ESTIMATING MOVEMENT AND PRODUCTION RATES IN AMERICAN BLACK DUCKS

by

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(Under the Direction of Michael Conroy)

ABSTRACT

American back duck (*Anas rubripes*) populations declined dramatically throughout much of the 1970's and 1980's, and recently have appeared to stabilize at wintering populations of approximately 300,000. Models were developed to estimate movement rates of black ducks among multiple breeding areas, migrations rates from Canadian breeding areas, to US harvest areas, and fidelity rates of individuals back to their respective breeding areas. We utilized banding and recovery data from 1965–1998 to estimate movement rates based on a model developed in program SURVIV. The best model as determined by AIC suggested that movement rates were sex specific. The movement pattern was similar among males and females. Black ducks banded in the western breeding area, exhibit the greatest movement rates to the Mississippi Flyway, and southern Atlantic Flyway, while black ducks banded in the eastern breeding area predominately move to the northern Atlantic Flyway. Fidelity rates were estimated in Program MARK using banding, recovery, and recapture data. The best model identified in Mark, suggested age- and sex-specific fidelity rates. Fidelity rates for adults were very high (>0.95), and rates for young were only slightly less with young females exhibiting the lowest fidelity rate, at 0.8870.

Second, we developed a model to predict production rates, as indexed by fall age-ratios, as a function of environmental and other intrinsic factors from 1990-2001. We utilized an exponential model which was log transformed. A model that included breeding area specific intercepts, black duck density, mallard density, spring temperature, and spring precipitation best predicted fall age-ratios. These models developed herein and their results can all be incorporated into an AHM strategy for American black ducks. Adaptive Harvest Management (AHM) offers the inherent strength of reducing uncertainty about the system through time, thus improving management capability, while striving towards a common objective.

INDEX WORDS: *Anas rubripes*, American black ducks, Adaptive harvest management, Migration, Fidelity rates, Reproduction

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CHAPTER 1

INTRODUCTION

Research Objective

American black duck (*Anas rubripes*; hereafter black duck) populations have experienced declines in population size since the mid 1950’s. The Mid-winter Inventory survey currently estimates around 300,000 (US Fish and Wildlife Service 1999) black ducks remaining in the population. This is down from the 500,000-700,000 (Martinson et al. 1968) routinely counted during Mid-winter Inventory survey in the early 1950’s (US Fish and Wildlife Service 1999). In recent years, black duck populations have appeared to stabilize with the implementation of harvest restrictions.

The objective of this research is to create predictive models to estimate black duck production rates and movement rates. Modeling production rates focus on identifying and quantifying the relationship between environmental conditions such as spring temperature and precipitation during the breeding season and the resulting recruitment of young into the fall population. Models of movement rates quantify the rate at which individuals move among breeding areas and the propensity with which individuals return to a given breeding area over time. These are two areas of black duck population dynamics that have received very little attention, but are necessary for a comprehensive multiple breeding population Adaptive Harvest Management (AHM) strategy for black ducks (Conroy et al. 2002, 2003).

Summary of Problem

American black duck populations declined an average of 3% per year between 1955-1988. However, during this same period, counts in the Atlantic Flyway declined 43%, and 64% in the Mississippi Flyway with most of the decline occurring between 1955-1959. This raised concern that a hunting moratorium would need to be imposed on black ducks. A moratorium on black ducks would result in a significant loss of hunting opportunity for the eastern portions of Canada and the United States, as the black duck is the dominant species of the waterfowl harvested. Disagreement among managers and biologists about the cause of population declines only serves to hinder efforts to restore black duck populations to previous levels.

In 1995 the US Fish and Wildlife Service began to use Adaptive Resource Management to manage mid-continental mallard populations (USFWS 1999). Briefly, the ARM paradigm provides a framework for which managers and biologists can recognize system uncertainty as an attribute of management, and attempt to reduce uncertainty through management while striving towards some long term objective (Williams and Johnson 1995). Managing black ducks under this paradigm could aid in restoring population levels through modification of harvest rates, while reducing uncertainties associated with population regulation.

Significance of Research

The results from this research will serve the research and management community in several ways. There exists a fairly comprehensive database about the ecology and management of the black duck after 50 years of research, yet key uncertainties still remain about the effect of management actions on the long-term trajectory of the population. There are general methodologies that allow us to examine movement patterns of black ducks, but often require the estimation of unnecessary or nuisance parameters. We hope to extend these methodologies to specifically suit the modeling of black ducks movement rates among breeding and harvest areas. Production or recruitment into the population is estimated on an annual basis through surveys and harvest data. Although estimates of production are available, it remains unclear what stochastic environmental processes affect reproductive rates and the impact that mallards (*Anas platyrhynchos*) have on the population, if any. From this research I plan to develop and apply statistical models for estimating movement rates of individuals from a harvested population. This research contributes important information the black duck AHM model currently under development, which, when completed, will aid managers in setting harvest regulations and facilitate the recovery of black duck populations.

Data Sources

Data for these analyses were obtained from the Canadian Wildlife Service (CWS), Environment Canada, the US Fish and Wildlife Service (USFWS), US Geological Survey (USGS), and the Bird Banding Laboratory (BBL). Data fall into four broad categories: 1) banding and recovery data; 2) harvest data; 3) population survey data; and 4) environmental data. Banding and recovery data are required to estimate survival and reproduction rates, as well as breeding and harvest area affinities. Harvest data are derived from two independent surveys: the parts collection survey and the hunter questionnaire survey. These sources are combined to determine harvest rates and age ratios for use in modeling black duck production rates. The United States and Canada use different survey methods to estimate population size. During the spring, the CWS surveys a sample of 250, 25-Km^2 plots, using helicopters over a portion the black duck breeding grounds (B. T. Collins CWS, Unpublished Report). During this same period the USFWS conducts an aerial transect survey using fixed-wing aircraft. These surveys serve to estimate breeding abundances of waterfowl, which are conducted annually in May. Summarized environmental data were obtained from Environment Canada, as the majority of black duck breeding occurs in Canada. These data serve as possible predictors of black duck production.

Literature Review

The 1950's and 1960's was a period of decline for continental waterfowl populations. At the time, annual surveys of waterfowl on the wintering grounds along the eastern United States indicated that black ducks were continuing to decline at a precipitous rate. In an attempt to halt the decline, harvest restrictions were implemented for black ducks in 1983, which remain in effect to date. While population levels have stabilized, it is unclear whether the stabilization is a result of harvest restrictions or changes in other contributing factors.

The management of the black duck has been hampered by a lack of understanding of factors that affect black duck populations, and disagreement among biologists and managers about the potential for recovery through management and harvest regulations (Conroy et al. 1998, 2002). To date there are four factors for which substantial support exists to attribute them in whole or part as the cause of black duck population decline. The four factors considered and summarized by Conroy et al. (2002) were: 1) harvest mortality, 2) decline in the quantity or quality of breeding habitat, 3) decline in the quantity or quality of wintering ground habitat, and 4) inter-specific competition or hybridization with mallards. Herein, I briefly review each of the potential factors for the black duck population decline.

Prior to 1969, the black duck constituted the species with the greatest numbers in a hunters bag in the Atlantic Flyway. In 1970, the mallard surpassed the black duck in total number harvested in the Atlantic Flyway, and by 1982 mallards outnumbered black ducks in the harvest by 2 to 1 (Blandin 1982, Rogers and Patterson 1984). Harvest was posed as a potential cause for the black duck decline when annual winter surveys indicated severe downward trends in the population. However, the extent that harvest has affected black duck populations has been a source of contention within the research and management community, as black duck counts vary significantly when examined on a regional basis. Changes in long-term numbers appear to be minimal in the northern Atlantic Flyway, while severe declines have occurred in the southern Atlantic Flyway (Rogers and Patterson 1984). Much of this contention lies in our lack of complete understanding of the relationship between harvest regulations, hunting kill rates, nonhunting mortality rates, and survival rates. If harvest mortality negatively impacts black duck populations, a relationship would exist between survival and harvest.

In a seminal report, Anderson and Burnham (1976) formulated two hypotheses that demonstrated possible extremes of the relationship between the harvest mortality rate and the annual survival rate. The additive mortality hypothesis (AMH) states that hunting kill rates are independent of nonhunting mortality rates and population density (Anderson and Burnham 1974, Nichols et al. 1984, Conroy and Krementz 1990). The compensatory mortality hypothesis states that there exists a negative (compensatory) relationship between nonhunting mortality rates and hunting kill rates. This relationship purports that below some threshold level, increases in hunting kill rates are compensated for by a reduction in nonhunting mortality rates, leaving annual survival rates unchanged. In order for compensation to occur, nonhunting mortality must act in a density-dependent manner, although the mechanism in which density-dependence occurs is not explicitly stated within the relationship (Nichols et al. 1984). If hunting kill rates exceed the threshold level, nonhunting mortality sources are unable to compensate, causing a reduction in annual survival rates, in accordance with the AMH. Nonhunting mortality rates are not directly estimable from band recovery data, but the two competing hypotheses can be expressed in terms of the relationship between kill rates and annual survival rates, which are estimable from banding data. The AMH predicts that a negative relationship exists between kill rates and annual survival rates, whereas the CMH predicts no relationship between kill rates and annual survival rates (Anderson and Burnham 1976, Nichols et al. 1984). These two hypotheses represent extremes in the relationship of kill rates, nonhunting mortality rates, and survival rates, and it is probable that the "true" relationship for a population lies at some intermediary between total additivity and total compensation (Nichols et al. 1984). An understanding of which relationship exists for black ducks has significant management implications, as well as determining the effect that harvest, and harvest regulations have on population status.

Several studies have attempted to marshal evidence in favor of the AMH or CMH. Geis et al. (1971) used the composite dynamic and relative recovery rate methods to estimate mortality rates from band recovery data. During years of liberal regulations, recovery rates were higher for immature black ducks than in years with restrictive regulations. Data relating recovery rate to regulations were inconclusive for adults. Geis et al. (1971) found a significant correlation between recovery rate and annual mortality rate suggesting the AMH for black ducks. It was later shown by Burnham and Anderson

(1976) that the composite dynamic methodology used by Geis et al. (1971) contained sampling correlations among estimators leading them to spurious conclusions.

Blandin (1982) used newly developed methodology described by Brownie et al. (1978) to study the population characteristics of black ducks. Blandin (1982) concluded that there was a great deal of variation in both survival and recovery rate estimates, and that harvest mortality is a greater proportion of the total mortality in black ducks than it is for mallards. In addition, Blandin (1982) found a significant negative correlation for adult males, and non-significant but negative correlation between recovery rates and winter survival rate, suggesting some relationship between harvest and survival. Blandin (1982) concluded that temporal and spatial variation existed in recovery rates based on preseason and winter bandings, but survival rates remained unchanged. An absence of a statistical relationship between recovery rates and survival rates is consistent with the compensatory mortality hypothesis. Conroy and Blandin (1984) used reward banded black ducks to estimate the band reporting rate and determine if geographical or temporal differences existed in the reporting rates for black ducks. There was little evidence that band reporting rates varied geographically or temporally (Conroy and Blandin 1984). Using additional years of banding and recovery data, Krementz et al. (1987) repeated Blandin’s (1982) work and found few differences in survival and recovery rate estimates using the updated band reporting rate estimated by Conroy and Blandin (1984). Krementz et al. (1987) also found temporal variation in the recovery rates, while survival rates remained constant suggesting weak evidence of compensatory mortality in black ducks. Nichols et al. (1987) acknowledged that temporal variation in survival and recovery rates existed in black ducks, and attempted to determine if the patterns of variation were similar in areas where black ducks and mallards were sympatric. Nichols et al. (1987) found that the mean recovery rates based on preseason bandings were similar for black ducks and northeastern mallards, and that the difference in population status cannot be attributed to higher harvest rates of black ducks. Correlation analysis showed that black ducks and mallards from the same breeding areas are exposed to similar patterns of year-to-year variation in hunting pressure suggesting that if mallards are increasing and black ducks decreasing, then the cause must lie in reproductive rates, immigration rates, or both (Nichols et al. 1987). A re-analysis of Blandin (1982) by Krementz et al. (1988) with six additional years of banding and recovery data increased the statistical power of their original tests. Additional data suggested that young males exhibit additive mortality, while evidence concerning adults remained unclear. They suggested that compensatory mortality occurs for adult females and adult males in the Atlantic flyway, but no evidence existed for either sex in the Mississippi flyway. Given these conclusions, young black ducks may be particularly vulnerable to hunting. Certain subpopulations may be of greater importance to the black duck population, because they may contribute a larger proportion of young to the fall population, and it may be unwise to manage the entire continental population on the assumption of compensatory mortality. Francis et al. (1998) estimated the effect of harvest restrictions on survival and recovery rates of black ducks. They postulated that restrictive regulations led to decreased harvest pressure and increased survival rates. They concluded that additive mortality existed for some age-sex classes of black ducks between 1955-1993, with adult's possibility exhibiting compensatory mortality post-1983 (Francis et al. 1998). Furthermore, they state that there was insufficient information to predict how compensatory thresholds change in response to varying population densities and available habitat (Francis et al. 1998).

Although no study has been able to conclusively support either the additive or compensatory mortality hypothesis, all suggest that harvest rates and harvest regulations do have some impact on black duck survival rates. The datasets that exist to determine the impacts of harvest on black ducks are often correlated with one another, thus, there are confounding issues that must be considered when estimating parameters. Parameters contained within the models used to estimate the effects of harvest are not independent (i.e., covariance is not zero). Partitioning the dataset, estimating only one parameter from each dataset, eliminates covariance among estimators. The drawback to dataset partitioning is that estimated parameters are of poorer precision. Second, the population status of black ducks and harvest regulations are not independent. Regulations for all duck species are set such that in years with high duck production, the harvest is liberalized, and in years with poor duck production harvest regulations are set very restrictive. This results in serial correlation of harvest regulations with population size and habitat conditions, in turn confounding any effect harvest may have on population status (Williams and Johnson 1995). In order to separate the variation that exists in black duck demographic parameters, and the effect harvest has on population status, manipulative experimentation with proper controls and replication (Anderson et al. 1987, Conroy and Krementz 1990) or adaptive management (Walters 1986, Conroy et al. 2002) is needed. Data for black ducks suggest different hypotheses about the effect of harvest on population status, and survival rates depending on the time series and dataset examined, thus, other factors must be examined for potential effects on black duck population trends.

The second putative factor is a reduction in the quantity and/or quality of breeding habitat. The breeding distribution of the black duck extends throughout eastern North

American from the Great Plains, east to the Maritime Provinces of Canada. The southern extents are the Great Lake states, and along the Atlantic coast to New Jersey, Delaware and Maryland (Bellrose 1980). These areas have witnessed considerable drainage of coastal marsh, and the clearing of large tracts of forest, particularly in southern Canada and northeast United States for timber, agriculture, and urban growth. It is hypothesized that these practices along with releases of captive-reared mallards (Rusch et al. 1989, Heusmann 1974) provided a route for mallards to infiltrate the black duck range and compete for resources (discussed later).

Agricultural and urban development within black duck breeding areas could have resulted in losses of critical habitats used by females for nesting and brood rearing in portions of the black duck breeding range. Nesting occurs in low densities across the breeding range, which may result from poor nutrient availability (Seymour and Jackson 1996), or territoriality among pairs (Dwyer and Baldassarre 1994). Habitats, in which black ducks have been documented to nest, include upland hardwood forests, abandoned nests of other bird species, sedge-meadow bogs, and tidal marsh areas (Kirby 1988). The dominant nesting habitats are forested wetlands in the boreal region, and coastal marshes in the southern extent of its breeding range (Bellrose 1980).

Habitat selection by black ducks has been examined through comparison of habitat use and habitat availability, or through the measure of specific habitat characteristics such as, water quality, invertebrate biomass, vegetation density, wetland size, and wetland area, in relation to some survival or reproductive output. These measures serve as indexes to habitat quality or quantity. During the breeding season black ducks require a variety of habitat types to fulfill the needs of nesting and brood rearing. Ringelman (1980) found that female black ducks prefer emergent, evergreen forested, and deciduous shrub wetlands. Specifically, black ducks selected small isolated wetlands with flooded timber, typical of beaver flowages (*Castor canadensis*). In the St. Lawrence river valley of Quebec, coastal breeding black ducks utilized saltmarsh habitats in greater proportion to man-made freshwater or brackish impoundments during nesting (Belanger and Lehoux 1994). Black ducks with broods utilized man-made impoundments with greater frequency than saltmarsh habitats (Belanger and Lehoux 1994). Merendino and Ankney (1994) evaluated habitat use by breeding black ducks and mallards in southern Ontario, and concluded that both black ducks and mallards utilize highly productive wetlands, but wetlands utilized by mallards were more fertile than those used by black ducks. Productivity of wetlands was determined by water chemistry (alkalinity, total phosphorous, magnesium, conductivity) and physical wetland characteristics (wetland size, shoreline irregularity).

The quantity of breeding habitat available to black ducks has declined over time. Between 1961 and 1991, eastern Canada lost 6.7 million hectares of forest, while during the same period the US lost 1.3 million hectares of forested wetlands (Conroy et al. 2002). Loss of this much habitat alone could have caused the decline witnessed by black duck populations. A major portion of the habitat loss occurred in southwestern Ontario, where surveys once recorded black ducks as being plentiful, are now recording mallards as the dominant species. Population declines in core breeding areas, like central Quebec, and the Maritime Provinces have not been as severe, and may have increased in certain areas. This may be because large tracts of forest remain relatively undisturbed in core breeding areas. Although it is possible and likely that the quality or quantity of black duck breeding habitat has declined over time, the quantification of what quality habitats are, and what habitats black ducks select, is difficult to determine with certainty. It has been difficult to quantify actual losses of black duck breeding habitat, as historical databases were not designed to measure wetlands from a wildlife perspective. The advent of remote sensing will eventually allow for better identification black duck breeding habitats and quantification of habitat changes through time.

If the quality or quantity of black duck habitat has declined the carrying capacity of these habitats are effectively reduced. This reduction could have a number of impacts on the population such as a decline in the breeding abundance, depressed reproduction rates, depressed survival rates, and reduced fledging success. If the quantity of breeding habitats were limiting the recovery of black duck populations, one would predict a correlation between habitat quantity and demographic parameters such as recruitment (fall age-ratio), survival, or breeding abundance (Conroy et al. 2002). If changes in the quality of breeding habitat were responsible, one would predict a correlation between indicators of habitat quality and breeding abundance, survival, or recruitment (Conroy et al. 2002).

Black ducks migrate and winter at various latitudes throughout the Mississippi and Atlantic flyways. The greatest proportion of black ducks winter along the Atlantic coast, concentrated in the Mid-Atlantic States, utilizing coastal estuarine marshes, and inland wetlands (Conroy et al. 2002). During the winter, black ducks require adequate food, open water, shelter from extreme temperatures, and minimal human disturbance (Lewis and Garrison 1984). The diet of wintering ducks consists of both plant and animal matter. Eelgrass (*Zostera marina*), pickerelweed (*Pontederia chordata*), widgeon grass (*Ruppia maritima*), smooth cordgrass (S*partina alternaflora*), wild rice (*Zizania aquatica*), and smartweeds (*Polygonum* spp.) are dominant plant species in the diet of wintering black ducks (Conroy et al. 2002). Coastal wintering black ducks rely on several species of mollusk, crustacean and insects commonly located on mudflats, which are accessible with receding tides. As latitude increases the proportion of animal matter in the diet increases (Conroy et al. 2002). Black ducks that winter in Tennessee predominately use palustrine emergent, or scrub-shrub wetlands, which are small bodies of water (Chipley 1995). In coastal areas black ducks typically use small bodies of water such as ponds that are generally dispersed throughout the salt marsh. When these freeze black ducks are forced to deeper lakes, and large rivers that remain ice free through the winter.

