EVALUATING THE EFFECTIVENESS OF POPULATION RECONSTRUCTION FOR BLACK BEAR (*Ursus americanus*) AND WHITE-TAILED DEER (*Odocoileus virginianus*) POPULATION MANAGEMENT

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Thesis submitted to the Faculty of the Virginia Polytechnic Institute and State University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE
IN
FISHERIES AND WILDLIFE SCIENCE

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14 September 2005
Blacksburg, Virginia

Keywords: White-tailed deer, black bear, population dynamics, population reconstruction, Downing reconstruction, model, harvest management

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(ABSTRACT)

This study was a comprehensive evaluation of population reconstruction techniques. Population reconstruction techniques are population estimation methods that calculate a minimum population size based on age-specific harvest data (Downing 1980, Roseberry and Woolf 1991). Population reconstruction techniques share the following characteristics: 1) utilization of catch-at-age data and 2) backward addition of cohorts to estimate a minimum population size. I developed a questionnaire to survey the biologists participating in this survey to determine the most common reconstruction technique used to estimate population sizes of exploited white-tailed deer (*Odocoileus virginianus)* and black bear *(Ursus americanus*). Downing reconstruction (Downing 1980) was the most commonly used reconstruction technique among biologists participating in this study. Based on a comprehensive literature review and discussions with state biologists, I decided to evaluate virtual reconstruction (Roseberry and Woolf 1991) and develop a new reconstruction technique: Reverse Order reconstruction.

I developed a quantitative population model in Microsoft Visual Basic 6.0 to evaluate the ability of the 3 reconstruction techniques to estimate population sizes given a variety of conditions. I evaluated the effects of stochasticity on reconstruction population

estimates by incorporating different levels of environmental stochasticity (*i.e.* process error) and measurement error in the generated or "known" population. I also evaluated the effects of collapsing age classes and aging biases on population estimates. In all conditions, Downing and virtual reconstruction were underestimates of the actual population size. Reverse Order reconstruction more closely estimated the actual population size, but is also more data-intensive than the other 2 methods. Measurement error introduces more uncertainty in the reconstructed population estimates than does process error. The population simulation model proved that Downing and virtual reconstruction are consistently underestimates and the percent underestimation is due to lack of inclusion of a natural mortality rates in population estimation.

I used the results of the questionnaire to characterize the harvest datasets of the states participating in this study. From these results, I chose two harvest datasets to further analyze: a white-tailed deer harvest dataset from North Carolina and a black bear harvest dataset from Pennsylvania. I analyzed these datasets with Downing and virtual reconstruction. I also applied the quantitative population model to these datasets to evaluate the effect of increasing levels of measurement error on the variance of the population estimates. I found that Downing and virtual reconstruction estimated the population sizes very closely to one another, within 5%, for both datasets, and the reconstructed estimates closely tracked the actual harvest numbers. I also found that increasing levels of measurement error increased the variance associated with reconstructed population estimates and may decrease the ability of these techniques to accurately capture population trends.

ACKNOWLEDGEMENTS

I would first like to thank my advisors, Dr. Jim Berkson and Dr. Mike Vaughan for allowing me the opportunity to pursue this research. Before I was even a student at Virginia Tech, they were both incredibly supportive and continued to be so throughout my tenure as a graduate student. Jim Berkson provided important guidance and mentoring throughout this project. His ability to help me solve programming problems instantly was much appreciated! Mike Vaughan was always available for giving advice on my thesis or anything else that I might need guidance with. His insightfulness and kindness was instrumental. I would also like to thank my committee member, Dr. Marcella Kelly. Marcella Kelly was available for help and for candid conversations about my thesis and otherwise.

My thesis was funded by eight state agencies: New York, Pennsylvania, Virginia, West Virginia, North Carolina, South Carolina, Georgia, and Mississippi. Funding was also provided by the Wildlife Management Institute and the US Forest Service. I would particularly like to thank Dave Steffen from the Virginia Department of Game and Inland Fisheries (VDGIF) for being the impetus for this project. Matt Knox and Cale Godfrey from VDGIF provided early guidance on the project. I'd also like to thank Mark Ternent from Pennsylvania and Evin Stanford from North Carolina for providing data.

Finally, I'd like to thank my family and friends. I like to thank my Mom for her continued encouragement and understanding. I thank my fellow graduate students, especially Colleen, Missy, Kate, and Adam, for making my time in Blacksburg memorable and enjoyable. And, lastly, I would like to thank David for helping to put it all in perspective and, at the end of it all, truly giving it meaning.

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CHAPTER 1 – REVIEW OF RECONSTRUCTION TECHNIQUES AND METHODS IN FISHERIES AND WILDLIFE LITERATURE

INTRODUCTION AND JUSTIFICATION

Population reconstruction techniques are population estimation methods that calculate a minimum population size based on age-specific harvest data (Downing 1980, Roseberry and Woolf 1991). Population reconstruction techniques are commonly used to estimate both harvested fish (Quinn and Deriso 1999) and wildlife populations (Gove et al. 2002). Population reconstruction techniques share the following characteristics: 1) utilization of catch-at-age data and 2) backward addition of cohorts to estimate a minimum population size. Minimum input data include total number of animals in the harvest, sex-specific, and age-specific harvest numbers. These data are readily available to most wildlife managers.

White-tailed deer (*Odocoileus virginianus*) and black bear (*Ursus americanus*) are two of the most important large game species in the eastern United States (Baker 1984). Wildlife biologists require an index of population size and/or trends, in order to set appropriate harvest levels for the desired population level effects (decrease, maintain, or increase) and desired levels of recreational hunting. Some wildlife managers currently use population reconstruction to produce population estimates from harvest data. From these estimates, estimates from other techniques, and independent indices, harvest limits are set and regulations are determined. It is essential that estimates produced from population reconstruction accurately represent the dynamics of the harvested population to ensure proper management actions.

Population reconstruction has received little critical evaluation of its effectiveness and accuracy. Roseberry and Woolf (1991) outlined several techniques used to analyze harvest data and applied each to a tightly managed white-tailed deer herd at Crab Orchard National Wildlife Refuge, Illinois. The authors cautioned that their analyses and evaluations were meant to be an overview and may not be applicable to all datasets or species (Roseberry and Woolf 1991). There have been no other published evaluations of this technique, though sophisticated statistical models and cost optimization equations for population reconstruction have been developed recently (Bender and Spencer 1999, Gove et al. 2002, Skalski and Millspaugh 2002). However, none of these papers addressed the robustness of population reconstruction to violations of assumptions or outlined datasets for which population reconstruction is appropriate.

WHITE-TAILED DEER NATURAL HISTORY

White-tailed deer are considered a premier large game species (Baker 1984) and are highly managed throughout their range (Lancia et al. 1988, Waller and Alverson 1997, Brown et al. 2000). Though white-tailed deer biology, ecology and management techniques are relatively well documented, uncertainties exist as to the most accurate methods of population and vital rate estimation and the establishment of appropriate harvest levels.

Distribution

White-tailed deer range throughout North and Central America, encompassing both northern-temperate and tropical environments. Throughout its distribution, there are 30 recognized subspecies of white-tailed deer (Baker 1984). White-tailed deer are one of

the wildlife species that have seemingly benefited from human-induced habitat manipulations. Forestry practices throughout much of the eastern United States, such as clear-cutting, have resulted in greater amounts of early successional forests and edge habitat. This habitat alteration has produced superior habitat for white-tailed deer, and in some cases, resulted in increased carrying capacity in those habitats (Alverson and Waller 1997).

The expansion of white-tailed deer distribution and increase in population size has lead to management concerns (Brown et al. 2000). Deer are finding suitable habitat in many types of landscapes including agricultural areas, often causing crop damage and subsequent economic losses (Matschke et al. 1984*b*, Alverson and Waller 1997, Waller and Alverson, 1997). Additionally, deer populations are increasing in some suburban and urban areas, as evidenced by increased vehicular collisions (Conover et al. 1995). These areas are difficult to manage, as hunter effort remains constant, or may decrease, while deer populations continue to increase (Brown et al. 2000). In some regions, public attitudes towards hunting are becoming increasingly negative, requiring managers to consider alternative management strategies, such as contraceptive techniques (DeNicola et al. 1997).

White-Tailed Deer Biology and Reproduction

Vital rates for white-tailed deer vary spatially and temporally. General factors that may decrease white-tailed deer survival rates are harvest, predation, winter weather, vehicular collisions, and density-dependent forage competition (Mech et al. 1987, Messier 1991, Patterson and Power 2002). In exploited deer populations, harvest is the

dominant cause of mortality (DePerno et al. 2000; Patterson and Power 2002; Patterson et al. 2002). Adult and yearling males are generally more vulnerable to harvest mortality than fawns and yearling and adult females, due to hunter selectivity, the decreased wariness of bucks in the fall, and larger male home ranges (Coe et al. 1980). Natural mortality rates are often higher in their northern range, as severe winter weather and natural predators, especially wolves, depress survival rates in these populations (Mech 1984, Messier 1991). Deer predators have been extirpated throughout much of white-tailed deer range; therefore predation is often not a significant limiting factor on many deer populations (Mech 1984).

Survival rates are lower for fawns than for adult deer. In a hunted whitetail population in Pennsylvania, fawn survival was estimated as 0.38 (95% confidence interval: 0.28 – 0.49) (Vreeland 2002). Vreeland (2002) found fawns had higher survival rates in agricultural landscapes than in forested areas. This differential survival may be a result of fewer predators and better forage in agricultural areas (Vreeland 2002). Adult survival has been estimated to be between 0.70 – 0.80 for unhunted populations (Hayne 1984, Creed et al. 1984). In a hunted Illinois whitetail population, survival rates for 2-year old males was estimated as 0.56 ± 0.05 (SE), 0.50 ± 0.06 (SE) for 3 year olds, and 0.39 ± 0.09 (SE) for 4 year old males (Nixon and Mankin 1999). The average life span of white-tailed deer is approximately 8 years, though the majority does not live past 4 or 5 years, primarily as a result of harvest-induced mortality (Matschke et al. 1984).

White-tailed deer have a very high reproductive potential (McCullough 1979). Female deer are most productive between 3 and 7 years of age, though winter malnutrition has been demonstrated to negatively affect fertility and viability of offspring

(Verme and Ullray 1984, Mech et al. 1987, Messier 1991). Female white-tailed deer are impregnated in October or November and give birth in March or April. White-tailed deer females reproduce annually, producing on average 1-2 fawns (Verme and Ullray 1984). Estimates of the intrinsic rate of increase (*r)* for white-tailed deer have been estimated for several populations (McCullough 1979, Fryxell et al. 1988). In an exploited whitetail population in Newfoundland, Fryxell et al. (1988) estimated the maximum population growth as r_{max} = 0.45, based on estimates of recruitment equal to 0.86 and survival equal to 0.80. Using an exponential growth model, McCullough (1979) estimated r_{max} for the hunted George Reserve deer herd as 0.8043. Estimates of *r* vary spatially and temporally, and with the type of model (logistic or exponential) selected to calculate this parameter (Lancia et al. 1988).

WHITE-TAILED DEER MANAGEMENT

Deer populations are highly managed across the United States to attain harvest and population goals (Lancia et al. 1988, Waller and Alverson 1997, Brown et al. 2000). Regulated hunting is the primary management mechanism used to control most deer populations (Brown et al. 2000). Hunting mortality can be directly controlled by management plans and harvest levels are often set according to the desired outcome: recreation, trophy hunting, population control, maintenance or increase (Lancia et al. 1988). Harvesting strategies directly affect the sex and age composition of the exploited population (Matschke et al. 1984, McCabe and McCabe 1997, DePerno et al. 2000, Brown et al. 2000, Patterson et al. 2002).

Management History

White-tailed deer were essential to the successful colonization of North America by Europeans in the 18th and 19th centuries (McCabe and McCabe 1984). Before Europeans settled North America, the historical whitetail distribution was similar to the current distribution. In the 1800's, there was a drastic decline in this species as a result of unlimited harvest, aided by the increased efficiency of guns, previously not utilized by Native American deer hunters (Smith and Coggin 1984). For example, whitetails were virtually extirpated from Massachusetts, only 18 years after the colonists landed at Plymouth Rock (Smith and Coggin 1984).

Initial enforcement of whitetail harvest seasons began around the 1890's throughout much of the U.S (McCabe and McCabe 1984). For the greater part of the 20th century, wildlife managers focused on protecting and enhancing deer populations. The early wildlife managers imposed bag limits, shortened hunting seasons, and enhanced habitat quality by increasing edge habitat, young heterogeneous forests, and clear cuts to encourage deer population growth (Waller and Alverson 1997). In the 1940's and 1950's, hunting was generally restricted to bucks to allow for the recovery of highly exploited populations. Buck-only harvesting strategies generally skew the sex and age distribution of the population towards younger male age classes and a higher proportion of females. Whitetail populations increased as the proportion of females in the population increased and recruitment exceeded mortality (natural and harvest).

Current Management Practices

Deer biologists employ management practices aimed at satisfying various goals, for example: 1) to protect the welfare of the species, 2) to maintain a high proportion of trophy-quality bucks in the population (*e.g.* Quality Deer Management), 3) to maintain the desired levels of yield for hunters, and/or 4) to ensure compatibility between deer and human populations, and other flora and fauna communities (VDGIF, 1999). The hunting season in most states is in the fall and varies in length and in the type of weaponry allowed. The majority of states currently allow rifles, shotguns, and bows for white-tailed deer harvest.

As a result of highly successful management techniques, some 21st century managers are faced with the task of controlling overabundant deer populations (see McShea et al. 1997). To maintain stable populations, it is necessary for harvest rates to equal recruitment rates (Lancia et al. 1988). Therefore, either-sex harvest was reinstated as whitetail populations increased, coinciding with increased bag limits and longer hunting seasons (McCabe and McCabe 1984). A particular difficulty encountered by managers is hunter selectivity for antlered bucks (Coe et al. 1980). In some regions, managers have enforced a "*one doe, one buck*" policy, such that before hunters can take an adult male, they must first take a female (Jenks et al. 2002).

Many hunters tend to select for antlered bucks when possible (Coe et al. 1980). Several studies have shown that hunters will pass up smaller, female deer to wait for a larger buck (Coe et al. 1980, Matschke et al. 1984). Towards the end of the harvest season, however, hunter selectivity tends to decrease, with a greater proportion of the

harvest consisting of fawns, yearlings, and does (Coe et al. 1980). Managers can be pressured by hunters to manage their deer herd for larger trophy males (Jenks et al. 2002)

Quality Deer Management (QDM; Brothers and Ray 1975) is a management technique that is employed by managers to produce a healthy deer herd that is in balance with the habitat (Harper 2002). QDM strives to direct hunter effort toward older bucks with large antlers, consequently encouraging hunters to restrain from harvesting young males. QDM also encourages removal of female white-tailed deer. This harvest strategy ideally results in a population with a more balanced sex and age structure, than populations managed for trophy males (Harper 2002). QDM can be difficult to enforce, as it requires ensuring that young bucks are not harvested and that a significant portion of the harvest is female (Harper 2002).

Wildlife biologists managing deer populations almost exclusively through the annual harvest face challenges imposed by public demands. Recently, there has been an increase in public concern about the ethical and biological validity of hunting, coinciding with an increase in human populations in suburban and urban areas. There has also been a generally stable, if not decreasing trend in the number of hunter licenses issued annually (Brown et al. 2000). Furthermore, annual harvest rates are often limited by other factors, including weather and access. Severe weather generally drives deer into dense forests for cover, making them difficult to detect. Inclement weather also deters hunters. Hunter access to deer can also be variable, as hunter effort tends to be concentrated around roads and well-developed trails (Matschke et al. 1984).

Despite public concern over the validity of hunting as population control, overabundant deer populations are causes for concern among biologists (Waller and

Alverson, 1997, Brown et al. 2000). Deer are altering the dynamics of entire ecosystems. Alverson and Waller (1997) found differential growth of hemlock seedlings from a deer exclosure experiment. In some forests, the elimination of palatable seedlings is resulting in a conversion of the forest to less palatable species (Waller and Alverson 1997). White-tailed deer also can act as an economic liability in agricultural landscapes (Creed et al. 1984, Alverson and Waller 1997, McShea and Rappole 1997, Waller and Alverson 1997). In extreme situations, severe deer browsing can result in the loss of an entire crop (Matschke et al. 1984*b*).

In general, management strategies for white-tailed deer vary geographically and greatly depend on public opinion. McCullough (1984) observed, "Science does not make the decision. People do. Once the goal has been established for a given management unit, then science…can be used to develop a program to achieve that goal and its associated objectives for the deer population."

BLACK BEAR NATURAL HISTORY

Distribution

Historically, black bears ranged throughout the forested areas of North America, from Canada to Mexico (Maehr 1984, Vaughan and Pelton 1999). Due to increasing human populations and subsequent habitat fragmentation, it is estimated that black bears now occupy approximately 62% of their historical range (Maehr 1984, Pelton and Van Manen 1994).

Black bear populations have been identified in 39 states in the United States (Pelton and Van Manen 1994, Vaughan and Pelton 1999). In all states, except New

Mexico and Idaho the populations are considered to be stable or slightly increasing (Pelton and Van Manen 1994, Vaughan and Pelton 1999). One of the primary reasons for the persistence of bear populations is their adaptability. Bears are opportunistic omnivores and can survive in many habitat types. Protected areas and refuges have alleviated harvest pressure on some populations (Powell et al. 1996).

Range expansion and population growth of black bears are causing some concern among managers (Miller 1990). As black bear populations and human populations increase simultaneously, there are bound to be conflicts with humans (Mattson 1990, Miller 1990, Pelton and Van Manen 1994). Human attitudes towards black bears are generally correlated with exposure and experience to bears (Bowman et al. 2001). People with limited exposure and no negative encounters with bears tend to be more tolerant than those who have had negative experience with bears (i.e. crop damage; Bowman et al. 2001).

Range extension of black bears may result in increased management policy and decisions regarding this species. Therefore it is critical to accurately estimate the vital rates that drive black bear populations in order to properly manage populations. Accurate population estimation and modeling techniques will be essential to ensure appropriate management actions for black bears.

Black Bear Biology and Reproduction

Survival rates for black bears vary geographically and with hunting status. Black bears in the wild can live to be ≥ 20 years old (Beecham 1983). In most areas, harvest is the primary source of mortality for adult black bears (Klenzendorf 2002). Adult bears in

a hunted Virginia population had a survival rate of 0.620 (95% confidence interval: 0.49 – 0.73) for males and 0.84 (95% confidence interval: 0.75 – 0.90) for females (Klenzendorf 2002). Adult male black bears tend to be more vulnerable to harvest than adult females. This increased vulnerability may be a result of hunter selectivity and male behavior, as females generally den earlier than males, and males have larger home ranges (Bunnell and Tait 1981, Higgins 1997).

Bear cubs and subadults have highly variable survival rates. Cubs are generally evicted by their mothers when 1.5 years old (Bunnell and Tait 1981). Cub survival depends upon many factors including maternal experience, nutrition, human interactions, predation, and disease (Elowe and Dodge 1989, Echols 2000). In a hunted Virginia black bear population, cub survival rates were estimated as 0.76 (95% confidence interval: 0.67 – 0.95) (Echols 2000). In a study of an exploited black bear population in Massachusetts, overall survival rates for cubs were 0.59 by one year and 0.39 after two and a half years (Elowe and Dodge 1989). Survival rates for yearlings in a hunted Virginia population ranged from 0.51 – 0.99 for females and 0.33 – 0.72 for males (Lee 2003). Survival rates for 2 and 3 year olds in the same hunted Virginia population ranged from 0.79 – 0.98 for females, and 0.32 – 0.72 for males (Lee 2003). Bunnell and Tait (1981) estimated survival rates for cubs to be approximately 0.70 to 0.75, and subadult mortality was estimated to be between 0.65 and 0.85.

Black bears have extremely low reproductive rates, among one of the lowest rates of all terrestrial mammals (Bunnell and Tait 1981). Low reproductive rates are primarily a result of late age at first reproduction, long breeding intervals, and small litter sizes. Female black bear become sexually mature between 3 and 7 years of age (Beecham 1980,

Miller 1990, Bunnell and Tait 1981). Sexual maturity is highly dependent upon nutritional condition. Rogers (1976) found that none of 16 females weighing less than 67 kilograms in October produced cubs, while 28 of 30 females weighing greater than 80 kilograms produced a litter. Breeding interval for black bears is also highly dependent upon habitat quality. Bears that live in highly productive habitat (e.g. eastern forests) may reproduce every 2 years. Bears in poorer quality habitat (e.g. western sagebrush habitat) have a mean breeding interval slightly greater than 3 years (Bunnell and Tait 1981, Miller 1990). Average litter size for black bear is about 2.25, with a range from 1 to 4 or more (Beecham 1983, Bunnell and Tait 1981, Elowe and Dodge 1989).

Though black bears are classified as carnivores, they are opportunistic omnivores, eating primarily berries and nuts. Adequate nutrition is essential to the survival and successful reproduction of this species. Eagle and Pelton (1983) classified 5 different seasonal patterns of food use in Great Smoky Mountains National Park. In early spring, black bears generally experience a weight loss, as forage quality is poor. Behaviorally, bears (except lactating females) respond to this nutritional deficiency by decreasing activity rates, thereby decreasing metabolic demands. Late spring, summer, and early fall are seasons of equal nutritional levels. Bears gain weight during these seasons, as there is ample high quality forage (including insects) available. Late fall differs in nutritional quality from the other seasons. During this time, bears consume a diet higher in carbohydrates and fat. This increases body fat stores necessary to survive winter denning.

BLACK BEAR MANAGEMENT

Management History

Historically, bears were considered a threat to human safety, dangerous predators, and "vermin". Bounties were offered to kill these nuisance animals (Miller 1990). As human populations spread throughout the country, bears were seen as an obstacle to successful and safe colonization, and were subsequently killed indiscriminately. The heavy harvest of black and grizzly bears in the continental United States led to the extirpation of the grizzly bear throughout much of its range, with the exception of protected populations in the Northern Rocky Mountains. Black bear populations were reduced as well, particularly in the southern and southeastern U.S. (Miller 1990).

Bears were classified as game species in most states in the 1920's. This change in status from a "nuisance" animal to a game species resulted in the implementation of management regulations (Miller 1990). Limitations were placed on the sale of fur, hides, and meat. There was also a reduction in the amount of allowable harvest. Hunting seasons and bag limits were enforced throughout the country. Further restrictions were implemented in areas where bear populations were severely depleted (Miller 1990).

Current Management Practices

Black bear populations have stabilized, or are growing, across most of the U.S. (Miller 1990, Pelton and Van Manen 1994). Several factors may be responsible for this stabilization and/or increase. First, management practices have improved with increased knowledge as a result of black bear research efforts. Biologists are more familiar with their biology, habitat requirements, and physiology. Increased knowledge allows for

more appropriate management actions, for example, setting harvest limits and maintaining adequate habitat. Furthermore, there has been an increase in the size and amount of protected areas and refuges (Pelton and Van Manen 1994). These areas provide black bears with a refuge from hunting pressure, thereby allowing migration into unprotected areas.

The most important consideration for bear biologists is the extremely low reproductive rate of black bears (Bunnell and Tait 1981). Miller (1990) described a simple deterministic model created to test the effects of overharvesting on the recovery rate of black bears. Simulations were performed in which the exploitation was double the sustainable harvest rate. Hunting was restricted when the population reached one-half of its original size, as a result of the simulated overharvest. With no hunting allowed on the depressed population, the population recovered in 6 years. When hunting levels were set at 75% of the sustainable harvest, recovery took 17 years. This simulation indicates the importance of accurate estimates of sustainable harvest rates and initial population size to ensure population stability (Miller 1990).

Public attitudes towards bears vary widely across the U.S. and even within states. Generally, in urban and suburban areas, people would like occasional viewing opportunities of bears and may not be not in favor of hunting as a population regulating technique (Bowman et al. 2001, VDGIF 2002). Black bears, however, are capable of causing property damage such as destroying bird feeders, rummaging through garbage cans, killing livestock, and destroying beehives (VDGIF 2002). In general, public opinion towards black bears varies from controlling nuisance populations to conserving populations for viewing and hunting opportunities, or to stabilizing populations to

maintain satisfactory population levels (Bowman et al. 2001, VDGIF 2002). These public opinions vary both spatially and temporally therefore management plans are frequently developed after assessing current public opinion (VDGIF 2002).

The approach to black bear management differs from that of white-tailed deer due to the significant differences in life history strategies and habitat requirements of these species. However, harvest data are routinely collected on both of these species and used to estimate changes or trends in population size.

POPULATION DYNAMICS AND ANALYSIS

Population dynamics of animal populations are defined by mortality, reproduction, movement, initial population size, and sex and age distribution (Caughley 1977). A cohort, a group of animals of the same age, is the basic unit of population dynamics (Hayne 1984). Population analyses evaluate survival and fecundity of cohorts over time. At any given time, a population is composed of a specific number of cohorts.

To manage populations that are subjected to harvest pressure, it is necessary to have accurate indices of population size to determine the most appropriate management actions. There have been many different techniques developed to determine trends in populations and to estimate population size and composition. Techniques used for estimating population size and setting harvest limits vary widely between agencies and researchers. In wildlife management, many of these techniques are not well described and are spread throughout journals, book chapters, and gray literature. Often, agencies adopt a particular population estimation technique without validating its appropriateness or accuracy (Roseberry and Woolf 1991).

