia perfoliata	miner's lettuce*
Osmorhiza chilensis	mountain sweet cicely
Osmorhiza depauperate	blunt fruit sweet cicely
+*Osmorhiza occidentalis	sweet cicely
Parnassia fimbriata	rocky mountain parnassia
*Pedicularis bracteosa	bracted lousewort
Pedicularis contorta	coiled lousewort
Pedicularis racemosa	sickletop lousewort
Petasites sagittatus	arrow-leaved coltsfoot
Pestemon spp.	
Penstemon albidus	white-flowered penstemon
Penstemon aridus	stiff-leaf penstemon
Penstemon confertus	yellow penstemon
Penstemon elegantulus	lovely penstemon
Penstemon ellipticus	rockyvine penstemon
Penstemon eriantherus	fuzzytongue penstemon
Penstemon procerus	
Penstemon wilcoxii	Wilcox's penstemon
Polemonium pulcherrimum	skunkleaf polemonium
Polygonum phytolaccaefolium	pokeweed fleeceflower
Potentilla gracitis	northwest cinquefoil
Potentilla paustris	marsh cinquefoil
Prunella vulgaris	commone selfheal
Ranunculus spp.	
Ranunculus macounii	Macoun's buttercup
Rubus pubescens	dewberry
Saxifraga spp.	
Saxifraga bronchialis	
Sedum stenopetalum	
Senecio triangularis	arrowleaf groundsel
Smilacina racemosa	false solomon's seal
Smilacina stellata	starry false solomon seal
Solidago spp.	goldenrods
Solidago canadensis	Canada goldenrod
Solidago missouriensis	Missouri goldenrod
Streptopus amplexifolius	claspleaf twistedstalk
Taraxacum spp.	
*Taraxacum officinale	common dandelion
Taraxacum occidentale	
Thalictrum occidentale	western meadowrue
Tofieldia glutinosa	tofieldia
+Trifolium spp.	clover
Trifolium dubium	least hop clover
Trifolium longipes	long-stalked clover
*Trifolium pratense	red clover
*Trifolium repens	white clover
Trillium ovatum	pacific trillium
Urtica dioica (for elev. dioica gracilis)	stinging nettle
Valeriana dicica	marsh valerian
*Valeriana sitchensis	sitka valerian
Veratrum viride	? hellabore
Verbascum thapsus	flannel mullein
Viola spp.	

Latin Name	Common Name
Viola adunca	hook violet
Viola canadensis	Canada violet
Viola glabella	pioneer violet
Viola nuttalii	yellow prairie violet
Viola orbiculata	western roundleaf violet
Xerophyllum tenax	beargrass
Ferns	
+Athyrium filix-femina	lady fern
Dryopteris expansa/assimilis	spiny wood fern
+*Equisetum arvense	field or common horsetail
Equisetum pratense	meadow horsetail
Equisetum fluviatile	swamp horsetail
Gymocarpium dryopteris	oakfern
Matteucia struthiopteris	ostrich fern
Pteridium aquilinum	western bracken fern
Grasses, Rushes, Sedges, etc.	
Agropyron caninum	
Agropyron dasystachyum	
Agropyron repens	quackgrass
Agropyron spicatum	bluebunch wheatgrass
Agropyron spp.	wheatgrass
Agrostis alba	redtop
Agrostis exarata	spike bentgrass
Agrostis interrupta	interrupted apera
Agrostis humilis	
Agrostis scabra	
Agrostis stonlonifera	
Alopecurus pratensis	
Aristida longiseta	red threeawn
Bromus spp.	brome
Bromus brizaeformis	nodding brome
Bromus carinatus	mountain brome
Bromus ciliatus	fringed brome
Bromus inermis	smooth brome
Bromus japonicus	Japanese brome*
Bromus mollis	soft brome
Bromus rigidus	ripgut
Bromus tectorum	cheatgrass*
Bromus vulgaris	Columbia brome
Calamagrostis canadensis	bluejoint reedgrass
Calamagrostis koelerioides	fire reedgrass
Calamagrostis montanensis	plains reedgrass
Calamagrostis purpurascens	purple reedgrass
Calamagrostis rubescens	pinegrass*
Calamagrostis spp.	reedgrass
Carex spp.	sedges
Cyperaceae	
Carex aquatilis	
Carex athrostachya	
Carex brunnescens	
Carex canescens	
Carex concinnoides	northwestern sedge*
Carex crawei	Craw's sedge
Carex deweyana	Dewey's sedge
Carex disperma	
Carex filifolia	