Increased agricultural, forestry, and urban development along the Atlantic Coast has resulted in the drainage of many wetlands for mosquito ditching, potentially reducing or eliminating important food sources required by black ducks to maintain body mass and energy reserves through the winter. It has been suggested that winter is the most stressful period for black ducks (Reinecke et al. 1982). The inability to obtain adequate resources could lead to reduced survival, abundance, or future recruitment. Conroy et al. (2002) compiled estimates of wetland acreage for states along the Atlantic Coast during 1955-98, to determine long-term changes in available wetland area. Significant loss of habitats have occurred in almost all states during some period between 1955-97 (Conroy et al. 2002). Most notable losses of coastal wetland area occurred in New Jersey, Florida and New York. In 1948, winter surveys in Florida counted 75,000 black ducks; the same survey in 1998 counted 0 black ducks (Conroy et al. 2002). Other states such as Maryland have also witnessed dramatic declines in winter counts of black ducks, yet the loss of coastal wetland area has been minimal. In contrast, New Jersey winter black duck counts between 1993-1997 were greater than counts conducted between 1955-1959, despite a 20% reduction in coastal wetland area (Conroy et al. 2002). In the last 50 years the amount of available wetlands has declined substantially, yet correlation between the decline of black duck populations and the quantity of wintering habitat cannot be interpreted as an ultimate cause for the decline of black ducks.

Black duck wintering grounds have undergone extensive changes. While a sufficient amount of habitat may remain to support large populations of wintering black ducks, it is plausible that the quality of these habitats have declined. Habitat quality has been addressed by examining factors such as contaminants, lead shot, nutrient enrichment, and human disturbance, but few have addressed their effects on waterfowl (Conroy et al. 2002). If the quality of wintering habitats is poor, one might expect the body condition of blacks ducks to be poor. The body condition of black ducks in Maine declined as the winter progressed, thus birds operated with negative energy budgets (Reinecke et al. 1982). The body condition of black ducks wintering in Virginia did not vary through the winter period and may have improved slightly (Morton et al. 1990). The body condition of black ducks wintering in New Jersey was intermediate to those wintering in Maine and Virginia (Costanzo 1988). It has been found that during periods of severe weather black ducks mobilize endogenous proteins and lipids to maintain nutritional requirements. The utilization of endogenous proteins and lipids are likely to negatively impact the survival rates of black ducks. If wintering habitats have had a significant influence on the regulation black duck populations, one would expect to predict a positive correlation between a measure of winter habitat and demographic parameters, such as winter survival or abundance. Conroy et al. (1989), and Pollock et al. (1989) detected a positive relationship between winter body condition and winter survival for adult black ducks. Declines in the quality or quantity of wintering habitats coincide with declines in the black duck population suggesting a possible linkage, however evidence of this is purely correlative.

The fourth putative causal factor of the black duck population decline is interactions with mallards through competition for resources, or introgressive hybridization. In recent years, the range of the mallard has expanded eastward to become confluent with that of the black duck. This increase in range is hypothesized to be a result of forest clearing for development, agricultural practices, and the creation of small marshes from federal assistance programs (Heusmann 1974). In addition to these forest practices, state agencies and private organizations have raised and released pen-reared mallards as part of stocking programs on state and private hunting reserves (Heusmann 1991, Longcore et al. 1987).

Mallards and black ducks have similar physical characteristics and courtship behaviors. In a study of captive mallards and black ducks, male mallards were shown to dominate over male black ducks and displace them when competing for receptive female black ducks (Brodsky and Weatherhead 1984; Brodsky et al. 1988; D’Eon, Seymour and Boer 1995). Although this has been shown in captive ducks, there is conflicting evidence that this pairing structure occurs in free-ranging black ducks and mallards (Morton 1998). When mixed pairing does occur, the resulting hybrids are fertile and show no evidence of reduced fertility or viability, indicating a lack of reproductive isolating mechanisms that typically exist between species (Hedrick 1984:307). This has led some to question the taxonomic classification of the black duck as a species versus dark color mallard morph (Ankney et al. 1986). Analysis between allopatric and sympatric black duck and mallard populations were virtually identical at the genetic level (Ankney et al. 1986). Further analysis of mitochondrial DNA by Avise et al. (1990) suggested a close evolutionary relationship between black ducks and mallards, and that the black duck is a recent derivative of a more broadly distributed mallard-black duck ancestor.

The lack of physical barriers isolating black ducks and mallards, and similar life histories, have caused some to hypothesize that mallards out compete black ducks for resources while on the breeding or wintering grounds. In areas where black ducks and mallards occur in sympatry on the breeding grounds, there are several competitive interactions in which mallards may exclude black ducks from necessary resources. D'Eon et al. (1995) reported that mallards in New Brunswick, Canada dispersed to initiate nesting up to 12 days earlier than black ducks. Dispersal of black ducks coincided with the removal of ice in areas that were subsequently used for territories (D'Eon et al. 1995). This suggests that mallards may be physiologically prepared to nest earlier than migrant black ducks. If high quality nesting habitats are limited this would afford mallards the advantage to access and defend these sites, displacing black ducks to inferior habitats (D'Eon et al. 1995). Once a pair has become established in a territory the resident male was able to successfully defend his territory from intruders, regardless of species (D'Eon et al. 1995). In contrast, Coulter and Miller (1968) noted that black ducks in the Lake Champlain region initiated nesting activities prior to that of mallards. The close evolutionary history between black ducks and mallards, and the degree, to which there is interspecific competition for mates and resources, could plausibly cause the decline of black duck populations. If there were a negative impact of mallards on black ducks, it would manifest itself in reduced nest success, or reduced survival in areas of sympatry.

There are several factors plausibly associated with the decline of black duck populations, but the evidence does not conclusively support one factor as the sole cause of population decline. It is also plausible that the decline of black ducks may be the result of multiple factors acting concurrently. The extensive scale and complexity of this problem is large enough to prevent manipulative experimentation, thus other methods must be employed. A solution to the problem of current and future black duck management must be both politically palatable, and compatible with the current regulatory and data gathering processes.

In an attempt to restore black duck population levels, biologists have proposed other management strategies. One strategy currently being explored is Adaptive Resource Management (ARM), which allows managers to evaluate management decisions in the face of uncertainty through a series of models that predict different population trajectories under each hypothesis being considered (Walters 1986). The goal of adaptive resource management is to obtain the greatest return from a resource based on some objective, while reducing key uncertainties associated with the system. The adaptive management framework differs from traditional hypothesis-testing framework in that multiple competing hypotheses can be evaluated simultaneously. Simultaneous comparison of several hypotheses, allows managers to apply gathered information to determine the relative importance of all hypotheses in a common framework.

ARM is a favorable strategy, because it is currently implemented for the management of mallard stocks. Previous work on mallard populations has identified three stocks across the United States and Canada, an eastern population, a western population, and a mid-continental population. The mid-continental population is the largest, numbering approximately 10.8 million, and is the most heavily exploited population (Martin et al. 1978). The mid-continental population nests in the parkland and prairie pothole region of the United States and Canada, and winters in the southern states of Texas, Louisiana, Arkansas, and Mississippi. The prairie pothole region is a simple grassland system with periods of rain and drought. An adaptive harvest management strategy was relatively simple to implement into this system for several reasons. The dynamics of this mallard population are well understood, a result of many studies and surveys that focused on estimating demographic parameters, population size, distribution of the population, and the response of the population to a changing environment.

Black duck population dynamics are more complex than those of mid-continental mallards. The population numbers approximately 300,000, an order of magnitude smaller than mallard populations (US Fish and Wildlife Service 1999). Thus, minor mistakes in management could have significant effects on the population. The Mid-winter Inventory (MWI), which is a survey conducted in January while birds are on the wintering grounds by the US Fish and Wildlife Service, and states within the Atlantic flyway is used as an index to population size. The lack of a rigorous statistical design and variation in methodology among participating states, mid-winter counts likely contain substantial unmeasured error in estimates of population size (Eggeman and Johnson 1989), and no way to estimate precision of population size estimates (Conroy et al. 1988). In addition to the MWI, the USFWS and CWS implemented breeding ground surveys in 1990 in an attempt to obtain better estimates of the breeding population and annual reproduction of eastern breeding waterfowl. The estimates obtained from these surveys often are of low precision due to the difficulty surveying a vast area of forest and locating significant concentrations of black ducks (Kazyinski and Chamberlain 1968).

Given the extensive research that has been focused on black ducks to date, there are still several aspects of population regulation that remain unstudied. One aspect is that a relationship that may exist between annual reproduction and abiotic or biotic factors.

Most notably, this type of relationship has been identified in mid-continental mallards. In years with extensive rainfall, recruitment of young into the population is high. In these years all of the potholes are at full capacity, which decreases competition among individuals for resources such as nest sites, and food for young. In addition, females are thought to be more dispersed across the landscape, potentially reducing predation. Identification of this type of relationship in black ducks has important implications for black duck harvest management. Models could be developed to predict recruitment based on spring surveys and auxiliary data. Managers would then have estimates of production, and thus fall flight prior to setting harvest regulations rather than estimating what the recruitment was from data collected post-hunting season, as it is currently done. This would allow managers to make better-informed management decisions regarding appropriate season lengths and bag limits. This type of relationship may be weak or undetectable in black ducks due to persistent inland wetlands on the breeding grounds, and the presence of coastal marshes. Adaptive management can be used as a tool to identify the best relationship from among several competing relationships (Figure 1.1).

Movement and migration patterns are another aspect that has received little attention at the continental level. Research conducted by Geis et al. (1971), Blandin (1982), and Pendleton and Sauer (1992) regarding movements and migration serve only to identify possible population units on the basis of survival and recovery rate characteristics, but assume no relationship among the units (i.e., spatial independence). Estimates of movement and migration rates would allow populations to be forecast through the hunting season. Estimates of fidelity to specific breeding areas are needed for transitioning birds back to respective breeding grounds in a population model. Fidelity rates would also aid in understanding the impact of harvest on the wintering grounds to specific breeding populations. Understanding movement and fidelity would allow the development of spatially stratified population models. Spatially stratified models would allow for a more realistic representation of true population dynamics, and in theory, lead to better recovery strategies with AHM (Figure 1.1).

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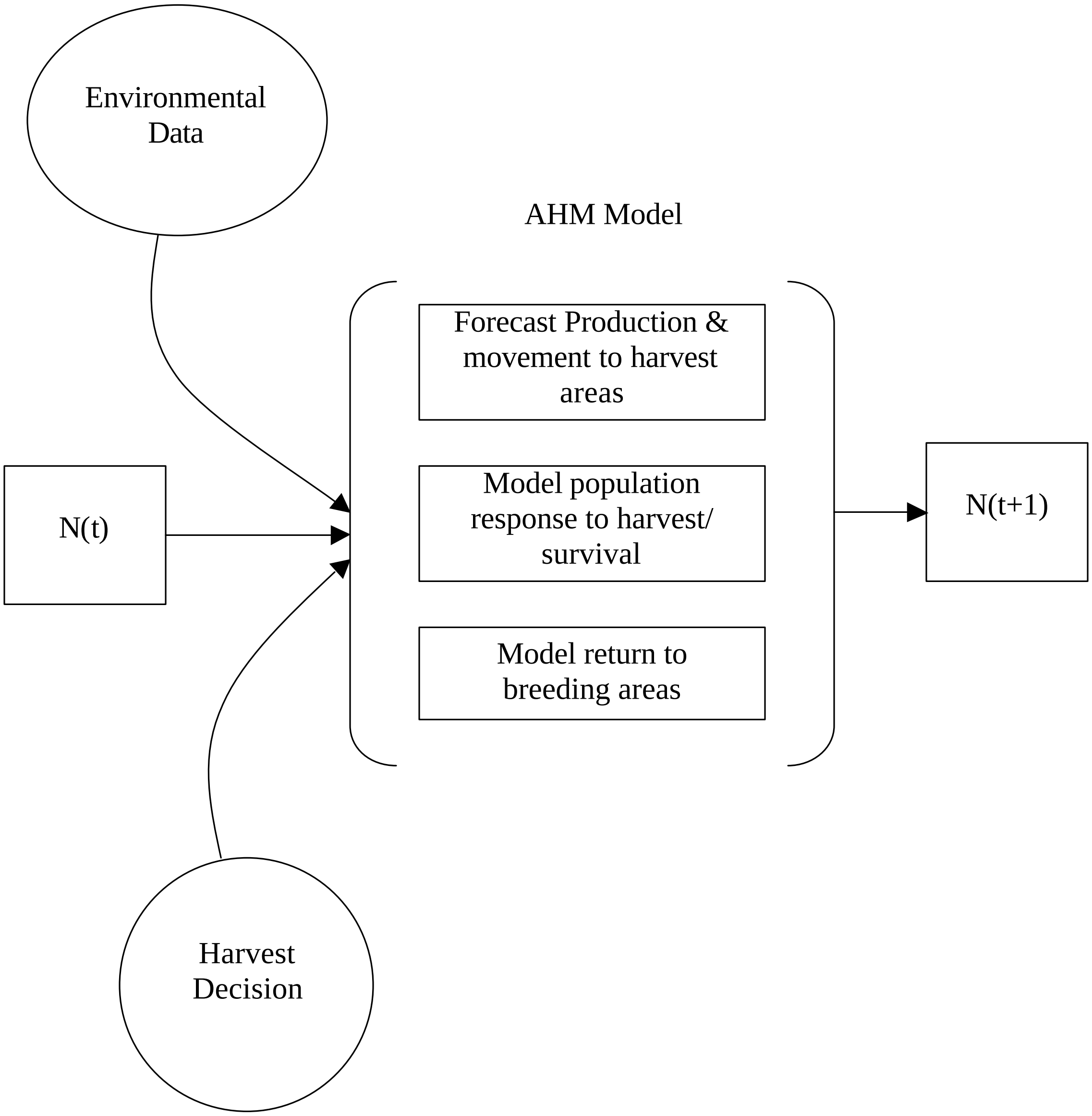
Figure 1.1. A conceptual model of the adaptive management process specifically highlighting areas of research investigated herein.



CHAPTER 2

ESTIMATING MOVEMENT AND FIDELTY RATES OF AMERICAN BLACK DUCKS [1]

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[1] Zimpfer, N. L., and M. J. Conroy. To be submitted to *The Journal of Wildlife Management*

The process by which waterfowl regulations are promulgated has evolved as research has documented a better understanding of the underlying biological processes that regulate waterfowl populations (Johnson et al. 1993). Increased knowledge of waterfowl population dynamics has resulted in additional complexity in population models for determining harvest regulations. The development of adaptive resource management (ARM; Walters 1986) has allowed waterfowl managers to incorporate alternative models and harvest management objectives into a common framework to identify regulations that achieve long-term objectives (Williams and Johnson 1996). Currently, black duck harvest regulations are set as if all black ducks originate from a common breeding population. Thus, black ducks in Ontario are treated identically to black ducks in the Maritime Provinces in terms of the underlying biological processes that drive their populations. However, survey data suggest that black duck numbers in Ontario are declining while black duck numbers in the Maritimes are stable or increasing (Conroy et al. 2002). Banding and recovery analyses also have concluded that black ducks from these areas exhibit differences in survival and recovery rates (Krementz et al. 1987,1988; Blandin 1982).

Black duck management may benefit from the use of models that incorporate multiple breeding stocks of black ducks. Within an ARM framework, spatial stratification may offer advantages over traditional single population models. Spatial stratification would aid in reducing uncertainty surrounding east-west differences in population size and vital rates that would not otherwise be captured if modeled as a single population. However, with finer scale resolution of management comes additional complexity, and the potential for logistical infeasibility. To examine these models for use in management we must identify how many breeding populations exist, what kind of relationship exists between these stocks, and what is the likelihood of individuals to return to a breeding area, given they were born or reproduced there (i.e., fidelity).

Several studies have proposed multiple breeding populations of black ducks on the basis of similarities in survival, recovery rates, and recovery distributions in adjacent banding reference areas. Using preseason banding and recovery data from 1946 to 1960 Geis et al. (1971) posed 25 banding reference areas for black ducks. In 1982, Blandin derived an additional two banding reference areas based on additional banding data. Pendleton and Sauer (1992) arrived at six distinct populations using additional banding and recovery data, and clustering techniques to group adjacent degree blocks. While these analyses are beneficial for identifying populations, information is still lacking about the movements of black ducks among potential populations as well as movement patterns from particular breeding populations to specific harvest areas.

In addition, there is a lack of sufficient quantitative information about fidelity of black ducks to specific breeding areas. It is suspected that that black ducks exhibit a high degree of fidelity (Blandin 1982), but this has not been studied extensively. In a study of black ducks breeding in Maine and Vermont, Coulter and Miller (1968) found that 25 percent of black duck hens were found to nest again in the same general area in later years. They suggested that the return rates of hens were likely to be greater as they were unable locate all nests, and capture hens known to have bands. Studies of other species have suggested that fidelity rates are likely to by high, but vary among ages and sexes (see Anderson et al. 1992).

We used banding and recovery data of black ducks with the objective of quantifying movement and fidelity rates for multiple breeding populations of black ducks across age, sex, and time. In this analysis, we define “fidelity” as the probability of individuals returning to a particular breeding area given that an individual had previously reproduced there, or was hatched there. We use this term interchangeably with the terms breeding philopatry, or natal philopatry originally defined by Greenwood (1980).

METHODS

Movement rates

Banding and recovery data were obtained from the Bird Banding laboratory (BBL), in Laurel, Maryland. Only "normal wild" black ducks banded preseason (1 July–30 Sept.) in Canada between 1965-1998 were included for analysis. Recoveries included only black ducks shot or found dead during the hunting season. Banding and recovery data were stratified by age, sex, time, banding, and recovery area. Banding, or breeding areas, were derived from the Black Duck Joint Venture (BDJV) breeding ground survey (Black Duck Joint Venture 1992).

The BDJV breeding ground survey consists of 250, 25-km^2 plots divided into four strata: 1) Atlantic Highlands, 2) Eastern Boreal Region, 3) Central Boreal Region, and 4) Western Boreal Region (Figure 2.1). Plots within the Atlantic highland strata are located throughout the provinces of Prince Edward Island, Nova Scotia, New Brunswick, and southern Quebec east of 76^o 30'. Plots within the eastern boreal region are those that lie within Newfoundland, Labrador, and in Quebec north of the St. Lawrence River (Figure 2.1). The central boreal strata are those plots located in Quebec from 70^o 30'-76^o 30'. Plots in the western boreal region fall within western Quebec, and Ontario. These four strata were divided to create three breeding areas (Figure 2.2). The Atlantic Highlands strata and the adjacent Eastern Boreal strata form the eastern breeding area. The remaining strata make up the central and western breeding areas, respectively. Harvest units were defined on the basis of recovery distributions from Canadian banded black ducks. Harvest areas in Canada coincide with breeding area definitions. Harvest areas in the United States were constructed under the constraint that they could not greatly alter the current structure in which regulations are set (i.e. flyways; Figure 2.2). The Mississippi Flyway was assigned a single harvest unit, as in recent years the Mississippi flyway contributes only a small proportion to the total black duck harvest. Recovery distributions in the Atlantic Flyway suggested that it might serve as wintering areas for two breeding populations of black ducks. The flyway was divided into a northern and southern harvest areas. The north Atlantic Flyway (AFN) included Maine, New Hampshire, Vermont, Rhode Island, Connecticut, Massachusetts, New Jersey, Delaware, and Eastern New York. The southern Atlantic Flyway (AFS) included Pennsylvania, West Virginia, Maryland, Virginia, North Carolina, South Carolina, Georgia, Florida, and western New York. The New York east-west dividing line follows the New York State Department of Environmental Conservation waterfowl hunting zone boundaries which occurs at 70^{o} 10’ (North-South Interstate I-81). Dividing New York improved the discrimination of movements from breeding units to harvest units. In total we considered three breeding areas, and six harvest areas for the estimation of movement rates.

