Non-Linear Density Dependence in a Stochastic Wild Turkey Harvest Model

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ABSTRACT

Current eastern wild turkey (*Meleagris gallopavo silvestris*) harvest models assume density-independent population dynamics despite indications that populations are subject to a form of density dependence. I suggest that both density-dependent and independent factors operate simultaneously on wild turkey populations, where the relative strength of each is governed by population density. I attempt to estimate the form of the density dependence relationship in wild turkey population growth using the theta-Ricker model. Density-independent relationships are explored between production and rainfall and temperature correlates for possible inclusion in the harvest model. Density-dependent and independent effects are then combined in the model to compare multiple harvest strategies.

To estimate a functional relationship between population growth and density, I fit the theta-Ricker model to harvest index time-series from 11 state wildlife agencies. To model density-independent effects on population growth, I explored the ability of rainfall, temperature, and mast during the nesting and brooding season to predict observed production indices for 7 states. I then built a harvest model incorporating estimates to determine their influence on the mean and variability of the fall and spring harvest.

Estimated density-dependent growth rates produced a left-skewed yield curve maximized at ~40% of carrying capacity, with large residuals. Density-independent models of production varied widely and were characterized by high model uncertainty.

Results indicate a non-linear density dependence effect strongest at low population densities. High residuals from the model fit indicate that extrinsic factors will overshadow density-dependent factors at most population densities. However, environmental models were weak, requiring more data with higher precision. This indicates that density-independence can be correctly and more easily modeled as random error. The constructed model uses both density dependence and density-independent stochastic error as a tool to explore harvest strategies for biologists. The inclusion of weak density dependence changes expected harvest rates little from density-independent models. However, it does lower the probability of overharvest at low densities. Alternatives to proportional harvesting are explored to reduce the uncertainty in annual harvests.

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Finally, here's a bit of wisdom about ol' *Meleagris gallopavo*…

"A turkey is more occult and awful than all the angels and archangels. In so far as God has partly revealed to us an angelic world, he has partly told us what an angel means. But God has never told us what a turkey means. And if you go and stare at a live turkey for an hour or two, you will find by the end of it that the enigma has rather increased than diminished."

– G. K. Chesterton. 1919. All Things Considered., Metheun, London.

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CHAPTER 1: LITERATURE REVIEW OF WILD TURKEY MODELS AND MANANGEMENT

Current harvest models for eastern wild turkey (*Meleagris gallopavo silvestris*) assume that annual variation in yield is determined entirely by density independent processes (Vangilder and Kurzejeski 1995, Alpizar-Jara et al. 2001). However, research based on radio-telemetry studies (Vander Haegan et al. 1988, Hurst et al. 1996), modeling of harvest indices (Porter et al. 1990a), and expert opinion (Healy and Powell 2001) suggest that density-dependent population growth may operate at the local population level, where density dependence is defined as the functional relationship between reproduction or survival and population density (Turchin 2003: 398). The presence of density-dependent growth could allow managers to recommend more liberal harvest strategies because it would increase the predictability of annual yields and provide a mechanism to stabilize populations undergoing periodic over-harvests (McCullough 1979: 237 – 238), and optimize growth rates in a stochastic environment (Saether et al. 2002). Conversely, environmental stochasticity causes uncertainty in the population dynamics of a harvested species, reduces the ability to predict yield and increases the probability of over-harvest if regulations assume a deterministic system (Lande et al. 2001: 81). Failure to account for environmental stochasticity may ultimately result in population decline or extirpation and long-term loss in hunting opportunity (Caughley 1977, Williams et al. 1996). This makes it important to understand the effects of both density dependence and environmental stochasticity on wild turkey populations (McCullough 1990).

Wild turkey managers are increasingly using population models to determine harvest strategies and population sensitivity to hunting (Suchy et al. 1990, Vangilder and Kurzejeski 1995, Alpizar-Jara et al. 2001). Currently, wild turkey population models ignore density-dependent effects and may overestimate stochastic effects by not allowing for covariance between demographic parameters (such as nesting and renesting rates: Vangilder and Kurzejeski 1995, Roberts and Porter 1995). This study examines the potential effect of density dependence on wild turkey population growth using McCullough's black box modeling approach, which accounts for covariances between vital rates (McCullough 1984). This approach is well suited to the time-series data collected by many state wildlife agencies, which attempt to measure annual population growth from harvest indices rather than from age-structured vital rates.

Analysis of density dependence from time-series requires large amounts of data for precise parameter estimates (>20 years: Woiwod and Hanski 1992, ≥30 generations: Solow and Steele 1990). Unfortunately, many agencies lack the number of years required for such precision, and, in addition, harvest index information is subject to a large amount of measurement error. Meta-analysis provides more precise estimates from a set of population time-series, assuming parameter estimates are common across populations (Myers 1997). Based on information from 11 state wildlife agencies (Fig. 1.1), I use meta-analysis techniques in this study, assuming a common response to increased population density for the eastern wild turkey, which can be measured both across populations and harvest indices. Based on these techniques, I then construct a new harvest model to examine the effects of multiple harvest strategies when both density dependence and environmental stochasticity are included.

In this chapter, I review the population biology and management history of wild turkey. This is followed by a discussion of four harvest models for the species, with comments on the results of each and the effect their common assumptions may have on harvest strategies. I then discuss the utility of the black box modeling approach and the relevance of density dependence to wild turkey population growth and harvesting. After this, I discuss the problems of detecting density dependence in time-series analysis and the potential for meta-analysis to address these problems. Finally, I discuss the strengths and weaknesses of meta-analysis, particularly in regards to time-series analysis.

Population Dynamics

Eastern wild turkey populations represent an important harvestable resource throughout the United States (Tapley et al. 2001). Annual population densities may fluctuate by as much as ± 50% of the long-term mean in a given region, however, making it difficult to predict harvestable yields from year to year (Mosby 1967). Causal factors for this variation are still poorly understood (Vangilder 1992), but are considered linked closely to reproduction and weather (Roberts and Porter 1996, Healy and Powell 2000).

The annual breeding cycle of the wild turkey begins in spring. Breeding behavior begins with an increase in daylight hours, and may vary among regions based on temperature differences, with cold weather delaying activity (Healy 1992). Winter brood flocks, composed of both males and females, with average sizes ranging from 11 – 125 individuals begin to disperse at this time (Porter 1978).

Breeding activity starts with the strutting and gobbling of males. These behaviors are concurrent with mating (Bailey and Rinell 1966). Mating is polygamous, and females are capable of reproducing during their first spring; a variable percentage of males may breed at this age, but all males ≥ 2 years can breed (Healy and Powell 2000). Impregnated hens disperse from their winter ranges, avoid other hens, and search for a nesting site (Healy 1992). The highest mortality occurs early in life with heaviest losses occurring from nest and brood predation of poults (Vangilder 1992, Hubbard et al. 1999). Although turkeys can live up to 15 years in the wild, their estimated mean life expectancy from hatching is approximately 1.3 – 1.6 years (Mosby 1967, Cardoza 1995). Mosby (1967) inferred from hunter-recovered banded wild turkeys that the mean expected lifespan after surviving the first six months was 0.81 years in West Virginia, and 1.16 years in Florida.

Predation and harvest are considered the largest mortality sources in wild turkey populations. Vangilder's (1992) review of wild turkey population dynamics reports the cause of death in nine studies. Predation in these studies accounts for 29 – 100% of deaths, while disease, starvation or unknown causes account for 0 – 18%. Legal harvest accounts for 0 – 50% and illegal harvest accounts for 0 – 22%. Given the large effect hunting has on the population dynamics of the species, the management history of the wild turkey is tightly linked to its life history.

Management History of the Eastern Wild Turkey

A decline in eastern wild turkey populations began with the colonization of North America by the Europeans (Aldrich 1967). Mosby and Handley (1943) suggested market hunting as a major reason for the decline of wild turkeys in the U.S. and gave four reasons for the decline of the eastern wild turkey in Virginia: 1) the clearing of forest for lumber or agriculture; 2) the increased human depredation as settlement expanded westward; 3) the human reduction of mast producing trees; and 4) the interaction of critical periods of severe weather and the loss of the American chestnut (*Castenea dentate*) in conjunction with the first two reasons.

Early management efforts to restore the wild turkey began in earnest in the late 1920's and early 1930's (Mosby 1975). These largely unsuccessful restoration efforts consisted of releasing farm-reared birds into the wild (Cantner 1955). The reasons for the failure of this strategy have been ascribed to a genetic loss of essential but unknown characteristics possessed by wild birds, increased disease and parasite loads under confined conditions, and the lack of proper survival mechanisms normally learned from wild maternal hens (Kennamer et al. 1992). For these reasons, despite the efforts of biologists, the eastern wild turkey probably occupied only 12% of its ancestral range by 1948 (Mosby 1949).

Some success in wild turkey restoration began with the onset of the Great Depression. People were forced to move toward urban industrial settings out of economic necessity and forests began to regenerate around abandoned family farms (Wunz and Pack 1992). This renewed habitat availability allowed turkeys to recolonize some of their former habitat. With the end of World War II came renewed efforts to re-establish wild turkey populations by releasing captured wild birds from existing flocks into other suitable habitats (Kennamer et al. 1992). This method soon emerged as the most efficient way of restoring wild turkeys to their former range. Bailey and Putnam (1979) reported an 83% success rate in establishing viable populations in 36 states. Restoration of wild turkey populations through the capture and release of birds from wild populations became a major focus for the conservation of the species (Lewis 2001, Tapley et al. 2001).

Current Management for Wild Turkey

Today all states in the U.S., with the exception of Alaska, have turkey populations of sufficient size for a spring hunting season. Wild turkeys occupy all states of their original range and 10 states not considered a part of their ancestral range (Kennamer et al. 1992). Consequent to this successful restoration of the wild turkey, management and research efforts have shifted from an emphasis on reintroduction to an emphasis on providing a sustained harvest (Tapley et al. 2001). Currently, biologists are confronted with the pressures of harvest management for a species subject to both highly variable annual harvests and natural population fluctuations (Mosby 1967, Weaver and Mosby 1979). Harvest strategies take three general forms considered the most practical options for turkey harvest management: spring gobblers-only harvests, spring gobblers-only harvests with limited fall either-sex harvests, or spring and fall harvests set to maximize the total harvest (Healy and Powell 2000, Healy and Powell 2001). The spring gobblers-only harvest represents the most conservative strategy, assuming that harvest mortality is additive, but is limited primarily to males such that it does not disrupt breeding behavior nor affect population growth (Healy and Powell 2001). In some regions, however, fall either-sex hunting is traditional and management needs to incorporate a fall season in conjunction with a spring gobblers-only season. The incorporation of a fall either-sex harvest typically requires the additional assumptions that the harvesting of hens may act to reduce population growth (Pack et al. 1999), populations are subject to annual fluctuations (Mosby 1967), and vulnerability to harvest in fall increases in poor mast years (Steffen et al. 2002, Healy and Powell 2000). A spring gobblers-only season with a limited fall either-sex harvest typically emphasizes spring hunting over fall hunting, minimizing the effect on population growth and the reduction of spring hunting opportunities (Healy and Powell 2001). Managers may also attempt to maximize both spring and fall harvests, with both seasons emphasized equally.

Increasingly, managers are using harvest models for wild turkey to explore options for balancing these desired harvest strategies with the high variability inherent to the system. In some cases, the assumptions of the 3 basic harvest strategies result from the same research that produced the harvest models (Suchy et al. 1983, Vangilder and Kurzejeski 1995). Thus the interplay between wild turkey harvest models and wild turkey harvest management is improving, and an understanding of current harvest management for this species relies on an understanding of current wild turkey harvest models.

Current Wild Turkey Harvest Models

Harvest models attempt to imitate the behavior of a population system, allowing managers to make predictions under an array of harvest strategies. McCullough (1984) classified these models as two types: accounting type or mechanistic models that follow the size and composition of a population by tracking the number of births and deaths via extensive bookkeeping, and simpler black box type models such as the stock-recruitment models often used in fisheries research.

Recent models for wild turkey are mechanistic. Vangilder and Kulowiec (1988), for example, produced a stochastic computer model that is both age and time-specific, requiring data that must be estimated from a radio-marked sample of wild turkeys (Vangilder 1992). Harvest mortality is determined by the user as the proportion of the population to be killed for fall harvests, and the number of males taken for the spring season. Natural mortality and illegal harvest are also included. Population projections are made by allowing model parameters to vary within a uniform distribution bounded by the 95% confidence interval around the mean. Vangilder and Kurzejeski (1995) used the same model, but bounded the uniform distribution within one standard deviation. The model assumes additive hunting mortality and density-independent survival and recruitment. Vangilder and Kurzejeski (1995) found that, under these assumptions, population growth could occur only if fall harvest was held at ≤10%, while the spring gobblers-only harvest had minimal effect.

Alpizar-Jara et al. (2001) produced a stochastic model to determine which parameters have the greatest effect on population growth, find the balance of spring and fall harvest strategies maximizing annual yield, and determine how annual variation in demographic parameters affect harvest and population growth predictions. The model incorporates both sexes and 3 age classes: juveniles (<1year old), yearlings (≥1 but <2 years old), and adults (≥ 2 years old). Recruitment rates were based on radio-telemetry data, but then calibrated to match the growth rates for 10 years of spring harvest data, assuming trends in the spring harvest were directly proportional to trends in population growth. Survival rates were time-specific (fall-winter, spring-summer) and represented the product of natural mortality, illegal harvest, and legal harvest. The data used in the model were collected in regions of both West Virginia and Virginia. Male demographic parameters were based on auxiliary data or taken from the literature (Vangilder and Kurzejeski 1995, Little et al. 1990, Suchy et al. 1990). The authors assumed density-independent population growth. Male and female harvests were assumed equal in fall based on the sex ratio of the harvest. Sensitivity analysis indicated fall harvest had the strongest effect on population growth and the proportion of males in the population, and suggested fall harvests of ≤10% would produce the greatest long-term annual and the greatest seasonal yields. Increasing the variability in demographic parameters increased the variation in population growth. Also, increases in fall harvests increased the variability in population growth.

Lobdell et al. (1972) produced a stochastic model to evaluate whether a fall-either sex harvest could be safely implemented. They used estimates of vital rates (annual mortality, harvest mortality, subadult: adult ratio) taken from the literature or harvest statistics. These parameters were assumed to be independent and allowed to vary according to a normal distribution. The authors assumed that the fall harvest was compensatory when less than half the natural mortality. Results indicated that the subadult:adult ratio had a greater effect on population growth than annual mortality (natural + harvest mortality). In addition, first year hens contributed little to annual production. Assuming complete compensation, populations could withstand fall harvests of 20 – 35% of the population (Vangilder 1992). The authors concluded that the assumption of additive mortality would require an unrealistically high reproductive rate to maintain the population. Therefore, the compensatory mortality assumption had intuitive appeal. They recommended a combined fall either-sex and spring gobblers-only harvest, based on their assumption of compensatory harvest mortality.

Suchy et al. (1983) produced a deterministic model to evaluate the potential effects of a fall harvest in Iowa. They tested the model under both additive and compensatory mortality assumptions. The authors specified a compensatory threshold (beyond which harvest was considered additive) for hens (5%) and gobblers (16%). They compared harvest rates based on the number of years it took to reach a 25% population decline. Under a 10% harvest rate with a compensatory threshold, a 25% decline took 73.6 years, while a 15% harvest rate under the same assumptions took only 6.2 years. Assuming completely additive mortality, a 10% harvest rate took only 6.5 years to reach a 25% decline in population size. The authors concluded that population growth was highly sensitive to hen survival, and recommended fall harvests of <10% to maintain population growth.

The general consensus of wild turkey models is that fall harvests of > 10% cause population decline. This decline may occur even under a compensatory harvest assumption. The agreement of these models, constructed using different parameters and different assumptions, make a strong case for a conservative fall harvest. Despite the differences in these models, however, they consistently assume high variability in vital rates without density dependence. This commonality among models, which may account for the agreement among results, should be questioned. It is likely that density dependence affects population growth at some level (Turchin 2003: 29) and it is unlikely that vital rates would vary independently of each other. For example, adult and subadult nest success should be highly correlated from year to year, and accounting for this would realistically reduce the variability in annual production.

McCullough (1984) proposed the use of empirical black box models for harvest management. These models use higher order variables to integrate the extensive demographic parameters in the accounting style models (the intrinsic rate of increase, *r*, for example, represents the integration of birth and death rates for a closed population). The stock-recruitment models used in fisheries, such as the Ricker model (1954) or the Beverton and Holt model (1957) are examples. McCullough (1979) used a stochastic Ricker-like model to compare a number of harvest strategies for the white-tailed deer (*Odocoileus virginianus*) population on the George Reserve and determined that only minor gains in harvest could be achieved through selective sex and age harvesting, and that, with stochastic population growth, harvesting a maximum sustained yield resulted in population extinction. These models, therefore, are useful for exploring consequences of management decisions, and require less information than their counterpart mechanistic models. Instead of estimates of age or stage-specific vital rates and their covariances, one needs only an estimate of population size or an index of the population, such as harvest indices (McCullough 1984). Porter et al. (1990b) and Suchy et al. (1990) have argued that the general models might be more useful in testing the effects of alternative management actions specific to wild turkey populations.

Current wild turkey models assume that density dependence does not act on population growth. This assumption reduces the number of viable harvest strategies available for the species because it does not allow for a biological feedback system in population growth. Biologists are forced to assume that density-independent factors, such as rainfall and temperature during the nesting and brood-rearing season, drive population growth (Roberts and Porter 1998a, Roberts and Porter 1998b). They are, therefore, consigned to manage harvests based on difficult to predict random variables, requiring a highly conservative approach when harvesting females (Healy and Powell 2001). In addition, the assumption of strict density independence assumes an unwarranted dichotomy between density-dependent and density-independent populations or species. Rather, populations are more likely undergo influences from both density-dependent and independent factors simultaneously with the strength of the effects of each waxing and waning at different population densities (McCullough 1990).

There is evidence that density dependence may strongly influence wild turkey population growth at some population densities. Examination of harvest indices in New York have indicated that wild turkey population growth may be maximized for population densities as low as 0 – 20% of the carrying capacity, with reduced growth rates as population density increases (Porter et al. 1990a). In support of this, there have been numerous observations of the rapid growth of reintroduced populations (Little and Varland 1981, Healy and Powell 2001). Other studies having observed low recruitment, suggest some wild turkey populations have reached carrying capacity (Glidden and Austin 1975,Vangilder et al. 1987, Vander Haegan 1988, Miller et al. 1998). Evidence for density-dependent growth has also been found for other galliforms, such as the willow ptarmigan (*Lagopus lagopus*), and the gray partridge (*Perdix perdix*: Blank et al. 1967, Dobson et al. 1988, Watson et al. 1998). In addition to this, theory specifying the strength of density dependence on population growth for species with different life histories (along the r-K continuum: Horn 1968, Fowler 1981), has been empirically examined for several bird species, including the willow ptarmigan (Saether et al. 2002). Thus, there is an established theoretical and taxonomic basis for examining the effects of density dependence on wild turkey population growth and harvest. Based on the theoretical and empirical framework that both density-dependent and independent factors influence wild turkey population growth, there is clearly a need to begin developing models that incorporate these factors and explore their simultaneous effect on harvest strategies.

The Inclusion of Density Dependence

The role of density dependence has been debated among population ecologists for many years. Verhulst formalized the concept in 1838, as the logistic curve of population growth. The idea that certain factors operate to affect population growth regardless of density (such as weather), while others operate in conjunction with density (such as competition) became increasingly important over the following years (Howard and Fiske 1911, Thompson 1928). Researchers have continued to scrutinize these density-independent and density-dependent factors (the terms proposed by Smith 1935), with little agreement on their importance relative to each other. While Nicholson (1933) claimed that environmental factors were incapable of regulating populations because they act irrespective of density, Andrewartha and Birch (1982) emphasized that the effects of environmental heterogeneity were sufficient to explain fluctuations in animal populations.

Today, many theorists hold population regulation (whereby a population returns to an equilibrium density) as logically inescapable, with its chief mechanism being density dependence (Berryman 1991, Krebs 2002, Turchin 2003). However, Krebs (2002) has criticized the lack of data in theoretical discussions of density dependence, calling for a synthesis of theory and empirical data. This has proven difficult. Much of the debate regarding density dependence centers on the difficulty in its detection in time-series data (Wolda and Dennis 1993). In general, the low power of designed statistical tests require the strength of density dependence to overcome not only demographic and environmental stochasticity, but also measurement error (error in the estimates due to the sampling mechanism, rather than error intrinsic to the system itself) to be detected (McCullough 1990). In order to meet this requirement, extensive data are required to detect density dependence effects in time-series data, ranging from 20 years to 30 or more generations (Solow and Steele 1990, Woiwod and Hanski 1992). In addition to the substantial data requirement, the presence of measurement error may bias parameter estimates (Solow 1998). This tends to produce spurious detection of density dependence effects (Dennis and Taper 1994). Unfortunately, time-series harvest-based population indices for wild turkey are often < 20 years and are subject to unknown amounts of measurement error. Further, the amount of measurement error must vary between states based on differences in regulations and other factors. Healy and Powell (2000) state that reporting rates vary both spatially and temporally and represent a serious source of error in harvest estimates. Clearly, steps must be taken to produce both accurate and precise estimates of density dependence effects for wild turkeys. Fortunately, although harvest index time-series are often short, many state wildlife agencies collect them. This allows for researchers to increase statistical power across populations rather than across time using meta-analysis.

Meta-Analysis for Parameter Estimation

Meta–analysis is the method used to combine research findings across studies to arrive at a consensus regarding some common hypothesis (Hedges and Olkin 1985). Scientists often combine the findings of a series of experiments by a vote-counting method such that a statistically significant result represents a vote for the hypothesized effect, and non-significant results represent a vote against it. The power of this method has been shown to be low and to actually decrease as studies are added to the analysis (Hedges and Olkin 1980). Meta-analysis provides a more sophisticated way of combining study findings by estimating combined effect sizes or correlation coefficients between experiments (Hedges and Olkin 1985). Effect size represents the strength at which a hypothesized phenomenon operates on population (Cohen 1977). For purposes of this study, I refer to the effect size as the degree to which an ecological parameter (either density dependence or environmental stochasticity) acts on the population (Wolf 1986).

Myers (2000) suggested that by treating the time-series of each population as a natural experiment, biologists could improve parameter estimates for an overall population. This is accomplished by determining a common estimate among multiple individual populations. In this case, the parameter estimate represents the effect size associated with statistical tests combined in other meta-analysis treatments. This effect size conveys the strength at which the parameter acts on the population over a variety of sizes or densities. The advantage to this technique is that it reduces the uncertainty inherent with the low sample size usually associated with time-series data by examining multiple time-series simultaneously. Myers and his associates have used this technique successfully to estimate stock-recruitment parameters for multiple fish stocks (Myers and Cadigan 1993, Myers 1997, Myers et al. 1999). Use of meta-analysis techniques appear well-suited to the examination of multiple wild turkey population index time-series, as these are often shorter than that required to precisely detect density dependence via statistical tests, or estimate a model parameter specifying density-dependent effects on population growth.