Population Models

Population models are useful to evaluate demographic data nested within harvest data and to determine optimal harvesting strategies (Hayne 1984). Models are simplified representations of mechanisms in natural systems, accompanied by a set of underlying assumptions (Bunnell and Tait 1980). In resource management, models are especially useful because it is possible to create and explore the effects of varying management strategies. The weaknesses of modeling natural systems are their application to reality and evaluating how accurately the model depicts natural processes.

There are two basic techniques used in population modeling: 1) accounting models, and 2) "black box" models (McCullough 1984). Accounting models record births and deaths to estimate the size, sex, and age composition of the managed population (e.g. population reconstruction). These models can become very complex due to the extensive amount of data required, especially for populations that have long-time series of data available. One of the greatest benefits of accounting-type models is that it is relatively easy to conduct sensitivity analyses. It is possible to change various parameters that control population growth (e.g. survival or recruitment rates) to estimate the effects of various harvesting strategies or stochastic events. An inherent disadvantage of these models is the amount of data required for accurate estimates. Wildlife managers need information on population size, sex and age composition, and birth and death rates by age class (McCullough 1984). McCullough (1984) aptly pointed out that if a manager possessed this data, a model would not be necessary.

Black box models, on the other hand, are more simplistic. McCullough (1984) stated that black box models rely on the fact that the population itself is a satisfactory

indicator of demographic parameters. Black box models, for example, use the intrinsic rate of increase, *r*, to represent the population birth and death rates. Though black box models require less input data, it is necessary at a minimum, to have an estimate (or index) of total population size (McCullough 1984).

Stock-recruitment models, such as the Ricker model (1954) and the Beverton-Holt model (cited in: Quinn and Deriso 1999) are commonly used models, especially in fisheries management. The stock-recruitment model is based on a deterministic, density dependent, sigmoid pattern of population growth through time. In this model, the per capita growth rate is high when the population is small, and decreases to zero when the population reaches carrying capacity (K). Carrying capacity is defined as the maximum population size that can be maintained by available habitat (Lancia et al. 1988).

POPULATION RECONSTRUCTION TECHNIQUES

Population reconstruction estimates minimum population size from sex and age harvest data. If survival and harvest rates are known, harvest data can be used to calculate estimates of abundance. This technique is intuitively appealing to managers, as it uses data often collected by state agencies. Often, the lack of analytical methods to reliably interpret these data leads managers to neglect the information available within harvest data (Gove et al. 2002). Similarly, there are few guidelines published and available to wildlife managers describing the most accurate techniques for analyzing harvest data (Roseberry and Woolf 1991). Population reconstruction has been used by management agencies for several different species including white-tailed deer (Downing 1980, Creed et al. 1984, Roseberry and Woolf 1991), black bear, elk (Bender and

Spencer 1999), wild turkeys (Boomer and Moen 2001) and moose (Fryxell et al. 1988, Ferguson 1993).

Population reconstruction recursively estimates the minimum number of individuals in a cohort by summing all of the individuals from that cohort recovered (from harvest, vehicular collisions, etc.) in subsequent years. This technique is also referred to as backward reconstruction (Downing 1980). The number of fawns entering the population at time step t can be determined by adding the number of fawns in the harvest at time step t to the one-year olds at time step $t+1$ to the two year olds in $t+2$ to t_{max}. It is possible to include estimates of natural mortality and/or crippling losses to more accurately assess initial population size or number of recruits at time t.

Population reconstruction is most appropriate for populations in which harvest mortality is the primary cause of death, or in cases where non-harvest mortality is known or can be accurately estimated. Sex and age-specific harvest mortality is the only *required* input data for population reconstruction. It is possible to estimate recruitment and mortality rates, sex and age ratios, in addition to a minimum population estimate from population reconstruction techniques; however, inherent errors and biases exist with these estimates. (Downing 1980, Fryxell et al. 1988, Roseberry and Woolf 1991, Bender and Spencer 1999, Gove et al. 2002, Skalski and Millspaugh 2002).

Population reconstruction, initially called cohort analysis, was first developed for a population of lake trout (Fry 1949). Hesselton et al. (1965) were the first to use population reconstruction for wildlife populations. They applied the technique to a hunted white-tailed deer population in New York. Since Hesselton et al. (1965) applied population reconstruction to wildlife harvest data the technique has evolved into several

variations including Downing reconstruction (Downing 1980), the Wisconsin method (Creed et al. 1984), and Fryxell et al. (1988) hybridization of reconstruction with catch per unit effort equations.

Variations of Population Reconstruction

There are several variations of reconstruction analysis published (Table 1.1). *Virtual reconstruction* is the most simplified reconstruction technique used to analyze age at harvest data. Virtual reconstruction is analogous to cohort analysis, a technique frequently used in fisheries management. The assumptions of virtual reconstruction are: 1) the proportion of deaths accounted for is constant over time for each age class and 2) age determination is accurate. This approach requires harvest mortality by sex and age class as input data and uses the following equations, with N as number of individuals, a as age in years (for 9 age classes), and t as time in years:

$$Nv_{a,t} = \sum_{i=9}^{a} H_{i,t+9-a}$$

where: $Nv_{a,,t}$ = number of individuals in age class a at time step t

$H_{a,t}$ = harvest of individuals in age class a at time step t.

The output from virtual reconstruction is a minimum population estimate for individual cohorts and, by summing cohorts, an estimate for the entire population (Roseberry and Woolf 1991). Virtual reconstruction (Roseberry and Woolf 1991) is most appropriate for datasets that have long time series, such that completed cohorts have passed through the population.

Downing reconstruction (1980) uses the same input data as virtual reconstruction (refer to equations in Appendix 2.1). The primary difference between the techniques is the treatment of the last 2 oldest age classes. Downing reconstruction collapses the older age classes into one category (e.g. ≥ 4.5 year olds for deer). This adds an assumption to Downing reconstruction, that the last 2 age classes have equal mortality rates. However, the collapsing of age classes decreases the amount of time required for cohorts to pass through the population, thus allowing managers a more current estimate of population size than virtual reconstruction. Similarly, collapsing age classes reduces the problems associated with incomplete cohorts in population estimation. Downing reconstruction uses the survival rate of the last 2 age classes to calculate an average survival rate for these age classes. This is the starting point for backward reconstruction of the younger age classes and for each year of data. In addition to the minimum population estimates calculated from virtual reconstruction, Downing includes recruitment rates, sex ratios and fawn/doe ratios as reconstruction outputs (Downing 1980).

The *Wisconsin method* (Creed et al. 1984) of population reconstruction differs from virtual reconstruction in the method of estimating total population size. This technique first uses virtual reconstruction to estimate the number of males in the population. The number of males is multiplied by an expansion factor that incorporates a recovery rate (percent of the population removed by harvest mortality), adult sex ratio, and recruitment rates to estimate total population size. The Wisconsin method requires more input data and has more assumptions than virtual and Downing reconstruction. Estimates of recovery rates, adult sex ratios, and recruitment rates from independent indices are necessary to calculate the expansion factor. An additional assumption in the

Wisconsin method to those from virtual reconstruction is that the estimates of the recovery rate, adult sex ratio, and fawn/doe ratio are accurate (Creed et al. 1984, Roseberry and Woolf 1991). The output from the Wisconsin method is an estimate of total population size.

Fryxell et al. (1988) combined virtual reconstruction with a Catch per Unit Effort technique to analyze Newfoundland moose populations. This analysis differs from the described reconstruction variations in its ability to estimate sizes of incomplete cohorts. Additional input data are necessary to estimate the size of incomplete cohorts. These input data include mortality by sex and age class (same as virtual reconstruction), and also an estimate of vulnerability to harvest and a measure of hunting effort. The vulnerability coefficient in reconstruction analysis is estimated from completed cohorts (Fryxell et al. 1988). The Ricker model (1954) and Baranov catch equations are used to estimate cohort specific harvest mortality and size of incomplete cohorts by:

$$f_{i,t} = q_i \mathrm{E}_i,$$

$$\mathrm{K}_{i,t} = \mathrm{N}_{i,t}(1-e^{-f_{i,t}})$$

where $\mathrm{N}_{i,t}$ is the number of age i individuals present prior to the harvest at time step t, and $\mathrm{K}_{i,t}$ is the number of animals killed in the hunt, $f_{i,t}$ = instantaneous rate of hunting mortality, E_i = total hunting effort, and q_i = a vulnerability coefficient defined as the proportion of the population killed by one unit of hunting effort. These additional input data require an additional assumption that harvest rate is a linear function of age-specific vulnerability and hunter effort. The output is the same as virtual reconstruction, but includes estimates of incomplete cohort size.

A commonly used technique to analyze harvest data (especially for white-tailed deer) is the Lang and Wood (1976) Pennsylvania Method. Lang and Wood (1976) developed a method to estimate current population size and predict prehunt abundance for the following year, using harvest data. This process calculates the average annual reduction rate (AARR) for adult males, using male age structure data from the harvest data. The number of adult males in the harvest is divided by the AARR to determine the number of males in the prehunt population. Using these data, the number of females and fawns in the prehunt population are estimated and population size is predicted for the following year. Roseberry and Woolf (1991) noted that this technique is more appropriate for large sample sizes as it tended to be sensitive to sampling errors in the AARR calculation, upon which all other parameters are calculated.

Population reconstruction has some inherent limitations. First, it is sensitive to changes in hunter effort and data on hunter effort can be difficult to obtain. If harvest rates are increased during the sampling period, reconstruction analysis will indicate an increasing population because a greater proportion of deaths are included in the estimation (Downing 1980). Sex ratios must be interpreted cautiously as they are dependent on the composition of the harvest (Fryxell et al. 1988, Roseberry and Woolf 1991). Furthermore, managers must recognize that population reconstruction produces *minimum* population estimates. Harvest rates will be too high if based on the minimum population size (Roseberry and Woolf 1991).

Recent Reconstruction Approaches

There have been recent studies evaluating population reconstruction techniques using more complex statistical analyses (Bender and Spencer 1999, Gove et al. 2002, Skalski and Millspaugh 2002). These studies had different objectives and methods concerning population reconstruction. Bender and Spencer (1999) compared population reconstruction with other population estimation techniques (mark-recapture, aerial sightability, and minimum count estimators) to determine if reconstruction estimates corroborated these other techniques (Bender and Spencer 1999). Skalski and Millspaugh (2002) developed generic equations for parameter and variance estimation. Gove et al. (2002) used auxiliary information (from telemetry data), reporting rates, and survival probabilities to create a maximum likelihood estimator of population size from harvest data.

Bender and Spencer (1999) applied reconstruction analysis to elk populations. Independent estimates were available for the preseason bull/cow and calf/cow ratios. The authors also assumed a stable and stationary age distribution of the population and that harvest mortality accounted for all of the deaths. Total population size and its associated variance were calculated using the estimated parameters from the reconstruction analysis. Confidence intervals around the mean population estimate were constructed using a parametric (Monte Carlo) bootstrapping approach. Bender and Spencer (1999) concluded that reconstruction analysis provided a population estimate with an equivalent degree of precision as aerial sightability techniques, with less sampling and economic effort.

Gove et al. (2002) used maximum likelihood estimators to jointly estimate harvest rates, survival, recruitment, and population size from harvest data. Gove et al. (2002) felt that harvest data alone was insufficient to generate estimates of abundance and survival. They calculated a joint likelihood that is a function of recruitment and survival, harvest, and reporting rates, in the form: $L_{joint} = L_{age\text{-}at\text{-}harvest} \times L_{auxiliary} \times L_{reporting}$. The auxiliary likelihood must be used to estimate either abundance, survival, or harvest to allow for estimation of the other parameters. The authors investigated four separate models varying from constant survival and harvest rate over all age classes to variable survival and harvest rate by age class. Gove et al. (2002) found that maximum likelihood methods allowed for "maximum information extraction." Parameters such as survival, harvest, age-specific abundance for each cohort and recruitment were estimated and 95% confidence intervals were calculated.

Skalski and Millspaugh (2002) developed equations for parameter and variance estimations for the Wisconsin Method of population reconstruction. They proposed general variance equations for adult male, adult female, juvenile, and total population abundance. From these variance expressions, it was possible to estimate how imprecision in individual input parameters effects the overall precision of the population estimate. They found that in order to reach a "rough management benchmark" (Robson and Regier 1964) all input parameters needed a coefficient of variation (CV) less than or equal to 0.10. In reality, this is difficult to attain in wildlife field studies. Skalski and Millspaugh (2002) also developed a cost optimization expression, to provide managers with a framework in which to allocate funding and research efforts. Bowden et al. (2000) also developed equations for optimal resource allocation for estimating population size,

recruitment rates of juveniles, and survival. Their optimization expressions are targeted towards wildlife managers of ungulate populations.

Other techniques for evaluating harvest data

Roseberry and Woolf (1991) reviewed many of the techniques used to analyze wildlife harvest data. They evaluated the effectiveness of each technique using a standard dataset from a closed, hunted deer population (Crab Orchard National Wildlife Refuge, IL). I will briefly outline these techniques below and have compiled a table of the required input data, assumptions, and output (Table 1.2).

The Catch per Unit Effort analysis is based on the assumption that the ratio of animals harvested to the effort expended (e.g. hours hunted, number of hunters or permits issued) is proportional to the number of animals in the pre-harvest population (Beverton and Holt 1957). The underlying premise of this technique is that harvest is a linear function of effort, from which it is possible to determine population size (Fryxell et al. 1988, Roseberry and Woolf 1991).

Change-in-Ratio analysis is another technique to estimate population size based on harvest data. Change-in-Ratio estimators calculate deer abundance based on differential harvest of the sexes in the population. Change-in-Ratio estimators are often considered unreliable due to the differential observability and vulnerability of sexes between seasons (Roseberry and Woolf 1991). In white-tailed deer, for example, bucks are less observable than does early in the breeding season and more observable later in the season (Downing 1980).

Roseberry and Woolf (1991) also described harvest age structure technique as an approach to analyze harvest data. Harvest age structured models use age frequencies to estimate the age structure of the population. Changes in the age structure over time will be indicative of changes in "harvest rate, growth rate, and/or relative density with respect to carrying capacity" (Roseberry and Woolf 1991). Downing (1980) and Burgoyne (1981) argue that the interpretation of this technique is difficult with potentially biased input data, such as harvest data, as the age structure tends to be skewed towards younger age classes.

Harvest sex ratio techniques have also been used to estimate population sizes of harvested populations. The Hayne-Gwynn (1977) method is the most cited variation of the harvest sex ratio technique. Hayne and Gwynn (1977) suggested that manipulating the proportion of females in the harvest could control herd growth. They contend that the population appeared to stabilize when does comprise 30-40% of the harvest. Downing (1981) argued that sex ratios in the harvest could be misleading as to the actual sex ratios and size of the population. According to Downing (1981), an increased ratio of does to bucks in the harvest could result from several scenarios, ranging from an increased number of does in the population to a decreased number of both sexes in the population, but bucks decreased at a faster rate than does.

The techniques briefly described above (see also Table 1.2) are similar in that each uses harvest data as input to estimate population size of an exploited population. Though the techniques vary in the amount of additional and independent input required and the output produced, a closer examination of these methods may be helpful to

determine alternative or hybrid methods to estimate population sizes and other population parameters from harvest data.

ALTERNATIVE POPULATION ANALYSES

Many techniques exist for analyzing harvest data, as these data are often the only information available to managers to assess the status of harvested populations. This is especially evident in fisheries management, where direct enumeration of the population is impossible. Fisheries biologists have managed fish stocks for decades using quantitative population estimation techniques such as cohort analysis (Derzhavin 1922, Fry 1949, Pope 1972) and stock recruitment curves (Ricker 1954). Quantitative population estimation techniques are well documented and tested in fisheries management. Wildlife biologists are increasingly applying quantitative fishery-based models to estimate wildlife population sizes and parameters (Fryxell et al. 1988, Gove et al. 2002, Skalski and Millspaugh 2002).

The dichotomy between fisheries and wildlife management prompted a divergence in the techniques used to analyze harvest, or catch, data. In some cases, techniques that are currently exclusively used to analyze fish catch data may be equally suitable to analyze wildlife harvest data.

Review of Fisheries Reconstruction Techniques

Cohort Analysis and Virtual Population Analysis (VPA) are techniques developed by fisheries biologists to estimate minimum population size from catch at age data. In the most basic VPA, deaths due to natural mortality are ignored, and subsequently, survival

is underestimated and mortality is overestimated (Quinn and Deriso 1999). Basic VPA is essentially equivalent to virtual population reconstruction (Roseberry and Woolf 1991). This technique assumes that catch is measured without sampling error. Therefore, the virtual population at each age class is estimated by: $V_a = V_{a+1} + C_a$, where V_a = the virtual population at the previous age and C_a = catch of age class *a* (Quinn and Deriso 1999).

Cohort analysis (Pope 1972) was developed to approximate VPA. Cohort analysis (particularly the Pope (1972) approach) was developed for a "pulse fishery" (Mertz and Myers 1996, Quinn and Deriso 1999). The equation and backward analysis is similar to a basic VPA, except that it includes a natural mortality term. Classic cohort analysis does not allow for estimation of variance. However, cohort analysis is robust for examining historical trends in abundance and fishing mortality. The disadvantage to cohort analysis is that it is sensitive to errors in natural mortality estimation, arbitrary estimates of fishing mortality for the last age class, errors in catch at age, and changes in population sizes and structure due to migration (Quinn and Deriso 1999).

The first published use of a reconstruction technique to estimate population size was by Derzhavin (1922). The input data for Derzhavin's reconstruction consisted of estimates of mean catch-at-age composition data for lake sturgeon (*Acipenser spp.*). Assumptions included natural mortality is negligible and no long-term trend in age composition over time. From this reconstruction, Derzhavin obtained absolute abundances of age groups, exploitation rates for each age class, and a minimum estimate of total population size (Derzhavin 1922, Ricker 1954, Megrey 1988). Ricker (1954) referred to Derzhavin's population estimate as utilized stock because it did not account for animals that die naturally.

In 1949, Fry published a widely cited example of a reconstruction technique that introduced the idea of a "virtual population," which he defined as an ideal population that does not experience natural mortality (Fry 1949). Fry improved upon Derzhavin's method by sampling the actual age structure of a lake trout (*Salvelinus namaycush*) population rather than using mean catch-at-age compositions. Similarly to Derzhavin, Fry retained the assumption that natural mortality is negligible. However, the abundance estimate was improved by using an age sample of the catch, rather than an average estimate of animals per age (Megrey 1988).

The 1950s saw increasing advances in reconstruction techniques. Most notably, Beverton (1954), Beverton and Holt (1957), and Paloheimo (1958) proposed age-structured models that emphasized the estimation of natural mortality and catch per unit effort. Their techniques allowed for estimation of fishing mortality rates as a product of fishing effort and vulnerability to catch. Additionally, each paper developed equations that allowed for incorporation of a natural mortality term (Beverton, 1954, Beverton and Holt 1957, Paloheimo 1958, Megrey 1988).

Murphy (1965) added complexity to the techniques published by Beverton, Holt and Paloheimo by proposing a nonlinear catch ratio model based on the Baranov catch equation. Murphy's equations had the following characteristics: 1) could be calculated forward in time, 2) fishing mortality was represented as a proportion of catch to estimate of total stock (as opposed to a product of effort and catchability as described above) and 3) estimated fishing mortality rates and population size based on catch-at-age data, assumed natural mortality rate, and a starting estimate of fishing mortality for the youngest fully exploited age group. Murphy's equations require recursive iterative

procedures to calculate population size; there are no simple algebraic equations to calculate population size (Murphy 1965, Megrey 1988).

In the same year, Gulland (1965) published a nonlinear sequential reconstruction technique combining the Baranov catch equation with Fry's concept of a virtual population (Megrey 1988). Gulland (1965) developed backwards equations to link successive age-groups over time in the catch and started this equation by providing a "best guess" of the fishing mortality for the terminal age group. Gulland's equations introduced problems with back projection equations, in that there is no estimate available for the most recent year, which would be of most interest to managers (Megrey 1988). Furthermore, the need to assume a terminal fishing mortality value for the last age class could prove to be arbitrary or incorrect (Megrey 1988).

Pope (1972) proposed a much less intensive model that simplified the equations needed to calculate the nonlinear catch equations developed by Murphy (1965) and Gulland (1965). Generally referred to as Pope's approximation, he provided an approximation to the nonlinear sequential model in which the exponential function describing a decrease in population size over time was replaced with a step function. Pope's approximation assumes that all fish caught in any age group are taken exactly halfway through the year (Pope 1972).

With Pope's approximation, population abundance estimates and vital rates could be estimated directly from catch data without the need for iterative calculations (Megrey 1988). Furthermore, Pope's approximation had a self-correcting property, in that the backwards calculation allowed for progressively smaller errors in estimates of fishing mortality and population abundance as the analysis moved backwards along cohorts

(Pope 1972, Megrey 1988). The self-correcting property was an important advancement because it lessened the importance of an exact assumption of terminal fishing mortality.

Another important advancement in reconstruction techniques was the development of the separability assumption, credited to Doubleday (1976), which is now incorporated in all recent model developments. The separability assumption states "in any one year, fishing mortality can be described by two factors, a full-recruitment fishing mortality (or exploitation) pattern and a factor to account for the differential effect of the annual exploitation pattern on various age groups in the stock" (Megrey 1988). In essence, the separability assumption is important because it allows for separation of mortality into age-specific effects (i.e. vulnerability) and temporal effects.

To overcome the difficulties associated with simultaneously estimating stock size and fishing mortality from catch-at-age data, recent efforts have concentrated on developing methods to "calibrate" results from stock assessment models with effort data or some other fishery-independent data including recruitment, catchability, spawner-recruit relationship, and fishing effort (Quinn and Deriso 1999). These models are increasingly complex and require varying amounts of auxiliary data to complete the equations.

Deriso et al. (1985) developed a cohort analysis program, CAGEAN. CAGEAN requires additional information as input data, including effort data, relationship between age and reproduction, and sources of random error. Ferguson (1993) used CAGEAN to estimate abundance, recruitment, and age-specific survival of a hunted Newfoundland moose population.

VPA and cohort analyses have been significantly expanded upon and modified since first developed (Fournier and Archibald 1982, Deriso et al. 1985, Mendelssohn 1988, Mertz and Myers 1996). Deriso et al. (1985) incorporated a tuning index into catch at age models. A tuning index incorporates auxiliary information, such as fishing effort or the relationship between spawners and recruits, to stabilize estimates calculated from catch at age data. Mertz and Myers (1996) developed alternate VPA equations that do not require the assumption that fishing mortality is constant throughout time. This variation of VPA is appropriate for pulse or seasonal fisheries. Fournier and Archibald (1982) have developed catch at age equations that incorporate error associated with sampling and stochasticity. Fournier and Archibald (1982) also allowed for the inclusion of auxiliary information (tuning index) in their catch at age equations.

These more complex catch at age models may also be appropriate for harvested wildlife populations. An examination of the assumptions, required input data, and output produced from these fisheries models will prove useful to evaluate potential utility or advantages for analyzing wildlife harvest data.

SUMMARY

Population reconstruction techniques are clearly an important tool for biologists managing exploited species. Harvest, or catch, data are sometimes the only source of information for many exploited species, and as a result, are used to understand and estimate the status of the population. Therefore, population reconstruction techniques using harvest data are practical and useful methods of estimating population sizes or monitoring trends. As discussed above, many variations of population reconstruction

techniques have been developed as computing and statistical skills improved over time. However, many of the more sophisticated reconstruction techniques require additional data beyond the harvest at age numbers.

Although these more complex models may provide more accurate population estimates, the goal of this study was to compare and evaluate reconstruction techniques that used input data similar to Downing reconstruction, which is commonly used by wildlife managers in the eastern United States (see Chapter 3). After a comprehensive literature review, I decided to evaluate two other reconstruction methods to compare to Downing reconstruction, virtual and Reverse Order reconstruction. As a quantitatively and theoretically simple method, virtual reconstruction was selected to evaluate the ability of a quantitatively simple model to estimate population size as a means of comparison to the relatively more complex equations of Downing reconstruction. Virtual reconstruction also uses the same input data (harvest at age numbers) as Downing reconstruction.

I surveyed the fisheries literature for a technique similar to Downing and virtual reconstruction, which used similar, minimal input data, but also incorporated natural mortality into the reconstruction equations. I was concerned about the lack of a natural mortality term in the other reconstruction methods, as Downing and virtual reconstruction do not account for deaths other than those due to harvest. Upon review of fisheries literature and a preliminary simulation study, we developed a new reconstruction method for the purposes of this study that includes a natural mortality term, but otherwise maintains the minimal data input requirements of age at harvest numbers. Reverse Order

reconstruction was designed as the reciprocal of Leslie Matrix forward population generation equations. These techniques are explained in more depth in Chapter 2.