Movement rates were estimated using a multinomial likelihood model constructed in program SURVIV (White 1983). The general likelihood methodology, for a single age-sex class is derived in Appendix A. Birds banded in one of three breeding areas may remain within the area of banding and be harvested, or move to an adjacent breeding area, and become eligible for harvest there (Figure 2.3). It is assumed that individuals that moved to an adjacent breeding area are not harvested differentially to individuals that did not move. Conditional on surviving the Canadian hunting season, banded individuals migrate to one of the three US harvest areas and are then either harvested or not harvested. Individuals that do not move from Canada to the US and are not harvested become part of the US non-harvest. The model estimates, area, age, sex, and time specific direct recovery rates, movement rates among breeding areas, and movement rates from breeding areas to harvest areas (Figure 2.3). Direct recovery rate (f) was defined as the probability that a banded bird was shot, recovered, and reported in the first hunting season after banding. Movement rates (m_{ij}) were defined as the probability that a bird banded in area i will be recovered in area j during the first hunting season after banding. However, movement parameters are not uniquely identifiable, without the implementation of constraints.

Fidelity rates

Definitions of breeding and harvest areas were identical to those used in the estimation of movement rates. Only "normal wild" black ducks banded preseason (1 Jul–30 Sept.) in Canada between 1966-2000 were included for analysis. Recoveries included only black ducks shot or found dead during the hunting season. Recaptures were obtained from the BBL recoveries file, and limited to encounters in years different than capture.

Fidelity rates were estimated in Program MARK (White and Burnham 1993) using the joint recapture-recovery model option developed by Burnham (1993). The dataset included 34 encounter occasions (1966-2000). Twelve attribute groups; three breeding areas, and four age-sex classes, were identified in which it was foreseeable that fidelity rates may vary. A logit link function was used to maintain the parameter space between 0.0 – 1.0.

Four parameters are estimated by the joint recapture-recovery model: apparent survival rate (*S*), capture probability (p), recovery rate (*r*), and fidelity rate (F). Apparent survival rate is the probability of surviving and not permanently emigrating over the interval *t* to *t+1*. Capture probability is the probability of capture, conditional on the individual being alive and in the sample (Cooch and White 2001). Recovery rate is the probability of being shot or found dead and reported between *t* and *t+1*. Fidelity rate is defined as the probability that an individual banded in area *j* at time *t* will return to area *j* in *t*+1, given it survives. We examined models that included both interactive and additive effects. Models were ranked using AIC_c. Mark-recapture data tend to be over-dispersed; because of a lack of independence among individuals being studied or heterogeneity in the parameters themselves resulting in underestimated variances (Anderson et al. 1994). This was accounted for this through the correction of AIC_c by $\hat{c}$ where

$$\hat{c} = deviance / df\ .$$

The standard calculation of $\hat{c}$ led to unrealistic estimates suspected to be a result of sparse recovery and recapture data, in that there were a number of cells that contained no recoveries or recaptures. Included in Program MARK was a bootstrap goodness-of-fit procedure which given a model evaluated goodness-of-fit from simulated data, thus, not violating assumptions of over-dispersion, and independence among individuals. We ran 100 bootstrap simulations, calculating the model deviance for each run. Based on these 100 simulations, we calculated $\hat{c}$ as the ratio of the deviance estimated from actual data to the average deviance from simulated data.

RESULTS AND DISCUSSION

Movement rates

Movement data included a total of 176,142 bandings and 16,598 recoveries over the 34 years (1965-1998) included in the analysis. We created models that included interactive effects for area, age, sex, and time. Models that included time specific movement or harvest rates failed to converge, precluding estimates of annual recovery or movement rates.

Black duck regulations in the US and Canada have become progressively more restrictive between 1965 and 1998 (Francis et al. 1998). In 1983, black duck regulations were further restricted resulting from a legal challenge regarding the management of the resource (Grandy 1983). In an attempt to estimate time specific recovery rates, the data were divided into periods, grouping years on the basis of regulations package: restrictive, moderate or liberal. Breakpoints were assigned in years where major changes in black duck regulations occurred, following Francis et al. (1998). In our dataset, 1983 represented an identifiable change in black duck regulations where regulations shifted from a moderate to restrictive package. Recovery rates were estimated over the two periods of regulations.

Under the full model parameterization, zero degrees of freedom remain when estimating area specific recovery rates (i.e., saturated model). Estimating parameters under the full parameterization produced poor parameter estimates due to parameter identifiably problems (see Appendix A). Constraining recovery rates to be equal across the Mississippi flyway, and the southern Atlantic flyway harvest areas eliminated the problem. Prior knowledge about black ducks and black duck movements suggested that this was a reasonable constraint.

The best approximating model, $f_{\text{age*period}}\ m_{\text{sex}}$, as identified by AIC, suggested that recovery rates were period and age specific, and sex specific movement rates (Table 2.1). Model weights were calculated as

$$w_i = \frac{e^{(-0.5\Delta_i)}}{\sum_{m=1}^{r} e^{(-0.5\Delta_m)}}$$

where $\Delta_i = \text{AIC}_i - \text{AIC}_{\min}$, and AIC_i is the score if the i^{th} model and $\text{AIC}_{\min}$ is the lowest scoring model (Burnham and Anderson 1998:124). Lower ranked models in which movement rates were constrained to be constant across age, and sex, and age specific contained a significant portion of the total AIC weight (0.3420), suggesting some parameter uncertainty around movement rates (Table 2.1). Model selection identified models with period and age-specific recovery rates as the best approximating models from those examined.

Under the best approximating model, recovery rates declined in all harvest areas over the two periods. The estimated decline in recovery rates coincides with increased restrictions on the harvest of black ducks implemented in the US in 1983 and Canada in 1984. In general, the recovery rates of young were greater than those of adults in all harvest areas, which was expected given the increased vulnerability of first year birds. However, the difference between adult recovery rates and young recovery rates was much more pronounced in Canadian harvest areas versus being almost identical in US harvest areas (Table 2.3). Estimated recovery rates were comparable to those found by Francis et al. (1998), who analyzed preseason banding data using similar time periods, but utilized the Pendleton and Sauer (1992) definition of harvest areas.

Very little movement occurred by males or females across breeding areas. Movement rates ranged from a low of 0.0146 by females moving from the eastern to central harvest area, to a high of 0.0479 by males moving from the central breeding area to the western harvest area. Movement rates from northern harvest areas to southern harvest areas varied depending on the originating area. Males from the western area predominately move to the Mississippi flyway at a rate of 0.5167 (SE = 0.0187). The remaining males move to the northern Atlantic flyway and southern Atlantic flyway at 0.2007 (SE = 0.0199) and 0.2826 (SE = 0.0355), respectively. Movement rates by male black ducks from the eastern and central areas indicate strong tendencies to the northern Atlantic flyway, at rates of 0.9124 (SE = 0.0072) and 0.6866 (SE = 0.0200), respectively. Females exhibit similar patters of movement to southern harvest areas with movements of western female black ducks tending to the Mississippi flyway, and central and eastern black ducks tending to the northern Atlantic flyway.

Surveys have documented greater declines of black ducks in western Canada whereas black ducks in central and eastern Canada, which have remained relatively stable or slightly increased (Conroy et al 2002). One could hypothesize that survey data could be explained by an eastward shift in the regional distribution of black ducks, and movement results would indicate greater movement rates eastward. However, our model results suggest very little movement occurred by adults and young among any of the breeding areas. The model assumes that an individual harvested in an area was not transient through the area. Violation of this assumption would result in movement rates being biased high. Thus, the declines from east to west are likely to result from something other than a change in the distribution of the breeding population.

The number of movement pathways utilized in this analysis may not reflect all of the true pathways individuals utilized. We estimated a direct movement rate from breeding area to harvest area. In reality, black ducks may pass through one or more harvest areas while migrating to southern harvest areas. It is plausible that movement rates estimated in northern harvest areas could be biased, if a large portion of the black ducks harvested in these areas were transient's. Repeated observations of banded birds as movement occurs from breeding areas to the point of being harvested would have allowed the estimation of movement rates on an incremental basis. In addition, it is also known that some black ducks, particularly those in coastal Atlantic Canada, may not migrate to the US. This portion of the population is not eligible for harvest in US harvest areas thus the potential for biasing harvest and movement rates to US harvest areas.

The model provided herein provides a framework to estimate such parameters in a common model. This analysis allows one to model the influence that regional harvest has on breeding populations. These models, and estimates serve a valuable tool for the exploration of spatially based harvest management models such as those currently being explored for black ducks under an Adaptive Harvest Management framework.

Fidelity rates

The data set contained 189,663 bandings, 2,545 unique recapture records (first recapture only), and 27,935 recoveries. We allowed for interactive and additive effects of area, age, sex, and time in all parameters during model development. Very general models often failed to converge, or were severely overfit as noted by small differences in the deviance between general and more constrained models. Small differences in model deviance also suggested over-dispersion in the data. Models were corrected for over-dispersion using $\hat{c} = 2.8900$, where $\hat{c}$ was estimated from the most general model fit ($S_{(area*age*sex)}, p_{(area*age)}, r_{(area*age*sex)}, F_{(area*age*sex)}$) containing 42 parameters. After correction of AIC_c for over dispersion, the top ranked model was $S_{(area*age*sex)}, p_{(age*sex)}, r_{(area*age*sex)}, F_{(age+sex)}$, which contained 97.48 percent of the total model weight (Table 2.4). All other models contained less than one percent of the total model weight, and were not retained in the model set.

Estimates of fidelity rate were age and sex-specific. The effects of age and sex were additive in the top model. Fidelity rates were greatest for the adult age class, at 0.9695 (SE = 0.0249) and 0.9554 (SE = 0.434) for males and females, respectively. The fidelity rates of young females (0.8870 ± 0.0475) were slightly less than young males (0.9210 ± 0.0931). The estimated fidelity rates could represent two situations. First, black ducks are extremely faithful to breeding areas, or natal areas in the case of young, in successive years. It is also plausible that the definition of breeding areas is masking movements of individuals within breeding areas in successive years (i.e. areas defined on a smaller scale such as degree blocks might suggest less fidelity to breeding or banding areas).

To date, the study conducted by Coulter and Miller (1968), is the only one to examine fidelity in black ducks. The return rates of hens were approximately 25 percent, based on a sample of 89-banded black ducks over the seven-year study. The estimates of Coulter and Miller (1968) are not adjusted for annual survival, precluding comparison to fidelity rates estimated herein. Failure to account for annual survival of individuals is likely to reduce estimates of return rates, as the estimator assumes that all individuals have equal opportunity to return, yet individuals harvested during the hunting season are not eligible to return to breed the next year (Anderson et al. 1992). In addition to this, Coulter and Miller (1968) also recognized that they were unable to find all the black duck nests or catch hens known to be banded, which potentially reduced their estimate of return rates. Arnold et al. (2002) used similar methodology to estimate breeding site fidelity of female redheads (*Aythya Americana*), and concluded that age-specific differences existed in fidelity rates, with adult females having a greater propensity to return to the same breeding area; 0.923 vs. 0.744 for adult and young females, respectively. Similar estimates by Arnold et al. (2002) suggest that our estimates of fidelity rates are not unrealistic.

Our results indicate that black ducks have a high probability of returning to the same general breeding area over time. Survey data have indicated that black duck populations in the western portion of the breeding range have experienced greater declines then populations in the eastern portion of their range. Our estimated fidelity rates suggest that the regional distribution of black ducks has not changed dramatically through time, and thus, observed changes in the status or distribution of black ducks in eastern and western Canada cannot be attributed to changes in distribution of the breeding populations. This type of modeling is beneficial to understanding relationships that may exist between breeding and harvest areas, especially harvest areas that are spatially disconnected from breeding areas. These estimates would aid the development of spatially stratified population models, and the advancement of the adaptive harvest management effort currently ongoing for black ducks.

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Table 2.1. Model selection of movement models for American black ducks, where *f* represents the recovery rate for each of the six harvest areas, and *m* are the movement rates to each harvest area.

Model Name	Number of parameters	Δ AIC	AIC Weight
*f(p*g) m(s)*	40	0.00	0.6580
*f(p*g) m(.)*	30	2.18	0.2212
*f(p*g) m(g)*	40	3.39	0.1208
f(p) m(g)	30	630.65	0.00
f(g) m(s)	30	707.98	0.00
*f(g) m(s*g)*	50	716.95	0.00
f(g) m(g)	30	720.80	0.00
f(g) m(.)	20	721.00	0.00
*f(p*s) m(g)*	40	1049.58	0.00
*f(p) m(s*g)*	50	1054.84	0.00
*f(p*s) m(s)*	40	1067.40	0.00
f(p) m(s)	30	1069.70	0.00
*f(p*s) m(.)*	30	1076.55	0.00
f(p) m(.)	20	1081.60	0.00
*f(a*g) m(s)*	24	1146.24	0.00
*f(a*g) m(s*g)*	44	1154.47	0.00
*f(a*g) m(.)*	14	1160.51	0.00
*f(a*g) m(g)*	24	1170.51	0.00
*f(s) m(s*g)*	50	1874.20	0.00
f(s) m(g)	30	1882.34	0.00
f(.) m(g)	25	1882.77	0.00
f(s) m(s)	30	1886.94	0.00
*f(.) m(s*g)*	45	1887.06	0.00
f(.) m(s)	25	1895.44	0.00
f(s) m(.)	20	1896.28	0.00
f(.) m(.)	15	1908.37	0.00
*f(a*s) m(s)*	24	2366.73	0.00
*f(a*s) m(s*g)*	44	2374.96	0.00
f(a) m(s)	22	2375.63	0.00
*f(a*s) m(g)*	24	2377.10	0.00
*f(a*s) m(.)*	14	2381.00	0.00
f(a) m(g)	22	2385.98	0.00
f(a) m(.)	12	2389.90	0.00

Table 2.1 continued. Model selection of movement models for American black ducks, where *f* represents the recovery rate for each of the six harvest areas, and *m* are the movement rates to each harvest area.

Model Name	Number of parameters	Δ AIC	AIC Weight
*f(a) m(s*g)*	42	2703.70	0.00
*f(g*s) m(g)*	40	3742.26	0.00
*f(g*s) m(s)*	40	3791.59	0.00
*f(g*s) m(.)*	30	4138.03	0.00
*f(p*g) m(s*g)*	60	296099.28	0.00
*f(g*s) m(s*g)*	60	526851.73	0.00
*f(p*s) m(s*g)*	60	778681.41	0.00
f(.) m(t)	1365	NC	---
f(a) m(t)	1362	NC	---
f(s) m(t)	1370	NC	---
*f(a*g) m(t)*	1364	NC	---
*f(a*s) m(t)*	1364	NC	---
*f(p*s) m(t)*	1380	NC	---
f(p) m(t)	1370	NC	---
*f(g*s) m(t)*	1380	NC	---
f(g) m(t)	1370	NC	---
*f(p*g) m(t)*	1380	NC	---

NC = non-convergence of model
a = country specific
g = age specific
s = sex specific
t = time specific
p = harvest period specific
. = constant

Table 2.2. Movement rates and standard errors for males and females from respective breeding areas to harvest areas.

	Sex		Breeding Area					
			West	SE	Central	SE	East	SE
Harvest Area	Females	East	--	--	0.0174	0.0042	0.9854	0.0019
		Central	0.0248	0.0045	0.9516	0.0076	0.0146	0.0019
		West	0.9752	0.0045	0.0310	0.0063	--	--
		MF	0.4668	0.0229	0.0649	0.0104	0.0000[1]	0.0000
		AFN	0.2430	0.0250	0.6786	0.0234	0.8907	0.0086
		AFS	0.2902	0.0438	0.2565	0.0297	0.1093	0.0086
	Males							
		East	--	--	0.0157	0.0033	0.9726	0.0025
		Central	0.0217	0.0035	0.9364	0.0073	0.0274	0.0025
		West	0.9783	0.0035	0.0479	0.0065	--	--
		MF	0.5167	0.0187	0.0477	0.0074	0.0019	0.0009
		AFN	0.2007	0.0199	0.6866	0.0200	0.9124	0.0072
		AFS	0.2826	0.0355	0.2657	0.2400	0.0857	0.0074

[1] Parameter estimate from SURVIV was 0.9121 x 10^{-16} (SE ± 0.2189 x 10^{-09})

Table 2.3. Direct recovery rates (standard errors) by age and regulations period of Canadian banded black ducks across the six defined harvest areas.

	Adult		Young	
Area	1965-1982[1]	1983-1998	1965-1982	1983-1998
West	0.3687 (0.0024)	0.0146 (0.0017)	0.0762 (0.0022)	0.0411 (0.0017)
Central	0.0394 (0.0031)	0.0340 (0.0029)	0.0956 (0.0025)	0.0926 (0.0024)
East	0.0362 (0.0025)	0.0212 (0.0014)	0.0899 (0.0014)	0.0612 (0.0012)
MF	0.0505 (0.0030)	0.0369 (0.0027)	0.0511 (0.0022)	0.0366 (0.0018)
AFN	0.0233 (0.0017)	0.0142 (0.0011)	0.0295 (0.0008)	0.0169 (0.0006)
AFS	0.0503 (0.0030)	0.0369 (0.0027)	0.0511 (0.0022)	0.0366 (0.0018)

[1] The average regulations, as determined by recovery and survival rates, became more restrictive between 1965-1982, and 1983-1998 periods. These restrictions were achieved through reduction in the season length and or daily bag limit (Francis et al. 1998).

Table 2.4. Selected models from Program MARK for estimating American black duck fidelity rates, and their associated QAIC$_c$ weights.