A requirement for using meta-analysis in population ecology is to find a parameter that can be compared across populations. Parameters with compatible units between populations can be combined, or a dimensionless parameter, such as a power term, can also be used (Charnov 1993, Myers and Mertz 1998). Density-dependent models for wild turkey must be designed, therefore, such that the parameters of interest are comparable across populations if meta-analysis is to be effective (Myers et al. 1997).

A disadvantage to the meta-analysis technique is that it does not eliminate or reduce biases inherent to the data (Myers and Mertz 1998). Parameter estimates are usually determined by treating observed time-series as though they were experimental units, subjecting them to traditional statistical techniques, such as linear regression. This procedure can lead to biases in these estimates because of autocorrelation among the residuals (Box and Jenkins 1976: 208 – 284). Measurement error (error inherent to sampling deficiencies) and process error (error inherent to the study system) may also cause biases in estimates (Ludwig and Walters 1981, Walters and Ludwig 1981, Walters 1985), and this is of particular concern when relying on time-series' of population indices, rather than more accurate estimates of population size or change (Anderson

2001). Meta-analysis cannot deal with these problems, so researchers must explore the effects of measurement and process error on parameter estimates using Monte Carlo simulations (Walters 1985).

Research Objectives

The aim of this study is to construct an improved harvest model for wild turkeys based on a meta-analysis of data collected by state agencies in the northeastern United States. Data contributed by agencies will take the form of spring gobbler's harvest numbers (Table 1.1), reported spring gobbler harvest/effort (Table 1.2), and a survey harvest/effort based on a small set of volunteer hunters ranging from 1 – 5% of the hunting population (Table 1.3). The model will incorporate density dependence, heretofore ignored by wild turkey harvest models. The model will also include density-independent environmental stochasticity. This is expected to increase the ecological relevance of the model, by increasing its realism. Given these goals, much work is needed. Specifically, in order to develop this model, the objectives of this study are to:

1. Estimate a density dependence parameter by fitting a population model to harvest index data provided by 11 state wildlife agencies, and explore the effects of measurement error on the parameter estimate;

2. Determine the feasability of including density-independent factors in the model using juvenile production indices; and

3. Construct a harvest management model that allows testing the effects of a range of harvest strategies when density-dependent and independent factors are assumed to act on populations simultaneously.

Including both density dependent and density-independent effects to the model should result in a simplified, though biologically realistic and theoretically sound model for wild turkey population growth. The final product of this research is a harvest model that allows managers to determine the effects of various harvest strategies on wild turkey populations. Optimal harvest strategies according to the model are identified under various assumptions.

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Table 1.1. Description of spring gobbler's-only harvest time-series data contributed by state and regions within states. Regions are listed by ecological region. Years represents the time period each regional index covers and n represents the number of years harvest information is available within the time period covered.

State	Region	Years	n
Maryland	Blue Ridge	1971-2001	30
	Coastal	1984-2001	17
	Appalachian Plateau	1970-2001	31
	Valley & Ridge	1970-2001	31
	Piedmont	1971-2001	30
New Jersey	Coastal	1983-2002	19
	Appalachian	1982-2002	20
	Ridge & Valley	1982-2002	20
	N.E. Highlands	1985-2002	17
	Piedmont, N.E. Highlands & Coastal	1986-2002	16
	Pine Barrens	1985-2002	17
North Carolina	Coastal	1977-2001	24
	Piedmont	1977-2001	24
	Mountains	1977-2001	24
Virginia	Tidewater	1963-2002	39
	E. Piedmont	1962-2002	40
	W. Piedmont	1963-2002	39
	SW Mountains	1963-2002	39
	Northern	1963-2002	39
	Central Mountains	1962-2002	40
West Virginia	E. Panhandle	1966-2001	35
	Mountains	1966-2001	35
	Southern	1966-2001	35
	Central	1966-2001	35
	Western	1966-2001	35
	Southwestern	1966-2001	35

Table 1.2. Description of the reported spring gobbler's-only harvest/effort time-series data contributed by state and regions within states. Regions are listed by state or ecological region or by New York Department of Environmental Conservation Region (DEC Region) or by Pennsylvania Turkey Management Area (TMA). Years represents the time period each regional index covers and n represents the number of years harvest information is available within the time period covered.

State	Region	Years	n
Maine	ME	1986-2001	14
Michigan	MI	1968-2002	26
New York	DEC Region 3	1983-2001	18
	DEC Region 4	1983-2001	18
	DEC Region 5	1983-2001	18
	DEC Region 6	1983-2001	18
	DEC Region 7	1983-2001	18
	DEC Region 8	1983-2001	18
	DEC Region 9	1983-2001	18
Pennsylvania	TMA 1	1990-2001	11
	TMA 2	1990-2001	11
	TMA 3	1990-2001	11
	TMA 4	1990-2001	11
	TMA 5	1990-2001	11
	TMA 6	1990-2001	11
	TMA 7	1990-2001	11
	TMA 8	1990-2001	11
	TMA 9	1990-2001	11
Rhode Island	RI	1993-2001	8

Table 1.3. Description of surveyed spring gobbler's-only harvest/effort time-series data contributed by state and regions within states. Regions are listed by Wildlife Management Area (WMA), ecological region or by New York Department of Environmental Conservation Region (DEC Region). Years represents the time period each regional index covers and n represents the number of years harvest information is available within the time period covered.

State	Region	Years	n
Mississippi	WMA 1	1996-2002	6
	WMA 2	1996-2002	6
	WMA 3	1996-2002	6
	WMA 4	1996-2002	6
	WMA 5	1996-2002	6
	WMA 6	1996-2002	6
New Jersey	Coastal	1996-2001	4
	Appalachian	1996-2001	4
	Ridge & Valley	1996-2001	4
	N.E. Highlands	1996-2001	4
	Piedmont, N.E. Highlands & Coastal	1996-2001	4
	Pine Barrens	1996-2001	4
New York	DEC Region 3	1985-2001	16
	DEC Region 4	1985-2001	16
	DEC Region 5	1985-2001	16
	DEC Region 6	1985-2001	16
	DEC Region 7	1985-2001	16
	DEC Region 8	1985-2001	16
	DEC Region 9	1985-2001	16
North Carolina	Coastal	1984-1999	6
	Piedmont	1984-1999	6
	Mountains	1984-1999	6
Virginia	Tidewater	1990-2002	12
	E. Piedmont	1990-2002	12
	W. Piedmont	1990-2002	12
	SW Mountains	1990-2002	12
	Northern	1990-2002	12
	Central Mountains	1990-2002	12

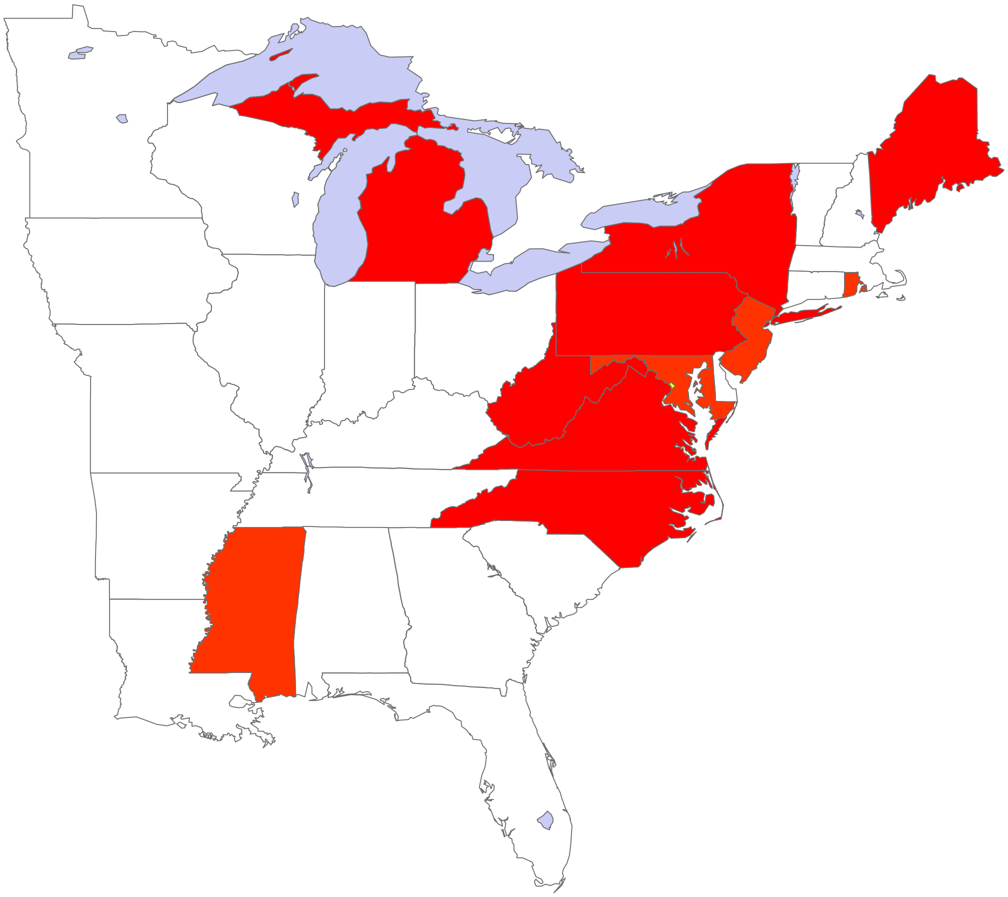

Figure 1.1. Map of the eastern U.S. highlighting the states contributing data to the meta – analysis and modeling project. Contributing states are shown in red.

CHAPTER 2: ESTIMATING THE FUNCTIONAL FORM OF DENSITY DEPENDENCE FOR REGIONAL WILD TURKEY POPULATIONS

ABSTRACT

Although previous research and theory has suggested that wild turkey populations may be subject to some form of density dependence, there has been no effort to estimate and incorporate a density dependence parameter into wild turkey population models. To estimate a functional relationship for density dependence in wild turkey, I analyzed a set of harvest index time-series from 11 state wildlife agencies. I tested for lagged correlations between annual harvest indices using partial autocorrelation analysis, and assessed the ability of the density dependent theta-Ricker model to explain harvest indices over time relative to exponential or random growth models. I tested the homogeneity of the density dependent parameter estimates (θ) from 3 differing harvest indices (spring harvest numbers, reported harvest/effort, survey harvest/effort) and calculated a weighted average based on each estimate's variance and its estimated covariance with the other indices. To estimate the potential bias in parameter estimates from measurement error, I conducted a simulation study using the theta-Ricker with known values and lognormally distributed measurement error. Partial autocorrelation function analysis (PACF) indicated that harvest indices were significantly correlated only with their value at the previous time step. The theta-Ricker model performed better than the exponential growth or random walk models for all 3 indices. Measurement error simulations indicated a strong positive upward bias in the density dependent parameter estimate, depending on the amount of measurement error. The density dependence estimate was averaged across indices, and, after correcting for measurement error, ranged $0.25 \leq \hat{\theta} \leq 0.49$, depending on the degree of measurement error, and assumed spring harvest rate. Density dependence appears to be non-linear in wild turkey, where growth rates are maximized at 39 – 42% of carrying capacity. The annual yield produced by density dependent population growth will tend to be less than that caused by extrinsic environmental factors. This study indicates that both density-dependent and density-independent processes are important to wild turkey population growth, and I make initial suggestions on incorporating both into harvest management strategies.

INTRODUCTION

With the increase in eastern wild turkey (*Meleagris gallopavo silvestris*) populations over past years, harvest management goals have shifted from protection and restoration to providing a sustainable harvest (Tapley et al. 2004). This shift in focus is reflected in three basic harvest strategies put forward by Healy and Powell (2000), ranging from the most conservative: a spring gobblers-only season, to a spring gobblers-only season with limited fall either-sex hunting, and a optimization of both the spring and fall harvests. With increasing fall harvests, which have the greatest potential to reduce population growth through the removal of hens (Kurzejeski and Vangilder 1992), managers need a precise understanding of wild turkey population dynamics to best determine the limits at which they can harvest while maintaining stable populations. Current harvest models for wild turkey assume density-independent processes drive annual variation in yield, with the general result being that ≤10% of the total fall population can be harvested without incurring population declines (Vangilder and Kurzejeski 1995, Alpizar-Jara et al. 2001). However, recent theoretical and observational research has suggested that wild turkey populations may be subject to density-dependent as well as density-independent factors, where density dependence describes the functional relationship between population growth rate and population density (Turchin 2003: 398). Theoretical studies suggest that those species subject to high environmental variability, such as wild turkey, where populations are often kept below carrying capacity (K) by extrinsic factors, will be selected for a high maximum growth rate when the environment is favorable. This results in populations being affected by competition for food at relatively low densities, such that growth rate declines in a convex relationship with increasing population density (Horn 1968, Fowler 1981, Sibly et al. 2005). This specific form of density dependence is associated with those species having high population growth rates, and subject to high environmental stochasticity (Horn 1968, Fowler 1981).

Porter et al. (1990) found evidence for this form of density dependence in their examination of New York township wild turkey harvest indices. Their results suggested that population growth was maximized for densities of 0 – 20%K. In addition, there have been numerous observations of the rapid growth of reintroduced populations (Little and Varland 1981, Healy and Powell 2001), while others have inferred from low recruitment estimates, that populations have reached K (Vangilder et al. 1987, Vander Haegan 1988, Miller et al. 1998). Clearly, density dependence may have importance in wild turkey population dynamics, and consequently, harvest management.

If density-dependent factors do have a significant impact on all or part of the range of possible population densities, we should be able to account for it in harvest models. Knowledge of the functional form of density dependence would allow managers to better predict yield, manipulate yield to fit preferred harvest strategies, or to stabilize populations undergoing intermittent overharvest, assuming population density can be estimated in relation to K (McCullough 1979: 237 – 238, Saether et al. 2002). Knowing the population densities where density dependence has the greatest impact will also provide insight into the interplay of density-dependent and density-independent factors in a species subject to large variability in annual abundance (Mosby 1967). This understanding would allow managers to begin modeling the effects of various harvest strategies on wild turkey populations undergoing both density dependent and density independent fluctuations. For this reason, the purpose of this study is to estimate a density-dependent parameter for wild turkey populations.

Unfortunately, estimation of density dependence is difficult because a large amount of information is required from time-series data, ranging from 20 years to 30 or more generations (Solow and Steele 1990, Woiwod and Hanski 1992, Wolda and Dennis 1993). Also, precision of single estimates decrease as the number of parameters to be estimated increases. Simpler models, in which higher order variables such as the intrinsic growth rate (*r*) are used to integrate age-specific vital rates, are likely to prove the most informative in determining functional forms of density dependence when data is sparse (McCullough 1984), and so I estimated parameters using a non-age-structured population growth model.

This approach is suited to the time-series data collected by many state wildlife agencies, which attempt to measure annual population growth from harvest indices rather than from age-structured vital rates. Harvest indices for wild turkey have several sources of measurement error, and are often < 20 yrs in length. Despite this, they are among the longest datasets available for wild turkey populations, and can be used for parameter estimation for non-age-structured models. To offset the lack of precision in indices and length of time-series, I used meta-analysis techniques to determine parameter estimates.

Meta-analysis is used to broaden inferences by quantitatively combining data across studies (Myers and Mertz 1998, Hedges and Olkin 1985). The independent study or experiment acts as the base unit for comparison, from which meta-analytic techniques produce summary statistics, often providing information on the generality of a hypothesis (Myers and Mertz 1998). Moving beyond the comparison of experimental studies, population ecologists have used meta-analysis techniques on time-series data for parameter estimation for some years (Osenberg et al. 1999, Myers 1997). In a similar manner here, I used time-series' of harvest-based population indices across regions to estimate a common density-dependent parameter.

Parameter estimation from time-series is often affected by measurement error. Measurement error represents the error inherent to sampling, and will bias parameter estimates (Ludwig and Walters 1981, Walters and Ludwig 1981, Walters 1985). This is of particular concern when relying on time-series' of population indices, rather than more accurate estimates of population size or change (Anderson 2001). Unfortunately, most wildlife agencies lack the funding needed to track the abundances or growth rates of the game populations they manage and must act on harvest-based population indices such as the number of animals harvested or harvest/effort. These indices assume information on population change over time, obscured by hunter behavior, weather, etc. These obscuring factors introduce error into the information we wish to track if not accounted for in some manner. A common solution to this, when data are lacking to account for these other factors, is to conduct simulations with known parameters to assess the effect of measurement error on parameter estimates (Hilborn and Mangel 1997: 152). Since much of the information needed to account for all the factors that determine harvest index values are unknown, I address the problem of measurement error through a simulation study.

METHODS

I estimated the functional form of density dependence for wild turkey using meta-analysis techniques, by combining information from 11 state wildlife agencies (MD, ME, MI, MS, NC, NJ, NY, PA, RI, VA, WV). After testing for lag effects in the time-series of harvest indices provided by these agencies, I estimated a density-dependent parameter by fitting a generalized Ricker model to the indices as grouped by region and harvest index type (spring harvest, spring harvest/effort, survey spring harvest/effort). I compared model fit to simpler models of exponential growth and random growth. I then calculated a mean density-dependent parameter estimate weighted by the variance of the individual estimates and their covariance between index types (Hedges and Olkin 1985). Parameter estimates were compared to estimates from separate data for validation.

Data Collection

Eleven participating state agencies provided harvest indices, which were subdivided by management or geographic region and by harvest index type. Times series length by state were: MD: 32 yrs, ME: 18 yrs, MI: 35 yrs, MS: 7 yrs, NC: 25 yrs, NJ: 21 yrs, NY: 19 yrs, PA: 12 yrs, RI: 9 yrs, VA: 41 yrs, WV: 36 yrs. Harvest index types were classified as spring reported harvest, where only the number of bearded wild turkey (primarily gobblers) killed is reported; spring reported harvest per effort (rh/e), where the number of gobblers killed and the number of hunter-days or hunter-hours are provided; and surveyed spring harvest per effort (sh/e), where a small set of volunteer hunters ranging from 1 – 5% of the hunting population provide the number of gobblers killed and the number of hunter-days or hunter-hours. I assumed these datasets served as an adequate index to population change for a given management region (Lint et al. 1995). To incorporate fall harvest information, I converted spring reported harvests into three population estimates assuming three constant spring harvest rates. Spring harvest rates were estimated from a review of banding and radio telemetry studies that estimated the harvest rate of gobblers (Mosby 1959, Lewis 1980, Weinrich et al. 1985, Palmer et al. 1990, Wright and Vangilder 2001). I applied gobbler harvest rates to the entire population by assuming a 50:50 sex ratio and dividing by 2. Since spring harvest rates are unlikely to remain constant over time or across management regions, I wanted to account for the maximum range observed in the literature, and calculated three population estimates using the minimum (3.1%), mean (10.1%), and maximum harvest rate (27.9%) observed in these studies. Since gobblers do not contribute to raising poults, I tracked hen numbers instead of the entire population. Calculation of population estimates allowed the addition of hens harvested during fall either-sex seasons in the calculation of annual growth rates between consecutive spring seasons (as if there had been no fall season, and assuming additive mortality). Subdividing the data by management region produced a total of 58 regions, where each region comprised of a time-series of spring harvest population estimates based on a 27.9% spring harvest, 10.1% spring harvest, 3.1% spring harvest, rh/e, sh/e, or some combination of two of these. I validated the model with data not used in the model's construction, by randomly selecting 12 regions to remove from the parameter estimation set to use for validation.

Population Models

I assessed the ability of three population models to describe the dynamics of harvest indices: random walk, exponential growth, and density-dependent growth. Let N_t represent the population size at year t, *r* represent the intrinsic growth rate (the maximum growth rate at small population sizes), and ε_p represent the process error (the error in the growth rate caused by density-independent environmental factors) such that

$$N_{t+1} = N_t e^{r+\varepsilon_p}$$

For this model, $r = 0$ represents random walk population growth, and $r \neq 0$ represents exponential growth. To model density-dependent growth, I used the theta-Ricker equation (Gilpin and Ayala 1973).

$$N_{t+1} = N_t e^{r\left[1-\left(\frac{N_t}{K}\right)^{\theta}\right]+\varepsilon_p}$$

In this model, *r* also represents the intrinsic growth rate; K represents the carrying capacity and θ represents the strength of density dependence. At $\theta = 1$, the population grows logistically; as $\theta \rightarrow 0$, density dependence acts most strongly at low population densities relative to K (N < 0.5K) and the N for which yield is maximized approaches 0.37K, and as $\theta \rightarrow \infty$, density dependence acts most strongly at high population densities relative to K (N > 0.5K), and the N for which yield is maximized approaches K (Fig. 2.1). The theta-Ricker model is highly flexible because it allows a non-linear density-dependent functional form across the range of possible population sizes. Also, because θ is a unit-less exponent, it is comparable between regions and indices, making it particularly useful for meta-analysis.

Model Selection and Fit

I used partial autocorrelation function analysis (PACF) to determine the number of lagged time steps required to fully account for density dependence in the time-series (Royama 1992). I calculated PACF to lag 6 (6 years previous), which accounts for two generations of wild turkey populations (Alpizar-Jara et al. 2001).

To determine how well harvest index information could be replicated by density-dependent growth as compared to exponential or random growth, I compared the ability of the three population models to account for the observed growth rates in the population indices (Morris and Doak 2002). I fit models with non-linear regression using Proc NLIN in SAS (SAS Institute 1985, Morris and Doak 2002). Models were fit on all regions simultaneously for each data type to increase the precision of parameter estimates, such that K differed by region, but r and θ did not. This assumes that the intrinsic or maximum physiological rate of population growth and the density dependent response to increased population size were the same for all eastern wild turkey populations, while habitats as measured by K differed between regions. This had the benefit of being biologically reasonable while increasing the precision in the θ estimate.

I specified an upper bound on r of 0.5158, the maximum I had seen for radio-tagged wild turkey in the literature, which allows populations to increase by 67.5% annually (Little and Varland 1981). Model performance was evaluated using Akaike's

Information Criterion for small samples, which has a bias correction derived for autoregressive time-series models (AIC_c: Hurvich and Tsai 1989). Residuals from model fits were studentized to allow for comparison between regions. For the best performing model, I examined the normality of the studentized residuals by region using a Shapiro-Wilks test (Zar 1999).

Parameter Estimation and Validation

To more precisely estimate θ (written as $\hat{\theta}$), I calculated a covariance matrix using an estimated correlation matrix between indices and the variance estimates of $\hat{\theta}$ (Hedges and Olkin 1985). The use of a covariance matrix increases the precision of the estimate by accounting for the overlap in information content of correlated datasets. Correlations were averaged from overlapping indices within the same regions.

When averaging parameter estimates across independent data, it is necessary to assess whether those estimates describe the same statistical population before pooling them (Hedges and Olkin 1985). To determine whether information on θ could be pooled across indices, a Q-test was conducted to determine the homogeneity of the separate index estimates (Hedges and Olkin 1985). Homogeneity of parameter estimates is rejected if the test statistic exceeds a critical value from the χ^2 distribution with k-1 degrees of freedom, where k represents the number of parameters compared. Failure to reject the hypothesis of homogeneity indicates that estimates may be assumed to originate from the same statistical population and can be averaged.