Latin Name	Common Name
Carex geyeri	elk sedge*
Carex hoodii	Hood's sedge
Carex interior	inland sedge
Carex microptera	
Carex obtusata	
Carex pachystachya	
Carex parryana	
Carex petasata	
Carex pennsylvanica	
Carex obtusata	
Carex retrorsa	retrorse sedge
Carex rossii	Ross sedge
Carex rostrata	
Carex rupestris	
Carex scirpoidea	
Carex scopulorum	
Carex stenophylla	
Carex stipata	sawbeak sedge
Cinna latifolia	drooping woodreed
Carex vallicola	
Dactylis glomerata	orchardgrass
Danthonia intermedia	
Deschampsia caespitosa	tufted hair grass
Deschampsia spp.	hairgrass
Deschampsia elongata	slender hairgrass
Festuca idahoensis	idaho fescue
Festuca occidentalis	western fescue
Festuca ovina	sheep fescue
Festuca rubra	red fescue
Festuca scabrella	rough fescue
Festuca subulata	bearded fescue
Festuca spp.	
Gramineae	
Glyceria elata	tall mannagrass
Glyceria grandis	American mannagrass
grass spp.	
Juncus spp.	rushes
Juncaceae	
Juncus balticus	
Juncus drummondii	Drummond's rush
Juncus ensifolius	dagger-leaf rush
Juncus hallii	
Juncus mertensianus	
Juncus parryi	
Koeleria cristata	prairie junegrass
Luzula campestris	field woodrush
Luzula hitchcockii	smooth woodrush
Luzula parviflora	small-flowered woodrush
Melica bulbosa	oniongrass
Melica subulata	Alaska oniongrass
Oryzopsis asperifolia	roughleaf ricegrass
Oryzopsis spp.	ricegrass
Panicum scribnerianum	few-flowered panic-grass
Phalaris arundinacea	reed canarygrass
Phleum alpinum	
Phleum pratense	timothy

Latin Name	Common Name
Poa spp.	bluegrass
Poa bulbosa	bulbous bluegrass*
Poa compressa	Canada bluegrass
Poa pulustris	fowl bluegrass
Poa pratensis	kentucky bluegrass
Poa sandbergii	
Poa secunda	
Scirpus spp.	bulrushes
Scirpus microcarpus	small-flowered bulrush
Sporobolus cryptandrus	sand dropseed
Stipa occidentalis	
Stipa spp.	
Trisetum canescens	tall trisetum
Trisetum spicatum	spike trisetum
Trifolium repens	white clover
Trifolium pratense	red clover
Trisetum wolfii	
Shrubs	
Acer glabrum	rocky mountain maple
Alnus sinuata	sitka alder
Alnus teneifolia	thinleaf alder
Amelanchier alnifolia	saskatoon serviceberry
Arctostaphylos uva-ursi	bearberry or kinnikinnik
Berberis repens	oregan grape
Cassiope mertensiana	mertens cassiope
Ceanothus sanguineus	redstem ceanothus
Ceanothus velutinus	snowvbrush ceanothus
Cornus stolonifera	red-osier dogwood
Crataegus douglasii	black hawthorn
Empetrum nigrum	Crowberry
Juniperis communis	common juniper
Kalmia polifolia	? Laurel
Linnaea borealis	twinflower
Lonicera involucrata	bearberry honeysuckle
Lonicera utahensis	utah honeysuckle
Menziesia ferruginea	menziesia
Oplopanax horridum	devil's club
Pachistima myrsinites	myrtle pachistima
Purnus virginiana	common chokecherry
Rhamnus alnifolia	alder buckthorn
Ribes lacustre	Bristly black currant
Ribes oxycantholdes	Wild gooseberry
Ribes viscosissimum	sticky currant
Rosa spp.	wild rose
Rosa acicularis	prickly rose
Rosa canine	dog rose
Rosa gymnocarpa	baldhip rose*
Rosa nutkana	bristly nootka rose
Rosa pisocarpa	clustered wild rose
Rosa woodsii	wood's rose*
Rubus idaeus (for elev. idaeus sachalinensis)	red raspberry
Rubus parviflorus	thimbleberry
Salix spp.	willows
Salix barclayi	
Salix boothii	