Reconstruction techniques have increased in complexity over time, incorporating various levels of auxiliary information into more sophisticated equations. However, the more quantitatively simple and less data intensive methods, such as Downing and virtual reconstruction, are still commonly used in white-tailed deer and black bear wildlife management to estimate population sizes and monitor trends. The decision as to which population reconstruction technique is most appropriate depends on the type and amount of data available, both harvest data and independent estimates of population parameters. Population reconstruction techniques are theoretically appealing to biologists managing exploited species, as these techniques use data that are readily available (Gove et al. 2002).

I conducted a survey of biologists participating in this study to ensure that I was evaluating the appropriate, and most commonly used reconstruction techniques: Downing and virtual reconstruction. I will describe the methods and results of the questionnaire developed below.

METHODS

Questionnaire development and implementation

I developed a questionnaire (IRB Registration Number: IRB00000667) with two primary goals: first, to assess current use of population reconstruction by state wildlife agencies, and second, to identify characteristics of each state's harvest dataset (Chapter 3). I developed similar, but separate, questionnaires for white-tailed deer and black bear

biologists (Appendices 3.1 and 3.2). The questionnaire was developed to limit open-ended questions. Wherever possible, questions were limited to yes/no or check-box answers. Subjective questions (i.e. biologists' confidence in harvest mortality rates) were limited to ranking on a 1 - 5 Likert scale to facilitate analysis.

The questionnaire was sent as an attachment via electronic mail (e-mail) to 13 white-tailed deer and black bear biologists representing the states participating in this study. The respondents had an opportunity to request a paper copy via U.S. postal service or a fax, if preferred. Respondents were asked to e-mail, fax, or mail their completed questionnaires to me. If I received no response from the respondent in two weeks, a reminder e-mail was sent. Another reminder e-mail or phone call was made in another two weeks if there was still no response.

Each biologist was first asked if he/she was currently using population reconstruction. If yes, the biologist was asked a series of questions about the type of reconstruction technique used, whether the reconstructed estimates were used for population management, the landscape level to which reconstruction estimates were applied, the applications for reconstruction estimates, if the oldest age classes were combined in a terminal "plus" age group, and if the reconstructed estimate was corrected with an estimate of natural mortality.

All biologists, regardless of current use of reconstruction, were asked to identify potential limitations with their dataset for analysis with population reconstruction, the degree to which harvest effort varies yearly in their state, the smallest landscape scale harvest data is collected and analyzed, if the harvest is aged to specific age classes or age

groups (e.g. cubs, juveniles, adults), the method used to estimate total harvest, the percent of the harvest aged, and the number of years of consecutive harvest data.

The white-tailed deer and black bear questionnaires were analyzed separately to determine species-specific differences. Where appropriate, percentages or average responses were calculated and reported.

RESULTS

Current use and application of reconstruction techniques

The questionnaire response rate was 84.6%. At least one biologist (white-tailed deer or black bear) responded from each state participating in this study. The responses were reported separately by species. In all results reported, the term "biologists" represents "biologists responding to the survey." One hundred percent (100%) of white-tailed deer biologists currently use some type of population reconstruction technique, while 83.3% of black bear biologists use population reconstruction.

Sixty percent (60 %) of white-tailed deer biologists use Downing reconstruction to estimate buck population sizes, then use Lang and Wood (1976) modification to estimate the total (or doe) population size; 67.7% of black bear biologists use Downing reconstruction and/or virtual reconstruction to estimate black bear population sizes. Sixty percent (60%) of white-tailed deer and 50% of black bear biologists rely on reconstruction population estimates for management. Eighty percent (80%) of white-tailed deer and 66.7% of black bear biologists use estimates from reconstruction techniques to estimate population size. One hundred percent (100%) of white-tailed deer

biologists and 50% of black bear biologists use estimates from reconstruction techniques to monitor or determine population trends.

In summary, at least half of the biologists who responded use population reconstruction estimates for management, while all responding white-tailed deer biologists and half of the responding black bear biologist use population reconstruction to assess population trends. Furthermore, Downing reconstruction (sometimes with modifications) is the reconstruction technique most commonly used among biologists responding to this survey.

Table 1.1. Population Reconstruction Variations

METHOD	ASSUMPTIONS	INPUT	OUTPUT
Virtual Reconstruction *(Fry 1949)*	1. Proportion of deaths accounted for constant over time for each age class 2. Age determination is accurate	Age-specific mortality numbers	1. Estimate of individual cohort size 2. Estimate of total population size
Downing Reconstruction (*Downing 1980)*	Same as virtual reconstruction and: 3. Equal mortality of the last two age classes	Age-specific mortality numbers	Same as standard and: 3. age-specific harvest rates 4. fawn/doe ratios 5. adult sex ratios
Wisconsin Method *(Creed et al. 1984)*	Same as virtual reconstruction and: 3. Estimates of adult sex ratio and female/progeny ratio are accurate	1. Age-specific mortality numbers 2. Estimate of productivity	1. Estimate of number of males in population 2. Estimate of absolute population size
Standard reconstruction and catch per unit effort *(Fryxell et al. 1988)*	Same as virtual reconstruction and: 3. Harvest rate is a linear function of effort and vulnerability	1. Age-specific mortality numbers 2. Estimates of age-specific survival rates 3. Estimate of hunting effort	Same as virtual reconstruction

(Roseberry and Woolf, 1991)

Table 1.1, continued. Population Reconstruction Variations

METHOD	ASSUMPTIONS	INPUT	OUTPUT
Pennsylvania Method *(Lang and Wood 1976)*	1. Total number of antlered males in harvest accurately estimated or known 2. Harvest sex ratios and female/progeny ratios are representative of population	1. Mortality by sex and age class	1. Estimate of population size 2. Predict prehunt population size for next harvest season

(Roseberry and Woolf, 1991)

Table 1.2. Alternative Techniques to Analyze Wildlife Harvest Data

METHOD	ASSUMPTIONS	INPUT	OUTPUT
Catch per Unit Effort (DeLury method) *(DeLury 1947)*	1. Proportion of population caught with 1 unit of effort does not vary with population size	1. Estimate of total harvest 2. Estimate of total effort 3. Estimate of proportion of population caught with one unit effort	1. With known catchability; an absolute estimate of population size 2. With arbitrary catchability; an index of population size
Change-In-Ratio *(Connor et al. 1986)*	1. "x- and y-type" individuals are equally likely to be sampled before and after harvest 2. The population is closed between sampling periods, except for known removals 3. Selective removal of individuals in harvest	1. Estimate of total harvest 2. Numbers of "x- and y-type" individuals in harvest 3. Estimate of numbers of "x- and y-type" before and after harvest	1. Estimate of absolute population size
Harvest Age Structure *(Downing 1980)*	1. Males and females have different age structures	1. Mortality by age class or category (i.e. fawns, yearlings, adults)	1. Index of population age structure
Harvest Sex Ratio *(Hayne and Gwynn 1977)*	1. Constant Recruitment and natural mortality rates 2. Harvest pressure differs between sexes 3. Vulnerability to harvest differs between sexes	1. Proportion of females in harvest	1. Indication of trends in future herds: increase, stable, decrease

(Roseberry and Woolf, 1991)

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CHAPTER 2 – EVALUATING POPULATION RECONSTRUCTION TECHNIQUES WITH SIMULATED DATA

ABSTRACT

I developed a quantitative population model in Microsoft Visual Basic 6.0 to evaluate 3 reconstruction techniques with simulated data. I evaluated Downing reconstruction (Downing 1980), virtual reconstruction (Roseberry and Woolf 1991) and Reverse Order reconstruction (specifically designed for this study). I generated a known population forward in time via Leslie Matrix equations, applied a specific harvest event and used the resulting harvest matrix to estimate population size via each of the 3 reconstruction techniques.

I evaluated the effect of incorporating stochasticity into population generation on reconstructed population estimates, by including different levels of process error to simulate environmental stochasticity. I also evaluated the effect of different levels of measurement error, collapsing age classes, variations in harvest rate mortalities, and biases in aging on population estimates by incorporating these errors in the simulation model.

I found that Downing and virtual reconstruction consistently underestimated the actual population size in all scenarios examined. The percent underestimate was related to the natural mortality rates chosen in the population generation. Because these reconstruction techniques do not include a natural mortality term, it is assumed that the lack of inclusion of natural mortality rates in these techniques results in the underestimate. Downing and virtual reconstruction estimate the population size similarly to one another, generally within 5% of each other. Reverse Order reconstruction more closely estimated the actual population size, but was more data intensive and included a

natural mortality rate. I also found that measurement error resulted in more uncertainty with population estimates than process error for all 3 reconstruction techniques evaluated. This is likely to due to the fact that measurement error acts independent of the actual population size; i.e. changes in the population size are not reflected in the harvest.

INTRODUCTION

Population reconstruction is a technique that estimates a minimum population size based on age-specific harvest data (Downing 1980, Roseberry and Woolf 1991). Population reconstruction techniques share the following characteristics: 1) utilization of catch-at-age data, and 2) backward addition of cohorts to estimate a minimum population size. Minimum input data include total number of animals in the harvest and age-specific harvest numbers (Williams et al. 2002). These data are readily available for most exploited species (Gove et al. 2002). Despite current use of these methods, the robustness of population reconstruction techniques to violations of assumptions has not been evaluated. I used simulation models to examine the robustness of population reconstruction to violations of assumptions and to evaluate the impact of biases and errors on reconstructed population estimates.

White-tailed deer (*Odocoileus virginianus*) and black bear (*Ursus americanus*) are two of the most important large game species in the eastern United States (Baker 1984, Bunnell and Tait 1981). Wildlife biologists require an index of population size and/or trends in order to set appropriate harvest regulations to achieve desired management goals (control, stability, or conservation) and set appropriate levels of harvest for these species. Some wildlife managers currently use population reconstruction techniques to produce population estimates from harvest data (see Chapter 3). From these estimates, estimates from other techniques, and/or independent indices, harvest limits can be set and regulations can be determined. If being used for wildlife management and policy, it is essential that estimates, or trends, produced from population reconstruction accurately represent the dynamics of the harvested population.

Population reconstruction techniques have received little critical evaluation of their effectiveness and accuracy in estimating wildlife population sizes. Roseberry and Woolf (1991) outlined several techniques used to analyze harvest data and applied each to a tightly managed white-tailed deer herd at Crab Orchard National Wildlife Refuge, Illinois. The authors cautioned that their analyses and evaluations were meant to be an overview and may not be applicable to all datasets or species (Roseberry and Woolf 1991). Roseberry and Woolf found that Downing reconstruction is a "powerful tool" for populations where most annual mortality can be accounted for (Roseberry and Woolf 1991). There are no other published evaluations of this technique, though sophisticated statistical models using auxiliary information and cost optimization equations for population reconstruction techniques have been developed recently (Bender and Spencer 1999, Gove et al. 2002, Skalski and Millspaugh 2002). However, none of these papers addressed the robustness of population reconstruction techniques to violations of assumptions or recommend situations for which population reconstruction techniques are appropriate.

I developed quantitative population models to evaluate the robustness of 2 specific reconstruction techniques as described by Roseberry and Woolf (1991): Downing reconstruction (Downing 1980, Roseberry and Woolf 1991) and virtual reconstruction (Roseberry and Woolf 1991). We also developed a more data-intensive reconstruction technique called Reverse Order reconstruction, specifically for this study, because we were concerned about the lack of incorporation of a natural mortality term in the other reconstruction techniques. These reconstruction techniques are discussed in more detail below.

Population Models in Wildlife Management

Models are simplified representations of mechanisms in natural systems, accompanied by a set of underlying assumptions (Bunnell and Tait 1980). Population models are representations of the real population and can be quite structurally complex, with the potential to include almost limitless biological and mathematical detail. Models are especially useful as evaluation tools, because they allow for complete control over variable manipulation and quantitative analysis of how changes in parameters affect model output (Williams et al. 2002).

In wildlife management, models are especially useful to create and explore the effects of varying management strategies (Hilborn and Mangel 1997, Williams et al. 2002). For population reconstruction techniques, models are useful tools to evaluate the effects of violations of assumptions, biases, changes in management strategies, and sampling errors on estimates. Population models that use harvest data are useful to evaluate demographic data nested within harvest data and to determine optimal management strategies (Hayne 1984).

Importance of Errors

Harvest data have inherent limitations for use in population estimation due to differential sex and age vulnerability to harvest, hunter selectivity, changes in hunter effort, and harvest regulations (e.g. size or age limits). Harvest data are affected by other sources of error, particularly process and measurement errors. These errors are often difficult to quantify, but can have substantial impacts on the actual population, the observed population, and the estimated population (Hilborn and Mangel 1997).

Process error is the error associated with uncertainties in vital rates or population growth rates (Hilborn and Mangel 1997). In this model, process error can affect fecundities, natural survival or harvest survival rates. Process error is difficult to quantify as it represents the stochasticity associated with natural growth of populations (Hilborn and Mangel 1997). Measurement error, or observation error, is independent error that does not act on the growth of the population or parameters affecting population growth. Rather, measurement error is the result of sampling errors or observation errors (Hilborn and Mangel 1997) and is present in the data, but not in the actual population. In summary, process error is stochasticity incorporated into the parameters that affects population growth rates. Measurement error is the result of independent error that affects the population as seen by the observer. Both types of error can result in high variances associated with point estimates, thereby making trend detection difficult or inaccurate.

Types of Model Simulations

The first simulation conducted was a "base run;" this simulation had no incorporated error. The base run was used to evaluate how each reconstruction technique performed given an ideal population and harvest matrix. After the base run, I conducted simulations that were divided into 3 categories: harvest characteristics, sampling characteristics, and environmental variability.

Simulations evaluating harvest characteristics determine the effect of variations in harvest rates on the reconstructed population estimates. Quality Deer Management (QDM), for example, is a management strategy that aims to minimize the harvest mortality rates on young deer, allowing for a higher harvest of the older, trophy animals

(Harper 2002). However, many exploited deer populations have a high harvest rate on all animals because there are no size or age regulations. I also varied harvest rates to violate the Downing Reconstruction assumptions that the mortality rates for the last 2 age classes are equal and that the proportion of harvest mortalities are constant over time.

Simulations evaluating sampling characteristics determine the effect of variations or errors in sampling on reconstruction population estimates. Observer, or measurement, error is an important consideration when evaluating harvest data. Poor reporting rates, incorrect recording, inaccurate aging, and collapsing age classes are factors that can affect harvest data used in reconstruction techniques.

These simulations included an evaluation of the effect of measurement error on population estimates, with and without the presence of process error. I also evaluated the effect of collapsing (or truncating) age classes, collapsing the last age classes into 3, 5, and 7-plus categories. Collapsing age classes is common practice for reconstruction techniques. Because the population cannot be estimated until all animals have passed through the population, managers often collapse the older ages to facilitate reconstruction analyses. However, when age classes are collapsed, multiple cohorts are combined into a single group that is treated as one age class. Theoretically, collapsing age classes should result in inaccuracies, because age-and cohort-specific differences in natural and harvest rates are no longer differentiated. I also evaluated the effect of systematic biases in aging.

Simulations that evaluated environmental variability were conducted to determine the effect of process error in population growth rates on the accuracy of estimates from the 3 population reconstruction techniques. In reality, it would be difficult to quantify

demographic or environmental variability, as there are many factors influencing vital rates. However, we do know that animal populations are affected by variability in the environment that results in changes in population growth rates; for example, a severe winter may result in increased white-tailed deer natural mortality rates. Conversely, a good mast year may increase black bear fecundity rates.

Summary

The purpose of this study was to provide a comprehensive evaluation of population reconstruction techniques. To date, no published studies have examined the performance or accuracy of estimates from reconstruction techniques using simulated data. I developed a quantitative population model to conduct simulations used to determine the accuracy of reconstruction estimates under a variety of scenarios. We developed Reverse Order reconstruction as a tool to compare the inclusion of a natural mortality term into reconstruction equations. Reverse Order reconstruction is not likely to be appropriate for most harvest datasets because of the intensive data requirements. I evaluated the effect that process and measurement errors have on the accuracy of population estimates. I also examined the effect of environmental variability, variations in harvest characteristics and different sampling errors and characteristics. This is the first study to evaluate population reconstruction techniques with simulated data and to provide recommendations for when population reconstruction techniques may, or may not, be appropriate.

METHODS

In order to evaluate the effectiveness of population reconstruction techniques to accurately estimate population size, I developed a quantitative population model in Microsoft Visual Basic 6.0.

Population Generation

The known population, with nine age classes, was generated forward in time via the Leslie Matrix equations:

$$N_{1,t+1} = \sum_{a=1}^{9} N_{a,t} * f_{a,t} * (1 - h_{a,t}) \quad \textbf{(1)}$$

$$N_{a+1,t+1} = N_{a,t} * s_{a,t} * (1 - h_{a,t}) \quad \textbf{(2)}$$

where: $N_{a,t}$ = the number of animals in age class *a* at time step *t*,

$s_{a,t}$ = the natural survival rate of animals in age class *a* at time step *t*,

$f_{a,t}$ = the fecundity of animals in age class *a* at time step *t*, and

$h_{a,t}$ = the harvest mortality rate of animals in age class *a* at time step *t*.

I used fecundities, natural survival rates, and harvest mortality rates realistic for deer populations (Table 2.1). I chose these vital rates based on literature review and wildlife managers' recommendations, and restricted to maintain a stable and stationary population. Each age class was initialized with 1,000 animals at time $t = 0$.

Process error was included in some specified population generation equations to simulate yearly stochasticity in population growth rates. In all cases, process error was the same across ages, but varied by year. I added process error by randomly selecting a

number from a log-normal distribution, with a mean of zero and a specified standard deviation. In all cases, process error I added to equations 1 and 2 by:

$$N_{1,t+1} = \sum_{a=1}^{9} N_{a,t} * f_{a,t} * (1 - h_{a,t}) * e^{\beta_t} \quad \textbf{(3)}$$

$$N_{a+1,t+1} = N_{a,t} * s_{,t} * (1 - h_{,t}) * e^{\beta_t} \quad \textbf{(4)}$$

where: β_t = a log-normally distributed random variable ~ N(0, σ^2) at time step *t*.

The total population size was determined by the summation of all individuals across all ages at time *t*:

$$N_{total,t} = \sum_{a=1}^{9} N_{a,t} \quad \textbf{(5)}$$

where: $N_{total,\,t}$ = the total population size at time step *t*.

I generated the population over 1,000 time steps in simulations where the annual growth rate was stable and stationary around 1.0. In cases where the inclusion of process error resulted in variability that made it impossible to maintain a stable population over 1,000 time steps, I generated 40 separate populations and each was run for 25 time steps. This was done to avoid having the population grow to unrealistic levels or crash.

Generating a Harvest Matrix

All population reconstruction techniques used age at harvest numbers as minimum input data. After I generated the population with a specific harvest rate, I created the matrix of actual harvest numbers (rounded to the nearest integer) by:

$$H_{a,t} = N_{a,t} * h_{a,t} \quad \textbf{(6)}$$

where: $H_{a,t}$ = the true number of animals in age class *a* harvested at time step *t*.

For each of the following simulations, I tested the 3 population reconstruction techniques using the actual harvest matrix, both with and without measurement error. I added measurement error (which affects only the observed data, not the actual population) to equation 6 by randomly selecting a number from a uniform distribution, with a mean of mean and specified bounds. I assumed measurement error affected each age class at each year differently; therefore a different random number was selected for each age over each year. I calculated an observed harvest matrix by:

$$\hat{H}_{a,t} = H_{a,t} * \alpha_{a,t} \quad \textbf{(7)}$$

where: $\hat{H}_{a,t}$ = observed harvest of age class *a* at time step *t*, and

$\alpha_{a,t}$ = a uniformly distributed random variable between 0.5 – 1.5, for age class *a*, at time step *t*.

A uniform distribution is appropriate for adding measurement error because, using a simple algorithm, the distribution has a mean of one and defined bounds (either

narrow or wide, depending on desired level of variance). I used 3 sets of bounds to represent high (0.5 – 1.5), medium (0.7 – 1.3) and low (0.9 – 1.1) levels of variance around the mean of one. An observed harvest matrix was calculated using this generic algorithm:

$$\alpha_{a,t} = (n_{a,t} * w) + b \quad \textbf{(8)}$$

$n_{a,t}$ = a randomly selected number from a uniform distribution, between 0 – 1 for age class *a* at time step *t*

w = the desired width of the bounds of the uniform distribution (*i.e.* 1.0, 0.6, or 0.2)

b = the low end of the bounds of the desired uniform distribution (*i.e.* 0.5, 0.7, or 0.9)

Reconstruction Analyses

Once I created the harvest matrices, I calculated population estimates with the 3 reconstruction methods using the harvest matrix calculated by Equations 6 and 7 (with and without added measurement error).

Virtual Reconstruction

Virtual reconstruction is the most simplified reconstruction technique used to provide population estimates from age at harvest data (Roseberry and Woolf 1991). Virtual reconstruction is analogous to cohort analysis, a technique frequently used in

fisheries management (Roseberry and Woolf 1991). The assumptions of virtual reconstruction are: 1) the proportion of deaths accounted for is constant over time for each age class and 2) age determination is accurate (Roseberry and Woolf 1991). Virtual reconstruction is most appropriate for datasets that have long time series, such that completed cohorts have passed through the population (Roseberry and Woolf 1991).

Virtual reconstruction uses only the harvest matrix (actual or observed) as input data in the following equation:

$$Nv_{a,t} = \sum_{i=9}^{a} H_{i,t+9-a} \quad \textbf{(9)}$$

where: $Nv_{a,t}$ = number of individuals in age class *a* at time step *t* as calculated using Virtual reconstruction method.

Downing Reconstruction

Downing reconstruction (1980) uses the same input data as virtual reconstruction. The primary difference between these techniques is the treatment of the last 2 age classes. Downing reconstruction collapses the older age classes into one category (e.g. ≥ 4.5 year olds for deer). This adds an assumption to Downing reconstruction, that the last 2 age classes have equal mortality rates.

Downing reconstruction uses an estimated survival rate of the last 2 age classes to calculate an average mortality rate for these age classes. This is the starting point for backward reconstruction of the younger age classes and for each year of data. All mortality rates for the oldest 2 age classes are calculated back over all years. These mortality rates are then used to estimate the population size, by multiplying the mortality

rate by the harvest numbers. I calculated the numbers of animals in the remainder of the age classes by backwards addition. Refer to Appendix 2.1 for equations used in Downing reconstruction.

Reverse Order Reconstruction

I designed Reverse order reconstruction specifically for comparison in this study and may not be always appropriate for actual harvest datasets. Assuming that a population moves forward in time given a particular sequence of births and deaths, it is possible to reconstruct that population backwards by reversing the forward projection equations. The input for Reverse Order reconstruction is harvest-at-age numbers, harvest mortality rates, and natural survival rates. Reverse Order reconstruction includes the additional assumptions that 1) the order of births and deaths is known and, 2) natural and harvest mortality rates are known. It should be noted that this information is most often unknown for most exploited wildlife populations and is therefore not always practical for wildlife managers, although useful for comparative purposes in this study.

The starting point for Reverse Order reconstruction is based on the assumption that there is a terminal age class past which no animals survive, i.e. the survival rate of the oldest age class is zero. Therefore, the first step was to assume that the number of oldest animals in the harvest is equal to the number of the oldest animals in the population, by:

$$N_{\max a,t} = H_{\max a,t} \quad \textbf{(10)}$$

After the estimate of the number of animals in the oldest age class was calculated, I calculated the numbers of animals in the younger ages by:

$$N_{a-1,t-1} = \frac{N_{a,t}}{s_{a-1}} + H_{a-1,t-1} \quad \textbf{(11)}$$

where: s_a = the natural survival rate of age class a.

These equations are reciprocal to the population generation equations. If the population is generated without error, then the population estimate using this method will be equal to the population number generated.

Model Simulations

Base Run

The first run conducted was the base run, which I used to evaluate the ability of each technique to estimate population size in ideal data conditions (i.e. no error or biases).

Sampling characteristics

I evaluated sampling characteristics in multiple simulations. The first simulation runs examined the effect of measurement error on population estimates. I applied measurement error to harvest numbers by selecting a log-normally distributed random number with a mean of zero and a standard deviation of 0.05, 0.15, 0.35, or 0.55. Measurement error was applied to the harvest numbers as described in equation 7.

I also evaluated the effect of collapsing age classes and aging biases on population estimates. I used the following categories for evaluating the effects of collapsed ages: 3 plus, 5 plus, and 7 plus. For example, the 5 plus category included all 5, 6, 7, 8 and 9 year olds.

I examined aging biases by simulating the systematic younger and older aging of animals. I applied these biases to the harvest matrix. The total number of animals in the harvest remained the same after applying a specified aging bias, but the number of harvested animals in each age class changed. For example, if the simulation examined under aging animals by 50%, 50% of 9 year olds were placed in the 8 year age class, 50% of the 8 year olds were aged as 7 year olds, etc. Therefore, the result of implementing aging biases was a change (either decrease or increase) in the proportion of each age in the harvest, but no change in the total harvest number. Aging biases were systematically applied to change the proportion of animals in each age class by 10, 20 or 50%, and applied to cause both over- and under-aging of animals (e.g. 50% of 2 year olds aged as 3 year olds or 50% of 3 year olds aged as 2 year olds).