Model Name	Number of Parameters	Δ QAIC$_c$	QAIC$_c$ Weight
S(_a*g*s_),_p(g*s),r(a*g*s)_,F(_g+s_)	31	0.00	0.97483
S(_a*g*s_),_p(g*s),r(a*g*s)_,F(_a*g*s_)	40	9.37	0.00901
S(_a*g*s_),_p(a*g*s),r(a*g*s)_,F(_g*s_)	40	9.42	0.00879
S(_a*g*s_),_p(a*g*s),r(a*g*s)_,F(_g+s_)	39	10.03	0.00648
S(_a*g*s_),_p(g),r(a*g*s)_,F(_a*g*s_)	38	14.16	0.00082
S(_a*g*s_),_p(a*g),r(a*g*s)_,F(_a*g*s_)	42	19.16	0.00007
S(_a+g+s_),_p(a+g+s),r(a+g+s)_,F(.)	16	26.78	0.000
S(_a+g+s_),_p(a+g+s),r(a+g+s)_,F(_g_)	17	26.96	0.000
S(_a+g+s_),_p(a+g+s),r(a+g+s)_,F(_g+s_)	18	28.94	0.000
S(_a*g*s_),_p(g*s),r(g)_,F(_s)_	22	29.70	0.000
S(_a+g+s_),_p(a+g+s),r(a+g+s)_,F(_a+g+s_)	18	30.08	0.000
S(_a*g*s_),_p(s),r(a*g*s)_,F(_a*g*s_)	38	31.83	0.000
S(_a*g*s_),_p(a*s),r(a*g*s)_,F(_a*g*s_)	42	36.33	0.000
S(_a*g*s_),_p(a),r(a*g*s)_,F(_a*g*s_)	39	38.50	0.000
S(_g*s_),_p(g*s),r(a*g*s)_,F(_a*g*s_)	32	47.52	0.000
S(_g*s_),_p(g),r(a*g*s)_,F(_a*g*s_)	30	53.78	0.000
S(_g*s_),_p(a*g),r(a*g*s)_,F(_a*g*s_)	34	54.65	0.000
S(_g*s_),_p(a*g*s),r(a*g*s)_,F(_a*g*s_)	40	55.43	0.000
S(_a*g*s_),_p(a*g*s),r(a*g)_,F(_a*g*s_)	42	65.23	0.000
S(_g*s_),_p(a*s),r(a*g*s)_,F(_a*g*s_)	34	70.44	0.000
S(_g*s_),_p(s),r(a*g*s)_,F(_a*g*s_)	30	70.55	0.000
S(_g*s_),_p(a),r(a*g*s)_,F(_a*g*s_)	31	73.78	0.000
S(_a*g*s_),_p(a*s),r(a*g)_,F(_a*g*s_)	36	80.90	0.000
S(_a*g_),_p(g*s),r(a*g*s)_,F(_a*g*s_)	34	81.58	0.000
S(_s*t_),_p(t),r(t)_,F(_t_)	165	82.55	0.000
S(_a*g_),_p(g),r(a*g*s)_,F(_a*g*s_)	32	82.79	0.000
S(_a*g_),_p(a*g),r(a*g*s)_,F(_a*g*s_)	36	88.06	0.000
S(_a*g_),_p(a*g*s),r(a*g*s)_,F(_a*g*s_)	42	92.64	0.000
S(_a*g_),_p(s),r(a*g*s)_,F(_a*g*s_)	32	104.54	0.000
S(_a*g_),_p(a),r(a*g*s)_,F(_a*g*s_)	33	108.29	0.000
S(_a*g_),_p(a*s),r(a*g*s)_,F(_a*g*s_)	36	108.72	0.000
S(_s*t_),_p(t),r(t)_,F(_s*t_)	197	122.20	0.000

Table 2.4 continued. Selected models from Program MARK for estimating American black duck fidelity rates, and their associated QAIC$_c$ weights.

Model Name	Number of Parameters	Δ QAIC$_c$	QAIC$_c$ Weight
S(_a*g*s_),_p(g+s),r(g*s)_,F(.)	20	131.34	0.000
S(_a*g*s_),_p(g*s),r(g*s)_,F(_s_)	22	131.53	0.000
S(_a*g*s_),_p(g*s),r(g*s)_,F(_g_)	22	132.51	0.000
S(_g_),_p(g*s),r(a*g*s)_,F(_a*g*s_)	30	132.52	0.000
S(_a*g*s_),_p(g*s),r(g*s)_,F(_g*s_)	24	133.11	0.000
S(_a*g*s_),_p(g*s),r(g*s)_,F(_g+s_)	23	133.46	0.000
S(_a*g*s_),_p(g+s),r(g*s)_,F(_g+s_)	22	133.90	0.000
S(_g_),_p(g),r(a*g*s)_,F(_a*g*s_)	28	134.23	0.000
S(_a*g*s_),_p(g*s),r(g*s)_,F(_a_)	23	135.51	0.000
S(_a*g*s_),_p(g*s),r(g*s)_,F(_a_)	23	135.51	0.000
S(_g_),_p(a*g),r(a*g*s)_,F(_a*g*s_)	32	135.56	0.000
S(_g_),_p(a*g*s),r(a*g*s)_,F(_a*g*s_)	38	140.19	0.000
S(_a*g*s_),_p(g*s),r(g*s)_,F(_a*g*s_)	32	143.40	0.000
S(_a*g*s_),_p(a*g*s),r(a*s)_,F(_a*g*s_)	42	144.66	0.000
S(_g_),_p(a),r(a*g*s)_,F(_a*g*s_)	29	155.08	0.000
S(_a*g*s_),_p(a*g*s),r(g*s)_,F(_a*g*s_)	40	155.67	0.000
S(_g_),_p(a*s),r(a*g*s)_,F(_a*g*s_)	32	156.08	0.000
S(g),_p(s),r(a*g*s)_,F(_a*g*s_)	28	156.23	0.000
S(_a*g*s_),_p(a*s),r(a*s)_,F(_a*g*s_)	36	160.94	0.000
S(_a*g*s_),_p(g*s),r(a)_,F(_g_)	21	162.57	0.000
S(_a*g*s_),_p(g*s),r(a)_,F(_s_)	21	164.20	0.000
S(_a*g*s_),_p(g*s),r(a)_,F(_g*s_)	23	164.67	0.000
S(_a*g*s_),_p(g*s),r(a)_,F(_a_)	22	167.96	0.000
S(_t_),_p(t),r(t)_,F(_t_)	131	169.92	0.000
S(_a*g*s_),_p(a*s),r(g*s)_,F(_a*g*s_)	34	170.91	0.000
S(_a*g*s_),_p(g*s),r(a)_,F(_a*g*s_)	31	175.28	0.000
S(_a*g*s_),_p(a*g*s),r(a)_,F(_a*g*s_)	39	188.35	0.000
S(_a*g*s_),_p(g*s),r(g)_,F(_s_)	20	190.44	0.000
S(_a*g*s_),_p(g*s),r(g)_,F(_g*s_)	22	191.62	0.000
S(_a*g*s_),_p(g*s),r(g)_,F(_g_)	20	192.05	0.000
S(_a*g*s_),_p(g*s),r(g)_,F(_a*g*s_)	30	201.74	0.000
S(_a*g*s_),_p(a*s),r(a)_,F(_a*g*s_)	33	204.64	0.000
S(_a*s_),_p(g*s),r(a*g*s)_,F(_a*g*s_)	34	207.47	0.000
S(_a*s_),_p(g),r(a*g*s)_,F(_a*g*s_)	32	214.35	0.000

Table 2.4 continued. Selected models from Program MARK for estimating American black duck fidelity rates, and their associated $\mathrm{QAIC_c}$ weights.

Model Name	Number of Parameters	$\Delta\ \mathrm{QAIC_c}$	$\mathrm{QAIC_c}$ Weight
S(a*s),p(a*g),r(a*g*s),F(a*g*s)	36	217.03	0.000
S(a*s),p(a*g*s),r(a*g*s),F(a*g*s)	42	217.11	0.000
S(a*s),p(s),r(a*g*s),F(a*g*s)	32	226.66	0.000
S(a*s),p(s),r(a*g*s),F(a*g*s)	32	226.66	0.000
S(s),p(g*s),r(a*g*s),F(a*g*s)	30	227.27	0.000
S(a*s),p(a*s),r(a*g*s),F(a*g*s)	36	229.37	0.000
S(a*s),p(a),r(a*g*s),F(a*g*s)	33	232.45	0.000
S(s),p(g),r(a*g*s),F(a*g*s)	28	234.29	0.000
S(g*s),p(g*s),r(g*s),F(g*s)	16	234.49	0.000
S(s),p(a*g),r(a*g*s),F(a*g*s)	32	235.75	0.000
S(s),p(a*g*s),r(a*g*s),F(a*g*s)	38	235.76	0.000
S(s),p(s),r(a*g*s),F(a*g*s)	28	246.39	0.000
S(s),p(a*s),r(a*g*s),F(a*g*s)	32	247.47	0.000
S(s),p(a),r(a*g*s),F(a*g*s)	29	250.96	0.000
S(a*g*s),p(g*s),r(s),F(g*s)	22	273.93	0.000
S(a*g*s),p(g*s),r(s),F(a*g*s)	30	285.22	0.000
S(a),p(g*s),r(a*g*s),F(a*g*s)	31	286.23	0.000
S(a),p(g),r(a*g*s),F(a*g*s)	29	288.96	0.000
S(a),p(a*g),r(a*g*s),F(a*g*s)	33	292.02	0.000
S(a),p(a*g*s),r(a*g*s),F(a*g*s)	39	296.13	0.000
S(a*g*s),p(a*g*s),r(s),F(a*g*s)	38	298.37	0.000
S(a),p(s),r(a*g*s),F(a*g*s)	29	304.23	0.000
S(a),p(a*s),r(a*g*s),F(a*g*s)	33	307.12	0.000
S(a),p(a),r(a*g*s),F(a*g*s)	30	308.76	0.000
S(a*g*s),p(a*s),r(s),F(a*g*s)	32	314.67	0.000
S(g),p(g),r(g),F(g)	8	380.15	0.000
S(a*s),p(.),r(a*s),F(a*s)	19	735.81	0.000
S(a*s),p(a*s),r(a*s),F(a*s)	24	736.43	0.000
S(a),p(a),r(a),F(a)	12	910.94	0.000
S(a),p(.),r(.),F(a)	8	1073.80	0.000
S(.),p(.),r(.),F(.)	4	1162.30	0.000

a = area
g = age
s = sex
t = time

Table 2.5. Parameter estimates from the top model selected in Program MARK where r is recovery rate, S is survival rate, p is capture probability, and F is the fidelity rate.

Age-Sex Class	Breeding Area	*r*	SE	S	SE	*p*	SE	F	SE
YF	East	0.1088	(0.0058)	0.6005	(0.0128)	0.01250	(0.0024)	0.8870	(0.0475)
	Central	0.1301	(0.0102)	0.5800	(0.0217)	0.01250	(0.0024)	0.8870	(0.0475)
	West	0.1168	(0.0086)	0.6157	(0.0200)	0.01250	(0.0024)	0.8870	(0.0475)
YM	East	0.1417	(0.0047)	0.4412	(0.0160)	0.17700	(0.0025)	0.9210	(0.0931)
	Central	0.1936	(0.0085)	0.4546	(0.0203)	0.17700	(0.0025)	0.9210	(0.0931)
	West	0.1554	(0.0082)	0.5495	(0.0209)	0.17700	(0.0025)	0.9210	(0.0931)
AF	East	0.1170	(0.0045)	0.6934	(0.0093)	0.00750	(0.0011)	0.9554	(0.0434)
	Central	0.1362	(0.0075)	0.6458	(0.0144)	0.00750	(0.0011)	0.9554	(0.0434)
	West	0.1468	(0.0072)	0.6683	(0.0136)	0.00750	(0.0011)	0.9554	(0.0434)
AM	East	0.1622	(0.0047)	0.5455	(0.0117)	0.01480	(0.0010)	0.9695	(0.0249)
	Central	0.2294	(0.0078)	0.5251	(0.0147)	0.01480	(0.0010)	0.9695	(0.0249)
	West	0.1971	(0.0067)	0.6216	(0.0117)	0.01480	(0.0010)	0.9695	(0.0249)

Figure 2.1. Location of the Black Duck Joint Venture survey plots and corresponding strata in Canada (Black Duck Joint Venture 1992).

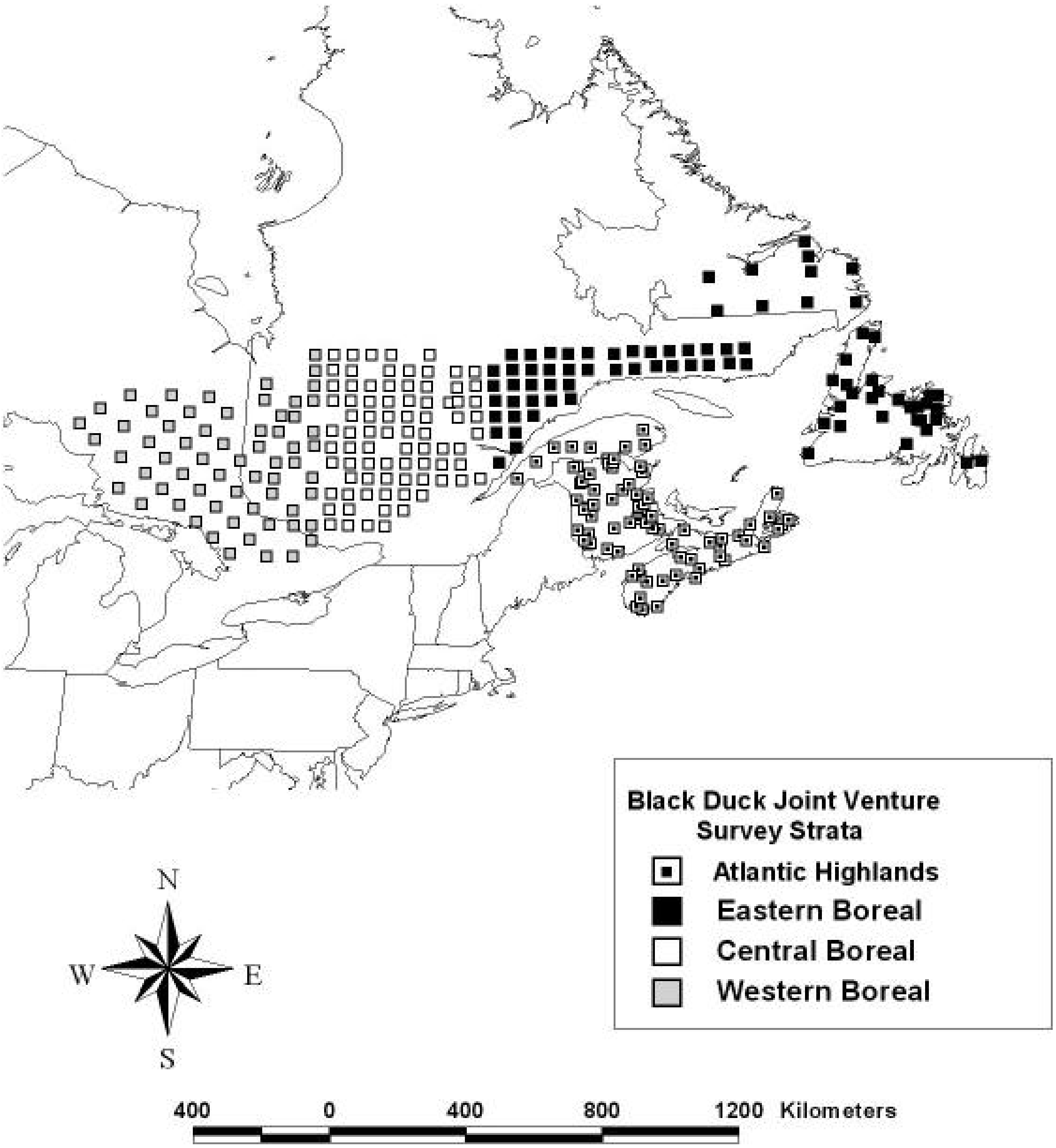


Figure 2.2. Breeding and Harvest area delineations used for modeling movement and fidelity rates for American black ducks, where W, C, and E represent the western, central, and eastern Canadian breeding and harvest areas. MF, AFN, and AFS correspond the US harvest areas in the Mississippi flyway, northern Atlantic flyway, and southern Atlantic flyway, respectively.

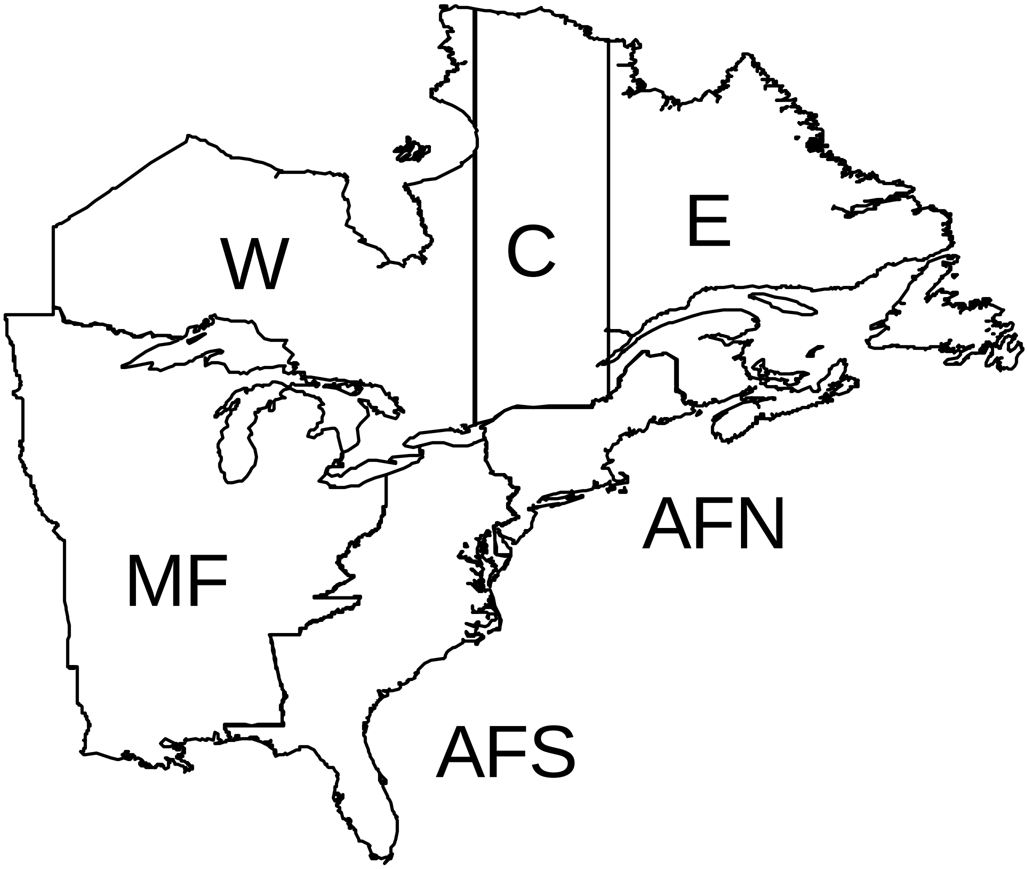
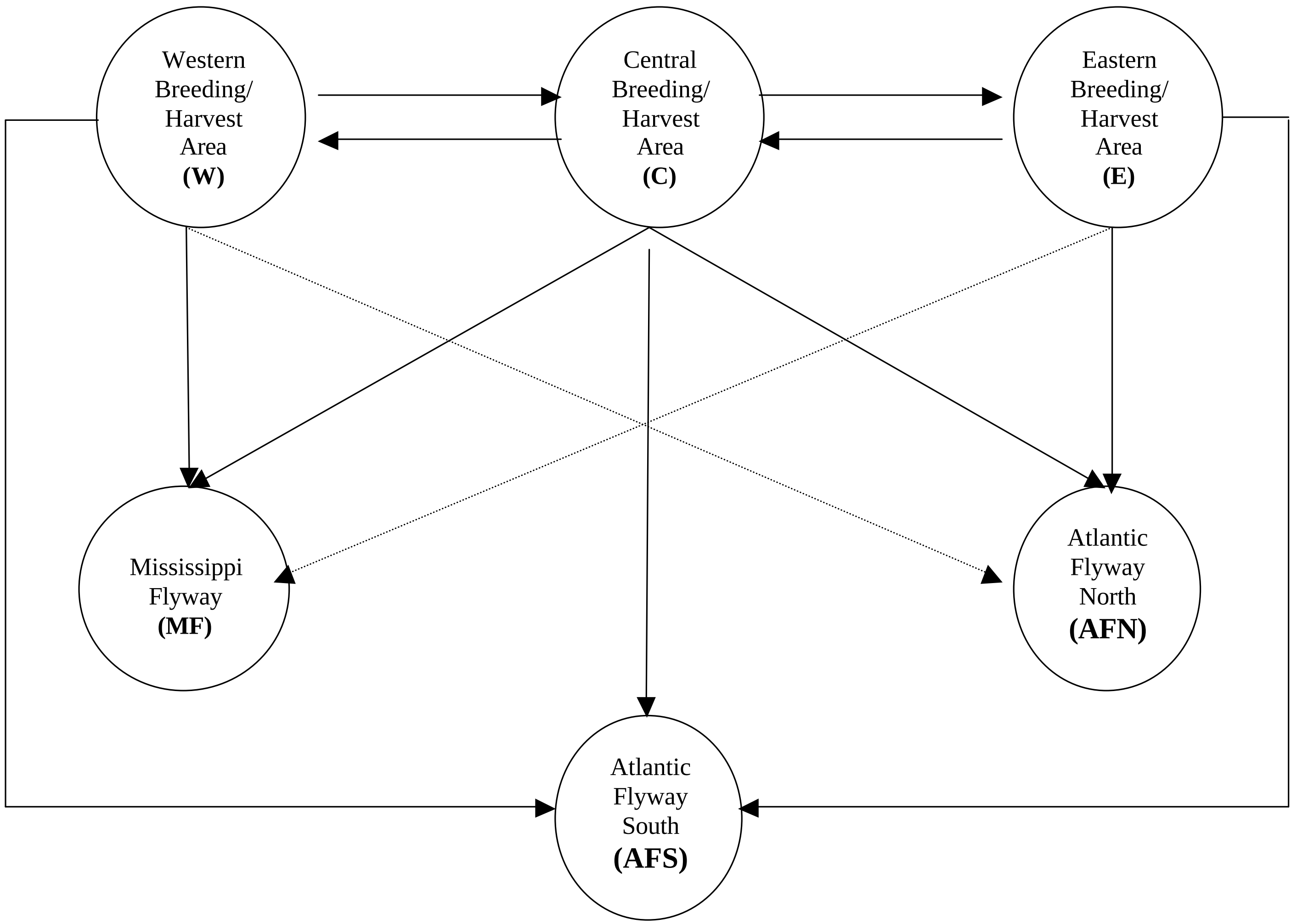