Latin Name	Common Name
Salix drummondiana	
Salix exigua	
Salix geyeriana	
Salix planifolia	
Salix scouleriana	
Sambucus racemosa	red elderberry
Sheperdia canadensis	russet buffaloberry
Sorbus scopulina	sitka mountain-ash
Sorbus scopulina	Western mountain ash
Spiraea betulifolia	white spirea
Spiraea densiflora	subalpine spirea
Spiraea douglasii	douglas' spirea
Symphoricarpos albus	common snowberry
Symphoricarpos oreophilus	mountain snowberry
Taxus brevifolia	pacific yew
Vaccinium caespitosum	Dwarf blueberry
Vaccinium globulare	globe huckleberry
Vaccinium membranaceum	Black huckleberry
Vaccinium myrtilloides	Velvet-leaved blueberry
Vaccinium ovafolium	Oval-leaved blueberry
Vaccinium oxycoccos	Bog cranberry
Vaccinium scoparium	grouse whortleberry
Vaccinium uliginosum	Bog blueberry
Vaccinium vitis-idaea	Lingonberry
Viburnum edule	Highbush cranberry

APPENDIX B

MODEL OUTPUT FILES – ONE SIMULATION RUN

Percent population in 1 of 10 inbreeding coefficient categories. Calculated each generation.

```
Generation      <.1     <.2     <.3     <.4     <.5     <.6     <.7     <.8     <.9     <1
 0              1.0     0.0     0.0     0.0     0.0     0.0     0.0     0.0     0.0     0.0
 1              0.95555555555556        0.022222222222223 0.022222222222223 0.0     0.0     0.0     0.0     0.0     0.0     0.0
 2              0.875   0.05    0.05    0.025   0.0     0.0     0.0     0.0     0.0     0.0
 3              0.6     0.12    0.16    0.04    0.08    0.0     0.0     0.0     0.0     0.0
 4              0.5     0.214285714285714       0.142857142857143       0.0     0.142857142857143       0.0     0.0     0.0     0.0     0.0
 5              0.28571428571429        0.28571428571429        0.28571428571429        0.0     0.142857142857143       0.0     0.0     0.0
        0.0     0.0
 6              0.33333333333333        0.33333333333333        0.0     0.33333333333333        0.0     0.0     0.0     0.0     0.0     0.0
 7              NaN     NaN     NaN     NaN     NaN     NaN     NaN     NaN     NaN     NaN
 8              NaN     NaN     NaN     NaN     NaN     NaN     NaN     NaN     NaN     NaN
 9              NaN     NaN     NaN     NaN     NaN     NaN     NaN     NaN     NaN     NaN
 10             NaN     NaN     NaN     NaN     NaN     NaN     NaN     NaN     NaN     NaN
```