I conducted Q-tests between the 3 indices (spring harvest, rh/e, sh/e) for each assumed spring harvest rate (27.9%, 10.1%, 3.1%). Values of $\hat{\theta}$ were averaged across data types using the estimated covariance matrix as a weighting factor. This method weights indices based on the amount of independent information each provides, and the correlation in regional overlapping series. Low correlation is associated with greater independent information, while high variability reflects imprecise estimation. This resulted in a separate grand mean θ ($\hat{\theta}*$) for the 3 index types. I calculated a $\hat{\theta}*$ for each of the 3 assumed harvest rates to determine the overall effect of harvest rate on our uncertainty of θ. To begin validating $\hat{\theta}*$, I fit the theta-Ricker model to the validation set (12 regions). Estimates of θ from the validation set were then compared to the original estimates by index.

To summarize, I used harvest indices from 11 states to estimate a non-linear density-dependent parameter (θ) for wild turkey. This parameter was assumed to represent a common mechanism across regions and to be correlated across harvest index types. I tested the homogeneity of estimates from differing indices and calculated a weighted average based on each estimate's variance and its covariance with the other indices. I then compared each index θ estimate with a validation set estimate to gauge their generality.

Measurement Error

I investigated the effects of measurement error on $\hat{\theta}$ using Monte Carlo simulations with known parameters and error distributions (Walters 1985). I built two types of datasets, one to mimic the harvest data and one to mimic the harvest/effort data.

Harvest datasets

Simulated harvest datasets were composed of 20 time-series, each with a length of 32 annual growth rates (the median of the true dataset). Each time-series was constructed using the theta-Ricker model with process error (e^{ε_p}), then multiplying each N_t by e^{ε_m}, where ε_m is the normally distributed measurement error ~N (0, σ_ε). Note that $\varepsilon_m = Z\sigma_\varepsilon$, where Z is a random variable from a standard normal distribution ~N (0, 1) and σ_ε is the pre-specified standard deviation of error distribution (Zschokke and Ludin 2001). This produced an index value for each N_t ($I_t = N_t\, e^{\varepsilon_m}$). Both process and measurement error are assumed to follow a lognormal distribution.

Observed growth rates were calculated as I_{t+1}/I_t. I set the total error standard deviation ($\sigma_{\varepsilon p} + \sigma_{\varepsilon m}$) at the median (0.22) value observed in the true harvest dataset, with measurement error covariances assumed to be zero (White et al. 2002, Mills and Lindberg 2002). There are no estimates of covariances in measurement error for wild turkey harvest data.

Datasets of time-series were then constructed for seven error treatments, where $\varepsilon_m \approx 0$, 20, 40, 50, 60, 80 or 100% of the total error. The proportion of total error due to measurement error, *r*, K, and θ were fixed for all time-series at 0.5158, 10,000, and 0.63 respectively for a given treatment. The length of, and changes in magnitude of, harvested birds over time in the true harvest datasets indicate that a wide range of population sizes was included in the time-series. To account for this, I set the starting population size to 0.10K. For each error treatment, I constructed 200 datasets (each comprising 20 time-series of 33 years length, or 32 annual growth rates), and estimated θ for each.

Harvest/ effort datasets

Simulation harvest/effort datasets comprised 16 time-series, each with a length of 12 annual growth rates (13 yrs, the median of the true dataset), with a total error standard deviation of 0.16 (median of the true dataset). I constructed datasets according to the same model as the simulation harvest datasets with the exception that the starting population size was set at K to reflect the observed behavior of the true harvest/effort dataset (apparent fluctuation around an equilibrium), which cover a much shorter and more recent time period than the harvest data.

RESULTS

Model Selection and Fit

PACF analysis indicated that all wild turkey population indices were significantly correlated with their value at the previous time step only, with the exception of the spring harvest data, which indicated a small negative correlation at lag 6, or 6 years previous. The average autocorrelation across regions by index are shown in Fig. 2.2. Comparison of the model fit between the theta-Ricker, exponential growth, and random walk model showed that the theta-Ricker model performed best in all cases (Table 2.1). The theta-Ricker explained spring harvest indices best, explaining 42 – 65% of their variation. The greatest amount of error (r^2) was explained for the spring harvest index when a 27.9% constant spring harvest rate was assumed, with r^2 declining with decreasing assumed harvest rate. The theta-Ricker performed more poorly with the harvest/effort indices, explaining 24 – 27% of their variation.

The magnitude of the residuals varied widely, but was comparable across indices. Standard deviations of the residuals ranged from 0.13 – 0.44 for a 27.9% harvest, 0.12 – 0.40 for an 10.1% harvest, 0.12 – 0.38 for a 3.9% harvest, 0.08 – 0.43 for the rh/e index, and 0.03 – 0.47 for the sh/e index. For most regions, studentized residuals did not differ from a normal distribution, indicating that the theta-Ricker model was sufficient to capture the intrinsic behavior of the system for most regions. However, a greater number of regions than expected by chance (5%) did differ from normal for the 25.5% spring harvest rate index (5 regions: 25%), 11.9% spring harvest rate index (6 regions: 30%), 3.1% spring harvest rate index (3 regions: 15%), rh/e index (5 regions: 33%), and sh/e index (2 regions: 8%).

Parameter Estimation and Validation

As the theta-Ricker model performed well relative to the other models tested, I conducted Q-tests for homogeneity of $\hat{\theta}$ across indices for each of 3 assumed spring harvest rates (27.9%, 10.1%, 3.1%). Assuming a 27.9% spring harvest rate, $\hat{\theta}$ was homogenous for the spring harvest index, rh/e, and sh/e (Q = 0.07, df = 2, P = 0.9656). Assuming an 11.9% spring harvest rate, $\hat{\theta}$ was homogenous for the spring harvest index, rh/e, and sh/e (Q = 0.08, df = 2, P = 0.9622). Assuming a 3.1% spring harvest rate, $\hat{\theta}$ was homogenous for the spring harvest index, rh/e, and sh/e (Q = 0.30, df = 2, P = 0.8594). Since $\hat{\theta}$ was homogenous across all harvest indices for each assumed spring harvest rate, I calculated θ^* (grand mean) weighted by the estimated covariance matrix for the index set (spring harvest, rh/e, sh/e) where harvest differed based on the three assumed harvest rates (resulting in 3 θ^*). The assumed spring harvest rate for the spring harvest index affected weights. The harvest index weight increased with a decrease in assumed spring harvest rate because the variance in $\hat{\theta}$ decreased with spring harvest rate as well. To summarize, since $\hat{\theta}$'s were homogenous across indices, regardless of the assumed harvest rate in the harvest index, it was reasonable to calculate a grand mean across indices for each index set. The θ^* ranged from 0.50 – 0.74 by index set (Table 2.2).

I fit the theta-Ricker model to the validation indices using the same non-linear regression procedure used to fit the original estimation indices. Estimates of θ from the validation set compared favorably with the original estimates (Fig. 2.3). Validation estimates tended to be larger than original estimates for the harvest index, with differences between the two increasing with assumed spring harvest rate. The validation estimate was much lower than the original estimate for the rh/e index, and higher for the sh/e index. In all cases, estimates of θ were < 1, and no validation estimate differed significantly from the original estimate for each index.

Measurement Error

I constructed 2,800 replicate datasets under different measurement error distributions for two types of data: spring harvest only and spring harvest/effort. Spring harvest only data was subject to greater total error, but covered a greater range of potential population sizes, provided information from more regions (20), with each region being of greater length (33 yrs). Spring harvest/effort data was subject to less error, covered a shorter range of potential population sizes, and provided information from fewer regions (16), with each region being of shorter length (13 yrs). As expected, there was substantial bias in the estimates of θ, which increased along with uncertainty as the proportion of measurement error increased (Table 2.3). The biases in $\hat{\theta}$ were uniformly positive, suggesting that the original estimates were overestimated. If the bias in $\hat{\theta}$ is accurately determined, the original estimates can be corrected by dividing the original estimate by the bias estimate. This gives a corrected range for $\hat{\theta}$ between 0.25 – 0.49, depending on the degree of measurement error in the indices, as well as the correct constant harvest rate. For these values of $\hat{\theta}$, annual yield for the wild turkey would be maximized between 39 – 42% of K (Fig. 2.4). Within each measurement error treatment, differences in assumed spring harvest rates had little effect on bias-corrected estimates of $\hat{\theta}$, resulting in greater agreement in corrected $\hat{\theta}$ between indices.

DISCUSSION

The results of this study indicate that wild turkey populations are subject to a non-linear form of density-dependence, with population growth rate maximized at densities between 39 – 42% of carrying capacity. This agrees with theory stating that organisms with high growth rates, subject to high environmental variation should experience maximum yield at lower population densities relative to K (Horn 1968). These organisms, such as the wild turkey, are often held below the limits of their habitat by environmental effects on birth or death rates. Individuals undergo selective pressure for high reproduction in favorable environments, resulting in yields maximized at densities < K (Horn 1968, Fowler 1981). In addition, these results agree with Porter et al. (1990), who analyzed a different population index at a smaller scale (county-level), suggesting that the results are general and robust. These results also agree with research on other phasianids. Using the similar theta-logistic model, Saether et al. (2002) report $\theta = 0.14$ for the willow ptarmigan (*Lagopus lagopus*). Aanes et al. (2002), using the same model, reported a similar relationship for a willow ptarmigan population in central Sweden.

Thomas et al. (1980) analytically determined the threshold at which a stable equilibrium is maintained in the theta-Ricker model as the product of the intrinsic growth rate (r) and θ at $0 < r\theta < 2$. At $r\theta > 2$, population abundances will cycle or become chaotic from intrinsic factors. My results indicate an $r\theta$ of $0.13 - 0.25$, indicating that the large annual variation in population growth typically observed for wild turkey is not intrinsically determined by a density-dependent growth rate, but is instead by extrinsic factors. This would have the benefit of increasing the stability of populations, offsetting the already high variation in growth rates caused by extrinsic factors.

However, because this causes maximized yields to occur at smaller population densities (< 0.5K), these yields will be less than those expected from logistic growth ($\theta = 1$) or yields from populations with maximum recruitment closer to K ($\theta > 1$: Fig. 2.4). For wild turkey, the maximum yield as determined by intrinsic density-dependent processes will be approximately 4 – 8% of K ($\theta = 0.25 - 0.49$), indicating that in some populations, extrinsic factors may contribute more to yield in a given year than density-dependent processes at all densities. The standard deviations of the residuals were large, and although they represented a mixture of both process and measurement error combined, suggest that these extrinsic density-independent factors will act to overshadow density-dependent processes in good or bad years.

Based on the PACF analysis, spring wild turkey population density is most correlated with population density during the previous spring. This indicates that lagged density dependence does not affect wild turkey population growth, and the theta-Ricker model does not have to be adjusted to account for population densities beyond the previous year. It also indicates that annual time steps should be used when modeling wild turkey populations instead of generation time steps. Alpizar-Jara et al. (2001) estimated generation times for wild turkeys at ~ 3 yrs, so that if wild turkey density dependence was based on the previous generation size, PACF analysis should have a significant correlation at lag 3 and possibly lag 6. While a significant correlation at lag 6 occurred in the harvest data, it failed to appear in either harvest/effort index, indicating that the correlation resulted from changes in hunting effort rather than the true population dynamics. It should be noted that the measurement error in the indexes could act to obscure correlations at lags > 1, especially if they are weak. I was able to detect the strongest correlation at lag 1, but smaller significant lags may exist for wild turkey populations.

The model selection procedure favored the theta-Ricker to the exponential or random growth models, implying density-dependent dynamics. It is conceivable that more complicated DI models, which include non-linear environmental factors, might explain the indices better than the theta-Ricker. However, this analysis assumed from the beginning that density dependence affected wild turkey population growth at some level. My purpose was not to perform a statistical test for density dependence, but rather to determine how useful the 3 harvest indices would be for estimating θ. A time-series that cannot be distinguished from random or exponential growth would provide little information regarding density dependence. I found that the theta-Ricker model best explained the harvest indices, as opposed to harvest/effort. Harvest indices tended to be longer and covered a greater range than harvest/effort indices. Harvest/effort indices were shorter, more recent and appeared to fluctuate around equilibrium. Harvest/effort indices would, therefore, be more difficult to fit than harvest indices, and this is probably why the theta-Ricker could better explain the harvest indices.

It is not surprising that the residuals from several of the regions did not appear normally distributed. I fit a simple model across several regions simultaneously for each index. While this resulted in a more precise $\hat{\theta}$, it would be extremely unlikely that $\hat{\theta}$ fixed across regions would produce a perfect fit to each regional time-series. In reality, each region's growth rate should be some combination of density-dependent growth and its own unique density-independent environmental factors (McCullough 1990). Overall, the increased precision gained from fitting across regions outweighs the need to fully explain any single region.

Estimates of θ from the 12-region validation set supported the original $\hat{\theta}$'s. While the validation estimate was more uncertain (less data used in estimation: 20 – 33% of original sample size), it agreed that $\theta < 1$. Because of the data requirements for parameter estimation, it is difficult to make inferences beyond this. While I used real data not used in model construction to validate $\hat{\theta}$, model behavior can be further validated by comparing its predictions against future regional harvests, or by comparing model behavior to observed harvest from other regions.

Both measurement error and process error acted to bias $\hat{\theta}$ upward. Measurement error increased bias in $\hat{\theta}$ to a greater degree than process error. Sibley et al. (2005)

reported that $\hat{\theta}$ could be determined without appreciable bias provided measurement error was less than half the environmental error. The positive bias could be substantial, and depended on the amount of information provided by the data. Bias was much lower for the spring harvest data because it covered a greater range of population sizes, providing more information on model behavior and parameter values. As might be expected, indices covering a greater range of population sizes or density over time will act to offset the estimation problems associated with harvest indices.

Meta-analysis techniques allow researchers to increase precision by using different sources of information, but cannot correct for hidden biases in the data. Failing to account for the positive bias in θ will result in expectations of higher yields, and a greater reliance by managers on density-dependent effects to determine yield than density-independent effects. When $\hat{\theta}$ is biased upward, managers will believe they have a smaller window of population densities at which a decline in population size will result in increased yields, and be tempted to maintain populations at higher levels as a more conservative strategy, but they may rely too heavily on intrinsically determined maximized yields to offset overharvests, when extrinsic effects such as weather or mast production, will often be a greater determinant of yield. Dealing with measurement error is, therefore, important.

Measurement error can be accounted for in some circumstances, such as when multiple samples are taken on the same population (Williams et al. 2003), however, there has been little done to examine the behavior of harvest indices and their relationship to true abundance, particularly in the case of wild turkey. Indices based on harvest numbers alone will be affected not only by changes in population size, but also hunter effort, regulation changes, reporting rates, weather, and landscape effects (the integration of agricultural and forested lands). Because of these factors, it is difficult to meet the underlying assumption that the harvest rate is constant (Lancia et al. 1994). This assumption that wild turkey harvest indices are proportional to population abundance appears to have resulted in a positive bias in $\hat{\theta}$.

Harvest/unit effort will standardize harvest rates, but will be less useful when harvest greatly reduces the population (Caughley 1977:17). Hunters may inflate numbers when filling out report cards, and if return rates are low, small sample sizes may increase variance (Healy and Powell 2000). In the case of surveyed harvest/effort, only a small proportion of total hunters report their effort and kills, and if highly experienced, as may be the case with National Wild Turkey Federation volunteers, they may not be representative of true hunting pressure in the region or state (their hunting success may be higher than average). Given these issues, reported harvest/effort is likely the better index of the three, and mark-recapture studies, such as Lint et al. (1995), may be useful in determining the amount of measurement error associated with this factor and its major contributors. While we examined the effects of bias under multiple scenarios, our understanding of the true effect of measurement error remains largely unknown. Yet, harvest indices represent the longest available times-series for wild turkey population studies, and will likely be used for future research. Studies relating indices to true abundance estimates are needed. Unless more research is undertaken, parameter estimation from time-series will remain problematic for this species.

MANAGEMENT IMPLICATIONS

The results of this study indicate the effect of density dependence as a component of wild turkey population dynamics, and consequently, harvest management. Current harvest models (Alpizar-Jara et al. 2001, Vangilder and Kurzejeski 1995) assume only density independent growth because no density-dependent mechanisms have been as yet determined. It is more likely, however, that both density-dependent and independent factors work in conjunction depending on population density and habitat limitations (McCullough 1990).

A specified density-dependent mechanism does not need to be fully determined before management can develop more effective harvest strategies assuming both density-dependent and independent factors operate. This study supports the hypothesis that density-dependent factors act most strongly at low population densities relative to K, with growth rates high at these low levels. Also, the degree to which yield can be determined by density dependence will tend to be low.

This finding allows managers to approach wild turkey harvest strategies from a yield curve paradigm (Fig. 2.5). Using the yield curve, managers can optimize population density or size to meet public desires and maintain wild turkey population stability (McCullough 1984). Ignoring environmental stochasticity, populations held nearer to K (scenario A: Fig. 2.5) will provide managers with greater opportunity to detect and respond to mistakes in harvest strategy, with low harvestable yield. Populations held at low densities < N_{msy} (scenario B: Fig. 2.5) will be very sensitive to overharvest with little opportunity for detection and correction, also with low harvestable yield. Populations held at or near N_{msy} (scenario C: Fig. 2.5) will also be sensitive to overharvest, and with still very little detection and response time, however, harvestable yield will tend to be larger.

Given the variability of growth rates due to density-independent factors, however, yields are likely to fluctuate to the extent that it may be difficult to detect problems or determine where a population lies along the yield curve. Because of this uncertainty, managers would be best advised to maintain populations well above N_{msy}, in order to provide a longer detection and response time. Further information on the variability in growth rates that can be explained by extrinsic factors is needed before setting more liberal harvest rates. Finally, this study demonstrates that both density-dependent and density-independent processes are important to wild turkey population growth, and that population models should account for both in order to provide the most useful results for wild turkey harvest management.

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Table 2.1. The theta-Ricker, exponential growth, and random walk models are compared by AIC$_c$, for each index type (spring harvest, reported spring harvest/effort, surveyed spring harvest/effort) and harvest rate assumption (27.9%, 10.1%, 3.1%). The number of regions and datapoints for all regions combined, n, are provided for each index. Competing models are compared by index. Model comparisons list the AIC$_c$ value; Δ_{AIC}, the difference from the best model; the sum of squared errors, SSE; the coefficients of determinations r^2 and r^2_{adj}; and the Akaike weights, ω_i. For all data, the theta-Ricker model performs substantially better than the exponential growth or random walk models.

Index	regions	n	Model	AIC$_c$	Δ_{AIC}	SSE	r^2	r^2_a	ω_i
27.9% spring harvest	20	533	Theta-Ricker	-1303.1	0.0	2.47	0.66	0.65	0.998
			Exponential Growth	-1161.1	142.0	3.30	0.51	0.51	0.001
			Random Walk	-771.1	532.0	6.78	0.00	0.00	0.001
10.1% spring harvest	20	533	Theta-Ricker	-1511.8	0.0	1.72	0.55	0.53	0.999
			Exponential Growth	-1417.0	94.8	2.27	0.44	0.43	>0.001
			Random Walk	-1132.0	379.8	4.03	0.00	0.00	>0.001
3.1% spring harvest	20	533	Theta-Ricker	-1544.2	0.0	1.57	0.43	0.42	0.999
			Exponential Growth	-1475.3	68.9	1.94	0.29	0.29	>0.001
			Random Walk	-1295.1	249.1	2.74	0.00	0.00	>0.001
Reported spring harvest /effort	15	207	Theta-Ricker	-609.4	0.0	0.53	0.28	0.27	0.999
			Exponential Growth	-584.5	24.9	0.71	0.04	0.03	>0.001
			Random Walk	-578.9	30.5	0.73	0.00	0.00	>0.001
Surveyed spring harvest /effort	23	210	Theta-Ricker	-549.4	0.0	0.68	0.25	0.24	0.998
			Exponential Growth	-546.1	3.3	0.89	0.01	-0.01	0.001
			Random Walk	-545.0	4.4	0.91	0.00	-0.01	0.001

Table 2.2. Weighted mean $\hat{\theta}$ (θ*) are calculated across indices for 3 separate harvest rate assumptions. Weights are calculated from an estimated covariance martix which was determined from correlations between indices in the same region and time period. For a set of indices, weights are multipled by index-specific $\hat{\theta}$ (se represents the standard error) which are summed to estimate θ*. These weighted means estimate the range of θ for wild turkey, given the potential differences in harvest rates based on multiple data sources.

Indices	weight	$\hat{\theta}$ ± se	θ* ± se
27.9% spring harvest	0.226	0.41 ± 0.06	0.74 ± 0.03
Reported spring harvest/effort	0.398	0.83 ± 0.08	
Surveyed spring harvest/effort	0.498	0.78 ± 0.07	
10.1% spring harvest	0.343	0.38 ± 0.05	0.63 ± 0.02
Reported spring harvest/effort	0.303	0.83 ± 0.08	
Surveyed spring harvest/effort	0.354	0.78 ± 0.07	
3.1% spring harvest	0.579	0.27 ± 0.03	0.50 ± 0.02
Reported spring harvest/effort	0.231	0.83 ± 0.08	
Surveyed spring harvest/effort	0.190	0.78 ± 0.07	

Table 2.3. Bias in θ is estimated for 7 measurement error treatments and 2 types of harvest indices. For each treatment, measurement error accounted for a different percentage of the total error. Total error was the sum of the process and measurement error and was set at 0.22 for the harvest simulation and 0.16 for the harvest/effort simulation. Harvest simulations were longer and covered a greater range of population sizes while harvest/effort simulations were shorter with population sizes near carrying capacity. Each treatment was run 200 times, and a mean θ was calculated and compared to its true value. Mean standard errors (se) are reported to reflect the variability in individual estimates of θ. Bias was calculated as the ratio of the true θ (0.63) to the estimated mean from simulation runs ($\bar{\theta}$). Bias values >1 represent positive bias and values <1 represent negative bias.