Figure 2.3. A graphical model representative of the movement pathways modeled in the likelihood



CHAPTER 3

ESTIMATING BREEDING AREA SPECIFIC AGE RATIOS OF AMERICAN BLACK DUCKS [1]

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[1] Zimpfer, N. L., and M. J. Conroy. To be submitted to *The Journal of Wildlife Management*

The productivity of waterfowl populations is largely determined by various biotic and abiotic factors, such as population density, climatic conditions, and habitat availability. Understanding how waterfowl populations are influenced by changes in these factors are important to further understanding their dynamics and for developing effective management programs (Sheaffer 1998). Considerable research has been done regarding the influence that abiotic and biotic factors have on American black duck production (*Anas rubripes*). Several studies have been conducted to identify biotic and abiotic factors which are thought to effect black duck production. Research has focused on factors such as wetland chemistry, habitat type, invertebrate composition, and the like. While insightful, these studies have been limited in spatial scale to individual wetlands, or wetland complexes, such that the data cannot be expanded to the entire range of the black duck. Conroy et al. (2002) attempted to address factors that may influence black duck production at the population level. However, the nature of the data limited their analysis to a single population level analysis. Second, their analysis utilized an index to black duck breeding abundance, since ongoing surveys that directly estimate breeding abundances had not been conducted for a sufficient time span for use in analysis. Additional years of breeding survey data have been collected, and their use for predicting reproductive rates is likely to be more beneficial than surrogate indexes.

Range wide, black ducks have been known to breed and nest in a variety of habitats. This diversity and their secretive nature make the identification of factors that may influence production difficult. It is hypothesized that production in black ducks may be influenced by various wetland characteristics such as the dominant vegetation type, wetland availability, or wetland fertility (Merendino and Ankney 1994). Abiotic factors such as population density, or interspecific competition/competitive exclusion with mallards (D'Eon et al. 1995) have been proposed as factors, which may also influence production.

Several studies have documented relationships between production and abiotic factors. For example, in mid-continental mallards (*A. platyrhynchos*), a well-documented relationship exists between the number of ponds in the spring and recruitment (Anderson 1975, Martin et al 1979, Heitmeyer and Fredrickson 1981). Modeling efforts for mid-continental mallards have been particularly successful because long-term population data exists, and the systems in which the population occurs are relatively simple, limiting the search for factors that may affect production. For eastern breeding mallards, which occur sympatrically with black ducks, Sheaffer (1998) concluded that spring and winter precipitation, and breeding population size were good indicators of recruitment. Predictive relationships between recruitment and biotic factors, such as those found in mid-continental mallards have yet to be identified for black ducks.

Previous survey attempts of black ducks on the breeding grounds have proved ineffective due to low breeding densities and low detection rates (Kazyinski and Chamberlain 1968). In 1990, the Canadian Wildlife Service (CWS) implemented a plot survey, and later in 1995 the US Fish and Wildlife Service (USFWS) added additional strata to their existing fixed wing aerial survey, to survey portions of the black duck breeding range. The relatively recent time frame in which these surveys have been implemented potentially limits their ability to detect relationships

Currently, the annual recruitment of black ducks is estimated from the age-ratio of harvested black ducks, corrected for the differential vulnerability of age groups. Black duck populations are assessed from the Midwinter Inventory (MWI) conducted annually in all states along the east coast of the US. Conroy et al. (2002) developed an exponential model, which described intrinsic (black duck abundance), and extrinsic factors (mallard abundance, mallard density, and breeding habitat density) that influence reproductive rates. Because of the data available to Conroy et al (2002) they were only able to construct a single, continental model that did not take into account important differences in factors across the black duck range. Our objective was to develop a predictive model relating annual reproductive success of black ducks to temporal and spatial variation in biotic and abiotic factors across the Canadian black duck breeding range on a breeding area specific basis.

METHODS

The Canadian black duck breeding range was divided into three principal areas, based on the Black Duck Joint Venture (BDJV) plot survey (Black Duck Joint Venture 1992). The eastern breeding area includes all of the Atlantic Provinces (New Brunswick, Prince Edward Island, Nova Scotia, Newfoundland) and the portion of Quebec lying east of 76° 30’ longitude. The central breeding area is that portion of Quebec lying between 70° 30’ and 76° 30’ longitude. The western breeding area is the province of Ontario (Figure 3.1). For modeling purposes, delineations of breeding areas also serve as Canadian harvest areas. We assumed that the Canadian harvest is composed principally of black ducks that breed within the western, central, and eastern breeding areas, respectively. A fall age ratio was used as the index of production for modeling. Age ratios were expressed as the number of young males per adult male. Recent research has suggested that expressing the age ratio in terms of males has less year-to-year variation, and may be a better reflection of true annual reproduction in the population (F. A.

Johnson, USFWS, Pers. Comm.). The reduction in the year-to-year variation is suspected to be from reduced mortality experienced by adult males over the summer period.

Unadjusted wing frequencies by age and breeding area were used to estimate the age ratio in the harvest for each area. Wing data were derived from the Canadian Parts Collection Survey (PCS), obtained from the Canadian Wildlife Service (J. F. Gobeil and B. T. Collins, CWS, Migratory bird population unit, unpublished data). All banding and recovery data were obtained from the Bird Banding Laboratory (BBL), in Laurel, Maryland. We included only bandings of "normal wild" male black ducks banded preseason (1 July – 30 Sept.) in Canada from 1990-2001. Recoveries included only black ducks shot or found dead during the hunting season. Direct recoveries of young and adult males banded in Canada and recovered in each of the respective harvest areas were then used to adjust the harvest age ratios for differential vulnerability to obtain the age ratio in the fall population.

For illustration, we derive model expectations for a single breeding population, but the methodology is readily extended to multiple breeding populations. A breeding population has some unknown total of birds N, which is composed of some unknown proportion of young and adults ($N = N_a + N_y$). Young (N_y) and adults (N_a) in the fall population are harvested at age specific harvest rates (h_j, j = a, y). We wish to estimate the age ratio, or the ratio young to adults in the fall population, where the age ratio is expressed as $A = N_y/N_a$. The proportion of young expected in the harvest is

$$E(a) = \frac{N_y h_y}{N_y h_y + N_a h_a} .$$

The expected ratio of young to adults in the harvest can be expressed as

$$E(a) = \frac{N_y / N_a}{(N_y / N_a) + h_a / h_y} = \frac{A}{(A + t)}$$

where $\tau = h_a/h_y$ and is a correction for the relative vulnerability of adults to young, and α is the proportion of young in fall population.

We observe a sample of harvested wings (W) from the Parts Collection Survey. The wing sample is apportioned into respective age classes, W_y and W_a for young wings and adult wings, respectively. Thus, the number of young wings in the sample is $W_y \sim Bin(a,W)$.

The relative vulnerability correction τ, is estimated from age specific bandings (R_j j = a, y) and recoveries (m_j j = a, y). The expected numbers of recoveries are modeled as

$$E(m_y \mid R_y) = h_y R_y$$
$$E(m_a \mid R_a) = h_a R_a$$

$m_\mathrm{a} \sim \mathrm{Bin}(f_\mathrm{a}, R_\mathrm{a})$ and $m_\mathrm{y} \sim \mathrm{Bin}(f_\mathrm{y}, R_\mathrm{y})$ where f_y and f_a are the recovery rates of young and adults, respectively. Expectations for the proportion of young in the fall population, and the number of young band recoveries are coded in SURVIV and are estimated simultaneously in a joint likelihood (Appendix B).

We examined several potential covariates that were thought to influence production rates in black ducks, chiefly black duck density (X_{ij}), mallard density (M_{ij}), and spring temperature (TMP_{ij}), and precipitation (PPT_{ij}). Environmental data were obtained from the Historical Canadian Climate Database (HCCD; http://www.cccma.bc.ec.gc.ca/hccd/), maintained by the Canadian Meteorological Service. The HCCD summarizes temperature (°C) and precipitation (mm) data, from 130 stations across Canada. Each weather station was assigned to a breeding area based on geo-referenced coordinates contained in the HCCD. The data contained in the database have been homogenized to account for known inhomogeneities such as changes in site location, collection procedures, and equipment differences (Mekis and Hogg 1999). Spring temperatures (March, April, May) for each station were averaged across all stations, and year in a given breeding area from 1990-2001. These averages were then standardized (Norm(0,1)) to the 12-year average, using

$$\frac{X_{ij} - \overline{X}_j}{SD_j}$$

where, *i* = mean annual spring temperature or precipitation, and *j* = breeding area (west, central, or east). Black duck and mallard abundance estimates were derived from the BDJV plot survey (Table B2). The BDJV plot survey consists of 250, 25-km^2 plots surveyed by helicopter, which are divided into four strata, the Atlantic highlands, eastern, central, and western boreal regions (Figure 3.1). The survey uses a rotating sample methodology, in which a group of plots are retained from one year to the next while others are discarded and replaced with other plots. The rotation is such that all plots are surveyed once every four years (B. T. Collins, CWS, Unpublished report).

We estimated area and time specific production rates in SURVIV (White 1983). Although τ is a nuisance parameter, it does affect estimated production rates, and thus we fit models where τ was constrained over space and time, while α was left unconstrained (Table B1). Area specific effects were modeled by constraining a covariate model, which estimates independent slopes and intercepts for each area, to constrain slopes across areas ($\log_e(P_i) = b_{0i} + b_{1i}X_i + b_{2i}M_i + b_{3i}TMP_i + b_{4i}PPT_i$), or constrain intercepts and slopes across areas ($\log_e(P_i) = b_0 + b_1X_i + b_2M_i + b_3TMP_i + b_4PPT_i$). The best fitting model, as determined by AIC, was utilized as the general model in which all covariate models were derived. We utilized a macro in SAS (SAS Institute, Inc. 1999; J. T. Peterson and W. L. Thompson, USGS, Unpublished data) which given a set of covariates, the macro will fit user specified models via general linear regression, calculate AIC_c, ΔAIC_c, and AIC model weights. This procedure served as a priori search for covariates and interactions, thought to be adequate predictors of black duck production. Models which were < 3 AIC units from the top ranked model were retained for further estimation in SURVIV.

RESULTS

All covariate models fit in SAS included effects for density dependence, and/or competition with mallards as these were identified as potential causal factors for the decline of black ducks. Linear modeling suggested that models that included standardized average spring temperature, average spring precipitation, or a black duck mallard interaction warranted further estimation in SURVIV. A total of 22 models were estimated in SURVIV. In all models τ was constrained to be area specific. Constraining of τ was done as they resulted in smaller AIC values when fitting more general models (Table B1). Results from initial SURVIV runs revealed that several models, typically those in which the coefficients were area specific produced estimates for slopes that were either counter intuitive (e.g. mallards having a positive effect on black duck production), or were biologically inadmissible. Constraining coefficients to fall within an admissible range resulted in non-convergence of some models. These models were deleted from the model set and AIC values, and model weights were normalized to reflect changes in the model set. Model weights were calculated as

$$w_i = \frac{e^{(-0.5\Delta_i)}}{\sum_{m=1}^{r} e^{(-0.5\Delta_m)}}$$

where $\Delta_i = AIC_i - AIC_{min}$, and AIC_i is the score if the i^{th} model and AIC_{min} is the lowest scoring model (Burnham and Anderson 1998:124). $QAIC_c$ was used as the ranking criteria for SURVIV models as some over dispersion ($\hat{c}$ = 1.2712) existed in the data. The AIC correction factor $\hat{c}$ was estimated as

$$\hat{c} = deviance / df$$

(Burnham and Anderson 2002).

Models with area specific intercepts consistently ranked higher than models with constant intercepts. Most of the selected models contained area specific intercepts, and constant slopes across areas for all covariates. One model contained area specific intercepts, and area specific effects for density dependence, and one model contained constant slopes for the intercept and a density dependent effect, but it received relatively low AIC model weight (w_i = 0.0011). The best approximating model ranked by $QAIC_c$ identified density dependence, mallard competition, precipitation, and spring temperature as covariates which were good predictors of reproduction, given area specific intercepts (Table 3.1). Coefficient estimates for density dependence and mallard competition were -0.4096 and -0.3465, respectively. Coefficient estimates for scaled precipitation and temperature were –0.1942 and 0.0820, respectively. Model results suggest that reproduction in black ducks is affected by spring temperature, spring precipitation, and the densities of mallards and black ducks present on the breeding grounds, it must be noted that 95% confidence intervals for temperature, precipitation, and competition coefficients all contain zero. Thus, one cannot say with complete confidence that these measures truly predict reproduction in black ducks. Second, the top model does not contain most of the total model weight, rather it is distributed across most of the models in the set indicating that with additional data, other models may be better predictors of black duck reproduction than the currently selected model. Interestingly, the model ranked second in the set has area specific intercepts, and area specific estimates of density dependence. Coefficients for this density dependent parameter, indicate that the density dependent effect is strongest in the central breeding area, and quite a bit less in the eastern and western breeding areas –0.7326 (SE = 0.2356) versus –0.2601 (SE = 0.3398) and –0.1984 (SE = 0.0939), respectively.

Model-averaged estimates of the parameters (Log (A), β_x, β_m, β_{tmp}, β_{ppt}) were calculated following Burnham and Anderson (1998). Averaging was done across the top five models for all parameters. Averaged parameter estimates, unconditional standard errors, and unconditional confidence intervals are reported in Table 3.1.

DISCUSSION

We were unable to identify a habitat variable suitable for use in modeling breeding area specific age ratios. Reproduction models, which included an environmental effect, contained only slightly more AIC weight than models that included only effects for density dependence and/or competition (Table 3.1). This may indicate that modeling habitat change could produce models that would better explain variation in age ratios. Variables such as beaver abundance, and total forest and swamp acreages (Conroy et al. 2002), water quality (Hanson 2001) have been used as predictors of black duck production but met with little success at large scales. A common theme that has appeared is the lack of long term data documenting changes in black duck habitat, and the inability to associate currently collected habitat data to the relevant scales needed to model black duck population dynamics.

Density dependence in waterfowl populations has always been considered a factor in reproduction rates. Typically, density dependence occurs when populations are high in relation to some measure of carrying capacity whereby reproductive rates are depressed through nest success, or fledgling survival. While we are not able to identify the mechanism by which density dependence occurs, in the case of black ducks, it is likely that the limiting factor is habitat related such as the number of suitable wetlands. Although we included a density dependent factor into all of our models, models in which density dependence was equal for all breeding areas, or area specific, received almost identical AIC weight 0.2631 versus 0.2492, respectively (Table 3.1). In models where the density dependent factor was constrained to be equal across areas, confidence intervals did not include zero. In the area specific model (Model 2), in only the eastern area, did the confidence interval of the density dependent factor include zero (Table 3.1). Based on our models, it is likely that density dependent reproduction is occurring in black duck populations, although the degree with which it occurs, and whether it varies across the breeding range is still debatable.

Given the recent increase in mallards across the black duck breeding range, competitive interactions with mallards may limit reproduction. In Ontario, Merendino et al. (1994) found that mallards would out compete black ducks for fertile wetlands. However, Mcauley et al. (1998) found that black ducks in Maine were not displaced by mallards on wetlands utilized for breeding, and brood rearing. Unfortunately, our models are unable to shed additional light on this topic, since models that included a competition effect, performed as well as models that did not.

Relationships between weather conditions and subsequent reproductive success as indexed by harvest age ratios have been identified for several species of waterfowl and arctic nesting geese (Johnson et al. 1992). It is suspected that weather conditions effect reproduction through modification of breeding ground habitat availability or quality. In mallards that breed in the prairie–parkland region of the U.S, spring precipitation determines the number of ponds available to be occupied by breeding pairs. In years of drought there are fewer ponds, and thus fewer available nest sites, a situation that may increase competition for prime nesting sites (Pospahala et al. 1974). Pairs without established territories are displaced into marginal habitats, which would negatively effect production. Eastern mallards and black ducks occupy similar geographic breeding ranges, with their numbers most prevalent in Ontario and Quebec and declining eastward. Most of the modeling has focused on those breeding in the northern Mississippi and Atlantic flyways. Sheaffer (1998) found a positive correlation between spring and winter precipitation and recruitment for mallards in northeastern United States. For black ducks breeding in the northeastern US, Conroy et al. (2002) found that mean minimum spring temperature and mean spring precipitation were poor indicators of black duck production. Our models of black duck production in Canada indicated an inverse relationship between black duck production and spring precipitation. Biologically, during years of above average rainfall, brood survival may be reduced because of their limited ability to thermo regulate when feathers become rain soaked. Black ducks prefer various types of forested wetlands with heavier cover, but females have been found to nest in a wide variety of habitats (Kirby 1988). In areas where black ducks and mallards occur sympatrically mallards may exclude black ducks from highly productive wetlands (Dwyer and Baldassarre 1994). Years with above normal precipitation could be ideal for mallards because additional nest sites would be created through lowland flooding, but detrimental to black ducks as wetlands fill with excess water and potentially reduce nest site availability. Temperatures during the spring may also have an effect on production, especially those just prior to nest initiation (Johnson et al. 1992). For black ducks we found that standardized mean annual spring temperatures had a positive effect on recruitment. Thus, black duck production is likely to decline in years with below average spring temperatures. Coefficients estimates for standardized precipitation and temperature are very small, which suggest that they may only marginally influence black duck production. However, the short times series of data available for predictors, may limit a full understanding of the relationship between black duck production and environmental conditions.

Adaptive harvest management (AHM) strategies are beginning to play a critical role in the way harvest regulations for many waterfowl species are set. AHM strategies are currently used for setting regulations of mid-continental mallards, and efforts are under way to develop strategies for other populations of mallards, American black ducks, and northern pintails (*A. acuta*; USWFS 2000). AHM incorporates uncertainties about system dynamics and the effect that management actions have on the system into the decision making process while using management as a tool to reduce these uncertainties through time (Williams and Johnson 1995). Uncertainty in system dynamics are represented as a series of alternative models which given a range of management actions will predict different population outcomes. Alternative models serve to describe our understanding about the relationships between waterfowl and the factors, which affect their demographics. The models developed here could serve as alternative models in an AHM strategy for black ducks. As currently formulated the model has the flexibility to model production rates as a single population or as multiple populations. As additional data area collected, AHM would allow for a better understanding of the relationship between production and environmental data, but also the ability to immediately incorporate this new information into decision making.