Genetic measures file. Measures recorded each generation.

```
Generation      aveHet          aveHetVar               likeInKind              lostFounderAlleles          meanKin             Fst
0               0.6075000000000002 0.7719374999999998 0.3924999999999996        0.0     0.016406250000000004
        0.058125000000000024
1               0.768888888888889   0.7236543209876548 0.2311111111111104       0.1333333333333333
        0.01987654320987654         0.0723
2               0.8775000000000001 0.5074375000000005 0.1225000000000001        0.2333333333333334
        0.028623046874999985        0.10353070175438597
3               0.8800000000000001 0.416   0.12    0.4166666666666667 0.052615625   0.1545873015873016
4               0.8142857142857143 0.5693877551020408 0.1857142857142857 0.45     0.09170220822704081
        0.22589285714285717
5               0.7285714285714286 0.5346938775510205 0.27142857142857146       0.7666666666666667 0.1831154336734694
        0.31734693877551023
6               0.7666666666666666 0.08888888888888895          0.2333333333333333 0.7833333333333333 0.2755262586805555
        0.36111111111111105
7               NaN     NaN     NaN     0.0     NaN     NaN
8               NaN     NaN     NaN     0.0     NaN     NaN
9               NaN     NaN     NaN     0.0     NaN     NaN
10              NaN     NaN     NaN     0.0     NaN     NaN
```

Demographics File. Recorded each year.

```
Year  Births Deaths     Pop.Size   Yaak Cabinet Juvs(suvival)     SubAdults(Survival)     Adults(Suvival)
1     0     3(2,0,1)    37          20    20    8(0.75)           10(1.0)           22(0.9545454545454546)
2     4     4(1,2,1)    37          20    21    6(0.8333333333333334)         10(0.8)           25(0.96)
3     5     2(2,0,0)    40          22    20    8(0.75)           7(1.0)            27(1.0)
4     6     5(1,1,3)    41          24    22    10(0.9)           8(0.875)          28(0.8928571428571429)
5     1     2(1,1,0)    40          24    18    6(0.8333333333333334)         7(0.8571428571428572)
      29(1.0)
6     8     7(4,1,2)    41          25    23    10(0.6)           8(0.875)          30(0.9333333333333333)
7     5     4(1,1,2)    42          23    23    10(0.9)           6(0.8333333333333334)
      30(0.9333333333333333)
8     4     4(4,0,0)    42          22    24    9(0.5555555555555556)         6(1.0)            31(1.0)
9     5     3(2,1,0)    44          23    24    9(0.7777777777777778)         5(0.8)            33(1.0)
10    8     9(6,1,2)    43          26    26    13(0.5384615384615384)        6(0.8333333333333334)
      33(0.9393939393939394)
11    2     2(0,2,0)    43          20    25    6(1.0)            4(0.5)            35(1.0)
12    4     3(3,0,0)    44          21    26    7(0.5714285714285714)         5(1.0)            35(1.0)
13    3     2(1,0,1)    45          23    24    6(0.8333333333333334)         5(1.0)
      36(0.9722222222222222)
14    3     5(3,0,2)    43          21    27    5(0.4)            6(1.0)            37(0.9459459459459459)
15    3     3(2,0,1)    43          24    22    4(0.5)            5(1.0)            37(0.972972972972973)
16    9     7(3,1,3)    45          31    21    10(0.7)           5(0.8)            37(0.9189189189189189)
17    2     4(1,0,3)    43          26    21    8(0.875)          3(1.0)            36(0.9166666666666666)
18    2     3(0,0,3)    42          25    20    4(1.0)            7(1.0)            34(0.9117647058823529)
19    6     8(1,3,4)    40          26    22    9(0.8888888888888888)         7(0.5714285714285714)
      32(0.875)
20    1     5(1,1,3)    36          23    18    7(0.8571428571428572)         5(0.8)
      29(0.896551724137931)
21    4     5(1,0,4)    35          19    21    5(0.8)            6(1.0)            29(0.8620689655172413)
22    8     6(4,1,1)    37          26    17    11(0.6363636363636364)        6(0.8333333333333334)
      26(0.9615384615384616)
23    3     5(2,1,2)    35          23    17    9(0.7777777777777778)         5(0.8)
      26(0.9230769230769231)
24    0     3(1,1,1)    32          22    13    4(0.75)           4(0.75)           27(0.962962962962963)
25    2     4(0,0,4)    30          23    11    2(1.0)            6(1.0)            26(0.8461538461538461)
26    4     5(1,0,4)    29          24    10    6(0.8333333333333334)         4(1.0)
```