% measurement error	Harvest simulation			Harvest/effort simulation		
	$\bar{\theta}$	mean se	Bias $\left(\theta/\bar{\theta}\right)$	$\bar{\theta}$	mean se	Bias $\left(\theta/\bar{\theta}\right)$
0	0.76	0.058	1.13	1.03	0.1409	1.54
20	0.75	0.050	1.12	1.07	0.1414	1.60
40	0.81	0.057	1.21	1.3	0.1479	1.94
50	0.87	0.064	1.30	1.49	0.1509	2.22
60	0.95	0.074	1.42	1.75	0.1544	2.61
80	1.23	0.100	1.84	1.96	0.1532	2.93
100	1.39	0.100	2.07	1.99	0.1538	2.97

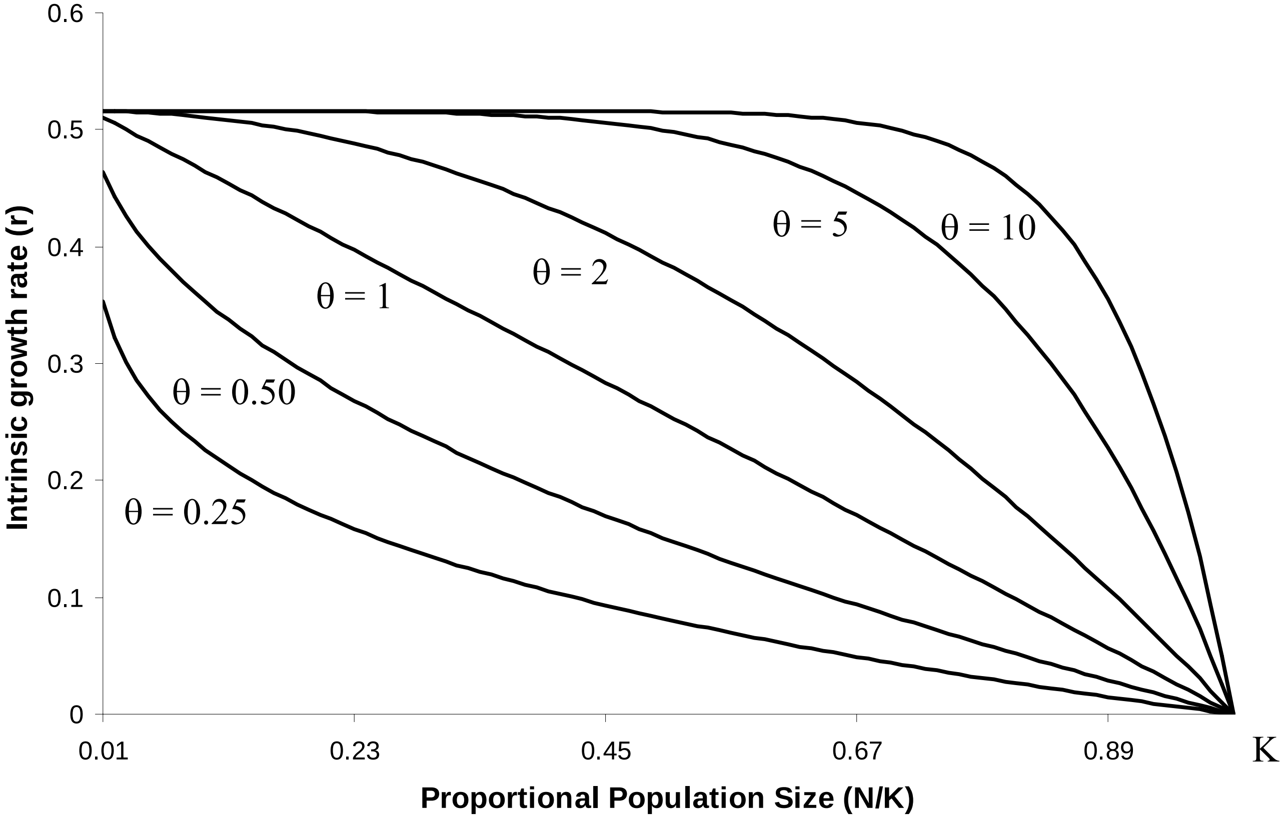
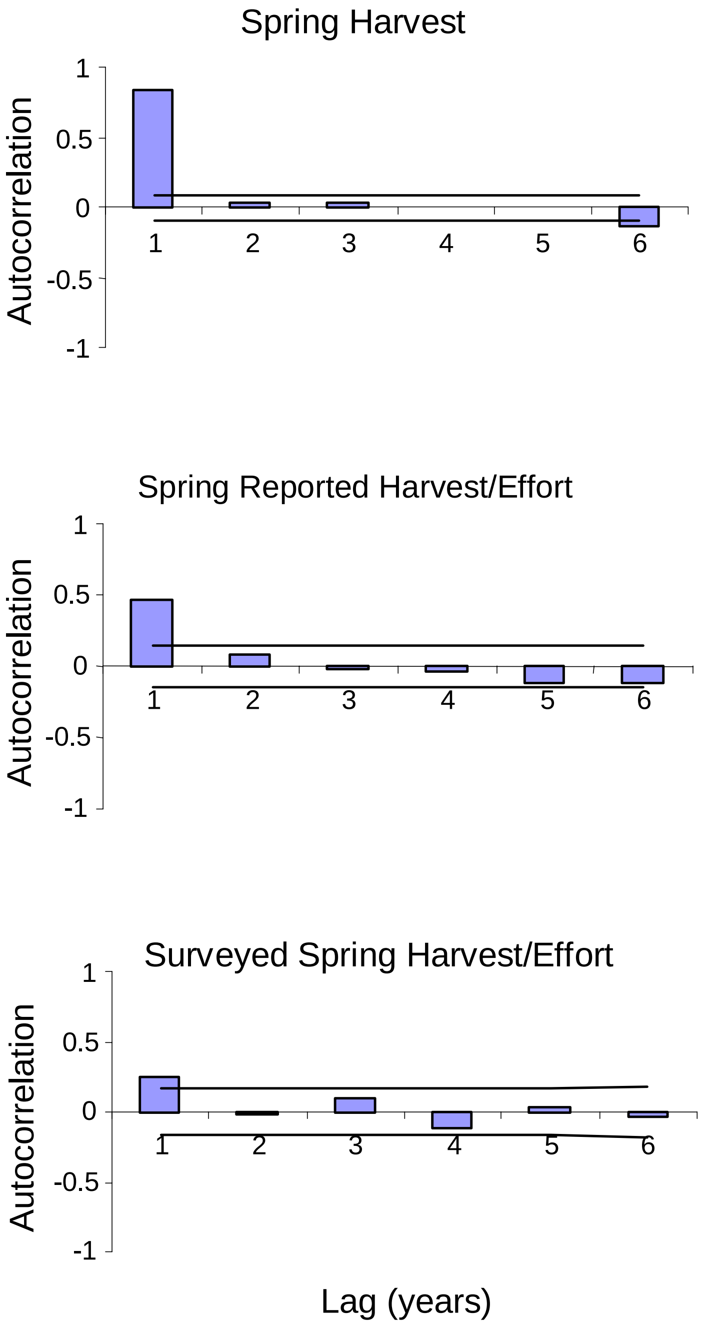


Figure 2.1. The behavior of the intrinsic growth rate under different values of θ. The intrinsic growth rate is set at 0.51, similar to maximum seen in reintroduced wild turkey populations. Minimum population size is 0.01K. For $\theta = 1$, the growth rate declines linearly, as in the logistic model. For $\theta < 1$, the growth rate declines quickly at low population sizes relative to K, producing a convex relationship. For $\theta > 1$, the growth rate is unaffected until population sizes are near K, whereupon the growth rate declines, producing a concave relationship.



Spring Harvest

Spring Reported Harvest/Effort

Surveyed Spring Harvest/Effort

Figure 2.2. PACF analysis of 3 harvest indices (spring harvest, n = 20 regions; spring reported harvest/effort, n = 15 regions; survey spring harvest/effort, n = 15 regions) with average correlation across regions shown at lags 1 – 6 years. The lines on either side of the x-axis represent 2 standard errors so that bars extending beyond these lines are considered significant correlations. In all cases, current spring harvest index value is significantly correlated with the previous spring harvest index value, indicating spring population densities are correlated with the previous spring population density only.

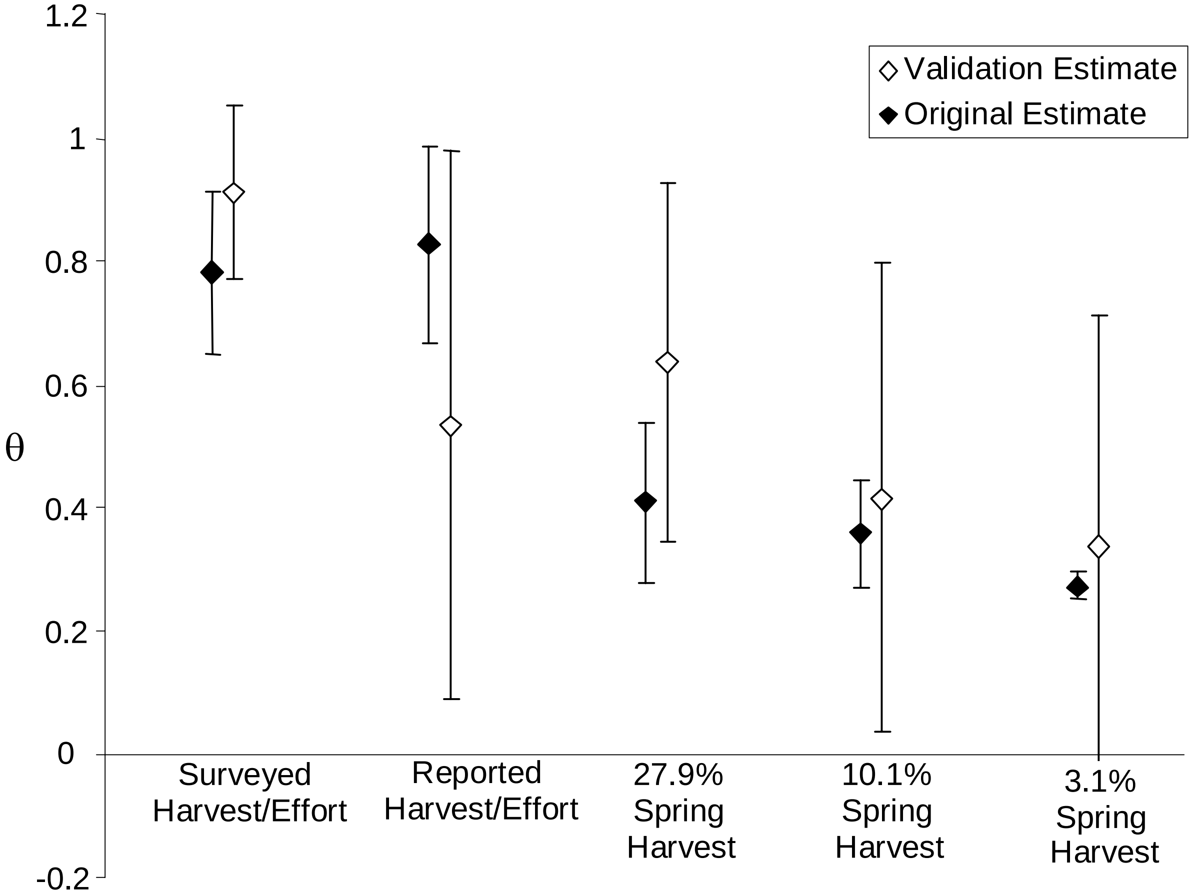


Figure 2.3. Comparison of θ parameter and validation estimates with 95% confidence intervals for 3 harvest indices (spring harvest, spring reported harvest/effort, survey spring harvest/effort). Parameter estimates from the validation set are shown in open shapes. 95% confidence intervals for validation estimates overlap original estimates for all indices and are uniformly < 1, indicating θ estimates are robust across regions.

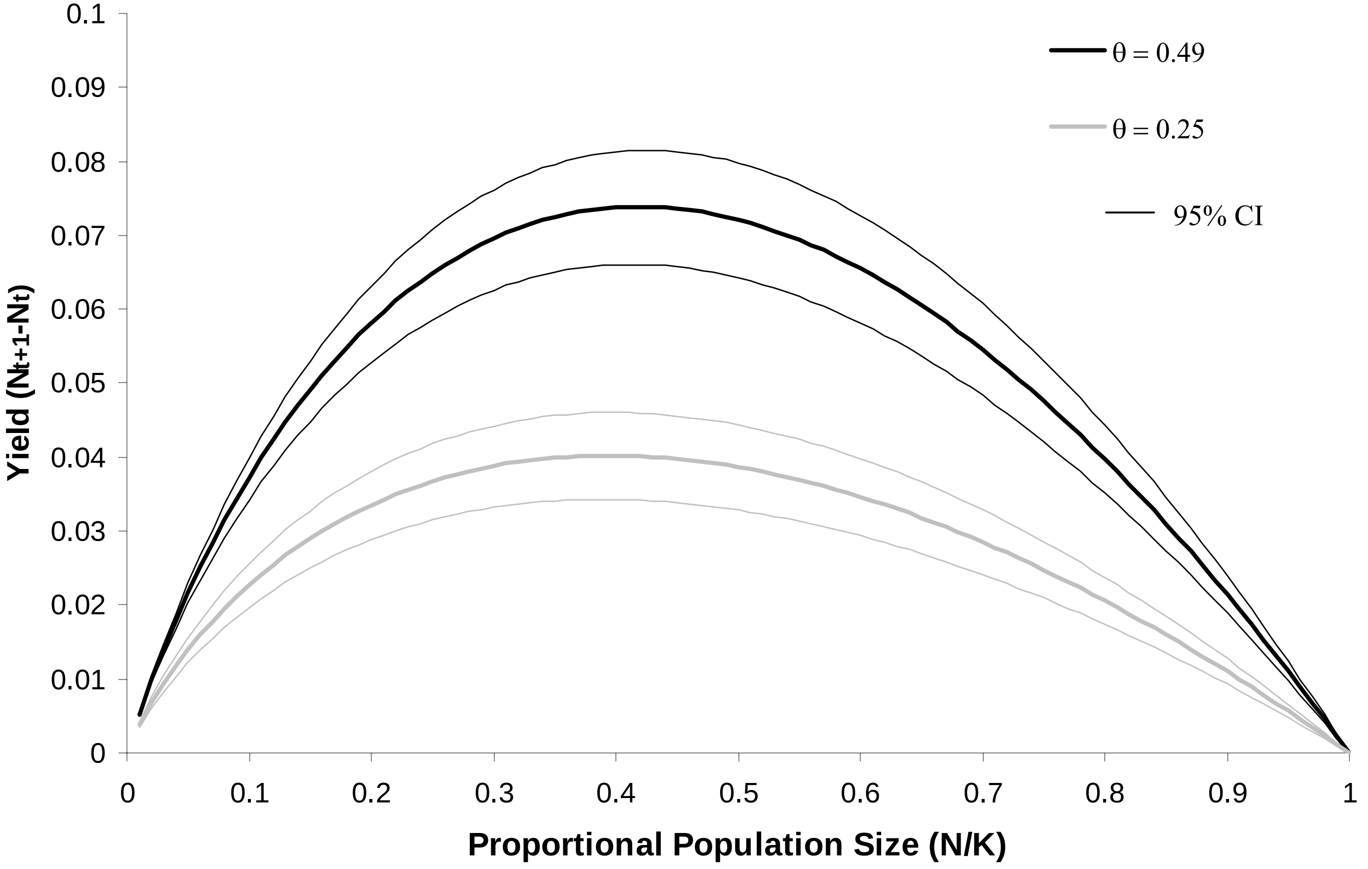


Figure 2.4. Yield curve for wild turkey for 2 values of θ (0.25, 0.49) where thin lines represent 95% confidence intervals. Expected yield (N_{t+1}-N_t) is shown for a given population size expressed as a proportion of K. Maximum yields occur between 0.39 – 0.42K while magnitude of yield decreases with θ for the deterministic theta-Ricker model.

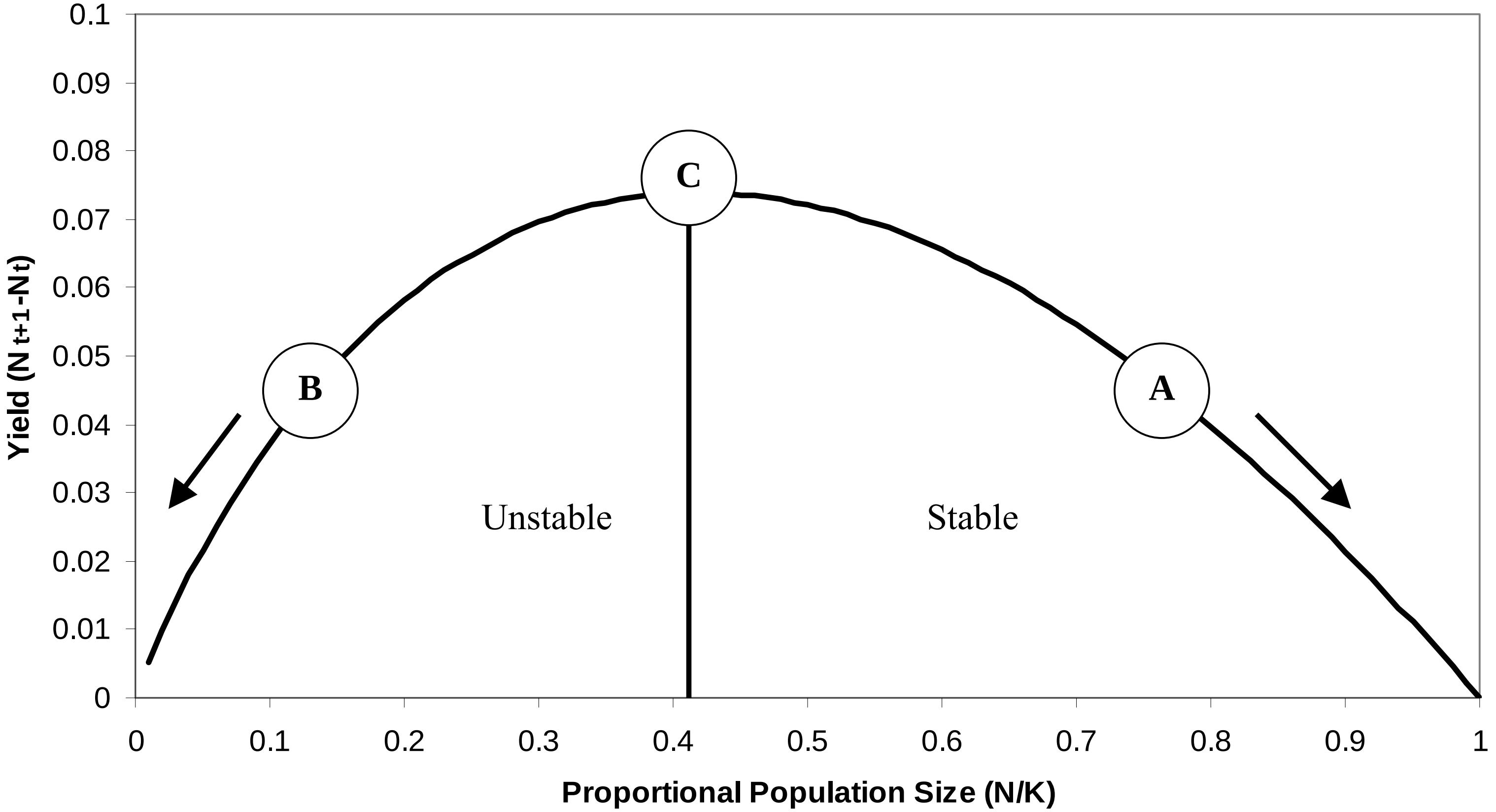


Figure 2.5. A hypothetical yield curve for wild turkey. The population size producing the maximum sustainable yield occurs at 42%K with a maximum expected yield of 8 % and is shown by the line bisecting the curve. Populations on the right side of the curve are stable because a decrease in population size results in an increase in yield so that population size is continually moving towards K. Populations on the left side of the curve are unstable because a decrease in population size results in a decrease in yield so that population size moves toward zero when overharvested. The circles labeled A, B and C represent three management scenarios discussed in the text.

CHAPTER 3: ENVIRONMENTAL CORRELATES OF WILD TURKEY PRODUCTION

ABSTRACT

Reproduction is a highly variable component of eastern wild turkey (*Meleagris gallopavo silvestris*) annual population growth, and is important in influencing summer cohort strength for fall either-sex harvests. I explored a set of models using environmental factors (departure from average rainfall, heating degree days, previous mast crop) during the nesting and brooding season to predict production index data at a regional scale for 7 states. The best models as selected by AIC_c varied widely by region and were typically characterized by high model uncertainty. Because time-series were brief, most selected models were limited to single predictors, while relative importance values for environmental predictors were roughly equal for a given state. While single predictor models may be useful over the short-term, managers should take care to validate and update models as new and better data are collected. Population and harvest models, especially those simulating population dynamics over multiple generations, should focus on better estimated intrinsic factors, such as density dependence, and model density independent environmental factors as random error in the growth rate, until better models can be determined.

INTRODUCTION

Reproduction is a key component of eastern wild turkey annual population growth, but can also be the most variable because of its apparent sensitivity to a suite of environmental factors during the nesting and brooding season (Roberts and Porter 1998a, Roberts et al. 1995, Healy 1992). This inherent variability makes it difficult to predict annual production, and hence, harvestable yield for fall either-sex hunting. For this reason, it is necessary to better understand the effects environmental factors have on annual production. Understanding the effects of environmental factors on production will consequently lead to a more complete understanding of the variation in annual wild turkey abundance. This will allow researchers to build more complete models of wild turkey dynamics, which include both intrinsic effects, such as density dependence along with the extrinsic environmental effects that operate in conjunction with the intrinsic to determine annual population growth.

This understanding is particularly important for those states incorporating a fall either-sex hunting season, as overharvest of females can cause population declines (Alpizar-Jara et al. 2001, Vangilder and Kurzejeski 1995, Suchy et al. 1983). Numerous studies have recommended monitoring production to assess a given population's ability to meet the demands of the fall harvest (Norman et al. 2001, Roberts and Porter 1998 a, b). However, monitoring production through summer brood surveys allows little time for managers to adjust fall harvest recommendations to match cohort strength, and accurate production models based on spring weather may be a suitable proxy, giving managers more time to make needed adjustments (Norman et al. 2004, Roberts and Porter 2001).

Previous studies have reported several environmental variables that may potentially affect annual production. These include change in May precipitation (Roberts and Porter 2001), temperature prior to incubation and during nesting and brood-rearing (Norman et al. 2004, Lowery et al. 2001, Roberts and Porter 1998a,b), rainfall during nesting and brood-rearing (Norman et al. 2004, Lowery et al. 2001, Healy and Nenno 1985), humidity during nesting (Roberts and Porter 1998a), and soil moisture storage in May and the previous August and September (Beasom and Pattee 1980). The majority of these studies has been conducted at local levels, such as wildlife management areas or counties, and has generally agreed that large deviations from the long-term means of early spring temperatures and rainfall in the nesting and brooding season have the strongest potential to negatively affect wild turkey production. However, only a few studies have attempted to estimate parameters from data directly relating production to environmental factors (Norman et al. 2004, Roberts and Porter 1998a, b).

Positive or negative weather effects on production could occur through several mechanisms. Generally, cold, wet seasons should reduce production. Two measures of deviations toward colder temperatures and high or low rainfall are heating degree-days (HD) and departure from normal precipitation (DP). Heating degree-days (65-mean daily temperature) measure cumulative heating demands, such that a large HD represents colder than average temperatures over a period of time, while a small HD represents average temperatures over a period of time. Departure from normal precipitation represents the departure from monthly average rainfalls.

Colder temperatures (high HD) during March or April may delay spring phenology, causing a delay in nesting, incubation, or lowered nesting rates in hens

(Norman et al. 2004, Vangilder and Kurzejeski 1995). Conversely, low HD may result in normal spring green-up and normal nesting and incubation times, resulting in average or higher production. High DP in March might cause a greater spring green-up, which hens might use to increase energy reserves more quickly and enjoy greater production success. Conversely, below-average rainfall may cause hens to increase energy reserves slowly, delaying nesting and reducing production. High rainfall during the nesting season may increase nest predation risk because predators may follow scents more easily in humid environments and find nests more readily (Roberts et al. 1995, Palmer et al. 1993). Therefore, high DP in April, May, and June might lower nesting success through increased predation and decrease poult survival after hatching (Lowery et al 2001, Roberts and Porter 2001, Roberts and Porter 1998a, b, Healy 1992). Conversely, low, negative values of DP may decrease predator's ability to find nests, increasing nest success. High rainfall (high DP) may also lower poult survival depending on the severity of storms, or if accompanied by low temperatures (low HD: Vangilder and Kurzejeski 1995, Healy and Nenno 1985, Kennamer et al. 1975). Roberts and Porter (1998a, b) found that daily nest survival and poult survival 25 days post-hatch was decreased with high rainfall and increased with heating demands respectively.