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Figure 3.1. Breeding and Harvest area delineations used for modeling movement and fidelity rates for American black ducks, where W, C, and E represent the western, central, and eastern Canadian breeding and harvest areas. MF, AFN, and AFS correspond the US harvest areas in the Mississippi flyway, northern Atlantic flyway, and southern Atlantic flyway, respectively.

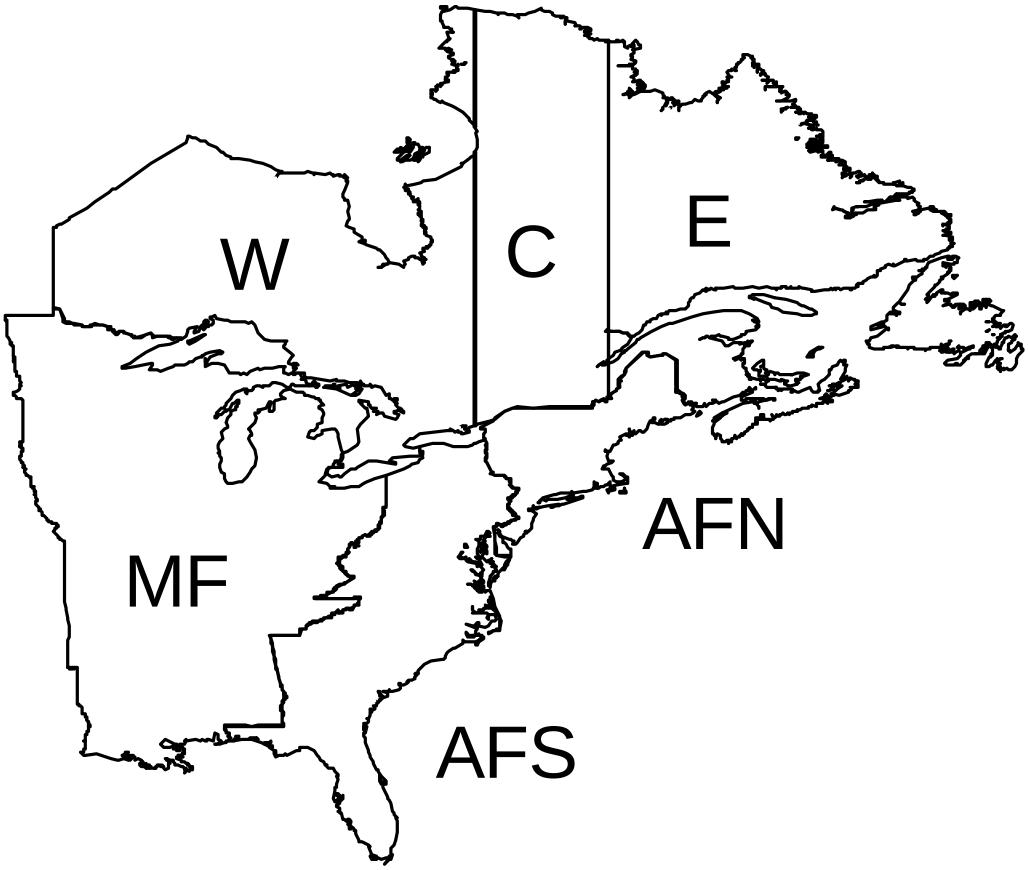

Figure 3.2. Location of the Black Duck Joint Venture survey plots and corresponding strata in Canada (Black Duck Joint Venture 1992).

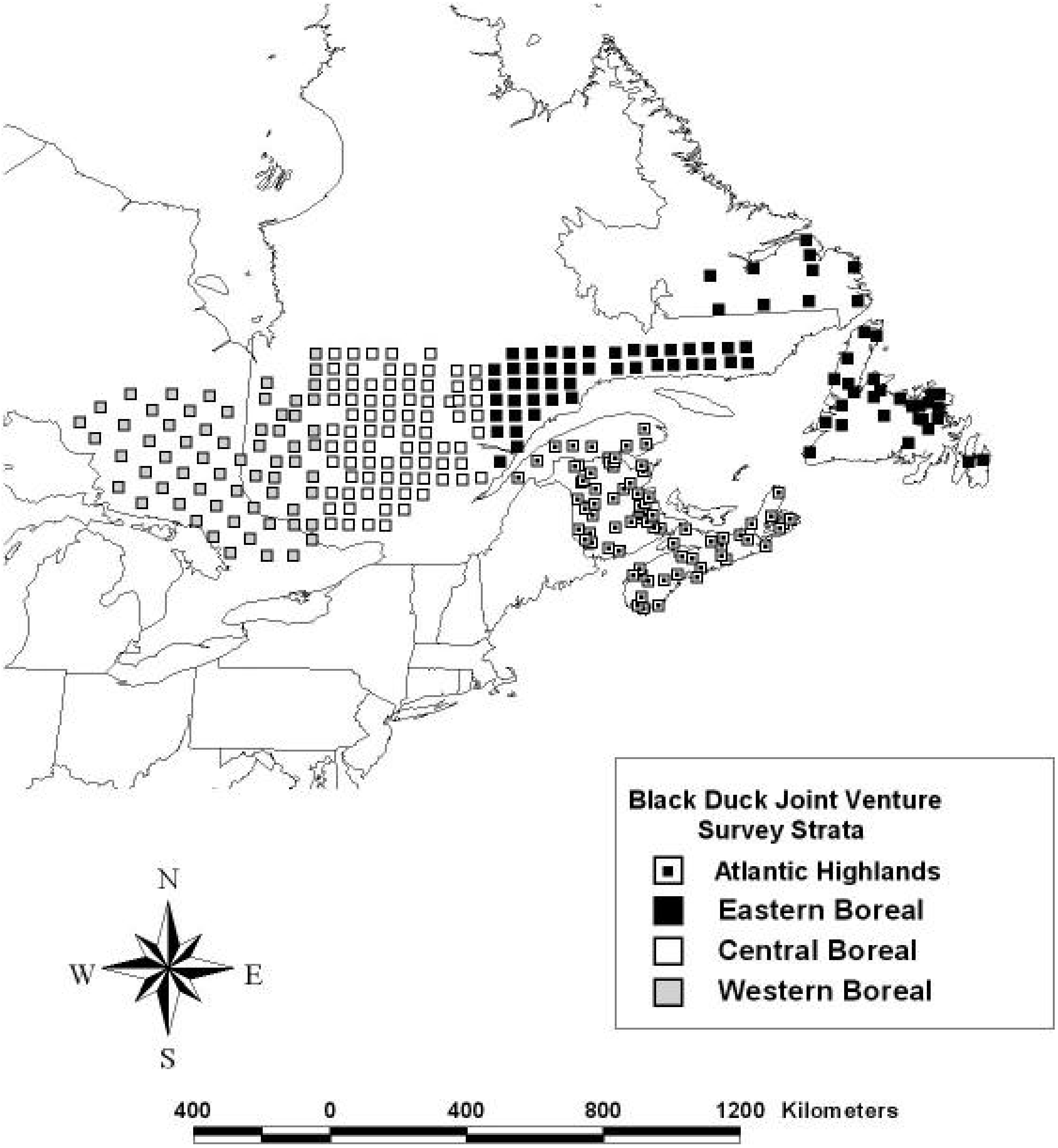

Table 3.1. Models and parameter estimates for predicting fall age-ratios of American black ducks where A_1, A_2, and A_3 represent intercept in the eastern, central and western breeding areas, respectively. β_X is the number of black ducks, and β_M is the number of mallards, in hundreds of thousands, estimated from the BDJV plot survey. β_{TMP} is the 12-year standardized spring temperature (^{o}C) across the black duck breeding range, and β_{PPT} is the 12-year standardized precipitation (mm) across the black duck breeding range.

				95% Confidence Interval			
Model	Predictor*	Coefficient Estimate	SE	Lower	Upper	Δ $QAIC_c$	*w*(i)
1	Log(A_1)	2.2478	0.3425	1.5765	2.9192	0.000	0.2631
	Log(A_2)	1.3557	0.1736	1.0155	1.6959		
	Log(A_3)	1.1790	0.2059	0.7757	2.9192		
	β_X	-0.4096	0.1294	-0.6632	-0.1561		
	β_M	-0.3465	0.2388	-0.8145	0.1215		
	β_{PPT}	-0.1942	0.1027	-0.3955	0.0072		
	β_{TMP}	0.0820	0.1476	-0.2072	0.3713		
2	Log(A_1)	1.5763	0.3740	0.8432	2.3093	0.108	0.2492
	Log(A_2)	1.6747	0.3049	1.0770	2.2724		
	Log(A_3)	0.8247	0.1742	0.4833	1.1662		
	β_{X1}	-0.2601	0.2356	-0.7218	0.2016		
	β_{X2}	-0.7326	0.3398	-1.3987	-0.0665		
	β_{X3}	-0.1984	0.0939	-0.3824	-0.0144		
3	Log(A_1)	1.5733	0.1761	1.2282	1.9184	0.473	0.2077
	Log(A_2)	1.1747	0.1506	0.8795	1.4700		
	Log(A_3)	0.9311	0.1603	0.6168	1.2454		
	β_X	-0.2584	0.0859	-0.4268	-0.0899		
4	Log(A_1)	1.8479	0.2713	1.3162	2.3795	0.939	0.1645
	Log(A_2)	1.1807	0.1505	0.8857	1.4756		
	Log(A_3)	0.9217	0.1609	0.6064	1.2371		
	β_X	-0.2475	0.0865	-0.4171	-0.0779		
	β_M	-0.2456	0.2086	-0.6545	0.1632		

Table 3.1 continued. Models and parameter estimates for predicting fall age-ratios of American black ducks where A_1, A_2, and A_3 represent intercept in the eastern, central and western breeding areas, respectively. β_X is the number of black ducks, and β_M is the number of mallards, in hundreds of thousands, estimated from the BDJV plot survey. β_{TMP} is the 12-year standardized spring temperature (^oC) across the black duck breeding range, and β_{PPT} is the 12-year standardized precipitation (mm) across the black duck breeding range.

Model	Predictor*	Coefficient Estimate	SE	95% Confidence Interval Lower	95% Confidence Interval Upper	Δ $QAIC_c$	*w*(i)
5	$Log(A_1)$	1.9120	0.2927	1.3382	2.4857	1.665	0.1144
	$Log(A_2)$	1.2366	0.1543	0.9342	1.5390		
	$Log(A_3)$	0.9831	0.1689	0.6521	1.3141		
	β_X	-0.3039	0.0930	-0.4862	-0.1216		
	β_M	-0.2162	0.2149	-0.6373	0.2050		
	β_{TMP}	0.0839	0.1441	-0.1985	0.3664		
6	Log(A)	1.1731	0.1295	0.9193	1.4269	10.996	0.0011
	β_X	-0.2664	0.0821	-0.4273	-0.1055		
Model Averaged	$Log(A_1)$	1.8337	0.5161	0.8274	2.8400		
	$Log(A_2)$	1.3537	0.4705	0.4363	2.2711		
	$Log(A_3)$	0.9732	0.3409	0.3084	1.6380		
	β_{X1}	-0.3017	0.2553	-0.7995	0.1961		
	β_{X2}	-0.4195	0.4042	-1.2076	0.3686		
	β_{X3}	-0.2864	0.2637	-0.8005	0.2277		
	β_M	-0.1563	0.3856	-0.9081	0.5955		
	β_{TMP}	0.0312	0.2010	-0.3608	0.4232		
	β_{PPT}	-0.0511	0.2745	-0.5864	0.4842		

CHAPTER 4

SUMMARY OF FINDINGS

At one time waterfowl regulations were set on the basis of survey data, and a biologist's understanding of environmental conditions and species biology. Models have seen greater use in waterfowl management with the advancement of modeling techniques. We have developed models that depict our understanding of a population's dynamics, and models that make predictions about such things as annual reproduction, and future population size after a set of management actions. Black duck population dynamics are complicated by the large degree of uncertainty regarding system dynamics, and causal factors surrounding past population declines. Conroy et al. (2002) developed a lifecycle population model for black ducks, which incorporated suspected causal factors for population declines, addressing black ducks as a single population. However, disparities in abundances in eastern Canada versus western Canada warrant further investigation. An understanding of movement and fidelity rates among breeding and harvest areas would extend the models of Conroy et al. (2002) with spatial stratification to examine differences among breeding areas.

The models developed by Conroy et al. (2002) utilized the Midwinter Inventory (MWI) as the index to breeding abundance, as other surveys covered too short of a time span, or were focused on species other than waterfowl. Although they recognized the deficiencies in the MWI, it provided the only sufficient long-term database for black duck population trends. Conroy et al. (2002) note that their needs to be continued monitoring of annual reproductive rates, and continued revision of the functional relationships between extrinsic and intrinsic variables. Migrating to a survey that directly estimates breeding abundances, could identify a better relationship between population size and reproductive rates.

Currently, black ducks are managed from the perspective of a single population or single stock. Surveys have indicated that black ducks have declined in the western portion of their range, while those found in the eastern portion of the range exhibited stable numbers or only minor declines. Are these differing trends a result of harvest pressure, influence of mallards (e.g. competition or hybridization), habitat differences, or differences in the underlying biological parameters of the population. Can we improve management performance, as measured by total harvest, by managing black ducks from a multiple population perspective? What are the costs associated with doing this, and how much additional return would be obtained from the system? These questions are beyond the scope of this research, but evaluation of these questions requires an understanding the dynamics that transition individuals from breeding areas to harvest areas, and fidelity to breeding areas.

The movement model consists of three breeding areas and six harvest areas, three of which are identical to the breeding areas, and models the transition of black ducks from the breeding areas to wintering areas. Movement rates among the breeding areas were modeled as the product of a movement rate, and a recovery rate using total banding and recoveries in each area as cell frequencies in a likelihood model. Model selection identified a model in which movement rates were sex specific. Estimated movement rates among the breeding areas by males and females were minimal. For instance, individuals breeding in the western breeding area were constrained to moving to the central breeding area. Estimated rates were 0.016 (SE ± 0.003) and 0.026 (SE ± 0.005) for males and females, respectively. Similar rates were estimated for males and females breeding in the eastern breeding area (Table 2.2). Black ducks breeding in the central breeding area could move east or west. For both sexes estimated movement rates were greater for the central to west pathway than for the central to east pathway, 0.081 (SE ± 0.008) for males and 0.052 (SE ± 0.008) for females, versus 0.015 (SE ± 0.003) for males, and 0.018 (SE ± 0.004) for females. Movement rates among the breeding areas were as expected, small. However, the large degree of movement from the central breeding area to the western breeding area by both males and females was unexpected. I suspect that this estimated rate is a result of the somewhat artificial means in which the breeding areas were created (see later discussion). One explanation for the resulting rate is that black ducks which bred in the central breeding area, and who would have ultimately migrated and wintered in the Mississippi flyway, move west and stop over in the freshwater marshes of Lake Erie and Lake Ontario, where they are then harvested (i.e. transients). Black ducks harvested on the Canadian side are considered in the western harvest area and would contribute to the movement rate from the central to western breeding area, while those harvested on the US side would contribute to the movement rate in the Mississippi flyway or northern Atlantic flyway.

Movement rates from the Canadian breeding areas to US harvest areas, are modeled on a conditional argument. Given that a bird survives the Canadian hunting season it is eligible to be harvested during the US hunting season. Movements by males and females from the eastern breeding area favor the northern Atlantic flyway harvest area, 0.914 (SE ± 0.007) and 0.890 (SE ± 0.008), respectively. The next largest movement rate is to the southern Atlantic flyway at 0.084 (SE ± 0.0073) and 0.108 (SE ± 0.0088) for males and females. Movement rates by black ducks from the central breeding area strongly favored the northern Atlantic flyway with rates for males at 0.689 (SE ± 0.020) and 0.686 (SE ± 0.0234) for females. However, there was increased movement to both the Mississippi flyway and southern Atlantic flyway. Movement rates by western breeding black ducks suggest an affinity for the Mississippi flyway, with movement rates to that area at 0.451 (SE ± 0.0227) for females and 0.506 (SE ± 0.0187) for males. Movement rates to the Atlantic flyway were split among the northern and southern areas for both males and females. Movement rates by males to the northern Atlantic flyway were 0.214 (SE ± 0.0205), and 0.280 (SE ± 0.0362) to the southern Atlantic flyway. Movement rates by females were 0.262 (SE ± 0.0255) to the northern Atlantic flyway and 0.287 (SE ± 0.0442) to the southern Atlantic flyway.

Movement rates to the US harvest areas indicate that while on the wintering grounds there is a great deal of mixing of birds from multiple breeding areas. Thus, setting harvest regulations in the US for black ducks should be done with care, because regulations could have an impact on the status of multiple breeding populations. This is particularly evident in the north Atlantic flyway harvest unit, where the movement rates to this area are large from all breeding areas, by both males and females.

From a US perspective the movement rates tend to follow what has been historically known regarding black ducks. The northern Atlantic Flyway states continue to harvest and winter more black ducks than any other state. It has been traditionally thought that black ducks breeding in the Ontario (western breeding area) migrated and wintered in the Mississippi flyway. Given that black duck numbers in Ontario have seen large declines, one could infer that the number of black ducks wintering in the Mississippi flyway would also see reduced numbers. However, the movement model is not without flaws. The largest being that any inconsistencies in the estimated rates probably results from weaknesses in the delineation of breeding areas. The delineation of these areas was limited by several factors. One, for this information to be palatable to stakeholders, we could not radically change the units in which waterfowl management occurred. In the US regulatory decisions are at the flyway level, and in Canada, at the provincial level. Second, there is consensus among the stakeholders to utilize a breeding ground survey for measuring abundance and production. Thus, spatial stratification was constrained to allow the estimation of production and abundance within each of the breeding areas. Utilizing the different strata in the CWS survey was an adequate solution to the problem. A more appropriate solution would be to examine banding and recoveries by 10' blocks and look for similarities in recovery distributions using multivariate techniques such as multi-response permutation procedures (MRPP), which has been done for mid-continental mallards and Wood Ducks (Kelly 1997; *Aix sponsa*). This type of analysis may result in better breeding areas, but estimating abundance and production rates in these areas may have failed or be of little value for management as breeding surveys would no longer index abundances in the breeding areas. As currently modeled, movement rates are based only on Canadian banding and recovery data. Thus, capture histories are limited to where they were banded, and where they were harvested. However, there are likely to be recoveries of black ducks that were harvested at some point during their migration, but had not yet reached their final wintering area, biasing movement rates. Unfortunately, we are unable to estimate the degree to which this occurs.

The second part of constructing spatially stratified models is transitioning the population from wintering areas back to respective breeding areas. Fidelity rates were modeled using Program MARK, using the Burnham (1993) model type, which incorporates bandings, recoveries, and recapture data into a common framework. AIC model selection, selected a model in which fidelity rates were age and sex specific. Fidelity rates for adults of both sexes were very high 0.9554 (SE ± 0.0434) for adult females, and 0.9695 (SE ± 0.0249) for adult males. Fidelity rates for juvenile black ducks were not that much less than adults, 0.9210 (SE ± 0.0931) for juvenile males and 0.8870 (SE ± 0.0475) for juvenile females.