Harvest characteristics

I evaluated harvest characteristics simulations by including variability in harvest mortality rates. These simulations included constant harvest of 40% for all ages in one scenario (Table 2.1), higher harvest for a young age group (1 - 3 year olds), in another (Table 2.2), and higher harvest for an older age group (4 – 9 year olds) in a third (Table 2.3).

Environmental variability

I examined the effect of environmental variability by incorporating process error into simulations. Process error was initially incorporated into equations 1 and 2 at specified standard deviations of: 0.05 and 0.35. Process error was year-specific in all simulations reported. This is based on the assumption that a bad (or good) year in population growth affects all age classes equivalently. Because process error causes the overall population to fluctuate, I was interested in determining the accuracy of each reconstruction technique to estimate the population size at particular time steps, rather than on average. Therefore, I calculated the deviation of the estimated population size from the actual population size for each reconstruction technique at each time step over all 1,000 iterations by:

$$d = \frac{\hat{N}_t - N_t}{N_t} \quad \textbf{(12)}$$

where: $\hat{N}_t$ = the estimated population size at time step *t*, and

N_t = the actual population size at time step *t*.

Comparing the effect of process and measurement error

All simulations included varying degrees of process and measurement error as specified with each simulation run. To compare the effect of both process and measurement errors on reconstruction estimates, I conducted simulation runs that included levels of 0.05 and 0.35 for process error and used low (bounds 0.9 – 1.1) and high (bounds 0.5 – 1.5) levels of measurement error. Measurement error was random for each age class at each year. Process error was constant over each year for each age class.

I compared the deviation of the estimated population from the actual population at each time step over all iterations for both process and measurement error to evaluate the effects of these different types of error on population estimates from the 3 reconstruction techniques.

Evaluation of reconstruction accuracy

I compared population estimates from reconstruction techniques to the actual population estimate. I calculated the standard deviation for all population estimates and reported on all figures. To compare population means among all estimates, I used an Analysis of Variance (ANOVA), followed by a post-hoc comparison of means to further evaluate differences between means. I considered all differences significant at the p = 0.05 level. Statistics were calculated in SPSS 11.0.

I calculated model fit by using a mean squared error (MSE) equation. The MSE results are provided as a means for comparison of model fit between methods, rather than to indicate statistical significance. I calculated an average model MSE by:

$$MSE = \frac{\sum_{t=1}^{m} \frac{(\hat{x}_t - x_t)^2}{x_t}}{m} \quad \textbf{(11)}$$

where: $\hat{x}_t =$ the estimated population size at time step t

x_t = the actual population size at time step t

m = number of estimated populations

RESULTS

I first calculated population estimates from each of the 3 techniques using simulated population data containing no error or other biases (e.g. base run). Then, I examined the effects measurement error, environmental stochasticity, harvest variability, and sampling characteristics on reconstruction estimates using the quantitative population model. All simulations involving process or measurement error will be identified using the specified standard deviation values used. I list all mean population estimates with their standard deviation.

Base Run

The base run (Figure 2.1) examined the accuracy of the population estimates from the reconstruction techniques in ideal data conditions. Simulating without stochasticity produced an actual population size equal to 10,743 animals. Reverse Order reconstruction most accurately estimated the population size with a population estimate of 10,594, underestimating the population size by 1.5%. Downing and virtual reconstruction estimates underestimated the population size by 28.1 and 28.2%, respectively. The population size estimated by Downing reconstruction was 7,721; the estimate from virtual reconstruction was 7,710. Since there was no stochasticity included in the base run, the reconstruction methods produced only a point estimate.

Sampling characteristics

Measurement error

The effect of measurement error on reconstruction estimates was evaluated using 3 different bounds for the uniform distribution used in the harvest matrix generation

equations: low (0.9 – 1.1), medium (0.7 – 1.3) and high (0.5 – 1.5). With low measurement error (Figure 2.2a), all reconstruction runs underestimated the actual population by the same percent as the base run. An ANOVA showed that all mean population estimates were different ($p < 0.001$). A post-hoc comparison of means showed that Downing and virtual reconstruction population estimates were not significantly different ($p = 0.137$).

Low measurement error resulted in an average MSE for each reconstruction technique of 1,455.46, 1,513.84, and 303.99 for Downing, virtual, and Reverse Order reconstruction.

With medium and high levels of measurement error all reconstruction techniques remained underestimates of the actual population size (Figure 2.2b and 2.2c). As expected, with increasing levels of measurement error, reconstructed population estimates also have increased variance (Figure 2.2b and 2.2c).

ANOVAs for the medium and high levels of standard deviations showed significant differences among group mean population sizes. A post-hoc comparison of means showed that Downing and virtual estimates were not different in either run ($p = 0.697$, for medium measurement error and $p = 0.813$, for high measurement error). This artificial inflation is evident in the improved MSE results for Downing (1,509.94), virtual (1,626.60) and Reverse Order (306.24) reconstruction in the highest measurement error runs.

Collapsed age classes

The effect of collapsing the oldest age classes into 3 categories was evaluated via simulations. The last age classes were collapsed either into a 3 plus, 5 plus, or 7 plus category.

The 7 plus category resulted in population estimates similar to that without collapsing ages. Reverse Order reconstruction most accurately estimated the population size, overestimating by 0.001%. Downing and virtual reconstruction were underestimates; each underestimated the population size by 27.9 and 28.8%, respectively.

The 5 plus category resulted in an overestimate by 3.6% for the Reverse Order reconstruction (Figure 2.3a). Downing and virtual underestimates were similar to those of the 7 plus category, by 27.7 and 31.7%, respectively.

The 3 plus category resulted in the same trends for Reverse Order reconstruction, but similar trends were seen for Downing and virtual reconstruction (Figure 2.3b). Reverse Order reconstruction overestimated the actual population by 4.5%. Downing reconstruction underestimated the population by 27.5%, while virtual reconstruction underestimated the population by 35.8%. A post-hoc means comparison for the 3-plus simulation showed differences between all mean population estimates with a $p < 0.001$ for all estimates.

Reverse Order reconstruction overestimated in these simulations because of the increase in the number of animals in the “plus” group. The plus group used the natural survival rate of the youngest animals in the group (i.e. 7, 5, or 3 year olds). Therefore, with more animals in the 3 plus group, the 7 year olds are given the same survival rate as the 3 year olds, thereby increasing the population estimate. Downing reconstruction, on

the other hand, performed similarly for all categories. This was expected as Downing reconstruction was designed to estimate population sizes with collapsed ages.

Collapsed age classes and the terminal assumption mortality

Downing reconstruction assumes that the last 2 age classes have equal mortality rates. I violated that assumption by changing the harvest rates such that 9 year olds had a harvest mortality rate of 40% and 8 year olds had a harvest mortality rate of 90%. When more ages were included in the last collapsed age class, the reconstruction population estimates decreased for all methods (Figure 2.4). Reverse Order reconstruction underestimated the population size by 8.2%, Downing reconstruction underestimated the population size by 26.8%, and virtual reconstruction underestimated 43.6% (Figure 2.4). Because there were fewer animals in the harvest, virtual reconstruction is more of an underestimate than other scenarios.

Aging biases

I evaluated the effect of biases in aging (e.g. animals consistently aged older or younger) on reconstructed population estimates. Aging bias resulted in a change in the proportion of animals in each age class. There was no change in the total number of animals in the harvest. The first set of simulations examined the effect of systematically over-aging animals. I will report results of 2 simulations here: 50% of each age class aged as the next oldest age class (e.g. 50% of one year olds aged as 2 year olds) and 20% of each class aged as the next oldest age class.

When 50% of each age class was aged as the next oldest age class (Figure 2.5a), Reverse Order reconstruction overestimated the population size by 26.9%. Downing and

virtual reconstruction calculated similarly, underestimating by 7.9 and 8.2%, respectively. An ANOVA showed among group differences in means with a $p < 0.001$. A post-hoc comparison of means revealed that Downing and virtual reconstruction population estimates were not significantly different ($p = 0.11$). The same trend in results was obtained when 20% of each age class was aged as the next oldest age class (Figure 2.5b).

I conducted the same simulations with biases for under aging animals. Aging animals younger resulted in underestimates of population size by all reconstruction techniques. I report results of systematically aging 50% of the animals to the next youngest age class here (Figure 2.6). Reverse Order reconstruction underestimated the population size by 16.8%, Downing reconstruction underestimated the population size by 36.1%, and virtual reconstruction underestimated the population size by 36.3%. An ANOVA showed among group differences with a $p < 0.001$. A post-hoc comparison of means showed that all means were different at the $p < 0.001$, except Downing and virtual reconstruction ($p = 0.452$).

Though underestimates for both under- and over-aging biases, Downing and virtual reconstruction both more accurately estimated the actual population size when animals are systematically over-aged. This is a result of a greater proportion of the animals being in the older age classes which biases the estimates from Downing and virtual reconstruction high as compared to the base run.

Harvest characteristics

Harvest characteristics were evaluated by simulating different harvest scenarios on the virtual population. I examined 3 harvest scenarios with 9 age classes: constant

harvest mortality rate of 40%, higher harvest of the younger age classes (e.g. 1 – 3 year olds), and higher harvest of the older age classes (e.g. 4 – 9 year olds). Refer to Tables 2.1 – 2.3 for a list of the harvest mortality rates used in the simulations. All simulations included a measurement error of 0.05. No results listed here included process error.

With a constant mortality rate of 40%, all reconstruction estimates underestimated the actual population size (Figure 2.7a). Reverse Order reconstruction underestimated by 1.2%, while Downing and virtual reconstruction underestimated by 27.7 and 27.8%, respectively. An ANOVA showed that the mean population sizes were different ($p < 0.001$). A post-hoc comparison of means showed that only Downing and virtual reconstruction were not different from each other ($p = 0.457$).

A high harvest mortality rate (60%) on age 1 and 80% on 2 and 3 year olds resulted in all reconstruction techniques underestimating population size (Figure 2.7b). Reverse Order reconstruction estimated the population size most closely, underestimating by 5.5%. Downing reconstruction underestimated the population size by 12.7% and virtual reconstruction underestimated by 43.5%. An ANOVA and post-hoc comparison of means showed that all mean population estimates were significantly different ($p < 0.001$ for all cases). In this case, virtual reconstruction was an underestimate because the majority of the harvest was in the younger animals, which were not added back into the population estimate multiple times.

A high harvest mortality rate (80%) on 4- 9 year olds resulted in all techniques underestimating population size by 2.9, 23.6, and 60.2% for Reverse Order, Downing and virtual reconstruction techniques, respectively (Figure 2.7c). Results from an ANOVA and post-hoc comparison of means showed that all mean population estimates were

significantly different ($p < 0.001$ for all cases). Virtual reconstruction underestimated the population by 60.2% because there were fewer animals in the harvest as a result of the higher harvest mortality on the ages that composed a smaller proportion of the population and harvest.

Environmental variability

The effect of environmental variability was evaluated by adding process error to Equations 1 and 2. Process error was year specific, i.e. one randomly selected random number was applied to all ages across a year. Process error was added with 2 standard deviation values for the log-normal distribution: 0.05 and 0.35. I evaluated the ability of each reconstruction technique to estimate the population size at time steps 5, 10, and 20 (Tables 2.4 and 2.5). At standard deviation of 0.05, the CVs from of all population estimates from the 3 reconstruction techniques were low, around 2.5 – 3.5% (Table 2.5). However with a process error standard deviation at 0.35, the CVs of the estimated population sizes increased to 15 – 25% (Table 2.4).

I also graphed the deviation of the estimated population size from the actual population size as described in equation 12. Process error at both levels of standard deviation increased the variance of the actual and estimated population sizes (Figures 2.8a and 2.8b). The figures show that as the level of process error increases, the mean and variance of the deviation of the estimated population from the actual population increases (note that with Downing and virtual reconstruction, the deviation is negative because these techniques produce underestimates).

Comparing the Effect of Process and Measurement Error

The following simulations compare the effect of process and measurement error on population estimates. I will present results with process error standard deviations set at 0.05 and 0.35 and low (bounds 0.9 – 1.1) and high (bounds 0.5 – 1.5) levels of measurement error.

With process and measurement error standard deviations set at low levels (Figure 2.9a), the average deviation of the estimated population size is similar with both measurement and process error (Table 2.6a).

However, with process and measurement error standard deviations set at high levels (Figure 2.9b), measurement error for all 3 reconstruction techniques resulted in a greater deviation from the actual population size and a greater variance of deviations than with process error (Table 2.6b). An ANOVA showed that the mean deviations were not different between estimates with process and measurement error for each reconstruction method (Downing, $p = 0.688$; Reverse Order, $p = 0.346$; Virtual, $p = 0.570$). However, Levine's test of homogeneity of variance showed that the variance of the deviations was different at $p < 0.001$ between process and measurement error for all 3 reconstruction techniques.

DISCUSSION

Population reconstruction techniques are commonly used population estimation tools for exploited species, such as white-tailed deer and black bear. At a minimum, the techniques require age-specific harvest numbers, which are commonly collected by

wildlife managers. I developed a quantitative population model to evaluate the accuracy of 3 population reconstruction techniques under a variety of conditions.

Base Run

In an ideal data situation, Reverse Order reconstruction performed as designed, underestimating the population size by merely 1.3%. Downing and virtual reconstruction underestimated the actual population size by 28.1 and 28.2%. The percent underestimate in this case, and throughout this simulation study, is likely a result of the natural survival rates chosen. Therefore, if managers are confident that their harvest data is without error, they may use a correction factor to compensate for lack of inclusion of a natural mortality term in Downing and virtual reconstruction.

Sampling Characteristics

Measurement error

Measurement error did not appear to have a large impact on the mean estimated population size. In fact, with higher measurement error, Downing and virtual reconstruction were closer to the actual population size. However, these results should be interpreted with caution. Though measurement error inflated the population estimates from Downing and virtual reconstruction, and therefore, on average, resulted in a closer approximation to the actual population, the variance associated with these estimates resulted in imprecision and uncertainty around the population estimate.

Measurement error will change the percent underestimate of Downing and virtual reconstruction as shown by the base run. This fact is particularly important for wildlife

managers using these techniques. Often wildlife managers will incorporate a correction factor to compensate for the underestimate (due to the lack of inclusion of a natural mortality term). If the measurement error associated with the reconstructed estimate results in a higher estimate than expected, that correction factor will be incorrect and lead to an overestimate of the population. This will have important management implications for wildlife managers using reconstruction techniques to set harvest limits or make regulations.

Measurement error is problematic because it does not act on the population itself, but rather is a result of observer or sampling error. As a result, managers can rarely quantify the amount of measurement error affecting the dataset, and therefore, will most likely be unable to correct for it. Estimates from reconstruction techniques will be highly unreliable if impacted by high levels of measurement error, because the observed errors are not actually representative of changes in the population, but rather changes in the observed data, which are difficult, if not impossible, to quantify.

Collapsed age classes

A collapsed age class is an important characteristic to study with population reconstruction techniques, because, intuitively, it should result in inaccuracies due to the combination of multiple cohorts and ages into one “plus” group. This “plus” group thereby ignores cohort- or age-specific differences and/or vulnerabilities to harvest or natural mortality. These results are particularly important for Downing reconstruction. However, as demonstrated in this study, collapsed age classes does not affect the underestimates of Downing reconstruction, increasing the percent underestimate by only

0.6% with 3 versus 9 age classes. In fact, Downing reconstruction was less of an underestimate with more ages included in the "plus" group. Downing (1980) designed this reconstruction technique to incorporate the grouping of the last ages to decrease the amount of time required to conduct reconstruction analyses. These results support that collapsing age classes for Downing reconstruction analysis does not increase the percent underestimate of this method.

Collapsing age classes does have an important effect on Reverse Order and virtual reconstruction. Virtual reconstruction is affected by fewer age classes, because it is a sequentially additive process in which the older animals are added back into the population estimate over all years of the cohort. Therefore, with fewer age classes, virtual reconstruction will be more of an underestimate. In reality, wildlife managers would not use virtual reconstruction with collapsed age classes (D. Steffen, pers. comm.). Reverse order reconstruction overestimated population size because of an inflated number of animals in the "plus" group, which is divided by the natural survival rate of the youngest age class. In all simulation runs here, the younger age classes have a higher natural survival rate than the older classes. Therefore, while collapsing age classes does not negatively affect Downing reconstruction estimates, it is not practical for virtual or Reverse Order reconstruction techniques.

Collapsed age classes and violation of equal mortality assumption

The violation of Downing reconstruction's assumption of equal mortality for the oldest 2 age classes did not greatly affect the results of Downing or Reverse Order reconstruction techniques. Virtual reconstruction was more of an underestimate in this

case for the same reasons listed above for collapsed age classes. Reverse Order reconstruction was able to compensate for the change in harvest rates because it is incorporated in the equations. It is possible that in this case, there were too few animals in the last 2 age classes to affect the results of Downing reconstruction. Further simulations should examine the impact of violating the assumption of equal mortality for the last 2 age classes by varying the proportion of the harvest in these age groups.

Aging biases

Aging biases are important considerations for reconstruction techniques, because all reconstruction techniques rely on the assumption of accurate aging. The results of this study showed different results whether animals were over- or under-aged. Aging biases that tended toward over-aging animals caused overestimates by all techniques, as compared to the base run. Downing and virtual reconstruction more closely estimated the actual population size when a higher proportion of the animals were in the older age classes. For Downing reconstruction, this makes sense because the number of animals in the oldest age classes will be increased, resulting in an increase in the total population size in the backwards calculations. The virtual reconstruction estimate is increased because of the sequential addition of more animals into the estimated population (as described above). Reverse Order reconstruction overestimated the actual population by 26.9%. This is because the natural and harvest mortality rates were used for the unbiased age classes. With a higher proportion of the harvest in the older age classes, the Reverse Order reconstruction estimate is inflated. The converse result is true for systematic

under-aging of animals for all techniques. All reconstruction techniques were underestimates when a higher proportion of the harvest was in the younger ages.

Data are often difficult to obtain on aging biases in exploited animals. If the aging biases are random, they may not have an important impact on the reconstructed estimates. However, this study shows that systematic over- or under-aging of animals will either over or underestimate the actual population, respectively.

Harvest Characteristics

Changes in harvest rate mortality did not affect the reconstruction estimates from Reverse Order reconstruction, as this technique is designed to incorporate those changes. Virtual reconstruction, however, was dramatically affected by these changes. Virtual reconstruction is highly influenced by the number of animals in the harvest, and the proportion of the harvest in the older age classes. In the higher harvest of the younger ages, there were fewer older animals in the harvest to be continuously added back into the population estimate. The simulation that examined higher harvest of the older ages was a significant underestimate because the total harvest number was decreased.

Downing reconstruction handled changes in harvest characteristics well; when the harvest mortality rate was higher on younger ages, Downing reconstruction underestimated the actual population size by 12.7%, which is closer to the actual population than the base run.

Environmental variability

Process error has a significant effect on the variance associated with the mean population estimates. Because process error acts directly on the population itself, the population reconstruction techniques were able to capture changes in population sizes. However, the variance associated with the mean population estimates causes these estimates to be very imprecise, especially in the runs with high process error (high CVs). In the cases with a process error standard deviation set at 0.05, the reconstruction techniques estimate the population size similarly to the base run, however, the variance with the mean estimates is higher. Process error set at a standard deviation of 0.35, resulted in highly variable population sizes (CVs of 15 – 25%), therefore making it more difficult to accurately estimate population sizes by reconstruction techniques.

Wildlife managers may be able to estimate, to some degree, the level of process error in the exploited population. For example, good mast years and severe winter weather have known effects on deer and bear population growth rates. Whenever possible, managers should evaluate the degree of environmental stochasticity likely to affect their managed population. Reconstruction techniques, especially those that do not incorporate a natural mortality term, may not be robust enough to incorporate stochasticity of vital rates.

Importance of Errors: comparing process and measurement error

Wildlife managers will rarely have enough data to quantify process and/or measurement error. Process error as environmental variability, may be easier to identify

by independent studies that estimate the effect of good mast years or severe winters, for example, on white-tailed deer populations. Measurement error, however, is much more difficult to quantify, as it is independent and does not act on the population itself. Because process error is actually acting on the population, it was expected that the reconstruction techniques should be able to capture variability caused by process error, because this variability would be transferred to the harvest matrix (which is used as input for the reconstruction methods). This expectation was confirmed when calculating the deviation of the estimated population size from the actual population size (Figures 2.9a and 2.9b) for low and high levels of measurement and process error. Because process error is actually changing the population size, the deviation of the estimated population size from the actual population is less than it is with measurement error (Table 2.6), as shown by the average MSE values for each reconstruction technique. Also, Figures 2.9a and 2.9b show that the variation in deviations of population estimates over 1,000 iterations is much greater with measurement error than with process error.

Clearly, any combination of both process and measurement error is problematic for wildlife managers, especially those that depend on harvest data as a source for monitoring population sizes or trends.

Summary of techniques

I evaluated the robustness of 3 population reconstruction techniques under a variety of conditions. This is the first study to use simulated data to evaluate the performance of Downing and virtual reconstruction under data conditions that would likely affect wildlife populations. We developed Reverse Order reconstruction as a

comparative method which incorporated a natural mortality term in population reconstruction equations.

Virtual Reconstruction

Virtual reconstruction is the simplest reconstruction technique analyzed in this study, both theoretically and quantitatively. Virtual reconstruction employs only addition of individuals in the harvest. The obvious drawback to virtual reconstruction is that a long time series of data is required to ensure that the entire cohort has passed through the population. For wildlife managers estimating black bear populations, for example, this can pose a problem as bears can live to be greater than 20 years old.

Virtual reconstruction is accepted to be a minimum population estimate (Roseberry and Woolf 1991), as it accounts only for animals in the harvest (or if animals are recovered and aged by other means). For most simulations I conducted, virtual reconstruction consistently underestimated the actual population size by approximately 25 – 30%. However, virtual reconstruction is particularly sensitive to changes in the older age classes, because of the nature of the cohort addition equations. If the oldest age class is artificially inflated by biases in aging or higher harvest mortality rates, virtual reconstruction will provide a higher population estimate. This inflated estimate may result in a population estimate that is closer to the actual population size, simply by the nature of the reconstruction technique.

Wildlife managers can be confident that virtual reconstruction is providing a minimum population estimate for all populations. Virtual reconstruction is appropriate for species that require conservative harvest strategies.

Reverse Order Reconstruction

The Reverse Order reconstruction method was designed for the purposes of this study. We were concerned the other reconstruction techniques did not include a natural survival term. After a comprehensive review of fisheries and wildlife literature, we decided to use a simple back projection of the Leslie Matrix equations, to keep the amount of input data similar to that of Downing and virtual reconstruction, but to also incorporate a natural survival term. I admit that it is unlikely that Reverse Order reconstruction would be practical for many exploited wildlife species due to the amount of data and knowledge of the order of mortalities required.

The Reverse Order method, as designed, estimated population sizes more accurately than Downing and virtual reconstruction in many simulations. However, many wildlife managers are unlikely to have the information required by Reverse Order reconstruction. Reverse Order reconstruction was a useful comparison to show that incorporation of a natural mortality term dramatically increases the accuracy of reconstruction estimates, except in situations with collapsed age classes. However, if these estimates are unavailable or highly uncertain, then the resulting population estimates will also be uncertain.

Downing Reconstruction

Downing reconstruction is accepted to be a minimum estimate of population size (Downing 1980, Roseberry and Woolf 1991). Downing reconstruction is quantitatively more complex than virtual reconstruction, but is still appealing to wildlife managers because of its minimal required input data and it does not require all animals in the cohort to pass through the population. Wildlife managers in the eastern United States commonly

use Downing reconstruction (see Chapter 3). However, the accuracy of Downing reconstruction has never been evaluated using simulated data.

For most exploited animal populations for which population reconstruction techniques would be used, harvest mortality is the dominant cause of death. These populations tend to have high natural survival rates to persist with substantial harvest pressure; therefore Downing's assumption of equal mortality is likely realistic, especially for species such as white-tailed deer that do not often live past 3 or 4 years old. Downing reconstruction performed consistently, underestimating the population by 25 – 30% in most scenarios.

Downing reconstruction must be used with caution for datasets with high, or unknown, levels of measurement and process error. For populations that are managed by changes in trends, rather than changes in point estimates, Downing reconstruction is not robust enough to capture changes in trends with high levels of associated measurement and/or process error.

Conclusions

In summary, wildlife managers accept that population reconstruction methods using only harvest data are minimum population estimates (Downing 1980, Roseberry and Woolf 1991). This simulation study showed that process and measurement error can lead to highly imprecise population estimates. This simulation study also showed that Downing reconstruction, the technique most commonly used by biologists (see Chapter 3), performed consistently, as an underestimate, in most scenarios. For a population in which harvest mortality is a dominant cause of death, reconstruction techniques can be

useful to provide an indication of population size and to monitor trends. However, wildlife managers should carefully assess their datasets prior to using reconstruction techniques to identify potential biases, errors, and other sources of mortality that may affect the population of concern, as a combination of these factors can result in imprecise and inaccurate population estimates.

Table 2.1. Specific rates used for population generation via the Leslie Matrix, using white-tailed deer vital rates as a template. Fecundities, natural survival and harvest mortality rates used in simulations with constant 40% harvest mortality rate on all age classes are listed below.