In addition to weather, the availability of hard mast (the hard fruit produced by trees: Scalet et al. 1996) over fall and winter may also affect production, such that in poor mast production years, hens may not acquire the energy reserves necessary to establish a nest or to renest. Porter et al. (1983) found that hen weights decreased over winter, with the severity of winter conditions accounting for 80% of the variation in hatching rates of yearling females. Similarly, Thogmartin and Johnson (1999) found that low hen weight was correlated with both smaller clutch sizes and later incubation dates. However, Norman et al. (2001) found no relationship between winter weight and reproduction.

To summarize, deviations in temperature during the pre-nesting and early nesting season, rainfall during nesting, and availability of acorns the previous fall and winter may account for much of the variability in annual wild turkey abundances through their effect on production, and useful predictors for production and harvest models. Several states maintain time-series data on production and abundance indices including poult:hen ratios, brood counts, and juvenile:hen ratios. Functional relationships between these production indices and weather may be tested using data collected from the National Climatic Data Center (NCDC) of the National Oceanic and Atmospheric Administration (NOAA: Asheville, North Carolina, USA).

The brevity of many current data sets will hinder complex model building, especially when multiple environmental factors can be expected to affect production (Ricker 1975: 277 – 278). Simpler models with fewer parameters may operate well over the short term by using those parameters that have the strongest detectable effect on production indices. Production models can be expected to differ by region in terms of which parameters work best and the magnitude of their effect, and because methodologies differ by state, models that combine information across regions via meta-analysis would be invalid (Hedges and Olkin 1985). Regional time-series must therefore, be examined separately, and because of the brevity of data, this will reduce the precision of parameter estimation. Despite this problem, independent regional model selection may still provide insights on how the importance of environmental variables may change across states.

My objective was to test for the presence of a set of functional relationships between environmental data and production, using data from multiple states, primarily to determine the potential of incorporating them into regional production models. Models of this nature would aid managers in estimating annual production potential and determining appropriate harvest strategies for a species subject to high environmental variation in its population growth rate (Mosby 1967). In this analysis, I assumed that both density dependent and density independent factors determine the growth rate of wild turkey, and that observed annual production may be determined primarily by weather or mast related factors. I tested a set of hypothesized models incorporating these factors, which are measured as departures from monthly expected temperature and rainfall for the months of March through June, the primary nesting and brooding period for wild turkeys, and hard mast abundance the previous fall.

METHODS

Data selection

I modeled deviations in production indices (brood surveys, fall harvest age ratios) over time using a combination of rainfall, temperature and mast variables at a regional scale for 7 states (MD, NJ, NY, PA, RI, VA, and WV). Regions were determined as pre-existing management regions set by state agencies or as geographical zones comprising of a set of counties conforming to Level III ecoregions as designated by the Environmental Protection Agency (Omernik 1987).

Summer brood surveys

I used poult:hen ratios from brood survey data from Maryland (9 yrs: 1993 – 2001), New Jersey (21 yrs: 1982 – 2002), New York (6 yrs: 1996 – 2001), and Rhode Island (9 yrs: 1993 – 2001) as an index to annual reproduction (Kurzejeski and Vangilder 1992). In addition, I used brood counts from West Virginia (16 yrs: 1986 – 2001) and summer sighting indices (broods observed/1000 km) from Pennsylvania (11 yrs: 1990 – 2000). Poult:hen ratios were based on all observed hens seen with the exception of RI, in which only brood hens were noted. State agencies collect brood survey data during summer over differing months by conservation officers or district biologists (MD, NJ, NY, WV, PA) and citizen volunteers (NY, RI). In most cases, brood surveys are conducted during routine fieldwork by staff, making standardization across samples difficult. This, in addition to the variable effort by volunteers, makes direct comparison of poult:hen ratios between states or management regions impossible (Healy and Powell 2000), so I modeled each state and region separately.

Fall harvest juvenile: hen ratios

I used juvenile:adult hen ratios based on fall harvest numbers as a separate index of recruitment from New York (20 yrs: 1983 – 2001), Virginia (10 yrs: 1994 – 2003), and West Virginia (29 yrs: 1964 – 1992). The juvenile class included both sexes. In NY and WV, hunters are required to complete a survey from which sex and age of fall harvested wild turkeys are determined. In VA, sex and age of fall harvested wild turkeys are determined from breast and wing feathers collected by mandatory check stations. I assume that the harvest age ratio reflects the population age ratio. However, adult males may be harvested in preference to juvenile males (Little et al. 1990), and differential harvest of adult females during mast failures (Steffen et al. 2002) would act to bias ratios towards low production.

I removed the trend from the time-series data using best-fit lines by year, and examined the residuals (Brockwell and Davis 1987: 15). I assume that the environmental effects discussed above act to create deviations from trends in production caused by intrinsic processes (such as density-dependence) that also act on population growth (Turchin 2003: 29, McCullough 1990).

Variable selection

Rainfall and Temperature

Much of the research correlating weather to wild turkey production has suggested that deviations from normal temperatures and rainfall levels are the most important determinants of fluctuations in production (Vangilder and Kurzejeski 1995). I chose 6 variables that reflected deviations from normal rainfall and temperature conditions during the pre-nesting, nesting, and brooding seasons. These variables were the regional averages for each month of the nesting season (Mar-Jun) for heating degree-days (HD), and departure from normal precipitation (DP). I examined HD in March and April, and DP in March, April, May, and June. I obtained weather data from the NCDC (NOAA: Asheville, North Carolina, USA). Variables for each month were calculated as the average from individual weather stations in a given region.

Hard Mast Production

Rhode Island, VA, and WV collect indices on annual mast production. I used these indices, focusing on hard mast, which may be the primary food for eastern wild turkeys in fall, winter, and spring (Steffen et al. 2002, Hurst 1992, Schroeder 1985). I did not separate estimates of red oak group and white oak group mast because wild turkeys do not appear to exhibit a preference for either (Steffen et al. 2002).

In VA, mast is classified by site into 5 categories based on observer perception (excellent, good, fair, poor, failure) on a per species basis. Indices are then averaged across region or state. In WV and RI, mast is classified by site into 4 categories (abundant, common, scarce, or not present) on a per species basis (Uhlig and Wilson 1952). Regional indices were calculated by adding the percentage of observers in a region that rated production as abundant plus half the percentage of observers that rated mast production as common.

Model determination and selection

I chose 17 a priori models to reflect the different periods of the nesting season where production might be most affected by environmental influences and the linear combination of those influences across the nesting season (Table 1). Linear models were chosen because graphs between poult:hen ratio residuals and explanatory variables did not appear to exhibit non-linear relationships.

I evaluated models using AIC_c, which is approximately unbiased for time-series models and performs better than standard AIC when sample sizes are small (Burnham and Anderson 1998, Hurvich and Tsai 1989). I compared models based on AIC_c

differences from the best model (Δ_i), explained variability (r^2, $r^2_{adj.}$), and Akaike weights (ω_i) which are normalized relative likelihoods of a model, given the data and the set of other models evaluated (Burnham and Anderson 1998: 124). I used the Shapiro-Wilks test to determine whether the residuals from models selected as best conformed to a normal distribution at an $\alpha = 0.05$ (Zar 1999). Mast time-series length was much shorter than ratio data for VA, so I compared these mast models to all other models in separate analyses using only the data for which mast data overlapped. Only regions with at least one model having a $\omega_i \geq 0.25$ are listed in the results. However, all models are presented in Appendix 1.

Finally, I wished to determine whether nesting and breeding season environmental models did better at predicting poult:hen ratios rather than fall harvest age-ratios. To do this I used the New York poult:hen ratios and fall age-ratios because NY collected both indices. I compared the best model weights between these production indices using a Wilcoxon paired-sample test, which does not assume a normal distribution for Akaike weights (Zar 1999).

RESULTS

Model Selection

Summer Brood Surveys

The variability in poult:hen ratios explained by the best regional models varied ($r^2 = 0.13 – 0.87$), and models with fewer parameters tended to be chosen as best (Table 3.2). Akaike weights also varied widely (cv = 0.42), but on average tended to be low

($\bar{x}$ = 0.54), indicating high model uncertainty. Residuals from the best models describing deviations in poult:hen ratios did not differ from normal (Table 3.2).

The variability in brood abundance explained by the best regional models varied (r^2 = 0.16 – 0.86), and models with fewer parameters tended to be chosen as best (Table 3.3). Akaike weights for the best models also varied widely (cv = 0.49), but on average tended to be low ($\bar{x}$ = 0.42), indicating high model uncertainty. The residuals for the top two WV mountains region models (a, b) and the top model for PA TMA 2 (a) did not conform to a normal distribution (Table 3.3).

Fall harvest juvenile: hen ratios

The variability in juvenile:hen ratios explained by the best regional models varied (r^2 = 0.13 – 0.50), and models with fewer parameters tended to be chosen as best (Table 3.4). Akaike weights also varied widely (cv = 0.33), but on average tended to be low ($\bar{x}$ = 0.39), indicating high model uncertainty. Model certainty was lower for fall juvenile:hen ratios than annual poult:hen ratios (Wilcoxon paired-sample test T- = 1, $P <$ 0.025) in New York (where both types of data were collected). The residuals for the top VA southern piedmont region model (a) did not conform to a normal distribution (Table 3.4).

Weather relationships to production indices

For the selected models, within indices, slope coefficients tended to be of the same magnitude, and relationships were often in the same direction, although the strength of the relationships were usually weak. Over all indices combined, high MarHD was associated with lower production in 3/6 of the best models for which it was selected. High AprHD was associated with lower production in 16/17 of the best models for which it was selected. High MarDP was associated with higher production in 7/13 of the best models for which it was selected. High AprDP was associated with lower production in 6/10 of the best models for which it was selected. High MayDP was associated with lower production in 18/20 of the best models for which it was selected. High JuneDP was associated with lower production in 11/16 of the best models for which it was selected. High Mast was associated with higher production in 2/2 of the best models for which it was selected.

DISCUSSION

The results of this study indicate that environmental variables prior to and during the nesting and brooding season have the potential to influence wild turkey production, but that the brevity of time-series (range: 6 – 29 yrs) precludes putting high confidence in most models, and models with multiple parameters tended to be heavily penalized because of the brevity of time-series. Consequently, most of the best models selected were limited to a single parameter; however, one would expect several environmental factors to contribute to variability in production. In some cases, simple models were well-supported given the data available (i.e. RI, MD Blue Ridge). However, as expected, model uncertainty was high for most regions, and limited model effectiveness.

Well-supported single factor models, such as April departure from normal precipitation (AprDP), determined from brief time-series detected strong but temporary effects that may shift over time. As data increases, model selection procedures may shift towards choosing multi-parameter models more often (Ricker 1975: 277–278). Managers should rely on environmental production models to estimate fall cohort strength only over the short-term, validating and calibrating them to new production index data as they become available.

Similar results were reported for the sharp-tailed grouse (*Tympanuchus phasianellus*), where the best weather models explained 16 – 57% of the variation in harvest age-ratios with model weights of ≤ 0.08 (Flanders-Wanner et al. 2004). The weak explanatory power of most models might be explained by hen parental behavior offsetting reductions in resource value through weather effects. Bradbury et al. (2003) found that temperature and precipitation poorly explained variation in nestling condition and body growth rate for 4 passerines species, surmising that parents compensated for poorer conditions with increased effort towards current reproductive success.

McCullough (1990) suggested that both density-dependent and independent factors would be important determinants of population growth rates. This view has been useful in explaining population growth rates for a number of bird species, as well as determining appropriate harvest strategies for hunted populations, including species whose population growth rates are considered sensitive to environmental variation (Aanes et al. 2002, Sæther et al. 2002, Watson et al. 1998). To model wild turkey population dynamics, and test the effect of harvest strategies, managers would be better served to focus on intrinsic population dynamics, such as density dependent effects, relegating environmental effects to random error until they can be better modeled.

Selected best models differed extensively among regions, which indicates that the appropriate scale for modeling annual production indices is at a within state regional level of multiple or single counties. In some cases, explanatory models fit well for concurrent regions (i.e. variations in poult:hen ratios in NY DEC regions 7–9 were all well explained by April departure from normal precipitation (AprDP). However, predictions may improve for models at more localized levels, such as counties, or townships. Poult:hen models tended to have higher weights on average than brood abundance or fall juvenile:hen ratios in general, and in NY, these differences were significant, indicating spring environmental correlates examined here are better at identifying summer production, rather than recruitment into the fall population.

Despite model uncertainty, some weather variables tended to be consistent predictors of variation in production. AprDP and May departure from normal precipitation (MayDP) were the most important predictors overall. In addition, April heating-degree days (AprHD) was consistently more important than March heating-degree days (MarHD). June departure from normal precipitation (JuneDP) was also often selected. Further modeling efforts for these regions should focus on these weather factors in future modeling attempts.

Important weather-related influences on production have been found for other bird species using time-series of similar length. Flanders-Wanner et al. (2004), using 21 yrs of data, reported that the cumulative precipitation from January 1 – July 31 was positively related to sharp-tailed grouse harvest age-ratios, possibly offsetting drought, and had high relative importance in model selection. However, the total precipitation in June was negatively related to the production index, possibly causing chilling or drowning of chicks. June temperature was thought to benefit production up until the point at which heat stress is generated.

Dorney and Kabat (1960), using 11 yrs of data, reported ruffed grouse (*Bonasa umbellus*) production was above average following high May temperatures, and below average following colder May temperatures, where high density populations were less responsive to favorable conditions than low density populations. Alternatively, Davies and Bergerud (1988) found that ruffed grouse chick survival was greater in years with warm Junes, but uncorrelated with mean and maximum May temperatures.

Potts (1986), using 17 yrs of data, developed a linear model that explained 58% of variation in chick survival for a gray partridge (*Perdix perdix*) population. Predictions were made from an estimated positive effect of preferred insect density and mean daily temperature from 10 June – 10 July. Similarly, breeding success of rock ptarmigan (*Lagopus mutus*) was related to the timing of blaeberry (*Vaccinium myrtillus*) growth and June temperature at one site and at June rain at a separate massifs > 10 km apart (Watson et al. 1998).

Smyth and Boag (1984), using 16 yrs of data, found no effect of spring green-up (or length of breeding season) on spruce grouse (*Dendragapus canadensis*) production, but did find that cold, wet conditions during incubation resulted in reduced productivity, while those same conditions immediately post-hatch were associated with high chick survival. The authors explained that this might occur through a lowered probability of predation from spending less time foraging and more time spent brooding in cold, wet conditions.

Similar to Norman et al. (2004), hard mast crops from the previous fall appeared to be relatively unimportant, although when considered, it was selected in the top models for the VA Southern Mountain and Northern and Southern Piedmont regions, as well as the WV Eastern Panhandle region (brood survey data). Nutritional deficiencies may reduce nesting rates, the temporal distribution of nesting, renesting rates, and brood survival (Porter et al. 1983, Vander Haegan et al. 1988, Steffen et al. 2002). Acorns are an important food source for wild turkey through most of the year (Hurst 1992), and may be particularly important in winter because of the high metabolizable energy they represent (Kirkpatrick and Pekins 2002). However, acorns are low in protein and phosphorus, which is important to egg production, and evidence for winter acorn availability directly affecting wild turkey production is scarce (Blankenship 1992, Kirkpatrick and Pekins 2002, Steffen et al. 2002). Norman et al. (2004) suggested that hard mast availability might be more important in areas with more severe winters. Unfortunately, estimates of mast production were only available from three states examined here (RI, VA, WV). Standardized mast production estimates are needed for multiple states across a variety of climate conditions before the effects of mast on wild turkey can be fully surmised.

Several studies have attempted to quantify the relationship between spring weather, fall mast crops and eastern wild turkey reproduction. Roberts and Porter (1998a, b) produced models incorporating HD, DP, and daily rainfall explaining 58% of the variation in 20-day nest survival, and 21% of the variation in 25-day poult survival. They later found that a negative association between the log annual rate of change in May precipitation and the annual rate of change in the fall harvest in the Western Plateau Climatic Division of NY ($r^2 = 0.73$: Roberts and Porter 2001). My study supports the conclusion that high rainfall during nesting (April and May) negatively affects production in NY, although I had less success predicting recruitment into the fall population ($r^2 =$

0.41) for a larger region encompassing the same area (DEC region 9). In addition, I found that DP in March – June was consistently important in predicting poult:hen ratios in DEC regions 3 – 6, while AprHD was consistently important in DEC regions 6 – 9.

Norman et al. (2004) produced models predicting variation in fall recruitment in the Allegheny Mountain Range of the Ridge and Valley Province of western Virginia. They found that high May and June rainfall events (≥75% quartile), combined with the number of days in March $\leq 0^{o}$C were able to explain 50% of the variation in fall juvenile:hen ratios. I show similar findings for the Northern Mountain and Southern Piedmont regions of VA, explaining 29% of the variation in juvenile:hen ratios. This includes the unexpected finding that increased June rainfall can have a positive effect on poult production in some regions. However, in 11 of 16 regions, June rainfall had a negative effect. Moderate increases in June rainfall may have beneficial effects that via incresed vegetative quality or insect abundance, that are lost in high June rainfall years (Beasom and Pattee 1980, Norman et al. 2004).

Norman et al.'s (2004) best models occurred using highly divergent rainfall events (≥75% quartile), and this implies that very large departures from average rainfall or cold may better predict recruitment during years in which they occur, while rainfall and temperatures closer to the long-term average may have less predictive power on an annual basis. This would support Healy and Nenno's (1985) contention that spring weather variables will only explain a portion of the annual variation in productivity, and therefore, may be more useful in predicting the direction rather than magnitude of change in the fall population. Nevertheless, my results suggest that temperature in March and

April, rainfall in May and June, and hard mast from the previous fall are important predictors of fall recruitment in VA.

Lowery et al. (2001) reported that fewer rainfall events were associated with higher annual nest success during March – June on the Tallahala Wildlife Management Area, while total rainfall over these months showed no association. Similarly, I found that above average rainfall March – June, particulary April and May, along with colder than average April temperatures tended to be important in predicting variation in summer production and fall recruitment.

MANAGEMENT IMPLICATIONS

This study demonstrates that spring temperature and rainfall variables have the potential to predict summer production and recruitment into the fall harvestable population, as well as account for the variability in annual wild turkey abundance. In many cases, however, time-series data were too short to build robust models with high certainty. Combining data across states and regions is a doubtful enterprise because methodologies differ between regions and lack the necessary standardization. In addition, one would not expect populations to undergo the same extrinsic pressures across states.

Given this, managers should continue collecting production and recruitment data while looking for ways to standardize surveys across regions and states, thereby reducing measurement error, and increasing statistical power. Heavily weighted, simple models can be used carefully in the short-term to estimate summer or fall cohort strength, but should be reevaluated against new data. Harvest strategies and annual population dynamics models should focus on intrinsic population dynamics until particular vital rates can be more reliably modeled by extrinsic environmental data. Modelers hoping to develop long-term harvest strategies (>3 yrs) should use the random error from their data to model environmental factors until data sets become long enough to estimate multiple environmental parameters.

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Table 3.1. Selected models to explain annual deviations in poult:hen ratios for regional management areas in 5 states (MD, NJ, NY, RI, WV). Model are shown in the left-hand column, while the rationale for the model is shown in the right-hand column.

Model	Rationale
MarHD	Delay of incubation
AprHD	Delay of incubation
MarHD + AprHD	Delay of incubation
MarDP	Early incubation, higher nest success
AprDP	Lowered early nest success
MayDP	Lowered nest success, lowered early poult survival
JunDP	Lowered poult survival
MarDP + AprDP	Early incubation, lowered early nest success
AprDP + MayDP	Lowered nest success
MarDP + MayDP	Early incubation, lowered nest success, lowered early poult survival
MarDP + AprDP + MayDP	Early incubation, lowered nest success, lowered early poult survival
MarDP + AprDP + MayDP + JunDP	Early incubation, lowered nest success, lowered poult survival
MarHD + AprDP + JunDP	Delay of incubation, lowered early nest success, lowered poult survival
AprHD + AprDP + JunDP	Delay of incubation, lowered early nest success, lowered poult survival
MarHD + MayDP + JunDP	Delay of incubation, lowered nest success, lowered poult survival
AprHD+ MayDP + JunDP	Delay of incubation, lowered nest success, lowered poult survival
Previous Fall Mast Production (Mast)	Hen condition

dp refers to departure from average monthly rainfall

hd refers to heating degree-days

Mast refers to hard mast as measured by state index data

Table 3.2. Top regional models for deviations in annual poult:hen ratios collected from summer brood surveys. States are divided by region, for which the best models are listed in order of preference (a, b, etc.). Intercepts (β_0) and coefficients (β_1, β_2) and standard errors (se) are listed. Akaike weights (ω_i) and coefficients of determination (r^2) estimate the relative likelihood and amount of variability explained by models respectively, n represents the number of years of data for each region. *P* represents the p-value for a Shapiro-Wilks test for normality of model residuals.

State	Region	Model	β_0	β_1	β_2	$\beta_1$se	$\beta_2$se	ω_i	r^2	n	*P*
RI	RI	AprDP	-0.11	-0.12	-	0.03	-	0.89	0.70	9	0.35
NJ	Ridge and Valley	AprHD	5.70	-0.01	-	0.01	-	0.27	0.13	17	0.37
	Appalachian-a	MayDP	-0.14	-0.20	-	0.11	-	0.28	0.21	15	0.98
	Appalachian-b	MarDP, MayDP	-0.66	0.29	-0.21	0.17	0.10	0.20	0.36	15	0.92
	Piedmont	MarDP	-0.31	0.33	-	0.15	-	0.50	0.30	13	0.68
	Pine Barrens	MayDP	-1.69	-1.01	-	0.25	-	0.40	0.66	12	0.82
	Coastal Plain	AprDP	-0.60	-0.60	-	0.26	-	0.51	0.34	12	0.63
	NE Highlands	MarHD	12.1	-0.10	-	0.01	-	0.35	0.25	10	0.56
MD	Appalachian	AprHD	4.74	-0.01	-	0.01	-	0.56	0.36	9	0.48
	Piedmont	MarDP	0.44	-0.10	-	0.04	-	0.59	0.44	9	0.27
	Ridge and Valley-a	AprHD	4.03	-0.01	-	0.01	-	0.35	0.32	9	0.65
	Ridge and Valley-b	JuneDP	-0.11	-0.24	-	0.14	-	0.31	0.30	9	0.72
	Coastal Plain-a	AprDP	-0.11	-0.27	-	0.15	-	0.27	0.33	9	0.62
	Coastal Plain-b	AprHD	3.34	-0.01	-	0.01	-	0.25	0.32	9	0.83
	Blue Ridge	AprHD	9.85	-0.03	-	0.01	-	0.53	0.49	7	0.99
NY	DEC Region 3	MayDP	0.13	-0.10	-	0.02	-	0.95	0.80	6	0.67
	DEC Region 4	MayDP	0.24	-0.24	-	0.07	-	0.69	0.74	6	0.69
	DEC Region 5-a	JuneDP	0.04	-0.04	-	0.03	-	0.28	0.33	6	0.21
	DEC Region 5-b	MarHD	-2.37	0.002	-	0.002	-	0.26	0.31	6	0.32
	DEC Region 6	JuneDP	0.02	-0.12	-	0.02	-	0.96	0.87	6	0.89
	DEC Region 7	AprDP	-0.05	-0.10	-	0.03	-	0.78	0.66	6	0.94
	DEC Region 8	AprDP	-0.07	-0.13	-	0.05	-	0.47	0.60	6	0.86
	DEC Region 9	AprDP	-0.06	0.07	-	0.03	-	0.60	0.70	6	0.55

Table 3.3. Top regional models for deviations in annual brood counts collected from summer brood surveys. States are divided by region, for which the best models are listed in order of preference (a, b, etc.). Intercepts (β_0) and coefficients (β_1, β_2) and standard errors (se) are listed. Akaike weights (ω_i) and coefficients of determination (r^2) estimate the relative likelihood and amount of variability explained by models respectively, n represents the number of years of data for each region. *P* represents the p-value for a Shapiro-Wilks test for normality of model residuals.