Fidelity rates have not been previously estimated for black ducks. However, it has been suggested that they were likely to be high given the fidelity, and philopatry of other duck species (Blandin 1982). Our results should not be confused with other studies, in that our purpose was not to estimate the fidelity to a previous nest site, or small scale breeding area, such as a previously used wetland complex, but the fidelity to a large scale breeding area. Intuitively, given the size of our breeding areas, one would expect our fidelity rates to be high, unless young birds or those who nest unsuccessfully disperse long distances.

The production model developed by Conroy et al. (2002) utilizes black duck counts from the MWI, and environmental variables measured in the northeastern US. Utilizing counts from statistically based breeding surveys, as well as environmental variables measured from core breeding areas may provide a model with greater predictive ability. Currently, the time series from these surveys is limited so, they are limited for historical analysis, but are of greater value for future prediction.

We utilized the CWS helicopter plot survey to develop a reproduction model, utilizing environmental factors and abundance estimates to predict breeding area specific fall age-ratios. Fall age-ratios corrected for differential vulnerability among the age classes were used as the index to production. A log-linear model was used to model fall age-ratios. The top candidate model from model selection included black duck abundance, mallard abundance, spring precipitation, and spring temperature as predictors of production in black ducks. Estimated coefficients for black duck abundance, which is used as an indicator of density dependent reproduction, mallard abundance which served as an indicator to competition, and spring precipitation were negative, indicating that these factors depress reproduction rates in black ducks. While we stipulated that all models must include an effect for density dependence, results suggest that it is occurring to some extent as confidence intervals in most cases do not include zero. The effects for competition, spring temperature, and spring precipitation explain some of the variation in black duck reproduction rates, but in all cases confidence intervals include zero.

A model with area specific intercepts and area specific coefficients contained almost an equal amount of the total AIC model weight as the top ranked model, 0.2631 versus 0.2492, respectively. The distribution of the AIC model weights across all of the models in the set suggests that the current time span of data which we have to model reproduction rates may be insufficient to identify which parameters have the greatest effect on reproduction rates. The data do suggest that models with area specific intercepts tend to perform better than models in which the intercepts are identical across areas. If this model is to be utilized, it may be best served to use the model averaged results, which incorporate parameter and model uncertainty into coefficient estimates.

As the CWS breeding survey continues, and re-estimation of parameters occur, model weights will shift to a model which identifies the true parameters for predicting reproduction. In addition, other variables may be identified which serve as good indicators of reproduction. It is felt that some measure of habitat would add to the predictive ability of the model, however, we were unable to identify any meaningful long-term measure of habitat which was collected uniformly across the black duck breeding range. Second, the failure to identify a model that contained a dominant proportion of the total model weight may result from the short-term nature of the survey data, and the manner in which other data are collected. It is generally assumed that black ducks banded in any year are representative of the total population. However, most black duck banding stations are located in the southern portion of the black duck breeding range, where biologists can efficiently trap and band large numbers of ducks. Attempts have been made to add additional banding stations, to cover more of the black duck breeding range, but the logistics of getting to these stations, and the small number of ducks banded has prevented their use on an annual basis (Black Duck Joint Venture November 2003 meeting, Avalon NJ, personal communication).

Adaptive harvest management is rapidly becoming a tool utilized by waterfowl managers for guiding harvest management decisions in systems where there is uncertainty surrounding population dynamics, and the effect that harvest regulations have on population status. AHM is currently in place for the management of mid-continental and eastern stocks of mallards, and efforts are underway to develop strategies for western stocks of mallards, and northern pintails. A successful adaptive harvest management strategy relies on several key elements. One, we have the ability to reliably determine population size, and the outcome of a management decision (i.e., total harvest). Second, there exists a finite set of regulatory options that can be applied to the population (Johnson et al. 1993). Third, there exist clearly stated objectives by which we can measure performance (Johnson et al. 1993). Fourth, there are a series of mathematical models that represent hypotheses about the impact of regulations on the population (Johnson et al. 1993). Last, there is a measure of model credibility to assess the performance of individual models (Johnson et al. 1993).

Currently, for black ducks there exists an institutional framework for assessing population size, harvest, and harvest rates. The US Fish and Wildlife Service added additional strata covering the eastern portion of Canada to its existing Waterfowl Breeding Population and Habitat Survey in 1994 (i.e., May Survey), and the Canadian Wildlife Service conducts a helicopter plot survey, in eastern Canada that was initiated in 1990. Black duck harvest is assessed through a two part survey, one where hunters submit a single wing from each duck harvested, by which age and sex can be assessed (Parts Collection Survey). The second survey asks a sample of hunters to keep a log of the days hunted and the number of ducks shot and retrieved, and the number shot but not retrieved (Mail Questionnaire Survey). From this, estimates the total number of black ducks harvested and the age and sex composition of the harvest can be derived. Regulatory options may not be needed immediately to implement an AHM strategy, but managers would need the ability to transform a harvest rate prescribed by AHM models into some season length, bag limit combination. Managers must be able to clearly define what the objectives of management are. This is often a difficult part of AHM, as different stakeholders have different objectives, and some objectives are purely subjective or socio-political in nature. By far the most technically difficult part of an AHM strategy is developing a set of models to represent meaningful hypotheses about black ducks. Research has identified harvest, habitat quality and quantity, and competition with mallards as plausible factors for population declines in black ducks. Conroy et al. (2002) synthesized these factors, for which data exist, into a life cycle model, which could be used in AHM. Initially, one could assume that all models in a set have equal credibility, and as data are collected annually, model weights will shift to models which best predict future population sizes.

Given the established institutional framework for setting waterfowl regulations, and our experiences with AHM for other species, an AHM strategy for black ducks could be implemented utilizing a single population model approach, given the work that has been completed to date. However, the disparity in counts across Canada suggests that that there may be underlying biological differences between eastern and western Canada and that a single population model approach may be insufficient. A single population AHM approach could result in harvest rates that are unsuitable to stakeholders, as it is possible to have excessive harvest rates where black duck numbers are depressed, and restrictive harvest rates where black ducks are considered plentiful. A single population model does not have the ability to account for the varying distribution of birds across the landscape, but rather assumes a uniform distribution across the landscape. The best way to explore these alternatives is through spatial stratification. The ability to spatially stratify black ducks, we could begin to address questions regarding management performance of a single population versus multiple population models. Ideally, this will result in an approach that is most palatable to stakeholders and logistically possible to implement from a management viewpoint.

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APPENDIX A

DERIVATION OF THE MODEL FOR ESTIMATING MOVEMENT RATES OF AMERICAN BLACK DUCKS

The structure of the movement model contains three banded samples, one for each breeding area, and six possible areas for recovery (Figure 2.3). Banding areas also serve as three of the recovery areas. From any area of banding there are five possible locations in which a recovery may occur. The pathway from an area of marking to a recovery area is estimated as a single step direct movement. This is necessary as no observations of banded individuals occur between the initial banding and time of recovery.

For the purposes of model derivation a single age-sex class will be used, but data can be stratified by age and sex. The total number of bandings (R_i, i=1-3), and direct recoveries (m_j, j=1N,2N,3N,1S,2S,3S) are the only data needed for estimation. Banded birds not recovered (either not harvested, harvested but not reported, or died from other causes) are obtained through the subtraction from total bandings, and from bands recovered in one of the other five defined harvest areas.

The model was developed to mimic the differences in the timing of the hunting seasons between Canada and the United States. Traditionally, the hunting season in Canada begins in September, and later in the US. Migrating waterfowl are exposed to the risk of harvest in a sequential fashion. For example, the expected number of recoveries in harvest area 1N of black ducks banded in area 1 is

$$E[m_{1,1N}] = R_1(1-p_{1,2})f_{1N}\,, \tag{A1}$$

where π_{iy} is the probability of not moving from area 1 to 2 and $f_j = H_j\lambda_j$ is the recovery rate in harvest area j, a product of the area-specific harvest and reporting rates. We have assumed that reporting rates are constant across areas. Expected number of recoveries in harvest area 1S from area 1, is

$$E[m_{1,1S}] = R_1(1-f_{1N})(1-p_{1,2})f_{1S}\,, \tag{A2}$$

whereas the expected number of recoveries in harvest are 1S from banding area 2 is

$$E[m_{1,1S}] = R_2(1 - f_{2N})(1 - p_{2,1} - p_{2,3}) f_{1S}\,, \tag{A3}$$

These expectations can be used to build a likelihood for estimating the parameters $\pi_{i.j}$, and f_j, j=1N,2N,3N,1S,2S,3S but these parameters are not uniquely identifiable. Parameter identification requires incorporation of a conditional likelihood, in which recoveries in each southern harvest area is conditioned on being recovered in the southern harvest area. Thus, the expected number of recoveries in harvest area 1S from banding area 1, conditional on recovery in 1S is,

$$E[m_{1,1S} \mid m_{.,1S}] = m_{.,1S}\left[\frac{R_1 p_{1,1S} f_{1S}}{1 - \left[(1 - p_{1,2n} - p_{1,3n}) f_{1n} + p_{1,2n} f_{2n} + p_{1,3n} f_{3n}\right]}\right]. \tag{A4}$$

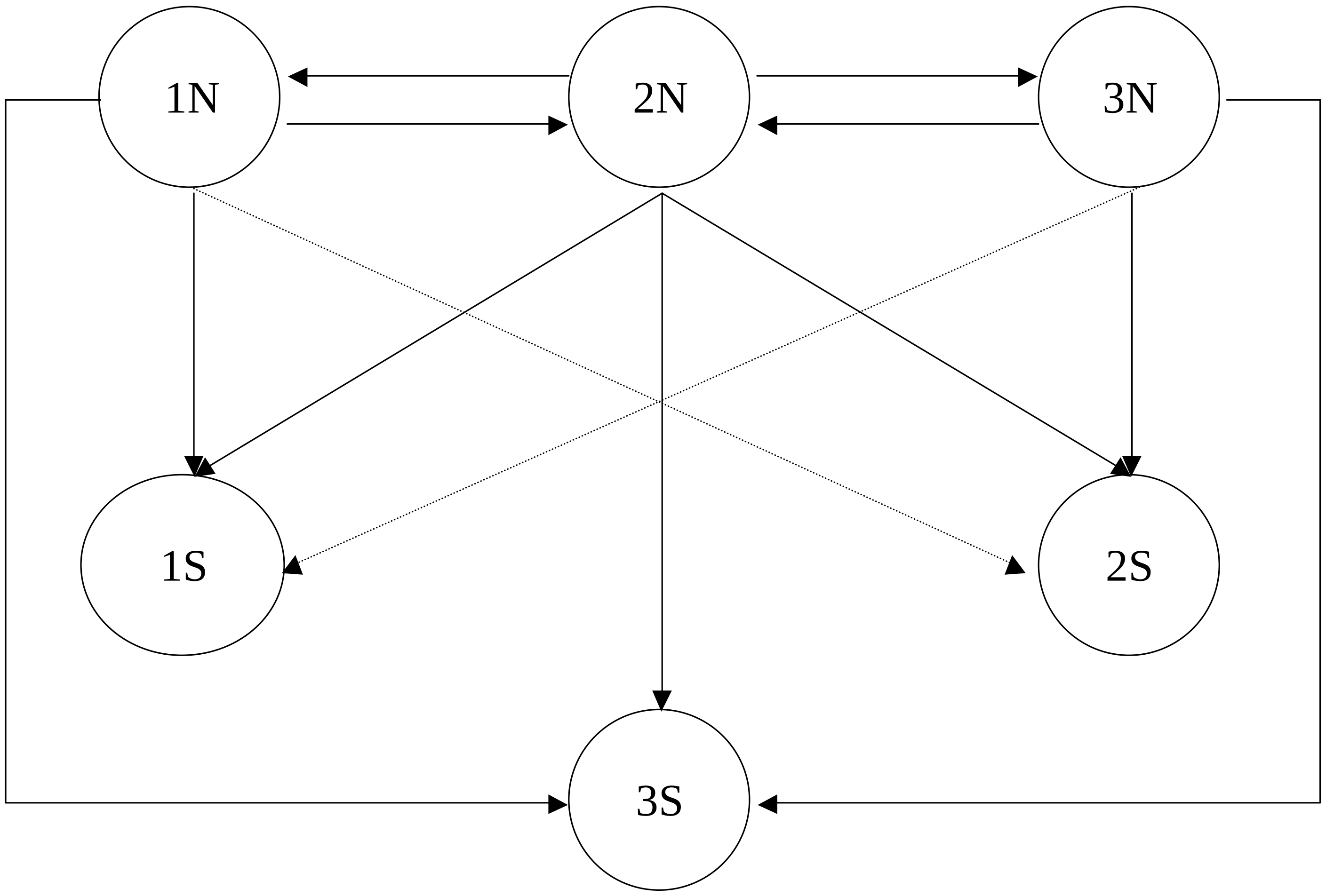
The total number of recoveries in any area is estimated by the product *n-1* movement rates, and *n* recovery rates.

Under a fully parameterized model, with three breeding areas and six harvest areas, there are 18 multinomial cells and 18 parameters leaving zero degrees of freedom. To estimate parameters it is necessary to constrain the model. For example, recovery rates for some harvest areas are equal, or eliminating movement pathways. Estimation occurs as a joint likelihood of the recoveries in northern areas and southern areas, in program SURVIV (White 1983).

Table A1. Expectations for the number of recoveries stratified by area of banding and recovery area for estimating movement rates in SURVIV. See figure A1 for a graphical representation.

Recovery Area		Banding Area 1	2	3
1	North	$R_1(1-p_{1,2}-p_{1,3})f_1$	$R_1 p_{1,2} f_2$	$R_1 p_{1,3} f_3$
	South	$\frac{p_{1,1s} f_{1s}}{1-\left[(1-p_{1,2}-p_{1,3})f_1+p_{1,2}f_2+p_{1,3}f_3\right]}$	$\frac{p_{2,1s} f_{1s}}{1-\left[(1-p_{1,2}-p_{1,3})f_1+p_{1,2}f_2+p_{1,3}f_3\right]}$	$\frac{p_{3,1s} f_{1s}}{1-\left[(1-p_{1,2}-p_{1,3})f_1+p_{1,2}f_2+p_{1,3}f_3\right]}$
2	North	$R_2 p_{2,1} f_1$	$R_2(1-p_{2,1}-p_{2,3})f_2$	$R_2 p_{2,3} f_3$
	South	$\frac{p_{1,2s} f_{2s}}{1-\left[p_{2,1}f_1+(1-p_{2,1}-p_{2,3})f_2+p_{2,3}f_3\right]}$	$\frac{p_{2,2s} f_{2s}}{1-\left[p_{2,1}f_1+(1-p_{2,1}-p_{2,3})f_2+p_{2,3}f_3\right]}$	$\frac{p_{3,2s} f_{2s}}{1-\left[p_{2,1}f_1+(1-p_{2,1}-p_{2,3})f_2+p_{2,3}f_3\right]}$
3	North	$R_3 p_{3,1} f_3$	$R_3 p_{3,2} f_3$	$R_3(1-p_{3,1}-p_{3,2})f_3$
	South	$\frac{p_{1,3s} f_{3s}}{1-\left[p_{3,1}f_1+p_{3,2}f_2+(1-p_{3,2}-p_{3,1})f_3\right]}$	$\frac{p_{2,3s} f_{3s}}{1-\left[p_{3,1}f_1+p_{3,2}f_2+(1-p_{3,2}-p_{3,1})f_3\right]}$	$\frac{p_{3,3s} f_{3s}}{1-\left[p_{3,1}f_1+p_{3,2}f_2+(1-p_{3,2}-p_{3,1})f_3\right]}$

Figure A1. A graphical model representative of the movement pathways modeled in the likelihood



APPENDIX B

PROGRAM SURVIV CODE FOR ESTIMATING PRODUCTION RATES IN AMERICAN BLACK DUCKS

Base Program SURVIV (1992) code used for fitting reproduction models for American Black Ducks. Code is based on modifications to Program SURVIV made by J. E. Hines (1999). Models are Created by inserting PROC MODEL statements with constraints.

```
PROC TITLE  'Age-Ratio calculation of Young Males in the
Fall Pop.';
PROC MODEL ADDCELL NPAR=123;
INLINE DECLARE REAL*8 HA(3,12), HY(3,12), TAU(3,12),A(3,12),
Y(3,12);
INLINE DECLARE REAL   BD(3,12), ML(3,12);
INLINE DECLARE REAL*8 B0(3,12), B1(3), B2(3), B3(3), B4(3),
B5(3);
INLINE DECLARE REAL*8 PPT(3,12), TMP(3,12), TPA(3,12),
BDML(3,12);
INLINE DECLARE INTEGER YRS, POPS;
INLINE BD(1,1) = 280684;
INLINE BD(1,2) = 162028;
INLINE BD(1,3) = 160612;
INLINE BD(1,4) = 136406;
INLINE BD(1,5) = 119176;
INLINE BD(1,6) = 114014;
INLINE BD(1,7) = 186512;
INLINE BD(1,8) = 144006;
INLINE BD(1,9) = 156584;
INLINE BD(1,10)= 211236;
INLINE BD(1,11)= 198658;
INLINE BD(1,12)= 150946;
INLINE BD(2,1) = 109130;
INLINE BD(2,2) = 95366;
INLINE BD(2,3) = 88730;
INLINE BD(2,4) = 77670;
INLINE BD(2,5) = 55548;
INLINE BD(2,6) = 65380;
INLINE BD(2,7) = 102040;
INLINE BD(2,8) = 90832;
INLINE BD(2,9) = 122822;
INLINE BD(2,10)= 144770;
INLINE BD(2,11)= 149440;
INLINE BD(2,12)= 131694;
INLINE BD(3,1) = 157238;
INLINE BD(3,2) = 134348;
INLINE BD(3,3) = 139918;
INLINE BD(3,4) = 127776;
INLINE BD(3,5) = 129704;
INLINE BD(3,6) = 133336;
```