								24(0.8333333333333334)
27	4	5(3,0,2)	28	25	8	7(0.5714285714285714)	4(1.0)	22(0.9090909090909091)
28	0	4(1,0,3)	24	20	8	2(0.5)	4(1.0)	22(0.8636363636363636)
29	3	2(0,1,1)	25	20	7	3(1.0)	5(0.8)	19(0.9473684210526316)
30	0	0(0,0,0)	25	18	7	3(1.0)	3(1.0)	19(1.0)
31	0	2(0,0,2)	23	18	7	0(NaN)	4(1.0)	21(0.9047619047619048)
32	2	0(0,0,0)	25	19	6	2(1.0)	3(1.0)	20(1.0)
33	3	5(3,1,1)	23	22	6	5(0.4)	3(0.6666666666666667)	20(0.95)
34	0	3(2,0,1)	20	17	6	2(0.0)	0(NaN)	21(0.9523809523809523)
35	4	4(1,0,3)	20	19	5	4(0.75)	0(NaN)	20(0.85)
36	2	2(1,0,1)	20	18	4	5(0.8)	0(NaN)	17(0.9411764705882353)
37	0	3(1,1,1)	17	17	3	3(0.6666666666666667)	1(0.0)	16(0.9375)
38	2	4(1,1,2)	15	17	2	2(0.5)	2(0.5)	15(0.8666666666666667)
39	0	1(1,0,0)	14	13	2	1(0.0)	1(1.0)	13(1.0)
40	0	0(0,0,0)	14	12	2	0(NaN)	1(1.0)	13(1.0)
41	0	1(0,0,1)	13	12	2	0(NaN)	0(NaN)	14(0.9285714285714286)
42	3	1(1,0,0)	15	14	2	3(0.6666666666666667)	0(NaN)	13(1.0)
43	1	2(0,0,2)	14	14	2	3(1.0)	0(NaN)	13(0.8461538461538461)
44	0	3(0,1,2)	11	12	2	2(1.0)	1(0.0)	11(0.8181818181818181)
45	0	0(0,0,0)	11	9	2	0(NaN)	2(1.0)	9(1.0)
46	0	2(0,0,2)	9	9	2	0(NaN)	2(1.0)	9(0.7777777777777778)
47	0	0(0,0,0)	9	8	1	0(NaN)	1(1.0)	8(1.0)
48	0	2(0,0,2)	7	8	1	0(NaN)	0(NaN)	9(0.7777777777777778)
49	0	0(0,0,0)	7	7	0	0(NaN)	0(NaN)	7(1.0)
50	1	1(0,0,1)	7	8	0	1(1.0)	0(NaN)	7(0.8571428571428572)
51	0	2(1,0,1)	5	7	0	1(0.0)	0(NaN)	6(0.8333333333333334)
52	0	1(0,0,1)	4	5	0	0(NaN)	0(NaN)	5(0.8)
53	1	0(0,0,0)	5	5	0	1(1.0)	0(NaN)	4(1.0)
54	0	2(0,0,2)	3	5	0	1(1.0)	0(NaN)	4(0.5)
55	0	0(0,0,0)	3	3	0	0(NaN)	1(1.0)	2(1.0)
56	0	0(0,0,0)	3	3	0	0(NaN)	1(1.0)	2(1.0)
57	0	0(0,0,0)	3	3	0	0(NaN)	1(1.0)	2(1.0)
58	0	0(0,0,0)	3	3	0	0(NaN)	0(NaN)	3(1.0)
59	0	0(0,0,0)	3	3	0	0(NaN)	0(NaN)	3(1.0)
60	0	0(0,0,0)	3	3	0	0(NaN)	0(NaN)	3(1.0)
61	0	1(0,0,1)	2	3	0	0(NaN)	0(NaN)	3(0.6666666666666667)