State	Region	Model	β_0	β_1	β_2	β_3	$\beta_1$se	$\beta_2$se	$\beta_3$se	ω_i	r^2	n	*P*
WV	E. Panhandle	Mast	-40.65	1.02	-	-	0.23	-	-	0.36	0.59	15	0.14
	Mountains-a	MarHD, AprDP, JuneDP	-213.31	0.12	1.62	-4.57	0.06	2.88	1.53	0.39	0.60	15	0.02
	Mountains-b	JuneDP	-110.76	-4.78	-	-	1.48	-	-	0.22	0.45	15	0.05
	Mountains-c	JuneDP, Mast	-145.67	-3.81	0.87	-	25.27	1.58	0.61	0.11	0.53	15	0.37
	Western	AprHD	282	-0.70	-	-	0.26	-	-	0.29	0.36	15	0.06
PA	TMA 1	AprHD	19.01	-0.04	-	-	0.02	-	-	0.63	0.40	11	0.76
	TMA 2-a	MayDP	-1.12	-1.03	-	-	0.76	-	-	0.26	0.17	11	0.03
	TMA 2-b	JuneDP	-1.15	-0.87	-	-	0.66	-	-	0.24	0.16	11	0.18
	TMA 4	MayDP	-0.78	-0.48	-	-	0.27	-	-	0.37	0.25	11	0.95
	TMA 5	JuneDP	-0.16	-0.77	-	-	0.25	-	-	0.80	0.52	11	0.60
	TMA 7	MarDP, AprDP	0.79	-0.44	0.16	-	0.07	0.06	-	0.73	0.86	11	0.40
	TMA 8	MarDP	0.36	-0.29	-	-	0.22	-	-	0.27	0.16	11	0.29
	TMA 9	MarHD	6.59	-0.01	-	-	0.01	-	-	0.29	0.16	11	0.93

Table 3.4. Top regional models for deviations in juvenile:hen ratios collected from fall harvest data. States are divided by region, for which the best models are listed in order of preference (a, b, etc.). Regional models selected from a smaller dataset to include a hard mast parameter are designated (m, ma, mb, etc.) and are listed only if results differed from non-mast datasets. Intercepts (β_0) and coefficients (β_1, β_2) and standard errors (se) are listed. Akaike weights (ω_i) and coefficients of determination (r^2) estimate the relative likelihood and amount of variability explained by models respectively, n represents the number of years of data for each region. *P* represents the p-value for a Shapiro-Wilks test for normality of model residuals.

State	Region	Model	β_0	β_1	β_2	β_3	$\beta_1$se	$\beta_2$se	$\beta_3$se	ω_i	r^2	n	P
NY	DEC Region 3	MayDP	-0.022	-0.067	-	-	0.023	-	-	0.44	0.35	19	0.16
	DEC Region 4-a	MarDP, MayDP	-0.071	0.131	-0.057	-	0.047	0.057	-	0.28	0.40	18	0.25
	DEC Region 4-b	MarDP	-0.103	0.127			0.05			0.26	0.28	18	0.98
	DEC Region 4-c	MarDP, AprDP, MayDP	-0.107	0.124	0.056	-0.075	0.044	0.033	0.031	0.20	0.5	18	0.91
	DEC Region 5-a	MayDP	0.051	-0.097	-	-	0.048	-	-	0.32	0.19	19	0.09
	DEC Region 5-b	AprDP	-0.007	-0.097	-	-	0.055	-	-	0.21	0.15	19	0.21
	DEC Region 6-a	JuneDP	0.020	-0.156	-	-	0.082	-	-	0.36	0.22	19	0.68
	DEC Region 6-b	AprHD, AprDP, JuneDP	5.048	-0.007	0.022	-0.230	0.004	0.066	0.090	0.19	0.42	19	0.16
	DEC Region 6-c	AprHD, MayDP, JuneDP	5.189	-0.008	0.023	-0.236	0.004	0.080	0.088	0.18	0.42	19	0.15
	DEC Region 7	AprHD	3.863	-0.007	-	-	0.002			0.48	0.38	16	0.86
	DEC Region 9	AprHD	3.860	-0.007	-	-	0.002	-	-	0.55	0.41	19	0.88
VA	N. Mountains-a	AprHD	2.940	0.008	-	-	0.004	-	-	0.25	0.13	25	0.84
	N. Mountains-b	AprHD, MayDP, JuneDP	4.065	0.010	-0.242	0.253	0.004	0.176	0.123	0.17	0.29	25	0.49
	S. Mountains-m	Mast	-2.911	1.423	-	-	0.915	-	-	0.25	0.23	10	0.87
	S. Piedmont-a	JuneDP	-0.095	0.159	-	-	0.076	-	-	0.26	0.16	25	0.04
	S. Piedmont-b	MarHD, MayDP, JuneDP	0.496	-0.001	-0.232	0.205	0.002	0.104	0.079	0.21	0.33	25	0.57
	S. Piedmont-c	AprHD, MayDP, JuneDP	0.326	-0.001	-0.237	0.223	0.003	0.104	0.078	0.21	0.33	25	0.22
	S. Piedmont-ma	Mast	-1.941	1.050	-	-	0.817	-	-	0.20	0.17	10	0.28
	S. Piedmont-mb	JuneDP	-0.219	0.099	-	-	0.079	-	-	0.19	0.16	10	0.08
	S. Piedmont-mc	MarHD	1.500	-0.003	-	-	0.002	-	-	0.19	0.16	10	0.57
	Tidewater	AprHD	2.854	-0.011	-	-	0.003	-	-	0.58	0.34	24	0.58
WV	Southern	AprHD	11.315	0.030	-	-	0.010	-	-	0.58	0.44	14	0.29
	Central	MarDP	-0.616	-0.413	-	-	0.187	-	-	0.38	0.29	14	0.48

CHAPTER 4: OPTIMAL HARVESTING FOR THE EASTERN WILD TURKEY USING A SEX-SPECIFIC STOCHASTIC DENSITY-DEPENDENT POPULATION MODEL

ABSTRACT

Current eastern wild turkey (*Meleagris gallopavo silvestris*) harvest models assume density-independent population dynamics with proportional spring and fall harvests. I develop a simulation model incorporating both density-dependent and density-independent effects on wild turkey populations, to compare multiple harvest strategies. I examined the influence of 4 strategies on mean spring and fall harvests and their variability: proportional harvesting, and 3 alternatives: restricted proportional harvesting, proportional threshold harvesting, and restricted proportional with a spring threshold. The model indicated that spring and fall proportional harvest numbers could be maximized at a fall harvest rate between 0 – 13% of the population. Variation in growth rates and harvest rate decreased the expected spring and fall harvest and increased uncertainty in harvest numbers. The alternative strategies increased expected spring harvests while lowering variability in spring harvests. Conversely, the alternative strategies decreased and fall harvest variability. Conversely, they decreased fall harvests while increasing fall harvest variability. One alternative: the restricted proportional harvest with spring threshold, allowing a fall permit harvest only if the spring harvest met a pre-determined harvest, provided greater control of the harvest and made use of spring harvest data, commonly available to wild turkey managers. This conservative strategy better accounts for the variation inherent to wild turkey population dynamics and is recommended for wider use.

INTRODUCTION

Harvest models allow managers to explore the effects of harvest strategies and regulations on populations. The effect of these strategies are always complex by nature, and can be subject to both density-dependent and density-independent factors. Current eastern wild turkey harvest models assume only density-independent dynamics (Vangilder and Kurzejeski 1995, Alpizar-Jara et al. 2001). However, evidence from time-series analysis in this study (Ch 2) and another (Porter et al. 1990b), radio-telemetry studies (Vander Haegan et al. 1988, Hurst et al. 1996), and expert opinion (Healy and Powell 2001) has suggested that density dependence does occur in wild turkey populations, where density dependence is defined as the functional relationship between reproduction or survival and population density (Turchin 2003: 398). Wild turkey are known to have high growth rates and are sensitive to environmental fluctuations (Ch 3, Roberts and Porter 1998 a,b), and should experience non-linear density dependence with the strongest effect occurring at low population densities (Ch 2, Horn 1968, Fowler 1981, Porter et al. 1990b).

Including density dependence in a wild turkey harvest model will change the current view of harvestable yield for wild turkey as a density-independent, increasing but highly fluctuating resource (Healy and Powell 2001). Similar harvest modeling stategies have already been developed for mallards (*Anas platyrhyncos*) and northern bobwhite (*Colinus virginianus*) that specifically include density-dependent reproduction (Guthery 2002, Johnson et al. 2002, Williams and Johnson 1995). Assuming density dependence requires that wild turkey population growth declines to zero at carrying capacity (K) or at a population size of zero (Fig. 2.4). Between these extremes, harvestable yield increases to a maximum level with increasing density, and declines as density dependent factors predominate. This apex of harvestable yield is the largest expected surplus of individuals above 1:1 replacement produced by some population density between 0 and K, and is considered the maximum sustainable yield (N_{msy}: Strickland et al. 1996). At higher densities, reductions in population size will result in higher yields, causing populations to be robust to overharvests when densities are between K and the density resulting in N_{msy}. Conversely, at densities between zero and N_{msy}, reductions in population size will result in decreased yields, causing populations to be very sensitive to overharvest (McCullough 1984).

Incorporating both density-dependent and independent effects increases a harvest model's biological realism, allowing us to better manage the species and determine the effects of alternative harvest strategies. It potentially increases the predictability of annual yields, specifies a mechanism by which populations might be stabilized or recovered from over-harvests, and provides unique information on the population ecology of eastern wild turkey populations (McCullough 1979: 237 – 238, McCullough 1990). While inferences from current density-independent models suggest that ≤10% of the total fall population can be harvested without incurring population declines, the inclusion of a density-dependent response may increase the proportion that can be sustainably harvested (Vangilder and Kurzejeski 1995, Alpizar-Jara et al. 2001).

Density-dependent and density-independent factors do not act in exclusion of each other, regardless of where they fit across the r –selected and K-selected life history spectrum. Several species have been shown to be demonstrably affected by both density-dependent and density-independent processes, including white-tailed deer (*Odocoileus* *virginianus*: Patterson and Power 2002), greater kudu (*Tragelaphus strepsiceros*: Owen-Smith 1990), magpie geese (*Anseranas semipalmata*: Bayliss 1989), and dungeness crab (*Cancer magister*: Higgins et al. 1997).

Random or stochastic density-independent effects will increase the uncertainty in annual abundance and yields (Hilborn and Walters 1992). This will, in turn, increase the potential for overharvest and population decline. Error in harvest rates will also increase the uncertainty of the harvest, as well as the probability of overharvest. A wild turkey harvest model must include variation from environmental stochasticity and hunter behavior to allow biologists to realistically judge between alternative management strategies and decide on the necessary balance between the spring and fall harvests that wild turkey populations may be subjected to.

By including the potential variation in harvest strategies that may be employed for wild turkeys, harvest models can be used by managers to compare the effects of alternative harvest strategies to meet specified criteria for hunted populations, such as the expected size and variability of the harvest (Porter et al. 1990a). A harvest model with both density-dependent and independent effects that allows managers to assess multiple harvest strategies will provide unique insights into wild turkey ecology and management actions.

Eastern wild turkey (*Meleagris gallopavo silvestris*) populations are traditionally harvested in the spring, when only males, or gobblers, may be legally hunted in a spring gobblers-only harvest. In some states, a fall hunting season is also held, where both males and females may be legally hunted in an either-sex harvest. This fall season is considered to have the greatest potential to impact population growth through a possible overharvest of hens (Alpizar-Jara et al. 2001, Vangilder and Kurzejeski 1995, Suchy et al. 1983).

Within this context, Healy and Powell (2000) listed 3 general harvest management strategies for wild turkey, differing by the degree to which a fall either-sex harvest is implemented.

> i) The spring gobblers-only harvest is considered the most conservative strategy because wild turkeys are polygynous, males do not help raise poults, and seasons are often timed so that the majority of hens are incubating nests and less subject to harvest risk (Healy and Powell 2000);
>
> ii) A spring gobblers-only with a limited fall either-sex season focuses on the spring season, but increases hunting opportunity by providing a restricted fall harvest that still allows population growth (Healy and Powell 2000); and
>
> iii) Maximizing both the spring gobblers-only and fall either-sex harvests represents the most liberal strategy, and aims to produce high harvests while still maintaining stable or growing populations (Healy and Powell 2000).

Managers may implement these strategies using an array of regulatory procedures that vary between states (Healy and Powell 2001, Pack et al. 1995). Many wild turkey models assume proportional harvesting, where a fixed percentage is removed from the population. However, agencies wishing to focus on the spring season, with limited fall hunting may want to more closely regulate the fall season. More restrictive harvest strategies include fall permit hunting, where only a pre-determined number of people are allowed to hunt (NJ, RI); or fall permit hunting dependent on meeting a pre-determined spring harvest threshold, where a pre-defined number of birds must be harvested during the spring season, before a fall season can be implemented (WV).

Other studies have examined the effects of harvest strategies beyond proportional harvesting, which may work well for species with growth rates that are sensitive to environmental variability, or where population abundance estimates are uncertain. These include the restricted proportional, where, similar to permit hunting, harvesting is proportional until a pre-determined harvest limit is reached and no further harvest is allowed, and proportional threshold harvesting strategies, where a proportion of all animals above a pre-determined threshold are harvested with no harvest below that threshold (Aanes et al. 2002, Engen et al. 1997).

My objective was to build a sex-specific harvest model to determine how the combination of density dependent and stochastic density independent effects might affect eastern wild turkey harvests under multiple harvest strategies. I first examine proportional harvesting, where a fixed percentage of the population is removed, when density dependence is included, because most wild turkey models assume proportional harvesting (Vangilder and Kurzejeski 1995, Alpizar-Jara 2001). I then compare proportional harvesting with 3 other fall harvest strategies of varying intensity in both the short-term and long-term for a hypothetical population at carrying capacity. Ultimately, the model will be provided as a tool to help managers to maximize a spring gobblers-only harvest, incorporate a limited fall either-sex harvest, or maximize both, using regional or state-specific population data and management strategies.

METHODS

I programmed a sex-specific model using Visual Basic software to model the spring gobbler's-only and fall either-sex harvest for a simulated wild turkey population. The state variable was annual population abundance, which was calculated from an annual growth rate incorporating both density-dependent and density-independent processes, and losses from spring gobbler's only and fall either-sex harvests. Males and females were linked by birth rate, the strength of density dependence, and the same annual stochastic effect of the environment. The model proceeded by annual time-steps, beginning in the spring, prior to nesting. Upon construction, I used the model to examine the effects of alternative fall either-sex harvest strategies.

In the model, gobblers were subjected to a proportional spring harvest while hens were subjected to proportional illegal kill, prior to or during nesting. The simulated population then grew according to the intrinsic population growth rate, modified by changes in sex ratio caused by differential survival and harvest rates between gobblers and hens. The intrinsic growth rate then incorporated a non-linear density dependence component using the theta-Ricker model (Thomas et al. 1980, Saether et al. 2002), along with a density-independent process error term (random environmental effects inherent to the system). Populations were subjected to a fall either-sex harvest under 4 alternative strategies: proportional harvesting, restricted proportional harvesting, proportional threshold harvesting, and restricted proportional with a spring threshold. Specific details of the model's structure are provided in the following paragraphs while parameters and variables are defined in table 4.1.

Estimating sex-specific birth rates

Because males and females are subjected to different levels of harvest, sex ratios are likely to differ from 1:1. Highly skewed sex ratios reduce growth rates by lowering the birth rate, even in polygynous species such as the wild turkey (Lindström and Kokko 1998). For this reason, it was necessary to incorporate the effects of a skewed sex ratio on the population growth rate.

To incorporate sex ratio differences, I calculated the number of births for each time step using a harmonic mean birth function (Caswell and Weeks 1986, Caswell 2001:574). This function takes the following form:

$$B_t = \frac{2kN_{G,t}N_{H,t}}{N_{G,t} + N_{H,t}h^{-1}} \tag{1}$$

where:

B_t = the number of births in year *t*,

k = ½ the male and female offspring per fertilized hen,

$N_{G,t}$ = The number of gobblers in year *t*,

$N_{H,t}$ = The number of hens in year *t*, and

h = a parameter accounting for both harem size and mate searching efficiency.

For a monogamous species, h ≥ 1, and for a polygynous species, h >> 1 (Lindström and Kokko 1998). As h increases, females become more important relative to males in determining population growth rates. I set h = 10, where the female-biased sex ratios have little effect on the birth rate until there are only ~3 males per 10 females and production is maximized at 3.16 hens/gobbler (Caswell and Weeks 1986: Fig. 4.1). I assumed female offspring per fertilized hen to be k = 2.105, This gives a poult:hen ratio of 2k or 4.21 poults/hen on average. This coincided well with a weighted average poult:hen ratio across 5 state agencies (MD, MS, NJ, NY, RI), and combined with the survival rates discussed later, produced an intrinsic growth rate very close to the highest I saw in the literature for a reintroduced population (and therefore not yet subject to densuity-dependent effects) of wild turkey (r = 0.5158: Little and Varland 1981). Sex ratio at birth is assumed 50:50.

Estimating modified intrinsic growth rates

Although the number of births of each sex is equal, natural survival rates differ, meaning that population sizes of the 2 sexes grow at different rates. I determined a birth rate for each sex from the ratio of sex-specific births and by the number of males or females in the population at a given annual time step. The gobbler-specific intrinsic growth rate, modified by the effect of sex ratio on the number of births, can be calculated from the function:

$$r_{G,t} = \ln\left[\frac{B_t}{2\left(N_{G,t} + N_{H,t}\right)} + m_G\right] \tag{2}$$

where:

$r_{G,t}$ = the gobbler-specific modified intrinsic growth rate in year *t*,

m_G = the gobbler survival rate.

Similarly, the hen-specific intrinsic growth rate, modified by the effect of sex ratio on the number of births, can be calculated from the function:

$$r_{H,t} = \ln\left[\frac{B_t}{2(N_{G,t} + N_{H,t})} + m_H\right] \tag{3}$$

where:

$r_{H,t}$ = the hen-specific modified intrinsic growth rate in year *t*, and

m_H = the hen survival rate.

Natural survival rates (independent of hunting or illegal mortality) were taken from a 4.5 year study on wild turkey populations in VA and WV, where $m_G = 0.74$ and $m_H = 0.64$ (Pack et al. 1999, Alpizar-Jara et al. 2001). Assuming an equal sex ratio, this results in a maximum intrinsic growth rate, averaged between males and females, of 0.50 ($\lambda = 1.65$). Based on a literature search, this growth rate approximates the maximum seen from a newly reintroduced population of wild turkey, presumably not yet subject to density-dependent effects (Little and Varland 1981).

Modeling density-dependent and independent effects

The modified intrinsic growth rates were then adjusted for density-dependent and density-independent effects using the theta-Ricker model (Ch. 2, Thomas et al. 1980). Population growth for gobblers in the absence of harvest was calculated using the following equation:

$$N_{G,t+1} = N_{G,t} e^{r_{G,t}\left(1 - \frac{N_{G,t}}{K_G}^{\theta}\right) + \varepsilon_{p,t}} \tag{4}$$

where:

K_G = the gobbler carrying capacity,

$\varepsilon_{p,t}$ is the density-independent process error in year *t*, and

θ = the nonlinearity in the density dependence effect.

Population growth for hens in the absence of harvest was calculated using the following equation:

$$N_{H,t+1} = N_{H,t} e^{r_{H}\left(1 - \frac{N_{H,t}}{K_H}^{\theta}\right) + \varepsilon_{p,t}} \tag{5}$$

where:

K_H = the hen carrying capacity.

For $\theta = 1$, density dependence follows the classic logistic model, and population growth declines linearly with increasing population density. For $\theta > 1$, density does not affect growth rates until population density is near K. For $\theta < 1$, density affects growth rates at low densities relative to K. I assumed $\theta = 0.36$, based on an average for the set of bias-corrected values calculated in chapter 2. This value falls within the range expected for species with high growth rates and sensitive to density-independent environmental variation (Fowler 1981). I set the starting population size for both sexes ($N_{G,0}$, $N_{H,0}$) in all simulations at equilibrium with carrying capacity, such that $N_{G,0} = N_{H,0}$

$= K_G = K_H = 10{,}000$. Population abundance for gobblers and hens was bounded at a minimum of 10.

Density-independent stochastic factors reflected annual changes in environmental effects (process error). The chapter 2 analysis used spring harvest and spring harvest/effort data from multiple states as abundance indices. I modeled growth rates from these indices using the theta-Ricker model to determine the strength of density dependence in wild turkeys (θ), using the most widely available information. The standardized residuals from model fitting were assumed to result from a combination of process error (environmental stochasticity) and measurement error (error inherent in the sampling process). The median residual standard deviation (sd) in the population growth rates was 0.22 for the spring harvest data and 0.16 for the spring harvest/effort data.

Mosby (1967) inferred from 2 studies and an analysis of Virginia harvest records that populations fluctuated within 50% of their long-term mean, although high abundance years had greater magnitude than low abundance years. For these reasons, I set the maximum error distribution of the growth rate as $\varepsilon_p \sim N\ (0, 0.25)$, corresponding to the median standard deviation from my harvest index analysis and to Mosby's findings (95% of abundances would fall between 65% above and 60% below the long-term mean).

Since the growth rate varied normally, abundance varied log normally, so that high abundance years had greater magnitude than low abundance years, and abundance could not fall below zero. Because process error is likely to impact both sexes similarly in any given year, it was not modeled to be sex-specific.

Spring Harvest

I incorporated a proportional gobblers-only spring harvest into the model by removing harvested gobblers after fertilization had taken place. The production of gobblers in year *t*+1 was independent of the spring harvest of gobblers in year *t*. The spring gobbler harvest was calculated as:

$$H_{s,t} = N_{G,t} s_t \tag{6}$$

where:

$H_{s,t}$ = the spring gobbler harvest in year *t*, and

s_t = the spring harvest rate in year *t*.