Age	Fecundity	Natural Survival	Harvest Mortality
1	0	0.55	0.40
2	1.5	0.85	0.40
3	1.5	0.85	0.40
4	1.5	0.85	0.40
5	1.5	0.85	0.40
6	1.5	0.85	0.40
7	1.5	0.75	0.40
8	1.5	0.65	0.40
9	0	0	0.40

Table 2.2. Specific rates used for population generation via the Leslie Matrix using white-tailed deer vital rates as a template. Fecundities, natural survival and harvest mortality rates used in simulations with higher harvest mortality rate on younger animals (1 – 3 year olds) are listed below.

Age	Fecundity	Natural Survival	Harvest Mortality
1	0	0.75	0.60
2	2.0	0.90	0.70
3	2.0	0.90	0.70
4	2.0	0.85	0.40
5	1.5	0.85	0.40
6	1.5	0.85	0.40
7	1.5	0.75	0.40
8	1.5	0.65	0.40
9	0	0	0.40

Table 2.3. Specific rates used for population generation via the Leslie Matrix using white-tailed deer vital rates as a template. Fecundities, natural survival and harvest mortality rates used in simulations with higher harvest mortality rates on the oldest animals (4 – 9 year olds) are listed below.

Age	Fecundity	Natural Survival	Harvest Mortality
1	0	0.55	0.40
2	1.5	0.65	0.40
3	1.5	0.65	0.40
4	1.5	0.90	0.80
5	1.5	0.90	0.80
6	1.5	0.90	0.80
7	1.5	0.90	0.80
8	1.5	0.90	0.80
9	0	0	0.80

Table 2.4 Means, standard deviations, and coefficients of variance (C.V.) for population estimates from the 3 reconstruction techniques (Downing, virtual, and Reverse Order reconstruction), with process error at a standard deviation set at 0.35. Table 2.4a shows time step 5, 2.4b represents time step 10, and 2.4c represents time step 20.

Table 2.4a. Process error with standard deviation set at 0.35; time step 5.

Reconstruction Method	Mean	Actual mean	S.D.	C.V.
Downing	7965	12081 ± 3804.64 (CV = 31.5%)	1930.36	24.2%
Virtual	7956		1928.38	24.2%
Reverse Order	11447		1819.67	15.7%

Table 2.4b. Process error with standard deviation set at 0.35; time step 10.

Reconstruction Method	Mean	Actual mean	S.D.	C.V.
Downing	8378	11019±3817.73 (CV = 34.6%)	1888.15	17.1%
Virtual	8370		1886.29	17.1%
Reverse Order	11101		1747.74	15.7%

Table 2.4c. Process error with standard deviation set at 0.35; time step 20.

Reconstruction Method	Mean	Actual mean	S.D.	C.V.
Downing	7990	11649 ± 4326.68 (CV = 37.1%)	1887.49	23.6%
Virtual	7983		1885.37	23.6%
Reverse Order	11638		2114.63	18.2%

Table 2.5 Means, standard deviations, and coefficients of variance (C.V.) for population estimates from the 3 reconstruction techniques (Downing, virtual, and Reverse Order reconstruction), with process error at a standard deviation set at 0.05. Table 2.5a shows time step 5, 2.5b represents time step 10, and 2.5c represents time step 20.

Table 2.5a. Process error with standard deviation set at 0.05; time step 5.

Reconstruction Method	Mean	Actual mean	S.D.	C.V.
Downing	7753	10789 ± 596.86 (CV = 5.5%)	239.02	3.1%
Virtual	7745		238.68	3.1%
Reverse Order	10601		370.28	3.5%

Table 2.5b. Process error with standard deviation set at 0.05; time step 10.

Reconstruction Method	Mean	Actual mean	S.D.	C.V.
Downing	7689	10650 ± 545.83 (CV = 5.1%)	210.01	2.7%
Virtual	7682		209.72	2.7%
Reverse Order	10675		255.32	2.4%

Table 2.5b. Process error with standard deviation set at 0.05; time step 20.

Reconstruction Method	Mean	Actual mean	S.D.	C.V.
Downing	7746	10737 ± 455.95 (CV = 4.2%)	210.11	2.7%
Virtual	7738		209.69	2.7%
Reverse Order	10663		318.16	3.0%

Table 2.6 Means and standard deviations for deviations of the estimated population from the actual population for each of the 3 reconstruction techniques: Downing, Reverse Order and Virtual reconstruction shown for low levels of measurement (bounds 0.9 – 1.1) and process (standard deviation 0.05) error (Table 2.6a) and high levels of measurement (bounds 0.5 – 1.5) and process (standard deviation 0.35) error (Table 2.6b).

Table 2.6a. Mean and standard deviations for the deviations of the estimated population from the actual at low levels of measurement and process error

Reconstruction Method	**Mean ± S.D.** *(process error)*	**Mean ± S.D.** *(measurement error)*
Downing	-0.284 ± 0.031	-0.285 ± 0.031
Reverse Order	-0.013 ± 0.026	-0.015 ± 0.032
Virtual	-0.401 ± 0.021	-0.405 ± 0.033

Table 2.6b. Mean and standard deviations for the deviations of the estimated population from the actual at high levels of measurement and process error

Reconstruction Method	**Mean ± S.D.** *(process error)*	**Mean ± S.D.** *(measurement error)*
Downing	-0.285 ± 0.042	-0.286 ± 0.085
Reverse Order	-0.015 ± 0.067	-0.017 ± 0.095
Virtual	-0.408 ± 0.025	-0.410 ± 0.082

Figure 2.1. Base Run. The point estimates of population size as approximated by Downing, Reverse Order, and virtual reconstruction. The actual population size is the first point on the graph.

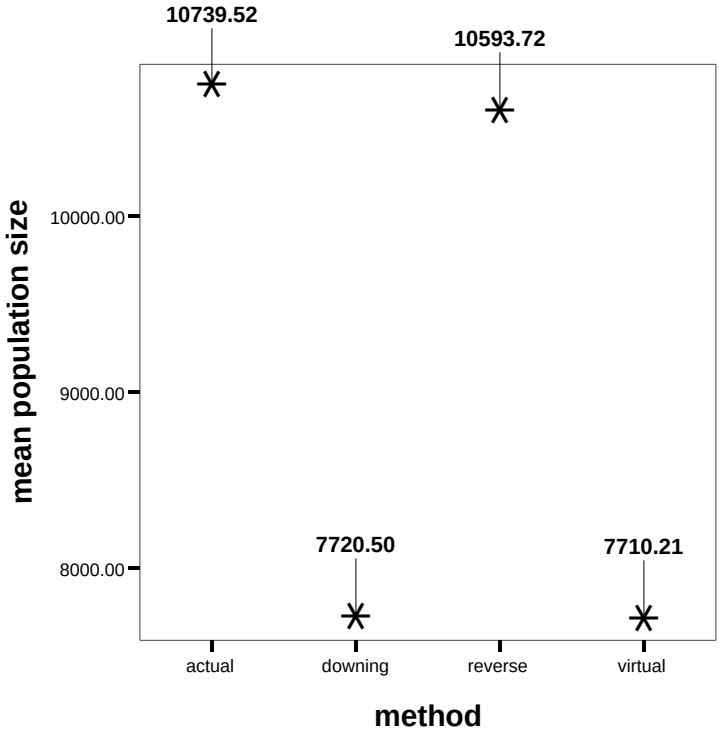


Figure 2.2a. Mean population estimates from 3 reconstruction techniques: Downing, Reverse Order and virtual reconstruction. This graph represents the simulation incorporating a low level of measurement error (bounds of 0.9 – 1.1 from the uniform distribution). The dashed line indicates actual population size. Error bars represent the mean and 95% confidence interval of the mean.

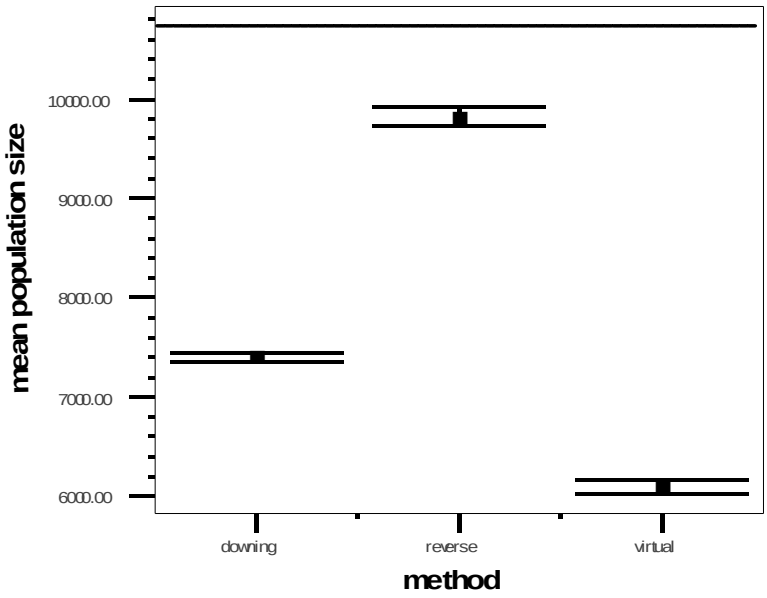


Figure 2.2b. Mean population estimates from 3 reconstruction techniques: Downing, Reverse Order and virtual reconstruction. This graph represents the simulation incorporating a middle level of measurement error (bounds of 0.7 – 1.3 from the uniform distribution). The dashed line indicates actual population size. Error bars represent the mean and 95% confidence interval of the mean.

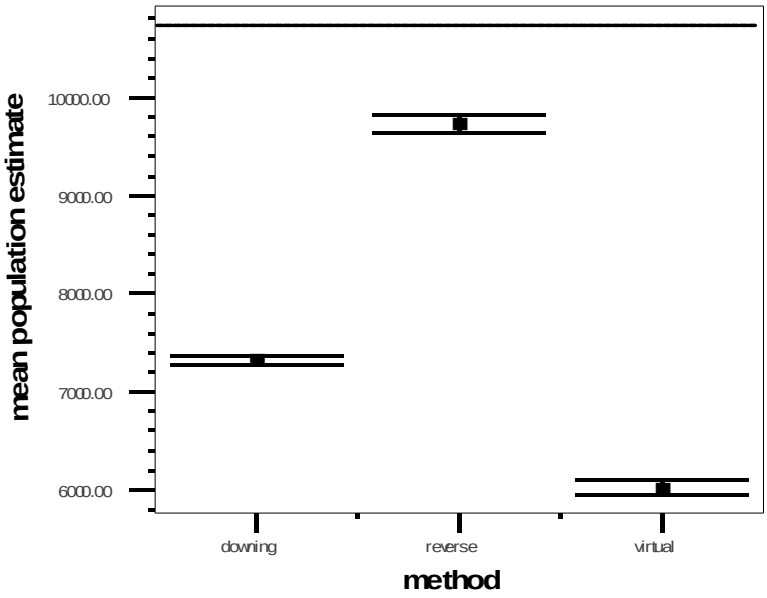


Figure 2.2c. Mean population estimates from 3 reconstruction techniques: Downing, Reverse Order and virtual reconstruction. This graph represents the simulation incorporating a high level of measurement error (bounds of 0.5 – 1.5 from the uniform distribution). The dashed line indicates actual population size. Error bars represent the mean and 95% confidence interval of the mean.

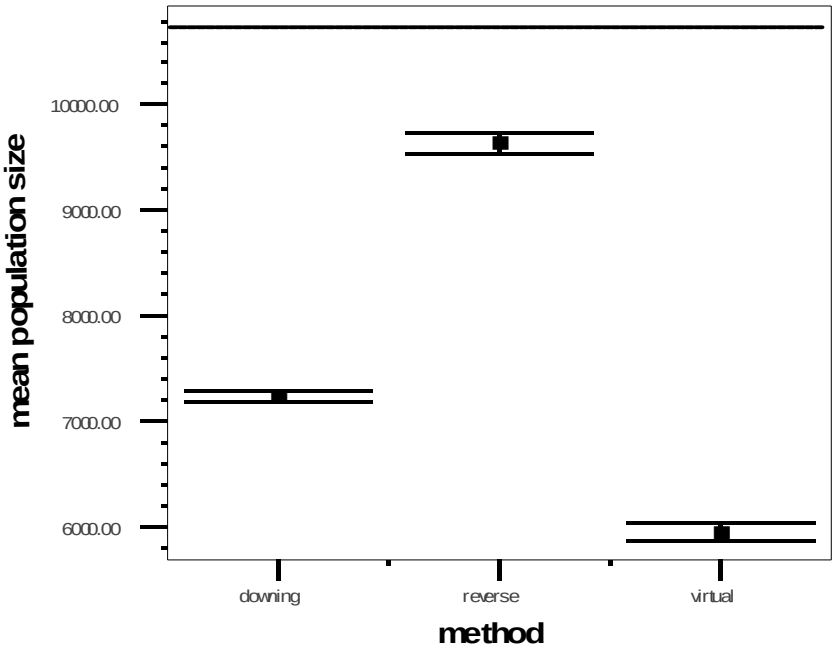


Figure 2.3a. The error bars below represent the mean population estimate of the 3 population reconstruction techniques: Downing, Reverse Order, and virtual reconstruction. The simulations evaluated the effect of collapsing the oldest age classes into a terminal "5-plus" group. The mean with associated 95% confidence interval is shown; the actual population is represented by the dashed line.

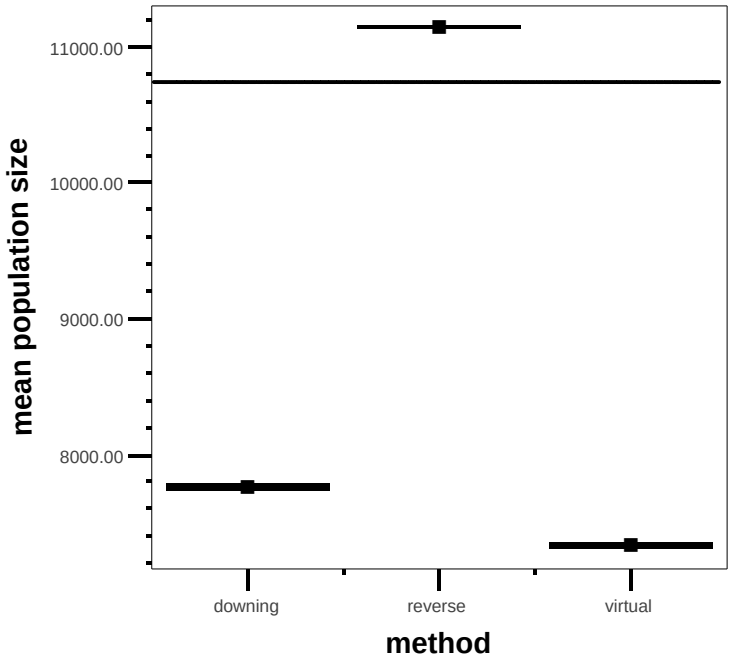


Figure 2.3b. The error bars below represent the mean population estimate of the 3 population reconstruction techniques: Downing, Reverse Order, and virtual reconstruction. The simulations evaluated the effect of collapsing the oldest age classes into a terminal "3-plus" group. The mean with associated 95% confidence interval is shown; the actual population is represented by the dashed line.

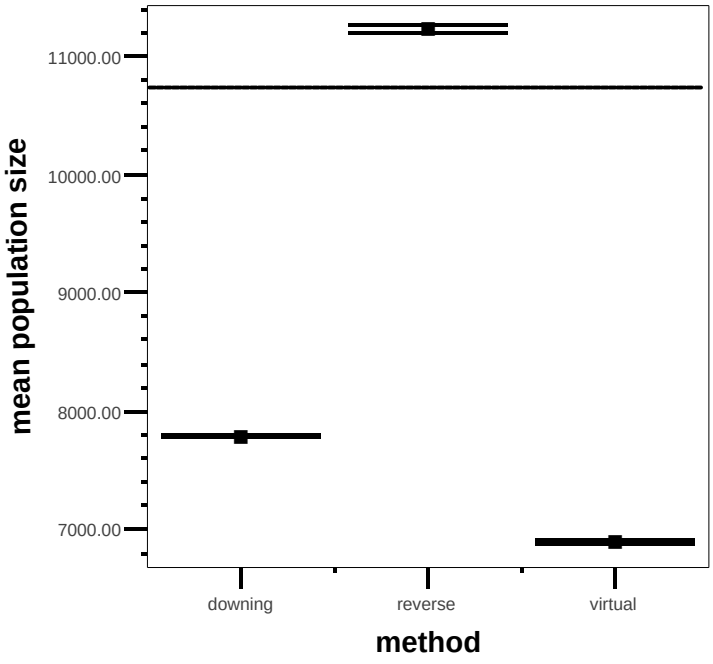


Figure 2.4. The error bars below represent the mean population estimate of the 3 population reconstruction techniques: Downing, Reverse Order, and virtual reconstruction. The simulations evaluated the effect of violating of the equal terminal mortality assumption (Downing reconstruction) with the 3 plus collapsed age group. The mean with associated 95% confidence interval is shown; the actual population is represented by the dashed line.

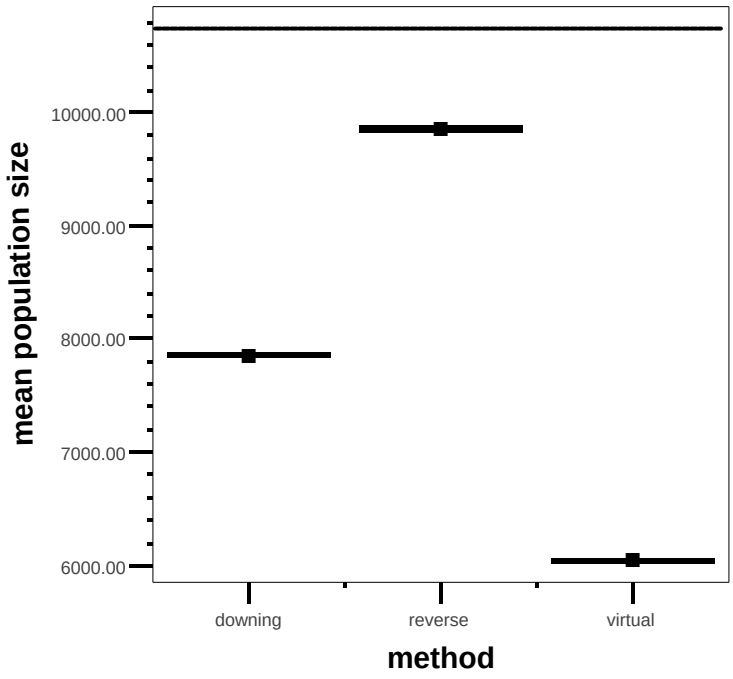


Figure 2.5a. The error bars below represent the mean population estimate of the 3 population reconstruction techniques: Downing, Reverse Order, and virtual reconstruction. The simulations evaluated the effect of aging biases, in this simulation 50% of animals aged to the next oldest age class. The mean with associated 95% confidence interval is shown; the actual population is represented by the dashed line

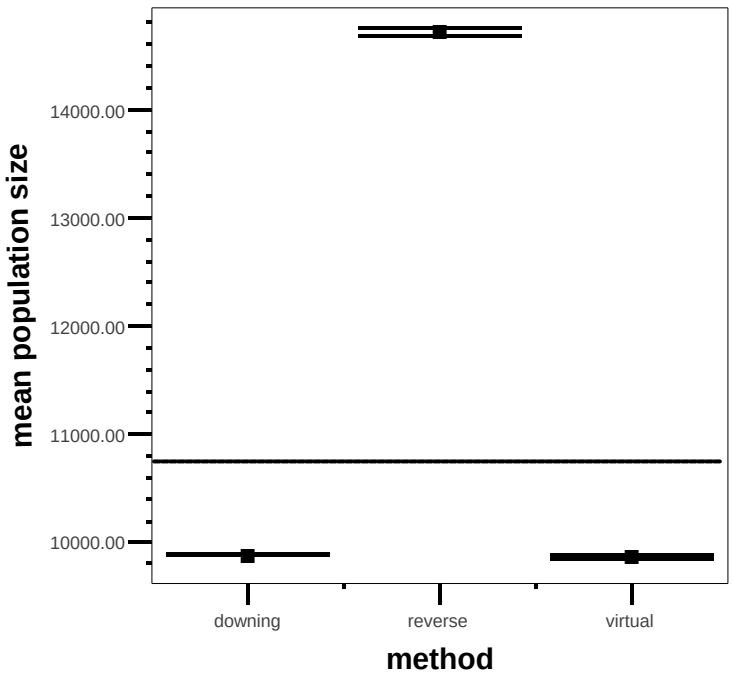


Figure 2.5b. The error bars below represent the mean population estimate of the 3 population reconstruction techniques: Downing, Reverse Order, and virtual reconstruction. The simulations evaluated the effect of aging biases, in this simulation 20% of animals aged to the next oldest age class. The mean with associated 95% confidence interval is shown; the actual population is represented by the dashed line.

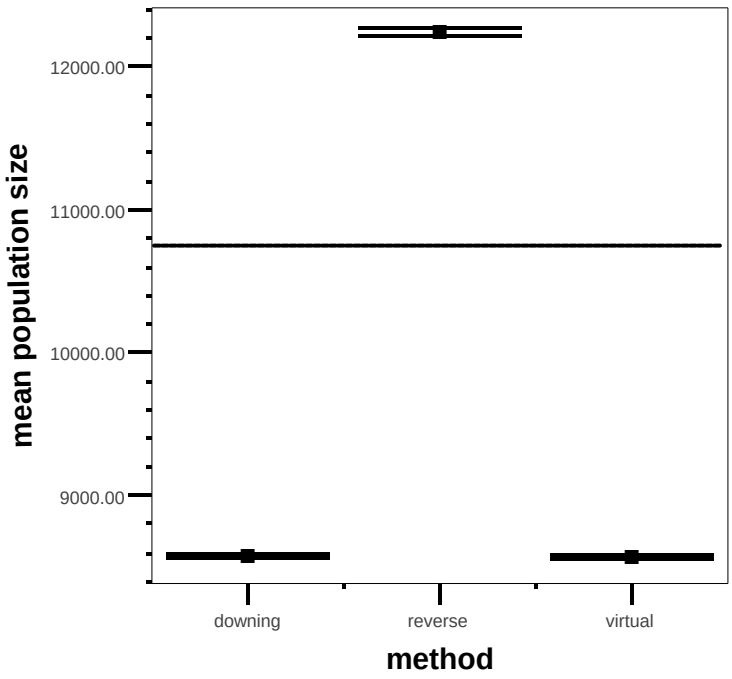


Figure 2.6. The error bars below represent the mean population estimate of the 3 population reconstruction techniques: Downing, Reverse Order, and virtual reconstruction. The simulations evaluated the effect of aging biases, in this simulation 50% of animals aged to the next youngest age class. The mean with associated 95% confidence interval is shown; the actual population is represented by the dashed line.

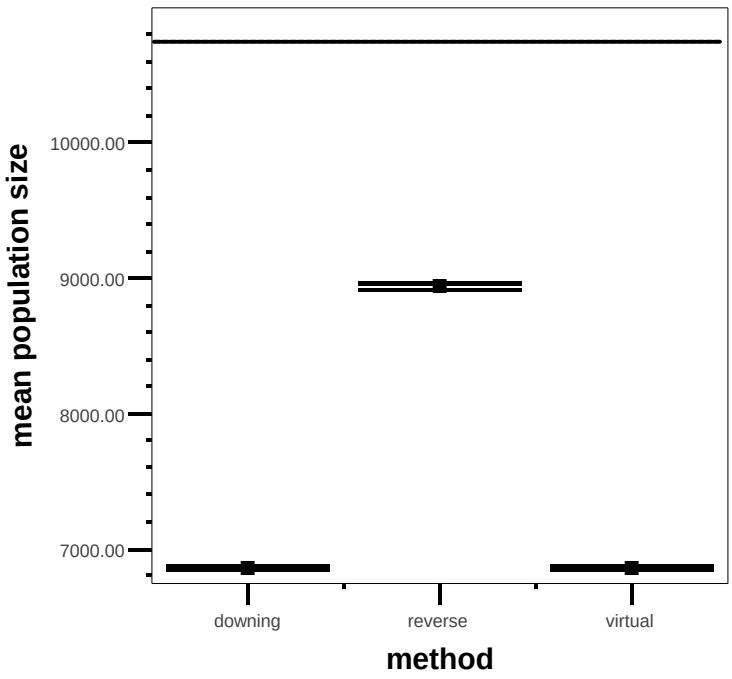


Figure 2.7a. The error bars below represent the mean population estimate of the 3 population reconstruction techniques: Downing, Reverse Order, and virtual reconstruction. The simulations evaluated the effect of a constant 40% harvest mortality rate across all age classes. The mean with associated 95% confidence interval is shown; the actual population is represented by the dashed line.