62	0	0(0,0,0)	2	2	0	0(NaN)	0(NaN)	2(1.0)
63	0	0(0,0,0)	2	2	0	0(NaN)	0(NaN)	2(1.0)
64	0	0(0,0,0)	2	2	0	0(NaN)	0(NaN)	2(1.0)
65	0	0(0,0,0)	2	2	0	0(NaN)	0(NaN)	2(1.0)
66	0	0(0,0,0)	2	2	0	0(NaN)	0(NaN)	2(1.0)
67	0	2(0,0,2)	0	2	0	0(NaN)	0(NaN)	2(0.0)
68	0	0(0,0,0)	0	0	0	0(NaN)	0(NaN)	0(NaN)
69	0	0(0,0,0)	0	0	0	0(NaN)	0(NaN)	0(NaN)
70	0	0(0,0,0)	0	0	0	0(NaN)	0(NaN)	0(NaN)
71	0	0(0,0,0)	0	0	0	0(NaN)	0(NaN)	0(NaN)
72	0	0(0,0,0)	0	0	0	0(NaN)	0(NaN)	0(NaN)
73	0	0(0,0,0)	0	0	0	0(NaN)	0(NaN)	0(NaN)
74	0	0(0,0,0)	0	0	0	0(NaN)	0(NaN)	0(NaN)
75	0	0(0,0,0)	0	0	0	0(NaN)	0(NaN)	0(NaN)
76	0	0(0,0,0)	0	0	0	0(NaN)	0(NaN)	0(NaN)
77	0	0(0,0,0)	0	0	0	0(NaN)	0(NaN)	0(NaN)
78	0	0(0,0,0)	0	0	0	0(NaN)	0(NaN)	0(NaN)
79	0	0(0,0,0)	0	0	0	0(NaN)	0(NaN)	0(NaN)
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91	0	0(0,0,0)	0	0	0	0(NaN)	0(NaN)	0(NaN)
92	0	0(0,0,0)	0	0	0	0(NaN)	0(NaN)	0(NaN)
93	0	0(0,0,0)	0	0	0	0(NaN)	0(NaN)	0(NaN)
94	0	0(0,0,0)	0	0	0	0(NaN)	0(NaN)	0(NaN)
95	0	0(0,0,0)	0	0	0	0(NaN)	0(NaN)	0(NaN)
96	0	0(0,0,0)	0	0	0	0(NaN)	0(NaN)	0(NaN)
97	0	0(0,0,0)	0	0	0	0(NaN)	0(NaN)	0(NaN)
98	0	0(0,0,0)	0	0	0	0(NaN)	0(NaN)	0(NaN)
99	0	0(0,0,0)	0	0	0	0(NaN)	0(NaN)	0(NaN)
100	0	0(0,0,0)	0	0	0	0(NaN)	0(NaN)	0(NaN)

Births File. Only part of file shown, the remainder of the file looks similar.

Year	Bear-ID	#Cub
2	F-5	2
2	F-10	1
2	F-22	1
3	F-9	2
3	F-25	1
3	F-26	2
4	F-17	2
4	F-29	2
4	F-30	2
5	F-5	1
6	F-9	2
6	F-14	1
6	F-22	2
6	F-32	2
6	F-33	1
7	F-17	1
7	F-25	2
7	F-30	2
8	F-14	1
8	F-29	2
8	F-35	1
9	F-32	2
9	F-33	2
9	F-49	1
10	F-5	2
10	F-14	2
10	F-22	2
10	F-50	2
11	F-35	2
12	F-17	1
12	F-30	2
12	F-33	1
13	F-22	1
13	F-50	2
14	F-32	2
14	F-55	1
15	F-33	2
15	F-77	1
16	F-9	2
16	F-17	1
16	F-29	1
16	F-50	1
16	F-57	2
16	F-85	2
17	F-30	2
18	F-29	1
18	F-77	1
19	F-22	2
19	F-33	1
19	F-35	1
19	F-85	1
19	F-95	1
20	F-50	1

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