In the absence of a fall harvest, the resulting growth of the gobbler population would be calculated as:

$$N_{G,t+1} = N_{G,t} e^{r_G \left(1 - \frac{N_{G,t}}{K_G}^{\theta}\right) + \varepsilon_{p,t}} - H_{s,t} \tag{7}$$

This assumes that the spring harvest is timed appropriately such that hens are participating in nesting and the loss of males will not affect production for that year. Spring harvest rates were allowed to vary according to a lognormal distribution and were bounded at 1. I set spring harvest rates to 0.15. This level of spring harvest approximates that used by previous wild turkey models (Vangilder and Kurzejeski 1995, Alpizar-Jara 2001).

Illegal spring hen kill

Unlike the spring gobbler harvest's affect on gobbler production, the illegal spring hen kill in year *t* was assumed to directly impact the production of hens in year *t*+1 by occurring prior to or during nesting. The illegal spring hen kill is calculated as:

$$I_t = N_{H,t} i_t \tag{8}$$

where:

I_t = the number of hens illegally killed in the spring in year *t*, and

i_t = the spring kill rate in year *t*.

It follows that $(1 - i_t)$ is equal to the spring kill survival rate in year *t*. In the absence of a fall harvest, the resulting growth of the hen population can be calculated using the following equation:

$$N_{H,t+1} = (1 - i_t) N_{H,t} e^{r_H\left(1 - \frac{N_{H,t}}{K_H}^{\theta}\right) + \varepsilon_{p,t}} \tag{9}$$

Illegal kill rates were allowed to vary according to a lognormal distribution and were bounded at 1. I set illegal kill rates to 0.05. While illegal kill is known to vary widely, this rate matches the expected level as reported by Vangilder andKurzejeski (1995) and Pack et al. (1999).

Alternative Fall Harvest Strategies

I considered 4 alternative fall either-sex harvest strategies, proportional harvesting, restricted proportional harvesting, proportional threshold harvesting, and restricted proportional harvesting with a spring threshold.

Proportional Harvesting

In proportional harvesting, a fixed percentage of wild turkeys are removed during the fall hunting season. Under a proportional harvesting strategy, fall harvest is calculated using the following equations:

$$H_{fH,t} = \left[(1-i_t) N_{H,t} e^{r_{H,t}\left(1-\frac{N_{H,t}}{K_H}^{\theta}\right)+\varepsilon_{p,t}} \right] f_t \tag{10}$$

$$H_{fG,t} = \left[N_{G,t} e^{r_{G,t}\left(1-\frac{N_{G,t}}{K_G}^{\theta}\right)+\varepsilon_{p,t}} - H_{s,t} \right] f_t \tag{11}$$

where:

$H_{fH,t}$ = the number of hens harvested in the fall of year *t*,

$H_{fG,t}$ = the number of gobblers harvested in the fall of year *t*, and

f_t = fall harvest rate in year *t*.

The resulting population growth equations under proportional harvest are the following:

$$N_{H,t+1} = \left[(1-i_t) N_{H,t} e^{r_H \left(1 - \frac{N_{H,t}{}^{\theta}}{K_H}\right) + \varepsilon_{p.t}} \right] (1 - f_t) \tag{12}$$

$$N_{G,t+1} = \left[N_{G,t} e^{r_G \left(1 - \frac{N_{G,t}{}^{\theta}}{K_G}\right) + \varepsilon_{p,t}} - H_{s,t} \right] (1 - f_t) \tag{13}$$

Restricted Proportional Harvesting

In restricted proportional harvesting, a fixed percentage of wild turkeys are removed during the hunting season up to a pre-determined upper limit, beyond which, no further harvesting is allowed (Aanes et al. 2002). This strategy can be likened to a permit system with a hunter bag limit. Under the restricted proportional harvesting strategy, expected total fall harvest numbers were calculated using equations (10) and (11) above, which estimate the proportional harvest, as follows:

$$E\left(H_{fG,fH,t}\right) = \left[(1-i_t) N_{H,t} e^{r_{H,t} \left(1 - \frac{N_{H,t}{}^{\theta}}{K_H}\right) + \varepsilon_{p,t}} \right] f_t + \left[N_{G,t} e^{r_{G,t} \left(1 - \frac{N_{G,t}{}^{\theta}}{K_G}\right) + \varepsilon_{p,t}} - H_{s,t} \right] f_t \tag{14}$$

where:

$E\left(H_{fG,fH,t}\right) =$ the expected total fall harvest in year t under a proportional harvest strategy.

If the expected harvest was less than the permitted level, as set by the manager, at any time step ($E\left(H_{fG,t}\right) < P_G$ or $E\left(H_{fH,t}\right) < P_H$), the proportional harvest equations (equations (9), (10), (11), and (12)) were used to calculate both the current harvests and resulting population growth. If the expected harvest was greater than or equal to the permitted level at any time step ($E(H_{fG,t}) \geq P_G$ or $E(H_{fH,t}) \geq P_H$), harvests were equal to the permitted size:

$$H_{fH,t} = P_H \tag{15}$$

$$H_{fG,t} = P_G \tag{16}$$

The resulting population growth is calculated as:

$$N_{H,t+1} = \left[(1-i_t) N_{H,t} e^{r_{H,t}\left(1-\frac{N_{H,t}}{K_H}^{\theta}\right)+\varepsilon_{p.t}} \right] - P_H \tag{17}$$

$$N_{G,t+1} = \left[N_{G,t} e^{r_{G,t}\left(1-\frac{N_{G,t}}{K_G}^{\theta}\right)+\varepsilon_{p,t}} - H_{s,t} \right] - P_G \tag{18}$$

Proportional Threshold Harvesting

In proportional threshold harvesting, a fixed percentage of the wild turkey population above a pre-determined threshold are removed during the hunting season, with no harvest occurring when populations are below the threshold (Engen et al. 1997, Lande et al. 1997). In this strategy, only a proportion of the expected yield of surplus individuals is harvested. Under the proportional threshold harvesting strategy, expected total fall harvest numbers were calculated using equation (14).

If the expected gobbler or hen population size was greater than the threshold fall population size (T) as set by the manager, at any time step ($N_{G,t} > T_G$ or $N_{H,t} > T_H$), fall harvest was calculated using the following equations:

$$H_{fH,t} = \left\{ \left[(1-i_t)N_{H,t}e^{r_{H,t}\left(1-\frac{N_{H,t}}{K_H}^{\theta}\right)+\varepsilon_{p,t}} \right] - T_H \right\} f_t \tag{19}$$

$$H_{fG,t} = \left\{ \left[N_{G,t}e^{r_{G,t}\left(1-\frac{N_{G,t}}{K_G}^{\theta}\right)+\varepsilon_{p,t}} - H_{s,t} \right] - T_G \right\} f_t \tag{20}$$

The resulting population growth is calculated as:

$$N_{H,t+1} = \left[(1-i_t)N_{H,t}e^{r_{H,t}\left(1-\frac{N_{H,t}}{K_H}^{\theta}\right)+\varepsilon_{p,t}} \right] - \left\{ \left[(1-i_t)N_{H,t}e^{r_{H,t}\left(1-\frac{N_{H,t}}{K_H}^{\theta}\right)+\varepsilon_{p,t}} \right] - T_H \right\} f_t \tag{21}$$

$$N_{G,t=1} = \left[N_{G,t}e^{r_{G,t}\left(1-\frac{N_{G,t}}{K_G}^{\theta}\right)+\varepsilon_{p,t}} - H_{s,t} \right] - \left\{ \left[N_{G,t}e^{r_{G,t}\left(1-\frac{N_{G,t}}{K_G}^{\theta}\right)+\varepsilon_{p,t}} - H_{s,t} \right] - T_G \right\} f_t \tag{22}$$

If the expected gobbler or hen population size was less than or equal to the threshold fall population size at any time step ($N_{G,t} \le T_G$ or $N_{H,t} \le T_H$), the fall harvest for that sex = 0 for year *t*.

Restricted Proportional Harvesting with Spring Threshold

In restricted proportional harvesting with a spring threshold, if, and only if, that year's spring harvest met a pre-determined threshold, a fixed percentage of wild turkeys are removed during the fall hunting season up to a pre-determined upper limit, beyond which, no further harvesting is allowed. For example, in West Virginia, a minimum spring harvest density of 1 bird/ sq. mi. of wild turkey habitat must be maintained for a county to keep a fall hunting season (Healy and Powell 2000, Pack et al. 1995). Under the restricted proportional with spring threshold harvesting strategy, expected total fall harvest numbers were calculated using equation (14).

If the expected harvest was less than the permitted level and the spring harvest threshold was met, as set by the manager, at any given time step ($E(H_{fG,t}) < P_G$ or $E(H_{fH,t}) < P_H$ and $H_{s,t} \geq D_G$), the proportional harvest equations (equations (9), (10), (11), and (12)) were used to calculate both the current harvests and resulting population growth. If the expected harvest was greater than or equal to the permitted level and the spring harvest threshold was met, at any time step ($E(H_{fG,t}) \geq P_G$ or $E(H_{fH,t}) \geq P_H$ and $H_{s,t} \geq D_G$), the permit harvest equations (equations (15), (16), (17), and (18)) were used to calculate both the current harvests and resulting population growth. If the spring threshold harvest was not met ($H_{s,t} < D_G$), the fall harvest for both sexes = 0 for year *t*.

Since the fall harvest for a given time at a given run could be equal to 0 under the proportional threshold and restricted proportional harvesting with spring threshold strategies, error in the spring and fall harvest were assumed to follow a delta log-normal distribution (Pennington 1996, 1983). This distribution assumes a log-normal error rate in the mean harvest, while accounting for the probability of no harvest. When a harvest of 0 does not occur in the data, the delta log-normal conforms to a log-normal distribution. Fall harvest rates were allowed to vary according to a lognormal distribution and were bounded at 1.

Model Analysis

Spring and Fall Harvest Relationship

I recorded the expected spring, fall and annual (spring + fall) harvests across a range of fall harvest rates (0.00 – 0.50) for simulation runs of 400 years, assuming no stochasticity. Simulations were run for 400 years to ensure population runs had stabilized at new equilibriums. I produced an expected yield curve for both sexes, and determined the expected equilibrium population and yield for a given harvest rate.

Stochastic proportional harvesting

I examined the mean harvest and harvest coefficient of variation (cv) for the proportional harvesting strategy when density-independent growth rate and harvest rate error were included. Stochastic simulations had 1000 runs for each fall harvest rate ranging from 0.00 – 0.50 at 0.05 intervals.

I allowed the growth rate to vary log-normally at 3 treatment levels ($\sigma_r = 0.05$, 0.15, 0.25). To include harvest rate variability, I allowed the spring gobbler harvest rate, fall either-sex harvest rate and illegal kill rate to vary log-normally at 2 treatment levels ($\sigma_{sif} = 0.10$, 0.25). I assumed the spring harvest rate, illegal kill rate, and fall harvest rate had the same standard deviation (0.10 or 0.25) for a given treatment. Consequently, population simulations fell within 6 possible error treatments:

i: $\sigma_r = 0.05$, $\sigma_{sif} = 0.10$;

ii: $\sigma_r = 0.15$, $\sigma_{sif} = 0.10$;

iii: $\sigma_r = 0.25$, $\sigma_{sif} = 0.10$;

iv: $\sigma_r = 0.05$, $\sigma_{sif} = 0.25$;

v: $\sigma_r = 0.15$, $\sigma_{sif} = 0.25$; and

vi: $\sigma_r = 0.25$, $\sigma_{sif} = 0.25$

for each of 11 possible proportional fall harvest treatments (0.00 – 0.50 at steps of 0.05).

Mean spring and fall harvests and their cv were examined over the short term, 3 years, or approximately 1 generation for wild turkeys and the long term, 10 years. Alpizar-Jara et al. (2001) reported a generation time of 2.78 years for wild turkey and suggested that 3 years was appropriate for an initial review of a harvest strategy. I chose year 10 as the long-term harvest because at year 10, populations tended to reach or approach equilibrium for a given harvest rate for the deterministic model. I recorded the difference between the expected harvest (deterministic) and the mean harvest (stochastic) at the 11 fall harvest treatments to assess the effects of stochasticity on the system.

Harvest Strategy Simulations

I compared the 4 alternative harvest strategies in terms of the mean annual harvest and harvest cv. The harvest mean and cv were examined in the short (3 year) and long (10 year) term for both the spring and fall harvests. I fixed the growth rate error (σ_r =

0.25) and the harvest rate error ($\sigma_{sif} = 0.10$) for all simulations. Fall harvest rate ranged from 0 – 30% at 5% intervals.

For the restricted proportional strategy, permit number (P_G, P_H), the upper limit of harvestable wild turkeys, ranged from 0.02 – 0.10K at intervals of 0.02 and 0.10 – 0.50K at intervals of 0.10. Permit number was equal for gobblers and hens ($P_G = P_H$).

For the proportional threshold strategy, threshold (T_G, T_H), above which the population could be proportionally harvested, ranged from 0.02 – 0.10K at intervals of 0.02 and 0.10 – 1.00K at intervals of 0.10. Threshold level was equal for gobblers and hens ($T_G = T_H$).

For the restricted proportional with spring threshold strategy, spring threshold (D_G), the minimum spring harvest required to allow a fall harvest that year, ranged from 0.02 – 0.10K at intervals at 0.02 intervals. A spring threshold harvest beyond this level resulted in harvesting during the first 2 years only in the deterministic model. Permit number (P_G, P_H) ranged from 0.02 – 0.10K at intervals of 0.02. Permit number was equal for gobblers and hens ($P_G = P_H$).

RESULTS

Spring and Fall Harvest Relationships

Over the range of fall harvest rates, the expected spring harvest was maximized at a fall harvest rate of 0, and declined as fall harvest rate increased (Fig. 4.2). Fall and annual harvests were parabolic across fall harvest rates. Fall harvest was maximized at a fall harvest rate of 0.13, while annual harvest was maximized at a fall harvest rate of 0.09.

Based on the hen and gobbler yield curves determined from the density-dependent model, maximum yield for gobblers and hens was 6.4% and 5.6% of K respectively (Fig. 4.3). At each combination of spring harvest, illegal kill, and fall harvest rate, populations declined to an equilibrium < K. Gobblers shifted to a lower equilibrium abundance than hens because they experienced a higher spring mortality than hens.

Gobbler populations shifted to the equilibrium producing a maximum yield at a fall harvest rate of 0.05. Hens shifted to the equilibrium producing a maximum yield at a fall harvest rate of 0.10. Fall harvest rates > 0.05 for gobblers and > 0.10 for hens shifted equilibrium abundance to the left side of the yield curve, producing lower yields than smaller harvest rates.

Environmental and harvest variation

As environmental variation in the growth rate (σ_r) and uncertainty in the harvest rate (σ_{sif}) increased, mean spring harvest decreased, particularly when fall harvest rates were low (Fig. 4.4a). As fall harvest rate increased, variation in growth and harvest rates had less effect on lowering the mean spring harvest as expected spring harvests declined. Similarly, as σ_r and σ_{sif} increased, mean fall harvest decreased, particularly when fall harvest rates were high (Fig. 4.4b). As fall harvest rate increased, increases in σ_r and σ_{sif} lowered the mean fall harvest to a greater degree. The differences between mean fall harvest and expected fall harvest was greatest at intermediate fall harvest rates.

Stochastic equilibrium populations shifted by 1 – 2%K lower than the deterministic equilibrium population, with maximum deviations ≤ 1% K. Increases in σ_r

and σ_{sif} lowered mean short-term and long-term harvests only slightly (Fig. 4.5). Spring and fall harvest cv increased with σ_r and σ_{sif} at 3 years and 10 years (Fig. 4.6).

Harvest Strategy Simulations

Restricted Proportional Harvesting

This strategy resulted in higher mean spring harvests than simple proportional harvesting, especially when fall permits were < 30% K for the 3 year and 10 year harvest. As permit levels decreased, and harvest became more restrictive, the mean spring harvest converged towards the expected harvest under a 0.00 fall harvest rate (no fall harvesting), regardless of the simulated fall harvest rate (Fig. 4.7). This occurred in both the short term (year 3) and the long term (year 10). Restricted proportional spring harvests did not differ from proportional harvesting until permits were ≤ 20%K. Similarly, as permit levels decreased, the mean fall harvest converged and lowered when permits were ≤ 20%K. Over the long term, fall harvests were highest at a fall harvest rate ≥ 0.20 and a fall permit level of 10%K.

The 3 year spring harvest cv ranged consistently between 40 – 60 (Fig. 4.8). The 10 year spring harvest cv increased as fall permits decreased, with the highest cv occurring when permit number equaled 6% K. Conversely, the 3 and 10 year fall harvest cv decreased when permits decreased from ≤ 10% K.

Proportional Threshold Harvesting

This strategy resulted in higher mean spring harvests than simple proportional harvesting when the threshold ≥ 10% K for the 3 year and 10 year harvest (Fig. 4.9). As the threshold above which populations could be proportionally harvested increased, and harvest became more restrictive, the mean spring harvest converged towards the expected harvest under a 0.00 fall harvest rate (no fall harvesting), regardless of the simulated fall harvest rate (Fig. 4.9). This occurred in both the short term (year 3) and the long term (year 10). Proportional threshold spring harvests did not differ from proportional harvesting until the population threshold was ≥ 10% K at 3 years and at 10 years. Similarly, as the population threshold increased, the mean fall harvest converged and lowered, especially when the threshold was ≥ 10%K at 3 years and at 10 years.

The 3 year spring harvest cv ranged consistently between 32 – 46 (Fig. 4.10). The 10 year spring harvest cv ranged between 38 – 63. Fall harvest cv increased by 16 – 33 times for increasing population thresholds ≥ 10% K at year 3 and by 9 – 17 times for population thresholds ≥ 10% K at year 10.

Restricted Proportional with Spring Threshold Harvesting

This strategy resulted in higher mean spring harvests than simple proportional harvesting at all spring harvest thresholds for the 3 year and 10 year harvest. As the spring harvest threshold, above which a fall harvest could occur, increased mean spring harvest changed little (Fig. 4.11). This occurred in both the short term (year 3) and the long term (year 10).

As fall permits increased, mean fall harvest increased, while mean spring harvest decreased across spring threshold levels. Similarly, as fall harvest rate increased, mean fall harvest increased, while mean spring harvests decreased, as shown for proportional harvesting. Increasing the spring harvest threshold caused mean fall harvests to decrease.

Spring harvest cv was not affected by changes in the spring harvest threshold, however, fall harvest cv increased as both spring threshold and fall permits increased (Fig. 4.12). Spring harvest cv ranged between 41 – 56 at year 3 and between 46 – 88 at year 10. Fall harvest cv ranged between 0 – 125 at year 3 and between 14 – 240 at year 10, depending on the spring threshold and number of fall permits.

DISCUSSION

Spring and fall harvest relationships

The results of this study set a framework for managing spring and fall harvests for wild turkey populations when both density dependence and independence are taken into account. In the absence of stochastic effects, under a proportional harvesting strategy with a 15% spring harvest, spring harvests will be maximized only when there is no fall harvest. Fall harvests will be maximized at a 0.13 fall harvest rate, assuming no spring harvest. Annual harvests will be maximized at a 0.09 fall harvest rate.

Examination of the sex-specific yield curves for wild turkeys in Figure 3 indicates that fall harvest rates > 10% in combination with a spring harvest and illegal kill will reduce populations to densities below N_{msy} (density at which a sustainable yield is maximized). Populations held below this threshold are sensitive to population reductions from overharvest because the reduced population will have a lower yield (McCullough 1984). This result is similar to the findings of previous models assuming density-independent dynamics only (Alpizar-Jara et al. 2001, Vangilder and Kurzejeski 1995). This strengthens the argument for weak density dependence in wild turkey population growth, where density-dependent factors exert their greatest influence at low population densities.

Alpizar-Jara et al. (2001) suggested that hen populations could withstand a 10 – 15% fall harvest. Similarly, Vangilder and Kurzejeski (1995) recommended a 5 – 10% fall harvest. Both included a 15% spring gobbler harvest, and illegal spring kill. Suchy et al. (1983) tested a deterministic model under both additive and compensatory mortality assumptions and recommended fall harvests of < 10% to maintain population growth. Lobdell et al. (1972), assuming complete compensation, suggested that populations could withstand fall harvests of 20 – 35% of the population. It seems that wild turkey populations can be considered to withstand high harvest rates only under an assumption of strong compensatory mortality or strong density dependence.

Compensatory thresholds are likely to be low for species with low mortality in the absence of hunting (Anderson and Burnham 1976). This might often be the case with wild turkeys (Suchy et al. 1983, Pack et al. 1999), and previous studies have indicated that harvest on wild turkeys is additive (Vangilder and Kurzejeski 1995, Pack et al. 1999).

In chapter 2, I demonstrated that density dependence is probably weak for most wild turkey densities, with a $\theta \leq 0.49$, and so environmental effects will act to overwhelm density-dependent effects, including compensatory mortality. Instead of testing the range of θ provided in ch. 2, I chose $\theta = 0.36$ because the population dynamics within that range were very similar, and using a single number would simplify interpretation. Assuming my estimate of $\theta = 0.36$ was reasonably correct, density-dependent effects are not substantial enough to allow for increases in fall harvest rate. As would be expected in a density-dependent model, spring harvests were reduced as fall harvest rate increased, because high fall harvests lowered the population equilibrium abundance. Steffen and Norman (1996) reported similar results after analyzing spring and fall harvest data in VA. This supports the inclusion of density dependence in a wild turkey harvest model.

Environmental and harvest variation

Including a weak form of density dependence allows managers to base harvest decisions using a yield curve paradigm. Depending on the level of environmental stochasticity, predictability of harvests will be increased, where at minimum, managers can expect yields to generally decrease from N_{msy} to K, or from N_{msy} to 0. As environmental variation and uncertainty in the harvest increases, however, these patterns will disappear. I found large uncertainties in the harvest in both the short-term and the long-term, due to both the inherent environmental variation to which wild turkey populations are subjected and the hypothesized uncertainty in harvest. Given this variation, the probability of overharvest is high, and populations could be easily overharvested to low population densities, with high uncertainties in yields increasing with harvest effort (Beddington and May 1977). For example, the 3-year spring harvest at the minimum level of variation tested ($\sigma_r = 0.05$, $\sigma_{sif} = 0.10$) and a 10% fall harvest rate, produced a cv of 0.62, meaning that one harvest standard deviation was 62% of the mean. So, for a given year, harvest may be more than double what is expected or sustainable.

Harvest for wild turkeys is strongly affected by environmental stochastic processes, which will act to lower the sustainable harvest (Roughgarden and Smith 1996, Hilborn and Walters 1992). Bayliss (1989) reported that adding environmental variation in the form of regional rainfall to a harvest model for magpie geese decreased the maximum harvest rate producing a yield and the maximum sustained yield by 25%. Similarly, Hunter and Runge (2004) reported that a fixed maximum sustained yield policy for white-tailed deer harvests would result in lower harvests than a state-dependent strategy when stochasiticity was high. Managers could reduce variation by acting to lower illegal hen kill, typically a significant mortality source in wild turkey populations (Vangilder 1992, Vangilder and Kurzejeski 1995). Assuming a 10% fall harvest rate, reducing illegal kill to zero would have shifted the expected hen equilibrium population from 40% K to 58% K and the gobbler equilibrium population from 26% K to 29% K.