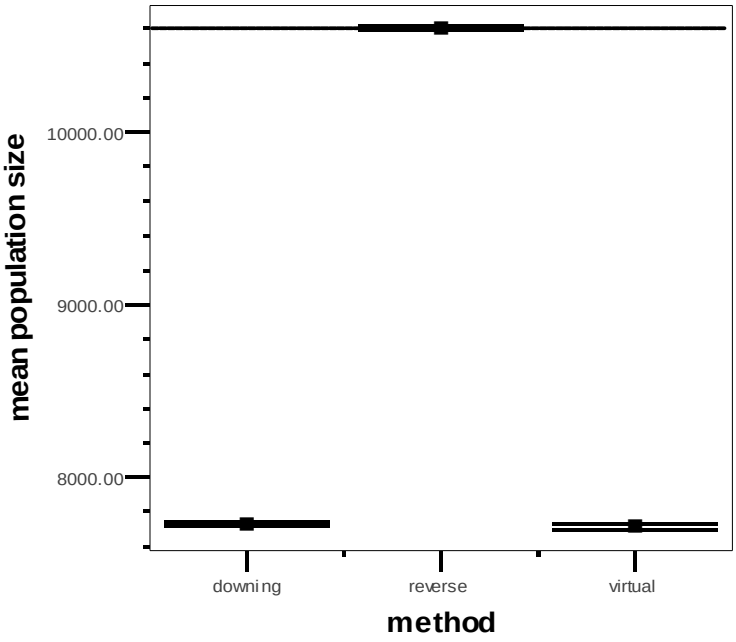


Figure 2.7b. The error bars below represent the mean population estimate of the 3 population reconstruction techniques: Downing, Reverse Order, and virtual reconstruction. The simulations evaluated the effect of variability in harvest characteristics; in this simulation there was higher harvest mortality on ages 1 – 3. The mean with associated 95% confidence interval is shown; the actual population is represented by the dashed line.

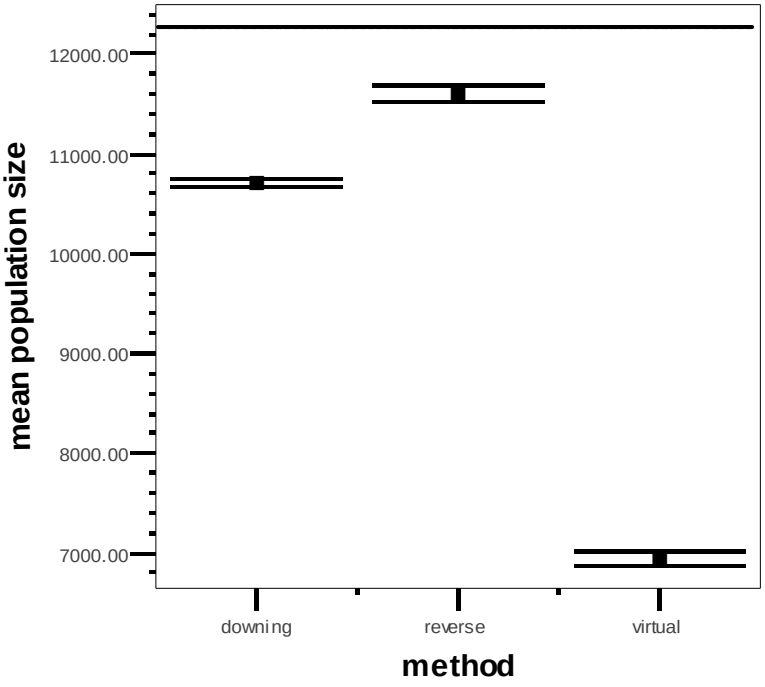


Figure 2.7c. The error bars below represent the mean population estimate of the 3 population reconstruction techniques: Downing, Reverse Order, and virtual reconstruction. The simulations evaluated the effect of variability in harvest characteristics; in this simulation there was higher harvest mortality on ages 4 - 8. The mean with associated 95% confidence interval is shown; the actual population is represented by the dashed line.

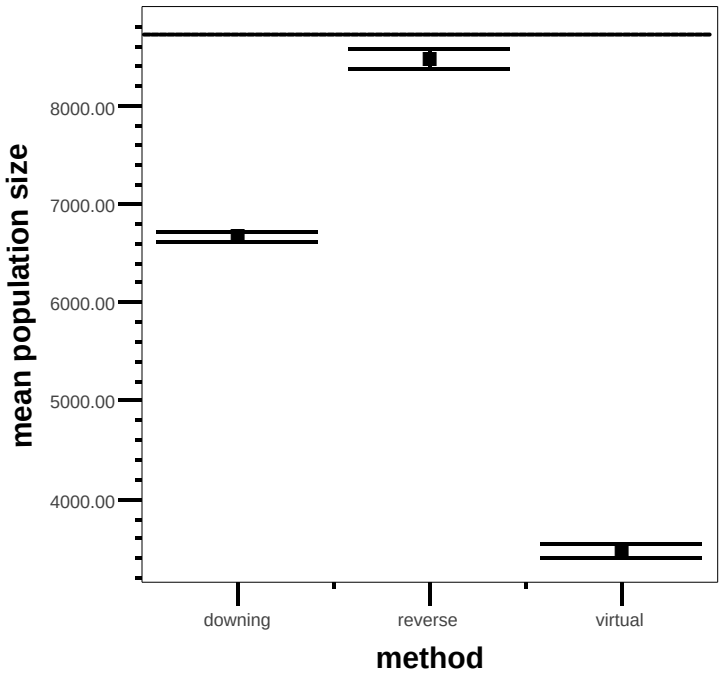


Figure 2.8a. The boxplots represent the deviation of the estimated population size from the actual population size by the 3 population reconstruction techniques: Downing, Reverse Order, and virtual reconstruction. These simulations evaluated the deviation of the estimated population from the actual population size as a result of environmental variability with the standard deviation set at 0.05 for process error. The mean with associated 95% confidence interval is shown..

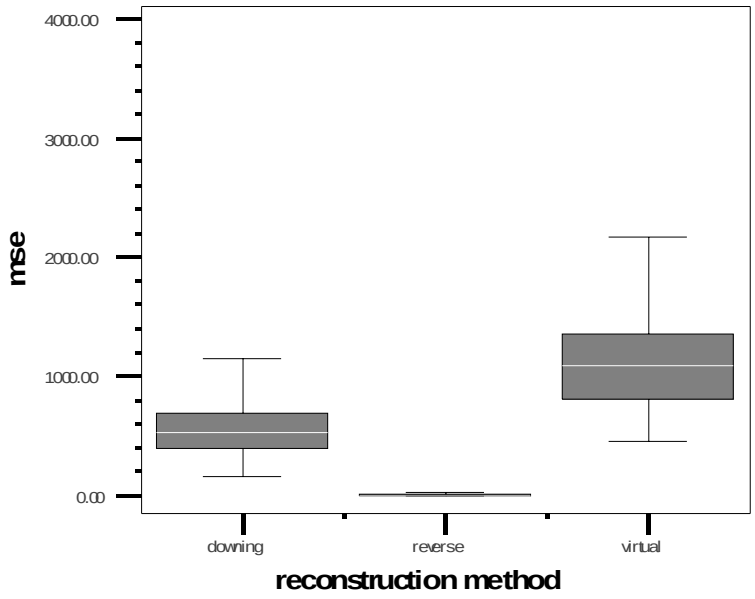


Figure 2.8b. The boxplots represent the deviation of the estimated population size from the actual population size by the 3 population reconstruction techniques: Downing, Reverse Order, and virtual reconstruction. These simulations evaluated the deviation of the estimated population from the actual population size as a result of environmental variability with the standard deviation set at 0.35 for process error. The mean with associated 95% confidence interval is shown.

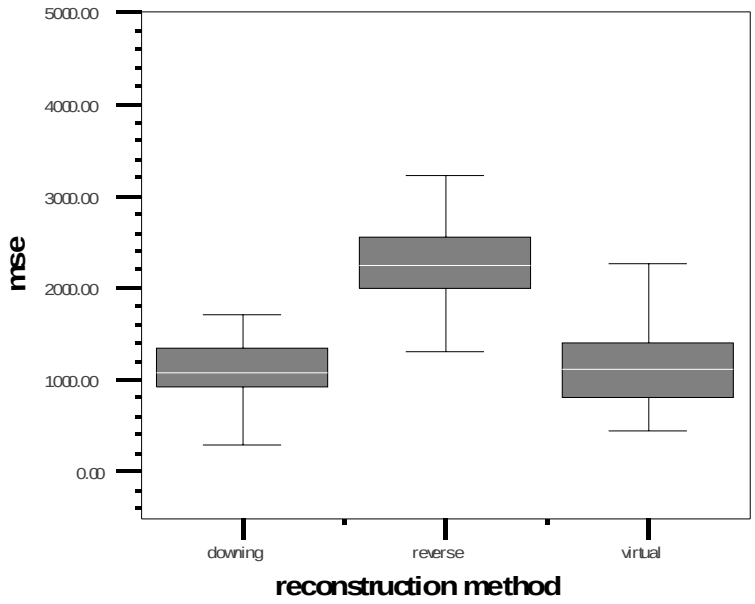


Figure 2.9a. The boxplots represent the deviation of the estimated population size from the actual population size of the 3 population reconstruction techniques: Downing, Reverse Order, and virtual reconstruction at low levels of measurement and process error. The levels of error shown here are process error with the standard deviation set at 0.05 and measurement error with bounds 0.9– 1.1. The mean deviation with associated 95% confidence interval is shown.

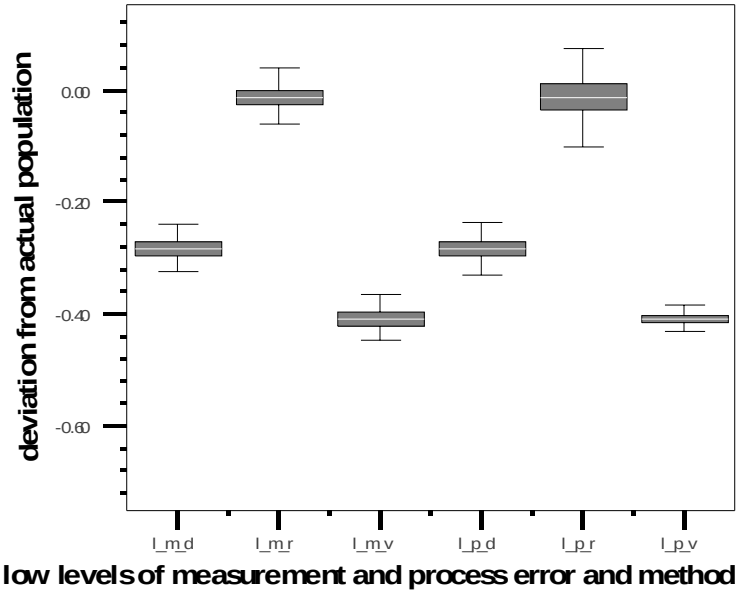
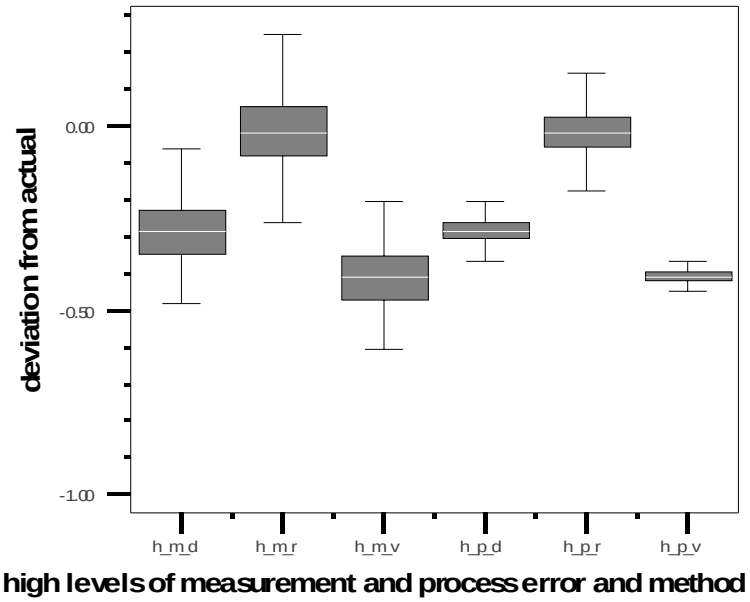


Figure 2.9b. The boxplots represent the deviation of the estimated population size from the actual population size of the 3 population reconstruction techniques: Downing, Reverse Order, and virtual reconstruction at high levels of measurement and process error. The levels of error shown here are process error with the standard deviation set at 0.35 and measurement error with bounds 0.5– 1.5. The mean deviation with associated 95% confidence interval is shown.



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Appendix 2.1. Equations for Downing Reconstruction.

Downing reconstruction (Downing 1980) has a more complex series of equations. The first step is to calculate mortality rates and the number of animals for the "average year." The "average year" is created as a starting point by averaging the harvest numbers for the oldest 2 age classes over the last 3 years. First, the average harvest numbers are calculated by:

$$\overline{H}_{\max a-1,avgt} = \frac{\sum_{i=0}^{2} H_{\max a-1,t-i}}{3} \quad \textbf{(1)} \qquad \overline{H}_{\max a,avgt} = \frac{\sum_{i=0}^{2} H_{\max a-1,t-i}}{3} \quad \textbf{(2)}$$

where: $H_{maxa,\,t}$ = harvest numbers of the oldest age class *a* at time *t*, and

$\overline{H}_{\max a,avgt}$ = the average harvest of the oldest age class *a* at the "average" time *t*.

The next step is to calculate the average mortality rate of the oldest 2 age classes. This is calculated by:

$$\overline{m}_{\max a,avgt} = 1 - \left(\frac{\overline{H}_{\max a-1,avgt}}{\overline{H}_{\max a-1,avgt} + \overline{H}_{\max a,avgt}}\right) \quad \textbf{(3)}$$

$$\overline{m}_{\max a-1,avgt} = \overline{m}_{\max a,avgt} \quad \textbf{(4)}$$

where: $\overline{m}_{\max a,avgt}$ = the average mortality rate of the oldest age class *a* at "average" time *t*.

After the average mortality rate is calculated for the oldest 2 age classes, the number of individuals in those age classes in the "average" year is calculated by:

$$\overline{N}_{\max a-1,avgt} = \frac{\overline{H}_{\max a-1,avgt}}{\overline{m}_{\max a-1,avgt}} \quad \textbf{(5)}$$

$$\overline{N}_{\max a,avgt} = \frac{\overline{H}_{\max a,avgt}}{\overline{m}_{\max,avgt}} \quad \textbf{(6)}$$

where: $\overline{N}_{\max a,avgt}$ = the number of animals in the oldest age class *a* at "average" time *t*.

Once the number of animals in the last 2 age classes in the "average" year is calculated, the backwards calculations for the oldest 2 ages for all years begin. The steps are the same for the calculations for the "average" year. First, the mortality rate is calculated by:

$$m_{\max a,\max t} = 1 - \left(\frac{\overline{N}_{\max a,avgt}}{\overline{N}_{\max a,avgt} + H_{\max a-1,\max t} + H_{\max a,\max t}}\right) \quad \textbf{(7)}$$

$$m_{\max a,\max t} = m_{\max a-1,\max t} \quad \textbf{(8)}$$

where: $H_{maxa,maxt}$ = the number of animals in the harvest in the oldest age class *a* at the last year *t*, and

$m_{maxa,\ maxt}$ = the mortality rate of the oldest age class *a* at the last year *t*.

After the mortality rate is calculated, the estimated population size for the oldest 2 age classes is calculated by:

$$N_{\max a,\max t} = \frac{H_{\max a,\max t}}{m_{\max a,\max t}} \quad \textbf{(9)}$$

$$N_{\max a-1,\max t} = \frac{H_{\max a-1,\max t}}{m_{\max a-1,\max t}} \quad \textbf{(10)}$$

where: $N_{maxa,maxt}$ = number of animals in the oldest age class *a* at the last year *t*,

$H_{maxa,maxt}$ = number of animals in the harvest of the oldest age class *a* at the last year *t*.

The backwards calculations continue for all remaining years following the equations listed above. First, the mortality rate for the second to last year of data is calculated by:

$$m_{\max a,\max t-1} = 1 - \left(\frac{\overline{N}_{\max a,\max t}}{\overline{N}_{\max a,\max t} + H_{\max a-1,\max t-1} + H_{\max a,\max t-1}}\right) \quad \textbf{(11)}$$

$$m_{\max a,\max t-1} = m_{\max a-1,\max t-1} \quad \textbf{(12)}$$

Then the average number of animals in the oldest 2 age classes is calculated by:

$$N_{\max a,\max t-1} = \frac{H_{\max a,\max t-1}}{m_{\max a,\max t-1}} \quad \textbf{(13)}$$

$$N_{\max a-1,\max t-1} = \frac{H_{\max a-1,\max t-1}}{m_{\max a-1,\max t-1}} \quad \textbf{(14)}$$

These calculations are continued back through all years of data. For example, for populations that I generated over 1,000 years, *max t* = 1,000. The back calculations continue over all years of data. When the population estimate for the oldest 2 age classes is completed, it is possible to calculate the number of animals in the remaining age classes by:

$$N_{\max a-2,\max t-1} = N_{\max a-1,\max t} + H_{\max a,\max t-1} \quad \textbf{(15)}$$

For example, if there are 5 age classes included in the harvest data, the numbers of 4 and 5 year olds are first calculated by equations ten through twenty-three. The number of one, 2 and 3 year olds is subsequently calculated by equation 15.

CHAPTER 3 –APPLICATION OF POPULATION RECONSTRUCTION TECHNIQUES TO STATE HARVEST DATASETS AND DEVELOPMENT OF A STOCHASTIC POPULATION SIMULATION MODEL

ABSTRACT

I developed a questionnaire to evaluate the characteristics of the white-tailed deer and black bear harvest datasets of the 8 states participating in this study. From the results of the questionnaire, I selected 2 state harvest datasets: Pennsylvania black bear harvest dataset and North Carolina white-tailed deer harvest dataset. I estimated the population size for both datasets using Downing (Downing 1980) and virtual (Roseberry and Woolf 1991) reconstruction. I found that the population estimates from Downing and virtual reconstruction were very similar, if not identical, for both datasets. I also found that the population estimates closely tracked the actual harvest numbers, thereby showing that artificial increases or decreases in harvest mortality will have an effect on the estimated population size.

I also used the 2 state harvest datasets as templates in a quantitative population model to evaluate the effect of different levels of measurement error on the variance of population estimates from Downing and virtual reconstruction. I used three levels of measurement error: low, medium, and high. Measurement error was added to the harvest matrix as a random number drawn from a uniform distribution with specified bounds and a mean of zero. The variance associated with the population estimates increased with increasing levels of measurement error. This has implications for managers dealing with high levels of measurement error in their harvest datasets. High variance around population estimates will make trend detection difficult. Managers are cautioned to evaluate the amount of measurement error that may affect their datasets.

INTRODUCTION

White-tailed deer (*Odocoileus virginianus*) and black bear (*Ursus americanus*) are 2 of the most important large game species in the eastern United States (Bunnell and Tait 1981). Wildlife biologists require an index of population size and/or trends in order to set appropriate harvest regulations to achieve desired management goals (control, stability, or conservation) and set appropriate levels of recreational harvest for these species. From population estimates, population trends, and/or independent indices, harvest limits are set and regulations are determined. It is essential that population estimates, and/or trends, accurately represent the dynamics of the harvested population to ensure population persistence and appropriate management actions.

Population reconstruction techniques are population estimation methods that calculate a minimum population size based on age-specific harvest data (Downing 1980, Roseberry and Woolf 1991). Population reconstruction techniques share the following characteristics: 1) utilization of catch-at-age data and 2) backward addition of cohorts to estimate a minimum population size. Minimum input data include total number of animals in the harvest and age-specific harvest numbers (Williams et al. 2002). These data are readily available for most exploited species (Gove et al. 2002). Despite comprehensive evaluation of the accuracy of reconstruction techniques, reconstruction techniques are often used as part of a management plan for white-tailed deer and black bear (D. Steffen, pers. comm.).

I developed a questionnaire to survey wildlife managers in the eight states participating in this study to inventory the current use of population reconstruction techniques; to identify the type of reconstruction technique(s) most commonly used by

these states; to identify the uses for the estimates obtained from reconstruction techniques (i.e. population estimation, monitoring population trends, etc.); and to identify potential biases, errors, and data limitations in state harvest datasets. With the data obtained from the surveys, I selected 2 black bear harvest datasets (from Pennsylvania and North Carolina), and a white-tailed deer dataset (from North Carolina) to analyze with the reconstruction methods evaluated in Chapter 2.

Using stochastic population simulation models, I used these datasets as input, combining them with measurement, or observation, error. The simulations accounted for likely error, as identified in previous chapters and from the questionnaire results, to provide a more realistic range of possible population estimates obtained from each dataset.

Assessment of state harvest datasets

Eight states (Pennsylvania, New York, Virginia, West Virginia, North Carolina, South Carolina, Georgia, and Mississippi) participated and funded this study because of an interest in an evaluation of the accuracy of population reconstruction, its potential for application to their deer and/or bear harvest datasets, and the utility of reconstruction estimates as a tool in wildlife population management. Population reconstruction techniques are practical tools for monitoring harvested wildlife populations because the required input data are simply the total number of animals in the harvest and the number of harvested animals in each age class (Williams et al. 2002). Wildlife managers in many eastern states rely on hunting effort as an integral component of the management strategy

for white-tailed deer and black bear populations (Bowman et al. 2001, Brown et al. 2000, and see McShea et al. 1997).

The first objective of this chapter was to assess the quality, quantity, and types of harvest data available and practical to be analyzed with population reconstruction from the states participating in this study. To that end, I developed a questionnaire (IRB Registration Number: IRB00000667) with 2 primary goals: first, to assess current use of population reconstruction (Chapter 1) and second, to identify characteristics of each state's harvest dataset. I used this information to select state harvest datasets to analyze with population reconstruction and to apply a population simulation model. I was interested in the following characteristics of state harvest datasets: the length of time series, sample size, proportion of the harvest aged, yearly variation in harvest effort, the landscape scale on which harvest data is collected and analyzed, if ages are collapsed into a "plus" group for reconstruction analyses, the biologists' perception of limitations within their datasets for use in population reconstruction techniques, and the biologists' confidence that the last 2 age classes have equal harvest mortality rates (important for Downing reconstruction).

Analysis of state harvest datasets with reconstruction techniques

The second objective of this chapter was to estimate population sizes from selected state harvest datasets with Downing (Downing 1980) and virtual reconstruction (Roseberry and Woolf 1991). From the results of the questionnaire, I selected 2 states datasets, 1 white-tailed deer harvest dataset and 1 black bear harvest dataset for contrast.

Application of population simulation models

Harvest data have inherent limitations for use in population estimation due to differential sex and age vulnerability to harvest, hunter selectivity, changes in hunter effort, and harvest regulations (e.g. size or age limits). Another significant limitation to harvest data is the effect of measurement error. Measurement error, or observation error, is independent error that does not act on the growth of the population or parameters affecting population growth. Rather, measurement error is the result of sampling errors or observation errors (Hilborn and Mangel 1997) and is present in the data, but not in the actual population. Measurement error includes all errors that affect observed data, *i.e.* inaccuracies in data reporting, data recording, errors in aging animals, or any other type of human-induced error on data collection and recording. Measurement errors are often difficult to identify in a dataset, and, perhaps more importantly, it is difficult to quantify the level to which measurement error affects a dataset. As a result, measurement error makes accurate population estimation difficult (Hilborn and Mangel 1997).

Estimation of population sizes with reconstruction techniques produces only a point estimate of population size (estimates of numbers of animals per age class, sex ratio, and recruitment rates can be calculated from this point estimate also). With only harvest data, there is no way to compare the reconstructed population estimate with the actual population size. In order to determine the possible range of population sizes based on harvest data, I developed a stochastic population simulation model to incorporate measurement error characteristics that effect harvest datasets and, as a result, may affect the population estimates calculated from this data. I incorporated measurement error into

the population simulation model. I used both a white-tailed deer and a black bear harvest dataset identified from the survey information as a template for the simulations.

METHODS

Questionnaire development and implementation

I developed a questionnaire with the goal of assessing characteristics of the harvest datasets of the states participating in this study. I developed similar, but separate, questionnaires for white-tailed deer and black bear biologists (Appendices 3.1 and 3.2). The questionnaire was designed to limit open-ended questions. Wherever possible, questions were limited to yes/no or check-box answers. Subjective questions (i.e. biologists' confidence in harvest mortality rates) were limited to ranking on a 1 - 5 Likert scale to facilitate analysis.

The questionnaire was sent as an attachment via electronic mail (e-mail) to 13 white-tailed deer and black bear biologists representing the states participating in this study. The respondents could request a paper copy via U.S. postal service or a fax, if preferred. Respondents were asked to e-mail, fax, or mail their completed questionnaires to me. If I received no response from the respondent in 2 weeks, a reminder e-mail was sent. Another reminder e-mail or phone call was made in another 2 weeks if there was still no response.

Each biologist was first asked if he/she currently used population reconstruction. If yes, the biologist was asked a series of questions about the type of reconstruction technique used, whether the reconstructed estimates were used for population management, the landscape level to which reconstruction estimates were applied, the

applications for reconstruction estimates, if the oldest age classes were combined in a terminal “plus” age group, and if the reconstructed estimate was corrected with an estimate of natural mortality.