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INLINE BD(3,7) = 166646;
INLINE BD(3,8) = 164910;
INLINE BD(3,9) = 229660;
INLINE BD(3,10)= 263048;
INLINE BD(3,11)= 270990;
INLINE BD(3,12)= 226654;
INLINE ML(1,1) = 49352;
INLINE ML(1,2) = 117272;
INLINE ML(1,3) = 117272;
INLINE ML(1,4) = 106254;
INLINE ML(1,5) = 92852;
INLINE ML(1,6) = 87246;
INLINE ML(1,7) = 136198;
INLINE ML(1,8) = 116246;
INLINE ML(1,9) = 76340;
INLINE ML(1,10)= 127522;
INLINE ML(1,11)= 236828;
INLINE ML(1,12)= 130992;
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INLINE ML(2,2) = 3442;
INLINE ML(2,3) = 4916;
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INLINE ML(2,7) = 10742;
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INLINE ML(2,9) = 9340;
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INLINE ML(2,11)= 6072;
INLINE ML(2,12)= 8874;
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INLINE ML(3,2) = 2212;
INLINE ML(3,3) = 1624;
INLINE ML(3,4) = 1600;
INLINE ML(3,5) = 864;
INLINE ML(3,6) = 1896;
INLINE ML(3,7) = 3500;
INLINE ML(3,8) = 4192;
INLINE ML(3,9) = 2806;
INLINE ML(3,10)= 10602;
INLINE ML(3,11)= 12746;
INLINE ML(3,12)= 5896;
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INLINE PPT(1,3) =  0.5863;
INLINE PPT(1,4) =  0.3891;
INLINE PPT(1,5) =  0.1389;
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INLINE PPT(3,11)= -0.5685;
INLINE PPT(3,12)= -0.4354;
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INLINE TMP(2,4) =  0.1192;
```

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INLINE TMP(3,7) =  0.0952;
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INLINE TMP(3,10) = 0.0968;

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INLINE POPS=3;
INLINE DO j=1, NYRS;
INLINE  DO i=1, POPS;
INLINE   B0(i,j)= S((j-1)*9+(i-1)*3+1);
INLINE   Hy(i,j)= S((j-1)*9+(i-1)*3+2);
INLINE  Tau(i,j)= S((j-1)*9+(i-1)*3+3);
INLINE  END DO;
INLINE END DO;
INLINE   B1(1)= S(NYRS*9+1)/*BD Density*/;
INLINE   B1(2)= S(NYRS*9+2);
INLINE   B1(3)= S(NYRS*9+3);
INLINE   B2(1)= S(NYRS*9+4)/*ML Density*/;
INLINE   B2(2)= S(NYRS*9+5);
INLINE   B2(3)= S(NYRS*9+6);
INLINE   B3(1)= S(NYRS*9+7)/*PPT*/;
INLINE   B3(2)= S(NYRS*9+8);
INLINE   B3(3)= S(NYRS*9+9);
INLINE   B4(1)= S(NYRS*9+10)/*TMP*/;
INLINE   B4(2)= S(NYRS*9+11);
INLINE   B4(3)= S(NYRS*9+12);
INLINE   B5(1)= S(NYRS*9+13)/*BD*ML*/;
INLINE   B5(2)= S(NYRS*9+14);
INLINE   B5(3)= S(NYRS*9+15);
INLINE DO j=1, NYRS;
INLINE  DO i=1, POPS;
INLINE   Ha(i,j)= Hy(i,j)*Tau(i,j);
INLINE   BDML(i,j)=(BD(i,j)/100000.)*(ML(i,j)/100000.);
```

```
INLINE   TPA(i,j)= B0(i,j)+B1(i)*(BD(i,j)/100000.)+
          B2(i)*(ML(i,j)/100000.);
INLINE   Y(i,j)=TPA(i,j)+B3(i)*PPT(i,j)+B4(i)
          *TMP(i,j)+B5(i)*BDML(i,j);
INLINE   A(i,j)= EXP(Y(i,j));
INLINE   P(1,(j-1)*9+(i-1)*3+1)= A(i,j)/(A(i,j)+Tau(i,j));
INLINE   P(2,(j-1)*9+(i-1)*3+1)= 1.- P(1,(j-1)*9+(i-1)*3+1);
INLINE   P(1,(j-1)*9+(i-1)*3+2)= Ha(i,j);
INLINE   P(2,(j-1)*9+(i-1)*3+2)= 1.- P(1,(j-1)*9+(i-1)*3+2);
INLINE   P(1,(j-1)*9+(i-1)*3+3)= Hy(i,j);
INLINE   P(2,(j-1)*9+(i-1)*3+3)= 1.-P(1,(j-1)*9+(i-1)*3+3);
INLINE  END DO;
INLINE END DO;

COHORT=  80;  60:;
COHORT= 275;   8:;
COHORT= 469;  36:;
COHORT= 155; 123:;
COHORT= 194;  10:;
COHORT= 239;  15:;
COHORT= 376; 287:;
COHORT= 378;  15:;
COHORT=1063;  84:;
COHORT=  83;  70:;
COHORT= 225;  10:;
COHORT= 707;  43:;
COHORT= 152; 129:;
COHORT= 158;  11:;
COHORT= 409;  41:;
COHORT= 350; 264:;
COHORT= 549;  16:;
COHORT=1949; 128:;
COHORT=  85;  63:;
COHORT= 353;  16:;
COHORT= 443;  28:;
COHORT= 198; 151:;
COHORT= 120;   3:;
COHORT= 241;  18:;
COHORT= 363; 263:;
COHORT= 331;   9:;
COHORT=1172;  72:;
COHORT=  59;  41:;
COHORT= 297;  13:;
COHORT= 649;  40:;
COHORT= 182; 154:;
COHORT= 126;   9:;
COHORT= 474;  61:;
```

```
COHORT= 322; 244:;
COHORT= 298;   4:;
COHORT=1481; 101:;
COHORT=  52;  45:;
COHORT= 307;  14:;
COHORT= 412;  16:;
COHORT= 141; 124:;
COHORT= 124;   4:;
COHORT= 274;  25:;
COHORT= 416; 377:;
COHORT= 260;   6:;
COHORT=1476;  86:;
COHORT=  60;  51:;
COHORT= 192;  13:;
COHORT= 410;  33:;
COHORT= 114; 100:;
COHORT=  45;   2:;
COHORT= 404;  33:;
COHORT= 425; 346:;
COHORT= 265;  14:;
COHORT=1560; 118:;
COHORT=  45;  32:;
COHORT= 288;  19:;
COHORT= 439;  23:;
COHORT= 155; 118:;
COHORT= 186;  16:;
COHORT= 113;   9:;
COHORT= 287; 229:;
COHORT= 374;   6:;
COHORT=1223; 116:;
COHORT=  93;  78:;
COHORT= 167;   9:;
COHORT= 786;  72:;
COHORT= 195; 167:;
COHORT=  87;   5:;
COHORT= 347;  45:;
COHORT= 212; 181:;
COHORT= 227;  11:;
COHORT=1226; 112:;
COHORT=  63;  52:;
COHORT= 157;  14:;
COHORT= 747;  60:;
COHORT= 128; 117:;
COHORT= 105;   7:;
COHORT= 376;  58:;
COHORT= 270; 224:;
COHORT= 414;  20:;
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```
COHORT=1810; 158:;
COHORT=  90;  73:;
COHORT= 212;  16:;
COHORT= 597;  39:;
COHORT= 157; 125:;
COHORT=  96;   9:;
COHORT= 179;  18:;
COHORT= 282; 204:;
COHORT= 446;  17:;
COHORT=1218; 111:;
COHORT=  77;  56:;
COHORT= 185;  23:;
COHORT= 487;  50:;
COHORT= 136;  92:;
COHORT= 251;  17:;
COHORT= 305;  49:;
COHORT= 250; 187:;
COHORT= 710;  34:;
COHORT=1168; 106:;
COHORT= 127;  98:;
COHORT= 155;  11:;
COHORT= 521;  64:;
COHORT= 202; 164:;
COHORT= 103;   5:;
COHORT= 218;  23:;
COHORT= 437; 335:;
COHORT= 380;  10:;
COHORT=1224; 104:;

LABELS;
S(1)= B0(1,1);
S(2)= Hy(1,1);
S(3)=tau(1,1);
S(4)= B0(2,1);
S(5)= Hy(2,1);
S(6)=tau(2,1);
S(7)= B0(3,1);
S(8)= Hy(3,1);
S(9)=tau(3,1);
S(10)= B0(1,2);
S(11)= Hy(1,2);
S(12)=tau(1,2);
S(13)= B0(2,2);
S(14)= Hy(2,2);
S(15)=tau(2,2);
S(16)= B0(3,2);
S(17)= Hy(3,2);
```

```
S(18)=tau(3,2);
S(19)= B0(1,3);
S(20)= Hy(1,3);
S(21)=tau(1,3);
S(22)= B0(2,3);
S(23)= Hy(2,3);
S(24)=tau(2,3);
S(25)= B0(3,3);
S(26)= Hy(3,3);
S(27)=tau(3,3);
S(28)= B0(1,4);
S(29)= Hy(1,4);
S(30)=tau(1,4);
S(31)= B0(2,4);
S(32)= Hy(2,4);
S(33)=tau(2,4);
S(34)= B0(3,4);
S(35)= Hy(3,4);
S(36)=tau(3,4);
S(37)= B0(1,5);
S(38)= Hy(1,5);
S(39)=tau(1,5);
S(40)= B0(2,5);
S(41)= Hy(2,5);
S(42)=tau(2,5);
S(43)= B0(3,5);
S(44)= Hy(3,5);
S(45)=tau(3,5);
S(46)= B0(1,6);
S(47)= Hy(1,6);
S(48)=tau(1,6);
S(49)= B0(2,6);
S(50)= Hy(2,6);
S(51)=tau(2,6);
S(52)= B0(3,6);
S(53)= Hy(3,6);
S(54)=tau(3,6);
S(55)= B0(1,7);
S(56)= Hy(1,7);
S(57)=tau(1,7);
S(58)= B0(2,7);
S(59)= Hy(2,7);
S(60)=tau(2,7);
S(61)= B0(3,7);
S(62)= Hy(3,7);
S(63)=tau(3,7);
S(64)= B0(1,8);
```

```
S(65)= Hy(1,8);
S(66)=tau(1,8);
S(67)= B0(2,8);
S(68)= Hy(2,8);
S(69)=tau(2,8);
S(70)= B0(3,8);
S(71)= Hy(3,8);
S(72)=tau(3,8);
S(73)= B0(1,9);
S(74)= Hy(1,9);
S(75)=tau(1,9);
S(76)= B0(2,9);
S(77)= Hy(2,9);
S(78)=tau(2,9);
S(79)= B0(3,9);
S(80)= Hy(3,9);
S(81)=tau(3,9);
S(82)= B0(1,10);
S(83)= Hy(1,10);
S(84)=tau(1,10);
S(85)= B0(2,10);
S(86)= Hy(2,10);
S(87)=tau(2,10);
S(88)= B0(3,10);
S(89)= Hy(3,10);
S(90)=tau(3,10);
S(91)= B0(1,11);
S(92)= Hy(1,11);
S(93)=tau(1,11);
S(94)= B0(2,11);
S(95)= Hy(2,11);
S(96)=tau(2,11);
S(97)= B0(3,11);
S(98)= Hy(3,11);
S(99)=tau(3,11);
S(100)= B0(1,12);
S(101)= Hy(1,12);
S(102)=tau(1,12);
S(103)= B0(2,12);
S(104)= Hy(2,12);
S(105)=tau(2,12);
S(106)= B0(3,12);
S(107)= Hy(3,12);
S(108)=tau(3,12);
S(109)=B1(1);
S(110)=B1(2);
S(111)=B1(3);
```

```
S(112)=B2(1);
S(113)=B2(2);
S(114)=B2(3);
S(115)=B3(1);
S(116)=B3(2);
S(117)=B3(3);
S(118)=B4(1);
S(119)=B4(2);
S(120)=B4(3);
S(121)=B5(1);
S(122)=B5(2);
S(123)=B5(3);

PROC TEST;
PROC STOP;
```

LITERATURE CITED

White, G.C. 1992. PC SURVIV Users Manual. Dept. of Fishery and Wildlife Biology, Colorado State University, Fort Collins, CO

Hines, J. E. 1999. Recent modifications to Program SURVIV. Patuxent Software Archive. Patuxent Wildlife Research Center, Laurel, MD.

APPENDIX C

PARAMETER ESTIMATES FOR PRODUCTION RATES OF AMERICAN BLACK DUCKS UNDER THE GENERAL MODEL

Table C1. Parameter estimates from Program SURVIV (Appendix B) for the general reproduction model $\tau(a)P(a*t)$ where τ is the relative vulnerability correction for adults to young, β_0 is the area and time specific age ratio, and f_y is the area and time specific recovery rates of young.

			95% Confidence Interval	
Parameter(*i*,*j*)*	Estimate	SE	Lower	Upper
$\tau(1,*)$	0.8390	0.0737	0.6946	0.9835
$\tau(2,*)$	0.5558	0.0622	0.4339	0.6777
$\tau(3,*)$	0.4354	0.0358	0.3652	0.5055
$\beta_0(1,1)$	0.9231	0.2727	0.3886	1.4577
$\beta_0(1,2)$	1.5081	0.3145	0.8916	2.1245
$\beta_0(1,3)$	0.8766	0.2628	0.3616	1.3916
$\beta_0(1,4)$	0.6477	0.2961	0.0674	1.2280
$\beta_0(1,5)$	1.6853	0.4157	0.8706	2.5000
$\beta_0(1,6)$	1.5591	0.3721	0.8299	2.2883
$\beta_0(1,7)$	0.7253	0.3404	0.0581	1.3925
$\beta_0(1,8)$	1.4732	0.2953	0.8944	2.0519
$\beta_0(1,9)$	1.3779	0.3433	0.7050	2.0507
$\beta_0(1,10)$	1.2818	0.2833	0.7266	1.8369
$\beta_0(1,11)$	0.8053	0.2705	0.2751	1.3356
$\beta_0(1,12)$	1.0422	0.2289	0.5935	1.4909
$\beta_0(2,1)$	0.7591	0.2278	0.3126	1.2056
$\beta_0(2,2)$	1.1370	0.2525	0.6422	1.6319
$\beta_0(2,3)$	0.5798	0.2010	0.1858	0.9739
$\beta_0(2,4)$	1.1174	0.2339	0.6589	1.5759
$\beta_0(2,5)$	1.3998	0.2818	0.8475	1.9520
$\beta_0(2,6)$	1.3788	0.3065	0.7781	1.9795
$\beta_0(2,7)$	0.5725	0.2191	0.1430	1.0020
$\beta_0(2,8)$	1.1985	0.2328	0.7421	1.6549
$\beta_0(2,9)$	1.7770	0.3346	1.1212	2.4328
$\beta_0(2,10)$	0.7753	0.2275	0.3293	1.2212
$\beta_0(2,11)$	0.1503	0.2147	-0.2706	0.5712
$\beta_0(2,12)$	0.8750	0.2120	0.4595	1.2904
$\beta_0(3,1)$	0.3392	0.1466	0.0520	0.6265
$\beta_0(3,2)$	0.2900	0.1489	-0.0019	0.5819
$\beta_0(3,3)$	0.1354	0.1434	-0.1457	0.4164
$\beta_0(3,4)$	0.3089	0.1539	0.0073	0.6105
$\beta_0(3,5)$	1.4371	0.1872	1.0702	1.8040

Table C1 Continued. Parameter estimates from Program SURVIV (Appendix B) for the general reproduction model τ(a)P(a*t) where τ is the relative vulnerability correction for adults to young, β_0 is the area and time specific age ratio, and f_y is the area and time specific recovery rates of young.

Parameter(*i*,*j*)*	Estimate	SE	95% Confidence Interval	
			Lower	Upper
β_0 (3,6)	0.6454	0.1494	0.3527	0.9381
β_0 (3,7)	0.5417	0.1684	0.2116	0.8718
β_0 (3,8)	0.9329	0.2110	0.5193	1.3466
β_0 (3,9)	0.7514	0.1815	0.3956	1.1072
β_0 (3,10)	0.1298	0.1565	-0.1769	0.4365
β_0 (3,11)	0.2564	0.1673	-0.0715	0.5842
β_0 (3,12)	0.3576	0.1398	0.0835	0.6316
f_y (1,1)	0.0630	0.0094	0.0446	0.0814
f_y (1,2)	0.0592	0.0080	0.0436	0.0748
f_y (1,3)	0.0595	0.0090	0.0420	0.0771
f_y (1,4)	0.0590	0.0080	0.0433	0.0747
f_y (1,5)	0.0448	0.0081	0.0288	0.0607
f_y (1,6)	0.0805	0.0116	0.0578	0.1032
f_y (1,7)	0.0616	0.0094	0.0432	0.0801
f_y (1,8)	0.0875	0.0094	0.0692	0.1059
f_y (1,9)	0.0842	0.0094	0.0657	0.1027
f_y (1,10)	0.0709	0.0093	0.0526	0.0892
f_y (1,11)	0.1135	0.0128	0.0885	0.1385
f_y (1,12)	0.1153	0.0127	0.0904	0.1402
f_y (2,1)	0.0719	0.0142	0.0441	0.0996
f_y (2,2)	0.1045	0.0139	0.0772	0.1318
f_y (2,3)	0.0684	0.0145	0.0399	0.0969
f_y (2,4)	0.1287	0.0145	0.1002	0.1571
f_y (2,5)	0.0848	0.0152	0.0550	0.1146
f_y (2,6)	0.0816	0.0132	0.0556	0.1075
f_y (2,7)	0.1145	0.0227	0.0700	0.1590
f_y (2,8)	0.1266	0.0169	0.0936	0.1597
f_y (2,9)	0.1499	0.0173	0.1159	0.1839
f_y (2,10)	0.1155	0.0213	0.0738	0.1573
f_y (2,11)	0.1491	0.0178	0.1142	0.1840
f_y (2,12)	0.1019	0.0185	0.0657	0.1381
f_y (3,1)	0.0806	0.0078	0.0652	0.0959
f_y (3,2)	0.0658	0.0053	0.0553	0.0763
f_y (3,3)	0.0615	0.0067	0.0485	0.0746
f_y (3,4)	0.0653	0.0062	0.0532	0.0774

Table C1 Continued. Parameter estimates from Program SURVIV (Appendix B) for the general reproduction model τ(a)P(a*t) where τ is the relative vulnerability correction for adults to younsg, β_0 is the area and time specific age ratio, and f_y is the area and time specific recovery rates of young.

Parameter(*i*,*j*)*	Estimate	SE	95% Confidence Interval	
			Lower	Upper
f_y (3,5)	0.0579	0.0059	0.0464	0.0694
f_y (3,6)	0.0787	0.0066	0.0657	0.0916
f_y (3,7)	0.0883	0.0077	0.0733	0.1034
f_y (3,8)	0.0928	0.0080	0.0771	0.1085
f_y (3,9)	0.0893	0.0064	0.0767	0.1020
f_y (3,10)	0.0907	0.0077	0.0755	0.1058
f_y (3,11)	0.0946	0.0078	0.0793	0.1099
f_y (3,12)	0.0822	0.0074	0.0676	0.0967

**i* corresponds to area where 1 = west, 2 = central, 3 = east, and *j* corresponds to year 1990-2002.

Table C2. Environmental and population data used for fitting models in SURVIV and SAS.

Area	Year (t)	N_t	M_t	PPT_t	TMP_t
Western	1990	280,684	49,352	0.6360	0.0748
	1991	162,028	117,272	0.6967	0.0778
	1992	160,612	117,272	0.5863	0.0724
	1993	136,406	106,254	0.3891	0.0734
	1994	119,176	92,852	0.1389	0.0720
	1995	114,014	87,246	0.0921	0.0736
	1996	186,512	136,198	-0.1079	0.0709
	1997	144,006	116,246	-0.2082	0.0709
	1998	156,584	76,340	-0.5543	0.0779
	1999	211,236	127,522	-0.5089	0.0767
	2000	198,658	236,828	-0.6052	-0.8817
	2001	150,946	130,992	-0.5546	0.0776
Central	1990	109,130	6,882	0.6835	0.1222
	1991	95,366	3,442	0.6982	0.1212
	1992	88,730	4,916	0.3550	0.1187
	1993	77,670	2,950	0.3685	0.1192
	1994	55,548	2,950	0.4322	0.1192
	1995	65,380	3,296	0.0986	0.1199
	1996	102,040	10,742	-0.1635	0.1198
	1997	90,832	8,874	-0.2294	0.1182
	1998	122,822	9,340	-0.5583	0.1226
	1999	144,770	13,544	-0.3675	0.1215
	2000	149,440	6,072	-0.9507	-1.2636
	2001	131,649	8,874	-0.3666	0.1213
Eastern	1990	157,238	1,766	0.4610	0.0929
	1991	134,348	2,212	0.4574	0.0942
	1992	139,918	1,624	0.3464	0.0925
	1993	127,776	1,600	0.3223	0.0933
	1994	129,704	864	0.3018	0.0931
	1995	133,336	1,896	0.0230	0.0934
	1996	166,646	3,500	-0.0047	0.0952
	1997	164,910	4,192	-0.1434	0.0920
	1998	229,660	2,806	-0.4264	0.0957
	1999	263,048	10,602	-0.3334	0.0968
	2000	270,990	12,746	-0.5685	-0.4390
	2001	226,654	5,896	-0.4354	-0.4675