All biologists, regardless of current use of reconstruction, were asked to identify potential limitations with their dataset for analysis with population reconstruction, the degree to which harvest effort varies yearly in their state, the smallest landscape scale harvest data is collected and analyzed, if the harvest is aged to specific age classes or age groups (e.g. cubs, juveniles, adults), the method used to estimate total harvest, the percent of the harvest aged, and the number of years of consecutive harvest data.

The white-tailed deer and black bear questionnaires were analyzed separately to determine species-specific differences. Where appropriate, percentages or average responses were calculated and reported.

Population reconstruction analyses

Using the results of the questionnaire, I selected black bear harvest dataset from Pennsylvania and a white-tailed deer harvest data from North Carolina identified from the survey analyses. The North Carolina white-tailed deer dataset covered 21 years, however only a small percent of the harvest was aged (approximately 10%). It should be noted that all population estimates reported here therefore represent only 10% of the population (*i.e.* the population estimate for management purposes would be divided by 90%).

In Chapter 2, I evaluated 3 reconstruction analyses: Downing reconstruction (Downing 1980), virtual reconstruction (Roseberry and Woolf 1991), and Reverse Order reconstruction (developed in Chapter 2). As detailed in Chapter 2, Reverse Order

reconstruction requires estimates of natural and harvest mortality rates. Neither of the datasets had reliable estimates of these rates; therefore I did not estimate a population size with Reverse Order reconstruction at this stage. I applied Downing and virtual reconstruction techniques to each dataset to estimate the reconstructed population sizes for all years of data.

Virtual Reconstruction

Virtual reconstruction is the most simplified reconstruction technique used to provide population estimates from age at harvest data (Roseberry and Woolf 1991). Virtual reconstruction is analogous to cohort analysis, a technique frequently used in fisheries management (Roseberry and Woolf 1991). The assumptions of virtual reconstruction are: 1) the proportion of deaths accounted for is constant over time for each age class and 2) age determination is accurate (Roseberry and Woolf 1991). Virtual reconstruction is most appropriate for datasets that have long time series, such that complete cohorts have passed through the population (Roseberry and Woolf 1991).

Virtual reconstruction uses only the harvest matrix (actual or observed) as input data in the following equation for a population with 9 age classes:

$$Nv_{a,t} = \sum_{i=9}^{a} H_{i,t+9-a} \quad \textbf{(1)}$$

where: $Nv_{a,t}$ = number of individuals in age class *a* at time step *t* as calculated using virtual reconstruction method.

Downing Reconstruction

Downing reconstruction (1980) uses the same input data as virtual reconstruction. The primary difference between these techniques is the treatment of the last 2 age classes. Downing reconstruction collapses the older age classes into one category (e.g. ≥ 4.5 year olds for deer). This adds an assumption to Downing reconstruction, that the last 2 age classes have equal mortality rates.

Downing reconstruction uses the survival rate of the last 2 age classes to calculate an average mortality rate for these age classes. This is the starting point for backward reconstruction of the younger age classes and for each year of data. All mortality rates for the oldest 2 age classes are calculated back over all years. These mortality rates are then used to estimate the population size, by multiplying the mortality rate by the harvest numbers. The numbers of animals in the remainder of the age classes are calculated backwards by addition. Refer to Appendix 2.1 for equations used in Downing reconstruction.

For the Downing reconstruction method, I collapsed black bear age classes into a terminal 8-plus age class. Pennsylvania had black bear aged to 31 years old, however there were very few bears aged older than 9 years old. I also collapsed the bear data to a 3-plus age class for comparison. I collapsed the white-tailed deer data into a terminal 7-plus and 3-plus age class. The population estimates were conducted separately for males and females and then combined for all datasets. Downing and virtual reconstruction produces a point estimate of the number of individuals in each age and sex class each year; those numbers are summed to produce the total population size.

For both Downing and virtual reconstruction, I included only the yearly population estimates for which complete cohorts were included in the population estimate. For this reason, the years reported in the population estimates were less than the number of years in the actual dataset.

Stochastic population simulation models

I developed a population simulation model using Microsoft Visual Basic 6.0. The population simulation model evaluated the effect of incorporating measurement error on the range of population estimates from Downing and virtual reconstruction.

For the population simulation model, the actual North Carolina white-tailed deer (7-plus age group) and Pennsylvania black bear harvest (8-plus age group) matrices were used, containing sex and age-specific harvest numbers. The simulations were performed both with and without measurement error:

$$\hat{H}_{a,t} = H_{a,t} \quad \textbf{(2)}$$

$$\hat{H}_{a,t} = H_{a,t} * \alpha_{a,t} \quad \textbf{(3)}$$

where: $\hat{H}_{a,t}$ = observed harvest of age class *a* at time step *t*, and

$H_{a,t}$ = actual harvest of age class *a* at time step *t*.

$\alpha_{a,t}$ = a uniformly distributed random variable between 0.5 – 1.5, for age class *a*, at time step *t*.

Measurement error was added to the actual harvest numbers by randomly selecting a number from a uniform distribution, with a mean of one and between

specified bounds. A uniform distribution is appropriate for adding measurement error because, using a simple algorithm, the distribution has a mean of one and defined bounds (either narrow or wide, depending on desired level of variance). I used 3 sets of bounds to represent high (0.5 – 1.5), medium (0.7 – 1.3) and low (0.9 – 1.1) levels of variance around the mean of one. Measurement error was assumed to affect each age class at each year differently; therefore a different random number was selected for each age over each year. An observed harvest matrix was calculated using this generic algorithm:

$$\alpha_{a,t} = (n_{a,t} * w) + b \quad \textbf{(3)}$$

$n_{a,t}$ = a randomly selected number from a uniform distribution, between 0 – 1 for age class *a* at time step *t*

w = the desired width of the bounds of the uniform distribution (*i.e.* 1.0, 0.6, or 0.2)

b = the low end of the bounds of the desired uniform distribution (*i.e.* 0.5, 0.7, or 0.9)

The population size was calculated using both the observed and actual harvest numbers in the stochastic simulation model. The harvest data with associated measurement error was entered into the appropriate equations for Downing and virtual reconstruction.

Model Simulation Runs

I used the North Carolina white-tailed deer and Pennsylvania black bear harvest data as a starting point for the population estimate. The N.C. deer dataset had 9 age classes over 22 years of data. The ages were collapsed to 7-plus group for Downing reconstruction. The harvest data was used to estimate population sizes with and without including measurement error. The Pennsylvania black bear harvest dataset, which had up to 30 age classes over 9 years of data. I collapsed the ages into an 8-plus class for Downing reconstruction. All simulations were done separately for males and females and then combined and reported here for a total population size. The population simulation model was run 50 times for all years for both datasets.

Evaluation of reconstruction population estimates

Population estimates from reconstruction techniques were compared to the population size estimated by Downing and virtual reconstruction without error. The standard error for all population estimates was calculated and reported on all figures. The interquartile range is reported to demonstrate the spread associated with the population estimates. To compare population means between all estimates, an Analysis of Variance (ANOVA) was performed and followed by a post-hoc comparison of means to further evaluate differences between means. I also conducted a Levine's test of homogeneity of variance to compare variances among time steps and among levels of measurement error (Ott and Longnecker 2001). All differences were considered significant at the $p = 0.05$ level. Statistical tests were conducted in SPSS 11.0.

RESULTS

Survey Results

Current use of reconstruction techniques

The questionnaire response rate was 84.6%. At least one biologist (white-tailed deer or black bear) responded from each state participating in this study; 5 white-tailed deer and 6 black bear biologists responded. The responses were reported separately by species. In all results reported, the term "biologists" represents "biologists responding to the survey." One hundred percent of white-tailed deer biologists currently use some type of population reconstruction technique, while 83.3% of black bear biologists use population reconstruction.

The questionnaires showed that harvest datasets for black bears were quite similar across the participating states with long time series (20 years or longer) and a high proportion of the harvest aged. Pennsylvania had 17 years of harvest data appropriate for analysis with reconstruction techniques and the biologist estimated that 100% of the harvest was aged ever year. Also, the dataset was particularly interesting because the state has never used reconstruction to estimate population sizes.

White-tailed deer datasets were more variable across the participating states, but overall tended to have more uncertainty associated with the harvest numbers, shorter or more inconsistent years of data and a smaller proportion of the harvested animals were aged, but bigger sample sizes. North Carolina white-tailed deer data set covered 22 years and approximately 10% of the harvest was aged each year.

Approaches to reconstruction and dataset characteristics

Eighty percent (80%) of both black bear and white-tailed deer biologists combine the oldest age classes into a “plus” age group for reconstruction analysis. Eighty percent (80%) of white-tailed deer biologists multiply their population estimate by a natural mortality correction term, while only 20% of the black bear biologists correct the reconstruction estimate for natural mortality.

There was no consistent pattern among biologists concerning limitations of their datasets for use in population reconstruction techniques. Half of black bear biologist respondents were concerned with their lack of information about harvest mortality rates, while 60% of white-tailed deer biologists were concerned with poor information concerning natural mortality rates. Forty percent (40%) of black bear and white-tailed deer biologists were concerned with inaccuracies in aging. All respondents reported that animals were aged to a particular age class, although as reported above, all biologists using Downing reconstruction create a “plus” age group for reconstruction analysis.

One hundred percent (100%) of black bear biologists reported that harvest was estimated by mandatory check-in of animals; white-tailed deer biologists reported much more varied methods of estimating harvest from telephone survey to mail survey to mandatory check-in; 60% of white-tailed deer biologists used a combination of the 3 reporting methods. The proportion of the white-tailed deer harvest that was aged ranged from 1 – 10%, while the proportion of the black bear harvest aged from 55 – 100%.

Population reconstruction analyses

I estimated population sizes using black bear harvest data from Pennsylvania with Downing and virtual reconstruction analyses. I also estimated population sizes using North Carolina white-tailed deer harvest data with Downing and virtual reconstruction.

The average population size for black bears in Pennsylvania as estimated by Downing reconstruction (8-plus age group) was 5,704, with a starting population estimate of 5,104 bears and the most recent population estimate was 6,313 bears (Figure 3.1); the average population size as estimated by virtual reconstruction was exactly the same as that of Downing reconstruction (Figure 3.1). The 3-plus age group allowed for more years of population estimation than the 8-plus age group and tracked the same population trajectory (Figure 3.1). The population estimate for the 3-plus group was, on average, an underestimate by 770 ± 58.2 (SD) as compared to the 8-plus group (Figure 3.1).

The average population size for white-tailed deer in North Carolina as estimated by Downing reconstruction for the 7-plus age group was 11,368 deer, with a starting population estimate in 1982 of 6,966 deer and the largest population estimate was 19,368 (Figure 3.2); the average population size as estimated by virtual reconstruction was slightly lower at 11,125, but followed a similar trajectory (Figure 3.2). The 3-plus age group allowed for more years of population estimation (Figure 3.2) and followed the trajectory of the 8-plus group closely, on average overestimating by 240 ± 249.48 (SD) animals.

It should be noted that all population estimates from Downing and virtual reconstruction are yearly point estimates, with no method for calculating variance within a year.

Population simulation models

The stochastic population simulation models were run 50 times using North Carolina white-tailed deer harvest data and Pennsylvania black bear harvest data as a template.

Measurement error: North Carolina white-tailed deer harvest dataset

The mean population estimates and the 95% confidence intervals of the mean calculated by Downing reconstruction with 3 levels of measurement error (0.05, 0.15, and 0.35) are shown in Figure 3.3. Three time steps are reported: year 5, year 10, and year 20. The population estimate at each year for each level of measurement error is shown. Figure 3.3 shows that increasing levels of measurement error results in more variance associated with the population estimates. The mean population size at time step 5, as calculated by the population simulation model with low variance is 19,054 ± 452.96 SD (IQ range = 701.24); at high variance the mean population size 19,176 ± 2,345.99 SD (IQ range = 3449.65). Downing reconstruction estimated the population as 19,062 deer. Levine's test of homogeneity of variance showed that the population estimate variances were significantly different among the three time steps evaluated and among all levels of measurement error, at $p < 0.001$ for all statistics. An ANOVA and showed that mean population estimates were not significantly different within a given year despite different levels of measurement error (for $t = 5$, $p = 0.988$; $t = 10$, $p = 0.887$; and $t = 20$, $p = 0.972$).

As expected based on the results from Chapter 2 and the analysis of state harvest datasets in this chapter, the population estimates from virtual reconstruction were similar to those from Downing reconstruction (Figure 3.4). Again, the mean population

estimates at each time step for each level of measurement error were not significantly different from each other, but the spread of estimates increased with increasing levels of measurement error. This is supported by results from an ANOVA comparing mean population sizes within a time step ($t = 5$, $p = 0.997$; $t = 10$, $p = 0.462$; and $t = 20$, $p = 0.997$). Again, the Levine's test showed that all variances were significantly different ($p < 0.001$) among the 3 years and e levels of measurement error.

Note in Figures 3.3 and 3.4 that the confidence interval associated with the mean population size decreased as the time step increased (*i.e*. from year 5 to 20).

Measurement error: Pennsylvania black bear harvest dataset

The mean population estimates and the 95% confidence intervals of the mean calculated by Downing reconstruction with 3 levels of measurement error are shown in Figure 3.5. Due to the shorter length of the time series of the harvest dataset, the time steps are shown at years 3, 5, and 7. Similar to the results from North Carolina, the mean population estimates closely approximate each other at all levels of variance. Unlike, the North Carolina dataset, however, the variance of the population estimates did not follow the same pattern. For example, at low variance the population estimate at time step 3, is 4,088 ± 42.27 SD, while at year 5, the standard deviation of the mean estimated population size was similar, though slightly higher at 4604 ± 56.64 SD. This is further supported by the Levine's test of variance which shows no significant difference of variances between years ($t = 3$, $p = 0.468$; $t = 5$, $p = 0.455$; and $t = 7$, $p = 0476$). Levine's test showed a significant difference of variances among levels of measurement error at $p < 0.001$ for all statistics. This may be a result of the shorter time series. An ANOVA

showed that means are not significantly different at each time step at different levels of variance ($t = 3$, $p = 0.565$; $t = 5$, $p = 0.448$; and $t = 7$, $p = 0.835$).

The population estimates and associated variances from virtual reconstruction, as well as ANOVA and Levine's test results followed the same trends as the Downing reconstruction population estimates (Figure 3.6).

DISCUSSION

Population reconstruction techniques are appealing as population estimators for wildlife managers because the input data are often already available, unlike data required for more complicated methods (Gove et al. 2002). In Chapter 2, I conducted simulations with a "virtual" population in order to quantify the amount of error in reconstructed population estimates given specific harvest and sampling characteristics, and environmental variability. In this chapter, I assessed characteristics of state harvest datasets, analyzed selected harvest datasets using reconstruction techniques, and developed a population simulation model based on actual harvest data, incorporating different levels of measurement error, to define a range of possible population estimates.

Assessment of characteristics of state harvest datasets

The results of the questionnaire showed that many wildlife managers in the eastern U.S. (92% of those surveyed) are currently using population reconstruction techniques. The questionnaire results also showed that the majority of both black bear and white-tailed deer biologists use Downing reconstruction, and as a result collapse the last age classes into one terminal "plus" age class. There has been very little critical

evaluation of Downing reconstruction since it was published in 1980 in Wildlife Management Techniques Manual (Schmenitz 1980). However, wildlife biologists have adopted this technique as a convenient method to estimate population sizes and monitor population trends. In Chapter 2, I provided a comprehensive evaluation of Downing reconstruction using simulated data. The results from Chapter 2 showed that while consistently underestimating population sizes, Downing reconstruction estimated the actual population sizes well with low levels of measurement error, environmental variability, and harvest mortality rate variations. As designed, Downing reconstruction estimates population sizes well with collapsed age classes.

The survey also showed that though the estimates from reconstruction techniques are used for a variety of reasons from estimating recruitment rates to setting the length of the hunting season, the majority of biologists use the reconstructed population estimate as a means to estimate population size and/or to monitor population trends. This was similar among black bear and white-tailed deer biologists. It was interesting to note that many of the biologists had different concerns about the limitations of their datasets; there was no one particular characteristic of a dataset that was limiting across all respondents. In fact, most respondents chose to check “other” and described a unique limitation. This showed that perceived limitations or problems with harvest datasets are unique among states and perhaps even to regions within the state (i.e. one respondent mentioned the selectivity bias encountered in white-tailed deer hunt clubs may skew the age and sex distribution in harvest data). The diversity of problems in harvest datasets across the region may make the use of one particular reconstruction technique inappropriate for all harvested populations.

Population reconstruction analyses

Virtual and Downing reconstruction analyses simply produce point estimates by year for each age class, allowing for calculation of the total population size. Despite the differences in calculations between virtual and Downing reconstruction, they produced surprisingly similar population estimates, often estimating exactly the same population size or within 5% of each other. This is supported by results from Chapter 2. The similarity in the estimates from both reconstruction techniques may provide managers with some reassurance that the reconstructed population estimates are accurate with either method; however, without independent estimates there is no method to determine how accurate the reconstructed estimates are. To increase the utility of the point estimates, it is useful if the manager is able to identify potential sources of error or biases in the harvest dataset, and then incorporate these into the analyses, as done with the stochastic simulation model. Often, it is impossible to quantify the degree or magnitude of errors or biases within the dataset, however, acknowledgement that these factors may affect estimates from reconstruction techniques would lead to a more accurate interpretation of the results. Downing (1980) clearly stated that the Downing reconstruction technique produces a population minimum estimate. If managers are using reconstruction techniques, they are (hopefully) aware that they are intrinsically accepting a level of uncertainty, because the harvest dataset can account only for animals that have been harvested.

The ability of the 3-plus collapsed age classes to track the same trajectory as the 7 and 8-plus age classes (Figures 3.1 and 3.2) support the benefit of using Downing reconstruction. Collapsing age classes to a terminal 3-plus group allows for more recent

population estimate (*i.e.* managers don't have to wait for all animals to pass through the population) and less reliance on accurate aging on animals older than 3 years old. It is accepted that deer can not be very accurately aged past 2.5 years old (Severinghaus 1949). The collapsed 3-plus age group with the Pennsylvania black bear data underestimated the 8-plus group by 770 bears on average, although the trajectories were similar (Figure 3.1). This is different from the North Carolina white-tailed deer data which estimated the population size within 240 deer, on average (Figure 3.2).

A possible explanation for this is the proportion of animals in the "plus" age group as compared to the total population. For example, in the Pennsylvania bear dataset, approximately 49.89% ± 0.6% (SD) of the total population was in the 3-plus group. On the other hand, for the North Carolina white-tailed deer population, 37.19% ± 7.3% (SD) of the total population was in the 3-plus group. Therefore, it is possible that the proportion of animals in the "plus" age group will affect the actual population estimate, however, the trajectory of the estimates remain consistent (Figures 3.1 and 3.2). This is particularly relevant for managers using reconstruction estimates as an index of population size.

Population simulation model

The purpose of the simulation model was to include measurement error into harvest data and estimate its impact on the resulting population estimates. Measurement error affects all datasets at some level, as it is a result of observer error (inaccurate observation, reporting, or recording of data, as examples). Estimating population sizes with Downing and virtual reconstruction from a harvest dataset produces a population

point estimate. It is simply a number. The population simulation model allowed for a more complex analysis of harvest data, creating a range of potential population sizes given an actual harvest dataset and realistic levels of measurement error.

The simulation model highlights this uncertainty by producing a wide range of possible population sizes around the point estimate. In simulations reported with high measurement error, the interquartile range (the range of 75% of the estimates) was within at least 10-15% of the mean population estimate. For example, when simulating high levels of measurement error in North Carolina deer harvest data the range of population sizes at time step 10 was 7,922 – 12,694 animals (Figure 3.3). For most wildlife populations, a range of 4,773 animals may not be precise enough to use to set wildlife policy or make management decisions. Therefore, these point estimates alone may not be precise enough to accurately capture the dynamics of the exploited population and set appropriate harvest regulations and policies.

Another important consideration in the use of reconstructed population estimates as a management tool is the use of these estimates as trends. All of the responding black bear biologists and 80% of the white-tailed deer biologists say they use estimates from reconstruction to monitor population trends. As seen in Figures 3.3 – 3.6, with varying levels of measurement error, it is difficult to detect the actual population trajectory when wide confidence intervals are associated with the mean population size. It is possible that the population follows a trajectory near the lower population sizes of the confidence interval, near the higher end, or bounces around through the middle. Levine's test of variance showed that the variances associated with the means were significantly different among the levels of measurement error used in this analysis, despite the fact that the

mean population estimates were not significantly different. A power analysis would be an appropriate next step in this analysis to detect whether the population estimates from population reconstruction techniques are appropriate for use in trend detection.

Harvest data as population estimation tools

This study evaluated 2 reconstruction techniques commonly used by wildlife managers in the eastern U.S.: Downing reconstruction and virtual reconstruction. These reconstruction techniques require only age-specific harvest numbers as input data (Downing 1980, Williams et al. 2002). For that reason, many wildlife managers with limited data for their harvested population, these reconstruction techniques are practical. However, more sophisticated population estimation techniques have been developed to estimate population sizes from harvest data. Gove et al. (2002) developed a statistical analysis based on maximum likelihood theory incorporating auxiliary information including reporting rates and vulnerability to harvest (Gove et al. 2002).

Fisheries managers have been estimating population sizes from catch (harvest) data for over a century (Megrey 1988). As computing technology has improved, more complex statistical methods have been developed to estimate stock sizes (Megrey 1988, Quinn and Deriso 1999). Some stock assessment models have increased to over 300 parameters (Davis 2004). Fisheries biologists also use tuning indices as an “anchor” for the population estimates (Quinn and Deriso 1999). These tuning indices include auxiliary information from fishery-independent population data. Wildlife managers with harvest-independent data may want to incorporate more sophisticated population estimation equations into their management strategies.

The drawback to more complex methods to estimate population sizes is the requirement of additional data (Quinn and Deriso 1999, Gove et al. 2002). Many wildlife managers, particularly white-tailed deer biologists, lack the necessary data to utilize these methods (D. Steffen, pers.comm.). It may be desirable for wildlife managers to use a population simulation model similar to the one I developed to incorporate a range of potential harvest mortality rates, environmental variability, measurement errors, and other characteristics known to affect the specific harvest dataset. The simulation model will produce a range of possible population sizes based on whatever data is available to him/her, based on a population generation equation that starts with age-specific harvest numbers, as is required for population reconstruction techniques, but also incorporates natural mortality and measurement error.

Summary

Most wildlife managers in the eastern United States use population reconstruction techniques, specifically Downing reconstruction, to estimate population sizes of harvested populations of black bear and white-tailed deer. The population simulation model in Chapter 3 showed that with real harvest data, increasing levels of measurement error result in a wide spread of population sizes estimated from the same set of harvest data.

Wildlife managers must determine the level of precision they require from reconstructed population estimates for the desired management actions. Managers of white-tailed deer populations, for example, may be more willing to accept errors in actual population estimates because white-tailed deer have an extremely fast growth rate

(McCullough 1979) and high population sizes in many areas of the eastern U.S. (Waller and Alverson 1997, Brown et al. 2000). Black bear populations, with a slower growth rate and smaller population sizes (Bunnell and Tait 1981) may require more precise population estimates and more exact population trend monitoring to ensure the appropriate harvest limits are set and population persistence.

Population reconstruction techniques are useful for managers with limited data availability on harvested wildlife species. However, these techniques have limitations when factors such as varying harvest mortality rates, environmental variability, and observation errors affect the input data. As shown, these factors result in a wide range of possible population sizes from the exact same input harvest dataset. Managers are cautioned to identify the factors that may result in errors or biases in their datasets and recognize these errors affect the interpretation of estimates from reconstruction techniques.

This was the first study to conduct simulation models with population reconstruction techniques. Further studies should be conducted to determine the effect of other biases and errors in harvest datasets on population estimates and a power analysis should be conducted to detect the ability of population estimates to accurately detect trends in populations.

Figure 3.1 Population estimates of Pennsylvania black bear harvest data as calculated by Downing and virtual reconstruction. The top line represents the population estimate with the 8-plus age group over 9 years of harvest data for both Downing (diamond) and virtual reconstruction (asterisk). The middle line represents the 3-plus age group (squares) over 16 years of data. The bottom line represents the actual harvest numbers over 16 years.

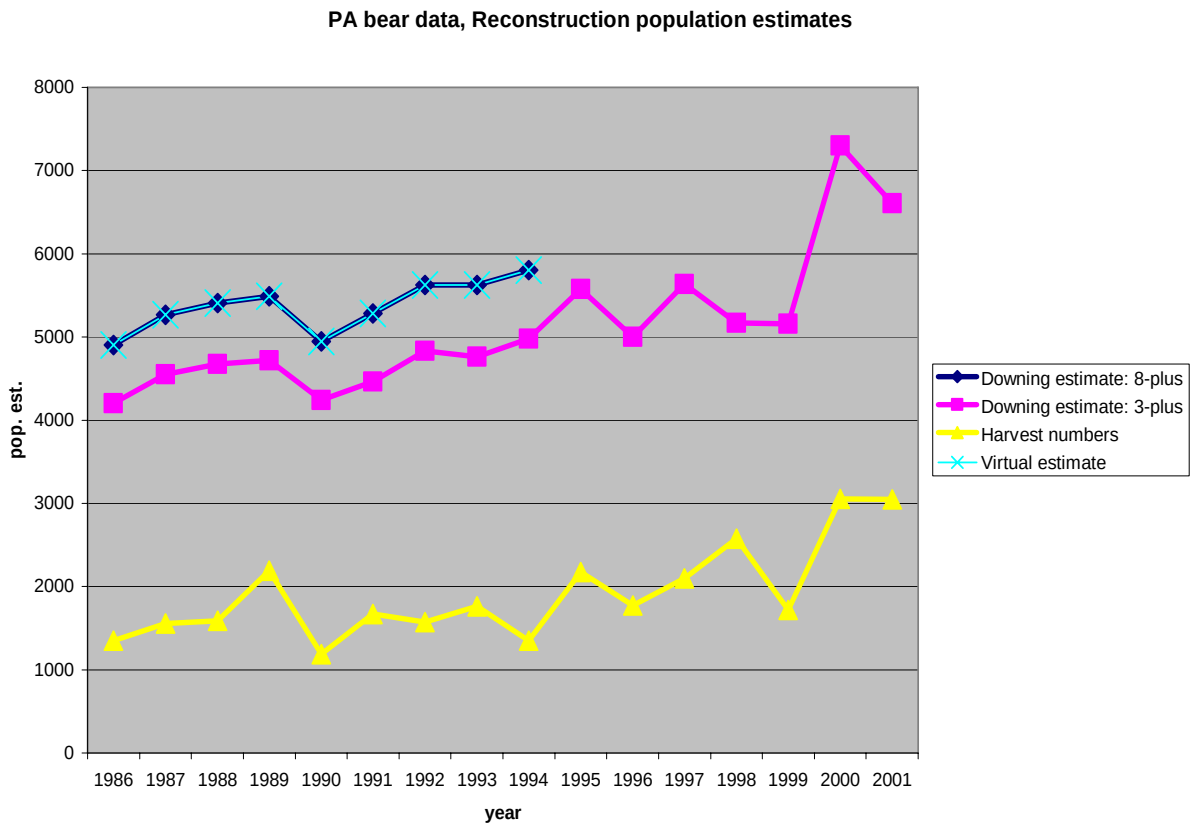


Figure 3.2 Population estimates of North Carolina white-tailed deer harvest data as calculated by Downing and virtual reconstruction. The top line represents the population estimate with the 7-plus age group over 17 years of harvest data for both Downing (circle) and virtual reconstruction (diamond). The middle line (asterisk) represents the 3-plus age group over 20 years of data. The bottom line represents the actual harvest numbers over 20 years.

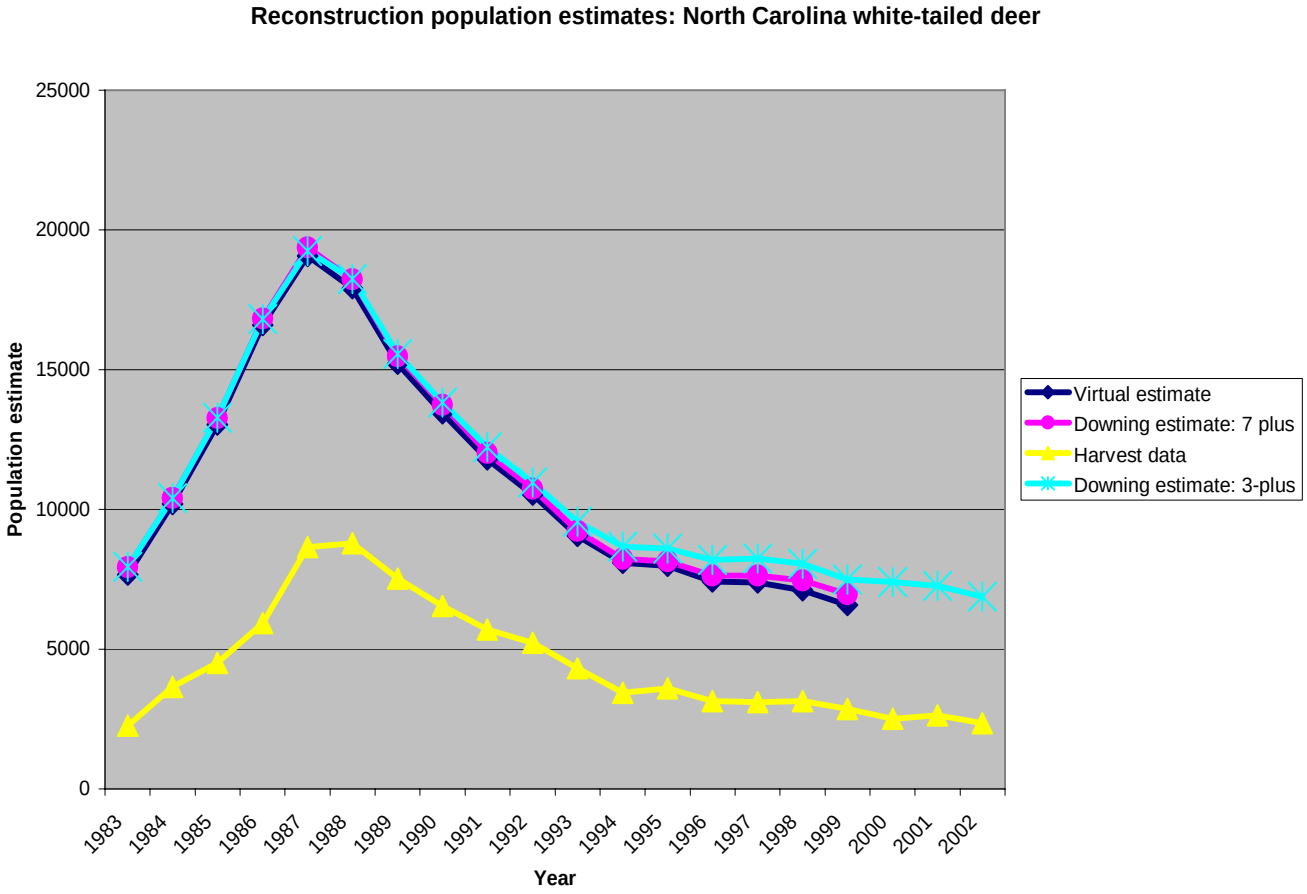


Figure 3.3 Mean population estimate and 95% confidence interval of the mean from Downing reconstruction based on different levels of measurement error from the uniform distribution with bounds of 0.9 – 1.1 (low), 0.7 – 1.3 (medium), and 0.5 – 1.5 (high). Results are shown over 50 model runs, using North Carolina white-tailed deer harvest data as a template, shown at time steps: 5, 10, and 20.

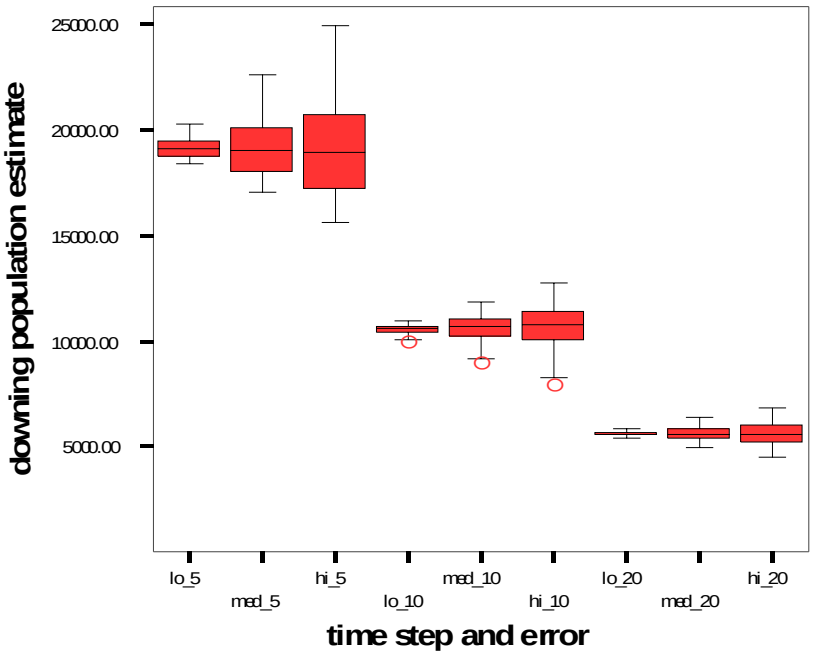


Figure 3.4 Mean population estimate and 95% confidence interval of the mean from virtual reconstruction based on different levels of measurement error, from the uniform distribution with bounds of 0.9 – 1.1 (low), 0.7 – 1.3 (medium), and 0.5 – 1.5 (high). Results are shown over 50 model runs, using North Carolina white-tailed deer harvest data as a template, shown at years 5, 10, and 20.

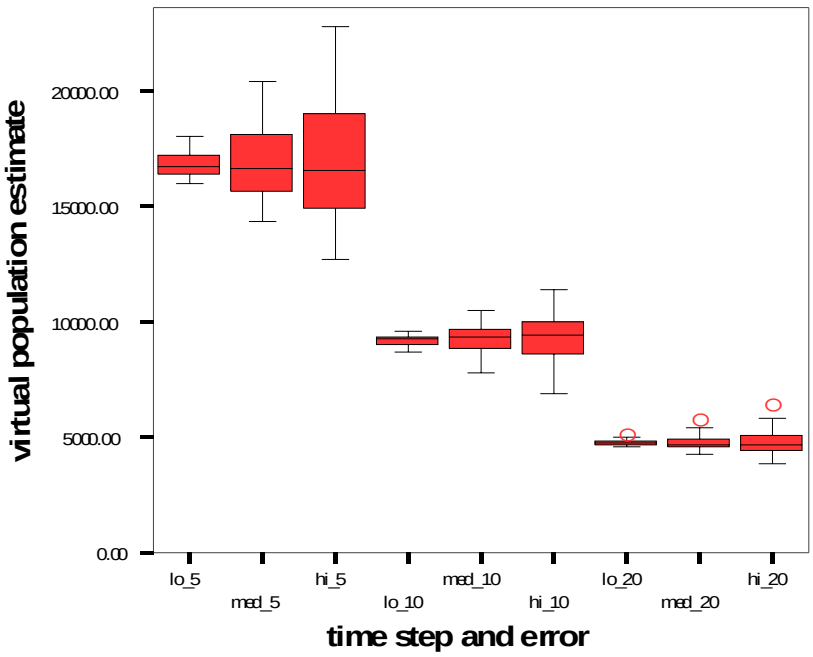


Figure 3.5 Mean population estimate and 95% confidence interval of the mean from Downing reconstruction based on different levels of measurement error, from the uniform distribution with bounds of 0.9 – 1.1 (low), 0.7 – 1.3 (medium), and 0.5 – 1.5 (high). Results are shown over 50 model runs, using Pennsylvania black bear harvest data as a template, shown at years 5, 10, and 15.

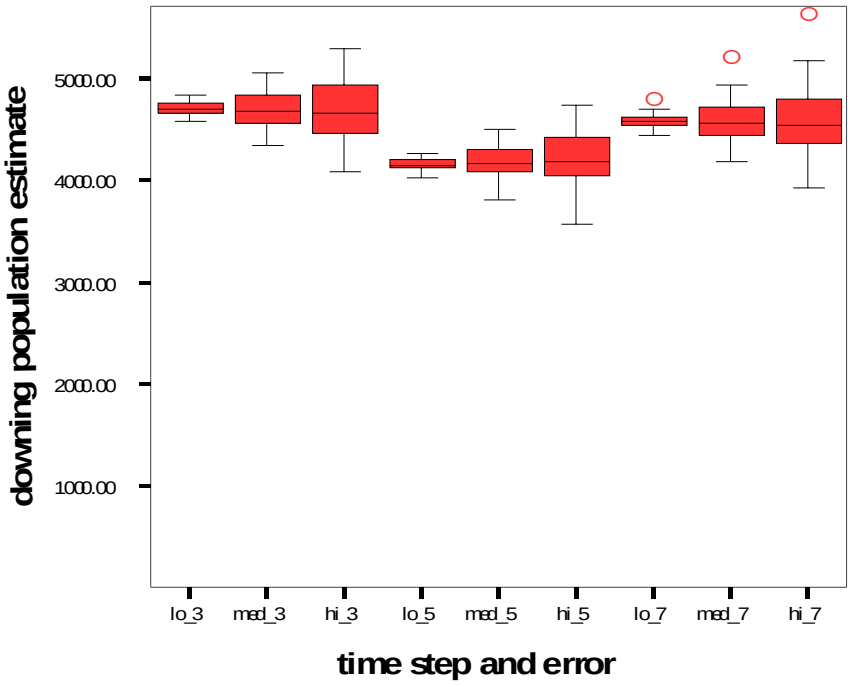
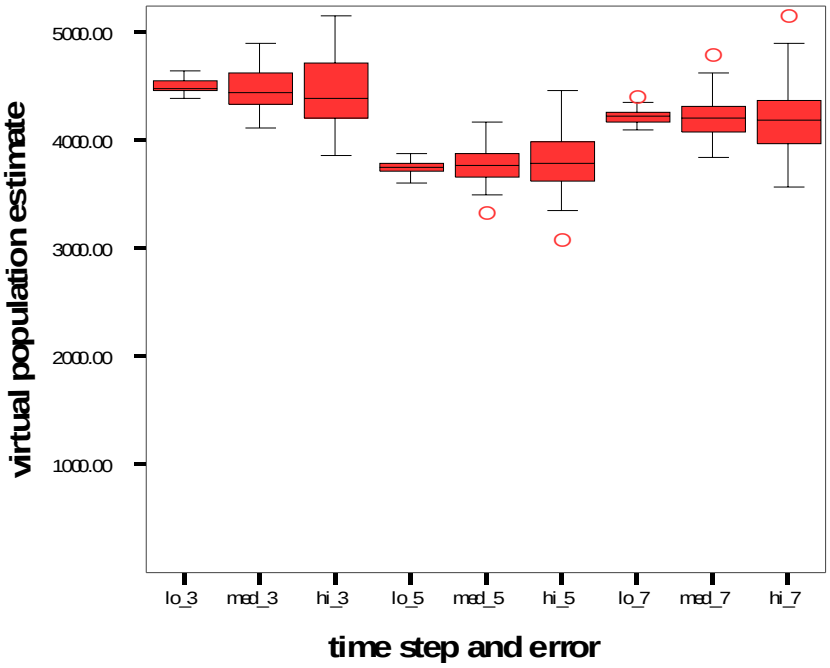


Figure 3.6 Mean population estimate and 95% confidence interval of the mean from virtual reconstruction based on different levels of measurement error, from the uniform distribution with bounds of 0.9 – 1.1 (low), 0.7 – 1.3 (medium), and 0.5 – 1.5 (high). Results are shown over 50 model runs, using Pennsylvania black bear harvest data as a template, shown at years 3, 5, and 7.



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Appendix 3.1 Black Bear Biologist Questionnaire

Thanks in advance for taking the time to complete this survey. Virginia Tech is conducting research to evaluate population reconstruction. Population reconstruction is defined, in this study, as a population estimation technique that uses sex and age-specific harvest data to back calculate population sizes (e.g. Downing reconstruction, virtual reconstruction, cohort analysis). Your responses will allow us to determine the types of datasets for which population reconstruction is an effective population estimator. Some datasets will require follow-up information. Please answer the following questions to the best of your ability. If possible, describe the source (e.g. common knowledge, assumed estimates, etc.) or study from which you received the data.

Thank you.
Mary Tilton (matilton@vt.edu)

1. Does your agency currently use population reconstruction methods to estimate black bear population sizes, trends, or other parameters?

- ☐ Yes (go to #2)
- ☐ No (go to #8)
- ☐ Not Sure (go to #8)

2. If yes, please describe the population reconstruction method(s) you use. Provide a general description and relevant citations, where available.

3. Do you rely on population reconstruction to set harvest management regulations for bears?

- ☐ Yes
- ☐ No
- ☐ Not Sure

4. Describe the smallest landscape scale for which you apply management regulations from the population reconstruction estimates (*e.g. county, wildlife management unit, state*)

5. Please indicate the applications for which you use population reconstruction (*check all that apply)*

- ☐ To estimate population size
- ☐ To determine population trends
- ☐ To estimate natural/non-hunting mortality rates
- ☐ To estimate harvest mortality rates
- ☐ To estimate recruitment rates
- ☐ As a means to set length of bear hunting season
- ☐ As a means to set/control total harvest
- ☐ Other, please specify:_____

6. When performing population reconstruction analyses, do you combine the oldest age classes for a final grouped age class (e.g., cubs, 1.5, 2.5, 3.5+)

- ☐ Yes
- ☐ No

If YES, please specify the specific age groupings you use for population reconstruction analyses.

7. Do you correct for natural/non-hunting mortality in your final population estimate?

- ☐ Yes
- ☐ No

IF YES, please specify the natural/non-hunting mortality correction percentage you use. Please provide a relevant citation, if available.

8. Please identify specific problems within your dataset that you believe may cause inaccurate estimates if you were to use population reconstruction:

- ☐ Inaccuracies in aging
- ☐ Short time series (i.e., only 5 years of consecutive sex at age harvest data)
- ☐ Too few animals in harvest aged
- ☐ Lack of information for annual variation in natural mortality rates
- ☐ Insufficient monitoring of annual variation in harvest mortality
- ☐ Annual variation in hunter effort
- ☐ Other, please specify:_____

9. Do you use other independent means to estimate (*i.e., not based on population reconstruction*):

	Overall	**Sex specific?**	**Age specific?**	**Year specific?**
Natural/non-hunting mortality rates	☐ Yes ☐ No	☐ Yes ☐ No	☐ Yes ☐ No	☐ Yes ☐ No
Harvest mortality rates	☐ Yes ☐ No	☐ Yes ☐ No	☐ Yes ☐ No	☐ Yes ☐ No
Reproduction rates	☐ Yes ☐ No	☐ Yes ☐ No	☐ Yes ☐ No	☐ Yes ☐ No

10. Please indicate the degree to which harvest effort in your state changes yearly:

0-10% **11-20%** **21-30%** **30+%** **don't know**

11. What is the smallest landscape scale at which your bear harvest data are **recorded**?
    - ☐ Hunt club
    - ☐ Township
    - ☐ County
    - ☐ Wildlife Management Unit
    - ☐ State
    - ☐ Other (please specify:_____)

12. What is the smallest landscape scale at which your bear harvest data are **analyzed**?
    - ☐ Hunt club
    - ☐ Township
    - ☐ County
    - ☐ Wildlife Management Unit
    - ☐ State
    - ☐ Other (please specify:_____)

13. How specific are the age data you collect from bears?

    - ☐ Bears are aged to the specific year class (e.g., 1, 2 , 3, ….to as old as possible)
    - ☐ Bears ages are only determined according to age groups (e.g., cubs, subadult (1-3), adult (4+)) (please specify the age groupings of the data you collect: _____)

14. In your opinion, how confident are you that the harvest rates are about the same for the oldest two age classes you use in population reconstruction?

Females?

Very Confident		***Somewhat Confident***		***Not Confident***
1	**2**	**3**	**4**	**5**

Males?

1	**2**	**3**	**4**	**5**

15. What is your most recent harvest estimate for bears: _____

16. How do you estimate total harvest of bears (check all that apply):

- ☐ Annual mail survey
- ☐ Mandatory check-in
- ☐ Mail-in report cards
- ☐ Other (specify:_____)

17. Approximately how many harvested bears do you age each year (*a percentage or number is acceptable here*)?

_____

18. How many consecutive years of age-specific harvest data are in your dataset?
_____years

Would you like to receive a summary of the results from this survey?

- ☐ Yes
- ☐ No

Appendix 3.2 White-tailed Deer Biologist Questionnaire

Thanks in advance for taking the time to complete this survey. Virginia Tech is conducting research to evaluate population reconstruction. Population reconstruction is defined, in this study, as a population estimation technique that uses sex and age-specific harvest data to back calculate population sizes (e.g. Downing reconstruction, virtual reconstruction, cohort analysis). Your responses will allow us to determine the types of datasets for which population reconstruction is an effective population estimator. Some datasets will require follow-up information. Please answer the following questions to the best of your ability. If possible, describe the source (e.g. common knowledge, assumed estimates, etc.) or study from which you received the data.

Thank you.
Mary Tilton (matilton@vt.edu)

1. Does your agency currently use population reconstruction methods to estimate white-tailed deer populations?
   - ☐ Yes (go to #2)
   - ☐ No (go to #8)
   - ☐ Not Sure (go to #8)

2. If yes, please describe the population reconstruction method(s) you use. Provide a general description and relevant citations, where available.

3. Do you rely on population reconstruction to set management regulations for deer?
   - ☐ Yes
   - ☐ No
   - ☐ Not Sure

4. Describe the smallest landscape scale for which you apply management regulations from the population reconstruction estimates (*e.g. county, wildlife management unit, state*)

5. Please indicate the applications for which you use population reconstruction (*check all that apply)*

- ☐ To estimate population size
- ☐ To determine population trends
- ☐ To estimate natural mortality rates
- ☐ To estimate harvest mortality rates
- ☐ To estimate recruitment rates
- ☐ As a means to set length of deer hunting season
- ☐ As a means to set number of does (antlerless deer) harvested per hunter
- ☐ As a means to set number of bucks harvested per hunter
- ☐ Other, please specify:_____

6. When performing population reconstruction analyses, do you combine the oldest age classes for a final grouped age class (e.g., fawns, 1.5, 2.5+, etc.)

- ☐ Yes
- ☐ No

If YES, please specify the specific age groupings you use for population reconstruction analyses?

7. Do you correct your estimate from population reconstruction for natural mortality?

- ☐ Yes
- ☐ No

IF YES, please specify the specific correction factor you use. Provide any relevant citations for this factor, if available.

8. Please identify specific problems within your dataset that you believe may cause inaccurate estimates if you were to use population reconstruction:

- ☐ Inaccuracies in aging
- ☐ Short time series (i.e., only 5 years of consecutive sex at age harvest data)
- ☐ Too few animals in harvest aged
- ☐ Lack of information for annual variation in natural mortality rates
- ☐ Insufficient monitoring of annual variation in harvest mortality
- ☐ Annual variation in hunter effort
- ☐ Other, please specify:_____

9. Do you use other independent means to estimate (*i.e., not based on population reconstruction*):

	Overall	**Sex specific?**	**Age specific?**	**Year specific?**
Natural/non-hunting mortality rates	☐ Yes ☐ No	☐ Yes ☐ No	☐ Yes ☐ No	☐ Yes ☐ No
Harvest mortality rates	☐ Yes ☐ No	☐ Yes ☐ No	☐ Yes ☐ No	☐ Yes ☐ No
Reproduction rates	☐ Yes ☐ No	☐ Yes ☐ No	☐ Yes ☐ No	☐ Yes ☐ No

10. Please indicate the degree to which harvest effort in your state changes yearly:

0-10% **10-20%** **20-30%** **30-40+%** **don't know**

11. What is the smallest landscape scale at which your deer harvest data are **recorded**?
    - ☐ Hunt club
    - ☐ Township
    - ☐ County
    - ☐ Wildlife Management Unit
    - ☐ State
    - ☐ Other (please specify:_____)

12. What is the smallest landscape scale at which your deer harvest data are **analyzed**?
    - ☐ Hunt club
    - ☐ Township
    - ☐ County
    - ☐ Wildlife Management Unit
    - ☐ State
    - ☐ Other (please specify:_____)

13. How specific are the age data you collect from deer?

    - ☐ Deer are aged to a specific year class (e.g., 1.5, 2.5,….to as old as possible)
    - ☐ Deer ages are only determined according to age groups (e.g., fawns, 1.5 years old, 2.5+ years old) (please specify the age groupings of the data you collect: _____)

14. In your opinion, how confident are you that the harvest rates are about the same for the oldest two age classes you use in population reconstruction?

Females?

Very Confident		***Somewhat Confident***		***Not Confident***
1	**2**	**3**	**4**	**5**

Males?

1	**2**	**3**	**4**	**5**

15. What is your most recent harvest estimate for deer: _____

16. How do you estimate total harvest of deer (check all that apply):

- ☐ Annual mail survey
- ☐ Mandatory check-in
- ☐ Mail-in report cards
- ☐ Other (specify:_____)

17. Approximately how many harvested animals do you age each year (*a percentage or number is acceptable here*)?

_____

18. How many consecutive years of sex at age harvest data are in your dataset?
_____years

Would you like to receive a summary of the results from this survey?

- ☐ Yes
- ☐ No

VITA

Mary Kathryn Tilton was born in Toms River, NJ. She grew up and attended high school in Marlborough, Connecticut. Mary attended the University of New Hampshire, in Durham, NH, where she earned a B.S. in Biology with a minor in Environmental Conservation in May 2000. As an undergraduate, she realized her passion for conservation and ecology during semesters abroad in Namibia and New Zealand. After taking some time off to work at a ski resort in Colorado, she worked as a state park naturalist in Oregon and as a researcher for The Nature Conservancy. Mary then entered the Department of Fisheries and Wildlife Sciences as a graduate research assistant at Virginia Tech in September 2002. Mary earned her M.S. in Fisheries and Wildlife Science in December 2005.

Mary K. Tilton