The inclusion of weak density dependence had little effect on harvest strategies compared to previous wild turkey models (Alpizar-Jara et al. 2001, Vangilder and Kurzejeski 1995). This implies that density-independent environmental factors will determine annual yields to a greater degree than population density. However, without long-term data, environmental parameters are difficult to estimate, especially for large multi-county regions (Ch. 3, Flanders-Wanner et al. 2004, Bradbury et al. 2003).

Furthermore, the importance of environmental factors may vary within the species range, particularly for peripheral populations in potentially more variable habitats. This has been indicated for northern bobwhite (*Colinus virginianus*) and ring-necked pheasants (*Phasianus colchcus*), as well as eastern cottontails (*Sylvilagus floridanus*) in

Kansas (Williams et al. 2003). Predictive models for wild turkey might work best at smaller habitat scales.

There is still a great deal of uncertainty in our understanding of wild turkey populations dynamics. The model developed here provides an additional framework to better predict population behaviors. Based on the vital rates used and the inclusion of non-linear weak density dependence, it can be surmised that population yields are maximized between 39 – 42% of carrying capacity. Ignoring environmental variation and harvest uncertainty, population densities at this level should experience higher population growth. The model assumes that wild turkey are typically held below carrying capacity by environmental effects on the vital rates, and individuals have been selected for high reproduction in favorable environments (Ch. 2, Horn 1968, Fowler 1981). Population growth can be expected to be highest after reintroductions or after overharvesting, and this trait may act as a mechanism for recovery, especially in stable habitats.

Most population models, including those for wild turkey, assume female dominance. Under female dominance, female abundance determines the population dynamics, assuming there are always enough males to fertilize females (Caswell 2001). Wild turkeys exhibit sex-specific survival rates, however, and this resulted in different growth rates and sex-specific yield curves (Pack et al. 1999). Sex-specific survival differences have been shown for other bird species, for example, great skuas (*Stercorarius skua*) and ovenbirds (*Seiurus aurocapilus*: Kalmbach et al. 2005, Bayne and Hobson 2002). Sex-related differences in vital rates and the variation in those vital rates might require differing harvest strategies for gobbler-only harvests and fall either-sex harvests.

Harvest Strategy Simulations

A proportional fall harvest in the fall might work well for states wishing to maximize the spring and fall hunting seasons. However, some states may wish to concentrate their efforts on providing a larger spring harvest while allowing limited fall hunting (Healy and Powell 2000). Managers can modify harvest variation and size by adjusting the proportional harvesting strategy to include greater restrictions. Such modifications would help biologists better match harvest strategies to the desires of the public.

Restricted Proportional Harvesting

This strategy produced higher spring harvests than simple proportional harvesting, while lowering fall harvests. Fall harvest variability was low as permits decreased, increasing the predictability of the fall harvest. Comparably, Aanes et al. (2002) reported that a restricted proportional harvest occurring 1 harvest/year produced a higher mean annual yield and lower variation in annual yield than proportional harvesting for a willow ptarmigan population in Sweden (*Lagopus lagopus*). However, for a 2 harvest/year system, I found that high fall harvest rates would result in less predictability in the spring harvest when permit levels were ≤ 20% K. Depending on fall harvest rates, incorporating a permit system will result in a trade-off in variability between the fall and subsequent spring harvest.

Proportional Threshold Harvesting

Under this strategy, increasing the threshold above which a population could be proportionally harvested increased the spring harvest towards the levels expected under no fall harvesting. Variability in the spring harvest did not change greatly and even decreased under higher fall harvest rates when the threshold was between 10 – 50% K.

As the required threshold increased, fall harvest decreased dramatically, especially over the short term. Similarly, because harvest would be 0 in years when the threshold was not met, variability in harvest increased quickly as the threshold increased.

Lande et al. (1997) reported that the expected cumulative yield before extinction could be maximized under the proportional threshold strategy, if the threshold was set to K, regardless of the dynamics of the system. This conservative strategy allows only those animals above carrying capacity to be harvested. Alternatively, a more aggressive strategy is to maximize mean annual yield, which depends more heavily on the harvest goal and population dynamics, but the threshold will tend to be closer to N_{msy} for populations with $\theta \leq 10$ (Sæther et al. 1996).

The conservative strategy of harvesting only those surplus individuals beyond K is problematic, as this allows wild turkey to grow to carrying capacity, and may have the unwanted effect of increasing the perception of damage to agricultural crops by wild turkey, along with reduced hunting opportunities due to restrictions (Swanson et al. 2001). Setting the threshold closer to N_{msy} would lower expected spring harvests only slightly, and depending on harvest rate, would produce a high expected fall harvest in the short term, but would have little effect on expected long-term harvests.

Restricted Proportional with Spring Threshold Harvesting

Under this strategy, spring harvests were similar to those expected under no fall harvesting. In addition, spring harvests were only weakly affected by changes in spring harvest threshold levels. Over the long term, spring harvests were highest when there was fewer available fall permits, combined with high spring harvest thresholds. Variability in the spring harvest was comparable to the restricted proportional strategy. At low spring harvest thresholds (~ 0.02K), fall harvest variability was low, especially when fewer fall permits were available. This strategy provides more control than proportional harvesting or restricted proportional harvesting by incorporating spring harvest information, and is less affected by changes in harvest rate than proportional threshold harvesting.

MANAGEMENT IMPLICATIONS

The results of this study provide a modeling framework from which to base harvest management decisions for an either-sex wild turkey harvest. Managers may wish to adapt the model framework shown here to more specific management options and data. Harvest strategies fall under 3 basic strategies: spring gobblers-only harvest, spring gobblers-only harvest with limited fall either-sex season, or maximizing both the fall and spring harvest (Healy and Powell 2000). My results show, that for a constant spring gobbler harvest, the spring and fall harvest may be maximized together by reducing the fall harvest rate from that level which would maximize the fall harvest. For simple proportional harvesting, this harvest rate should be further reduced as interest in the spring season increases, and fall harvest rates must be maintained below 10%, although this may be adjusted upward as illegal kill is reduced and/or the spring harvest rate is lowered.

For managers wishing to maximize their spring and fall either-sex harvest, proportional harvesting may be an appropriate strategy, requiring fewer regulations and safeguards compared to the other strategies. This strategy does not necessarily require knowledge of population size or carrying capacity if a fixed harvesting effort can be maintained that corresponds to the desired harvest rate (Aanes et al. 2002). However, Lande et al. (1995) concluded that when demographic stochasticity is included in harvest model simulations, extinction risks are higher for proportional harvesting than threshold harvests. Demographic stochasticity is unlikely to be an important factor in the population dynamics, considering the large sizes of many wild turkey populations. However, the simulations in this study indicated that stochasticity reduced expected harvests, increasing the risk of overharvest if environmental effects are underestimated. In addition, illegal harvest and the risk of overharvesting (harvest stochasticity) will confound the true harvest rate; so targeted proportional harvests should be low (< 10%).

For managers wishing to maximize or maintain the spring harvest while allowing limited fall harvesting, I recommend a more conservative harvest that accounts for the variation inherent to wild turkey population dynamics, and allows managers to more fully use the harvest information they have. The restricted proportional harvest with spring harvest threshold allows managers to use information from the spring harvest to manage the fall hunting season. This strategy causes little reduction in annual spring harvests and for low permit levels and spring harvest thresholds, there is low variability in the fall harvest. The West Virginia Division of Natural Resources uses a very similar strategy, requiring a spring harvest of 1 gobbler/mi^2 of wild turkey habitat but this threshold must be met for 2 years in succession after failing to meet the threshold (Healy and Powell 2000, Pack et al. 1995). I agree with Healy and Powell's (2000) recommendation of this strategy. While the proportional threshold strategy would require knowledge of K or N_{msy} and the populations relation to those abundance levels, it is not required for the spring threshold strategy. Knowledge of K would be useful, but not vital, and managers may adjust both permit and threshold levels in an adaptive management framework to best determine what works best. This can be done either by an actively adaptive framework where strategies are tested experimentally at the county or regional level, or the trial and error adaptive strategy for a given region, although this will limit that amount the manager can learn from the system (Hilborn and Walters 1992).

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Table 4.1. Sex-specific parameters for the wild turkey model.

Parameter	Explanation
$N_{H,t}$	The number of hens at time t
$N_{G,t}$	The number of gobblers at time t
N_t	The total abundance (hens and gobblers) at time t
$r_{H,t}$	Hen intrinsic growth rate
$r_{G,t}$	Gobbler intrinsic growth rate
B_t	Number of births at time t
m_G	User-defined gobbler natural survival rate
m_H	User-defined hen natural survival rate
K_H	User-defined hen carrying capacity
K_G	User-defined gobbler carrying capacity
θ	User-defined sex-independent non-linearity in density dependence
$\varepsilon_{p,t}$	User-defined process error term for the growth rate (r) at time t, $\sim N(0, \sigma_r)$
k	User-defined expected female offspring per fertilized hen
h	User-defined synthesis of gobbler harem size and mate searching efficiency
f	User-defined fall harvest rate
s	User-defined spring gobbler harvest rate
i	User-defined illegal kill rate of hens prior to nesting
$\varepsilon_{f,t}$	User-defined error term for the fall harvest rate at time t, $\sim N(0, \sigma_f)$
$\varepsilon_{s,t}$	User-defined process error term for the spring harvest rate at time t, $\sim N(0, \sigma_s)$
$\varepsilon_{i,t}$	User-defined process error term for the spring illegal hen kill rate at time t, $\sim N(0, \sigma_i)$
$H_{fH,t}$	Fall hen harvest at time t
$H_{fG,t}$	Fall gobbler harvest at time t
$H_{f,t}$	Total Fall Harvest (hens and gobblers combined) at time t
$H_{s,t}$	Spring gobbler harvest at time t
P_H	User-defined hen permit number for a restricted proportional harvest
P_G	User-defined gobbler permit number for a restricted proportional harvest
T_H	User-defined threshold hen population size for a proportional threshold harvest
T_G	User-defined threshold gobbler population size for a proportional threshold harvest
D_G	User-defined spring gobbler harvest threshold for a restricted proportional harvest with spring threshold

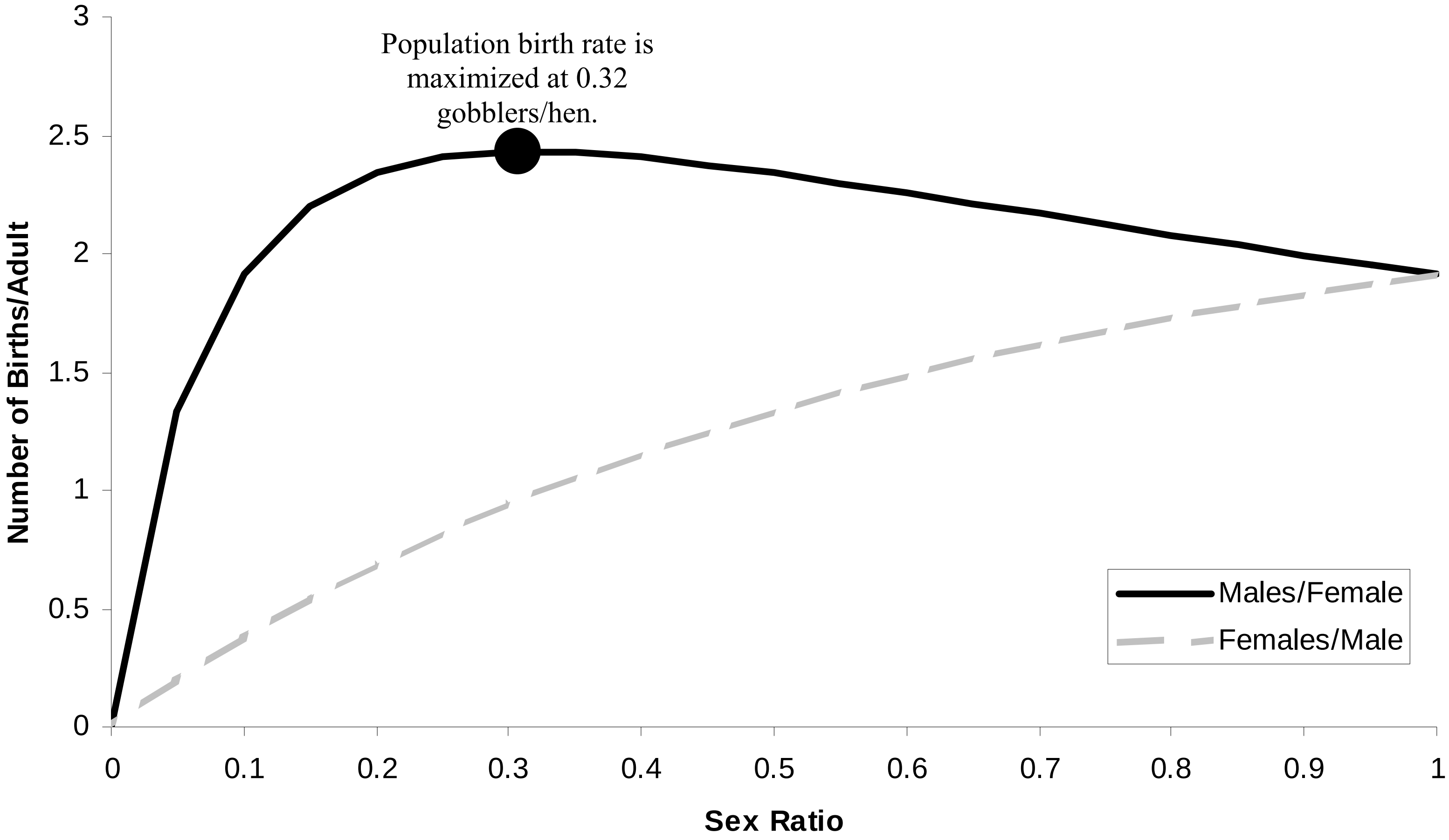

Figure 4.1. Harmonic mean frequency dependent birth rate function for gobbler or hen limited populations. Total offspring per fertilized hen was set to 4.21 when sex ratios are equal. Females fertilized/male was set to 10. The black line indicates the expected number of births/adults of both sexes for male-limited populations (0 – 1 males/female). Because males may fertilize many females, fewer gobblers than hens do not decrease birth rates until there are < 0.3 gobblers per hen. Birth rate is maximized at 0.32 gobblers/hen and this point is marked by the black dot. The dashed gray line indicates the expected number of births/total population size for female-limited populations (0 – 1 females/male). Birth rate declines in a nearly linear fashion as hens become limited.

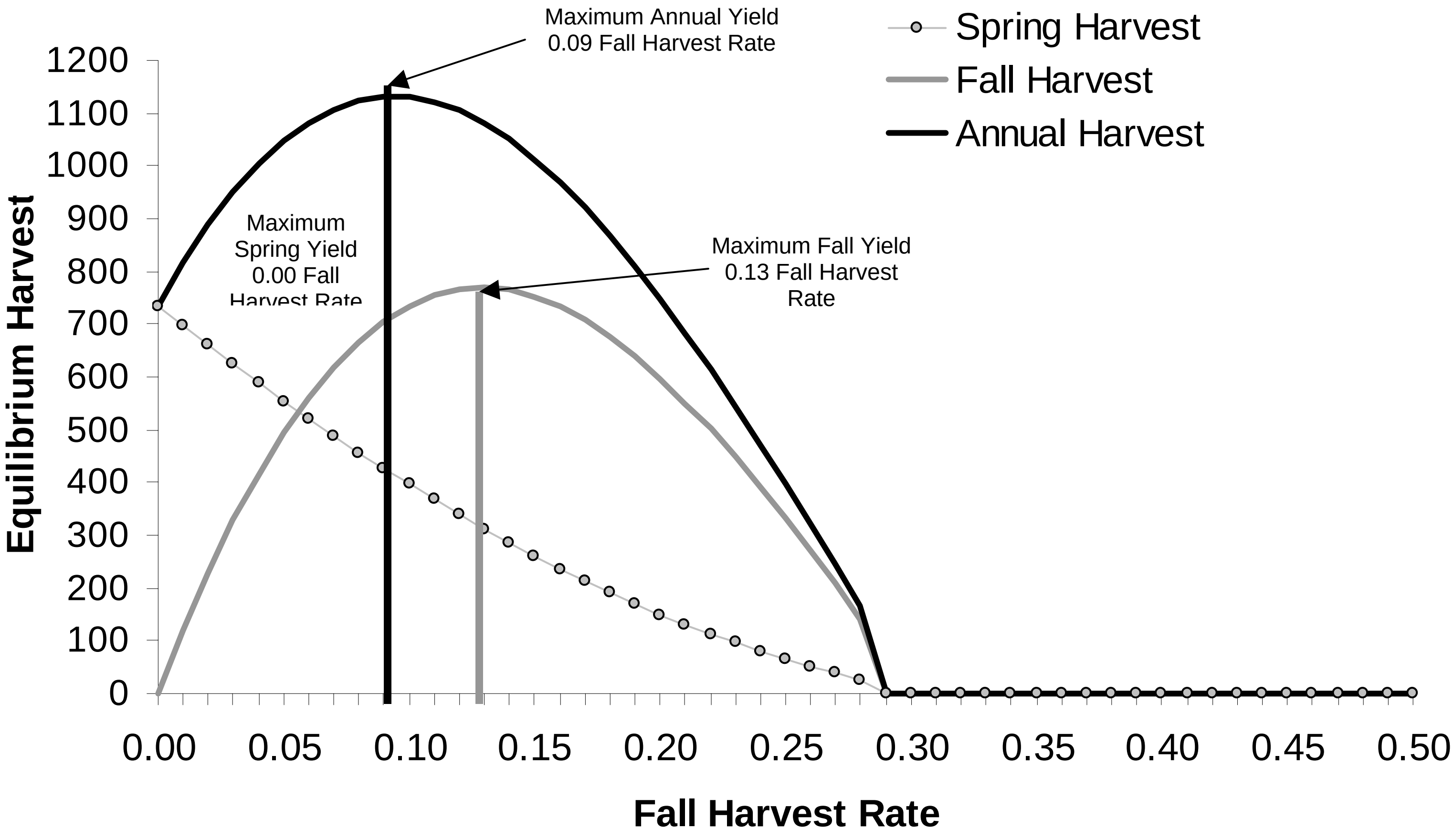

Figure 4.2. Deterministic harvests at population equilibrium are shown by fall harvest rate (0.00 – 0.50) where s = 0.15, i = 0.05, N_o = K = 10,000. As fall harvest rates increase, spring harvest declines. Fall harvest is maximized at 0.13 and annual harvest is maximized at 0.09. Fall and annual harvests abruptly decrease to 0 at a fall harvest rate of 0.30, caused by the decrease in birth rate as hen numbers decline.

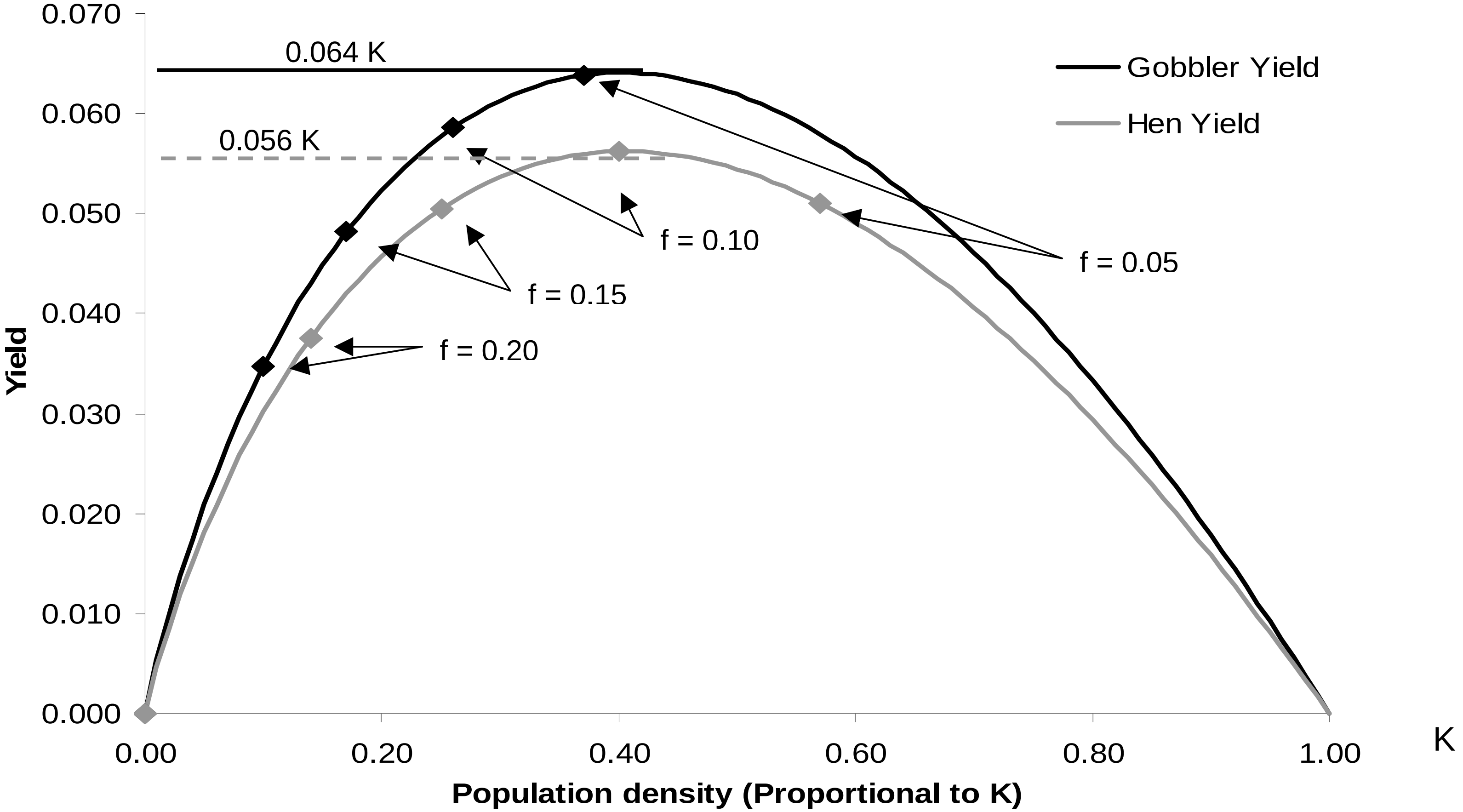

Figure 4.3. The proportional yield curve for gobbler and hen populations for s = 0.15, i = 0.05, N_o = K = 1. Population size is shown as proportional to carrying capacity (K). Horizontal lines show maximum expected yield for gobblers (0.064K) and hens (0.056K). Diamonds represent the expected long-term yield and equilibrium population for a given fall harvest rate (f). Populations on the left side of the curve are less robust to overharvest. A fall harvest rate of 0.10 maximizes hen yield but reduces gobbler yield and lowers gobbler equilibrium to the left side of the curve.

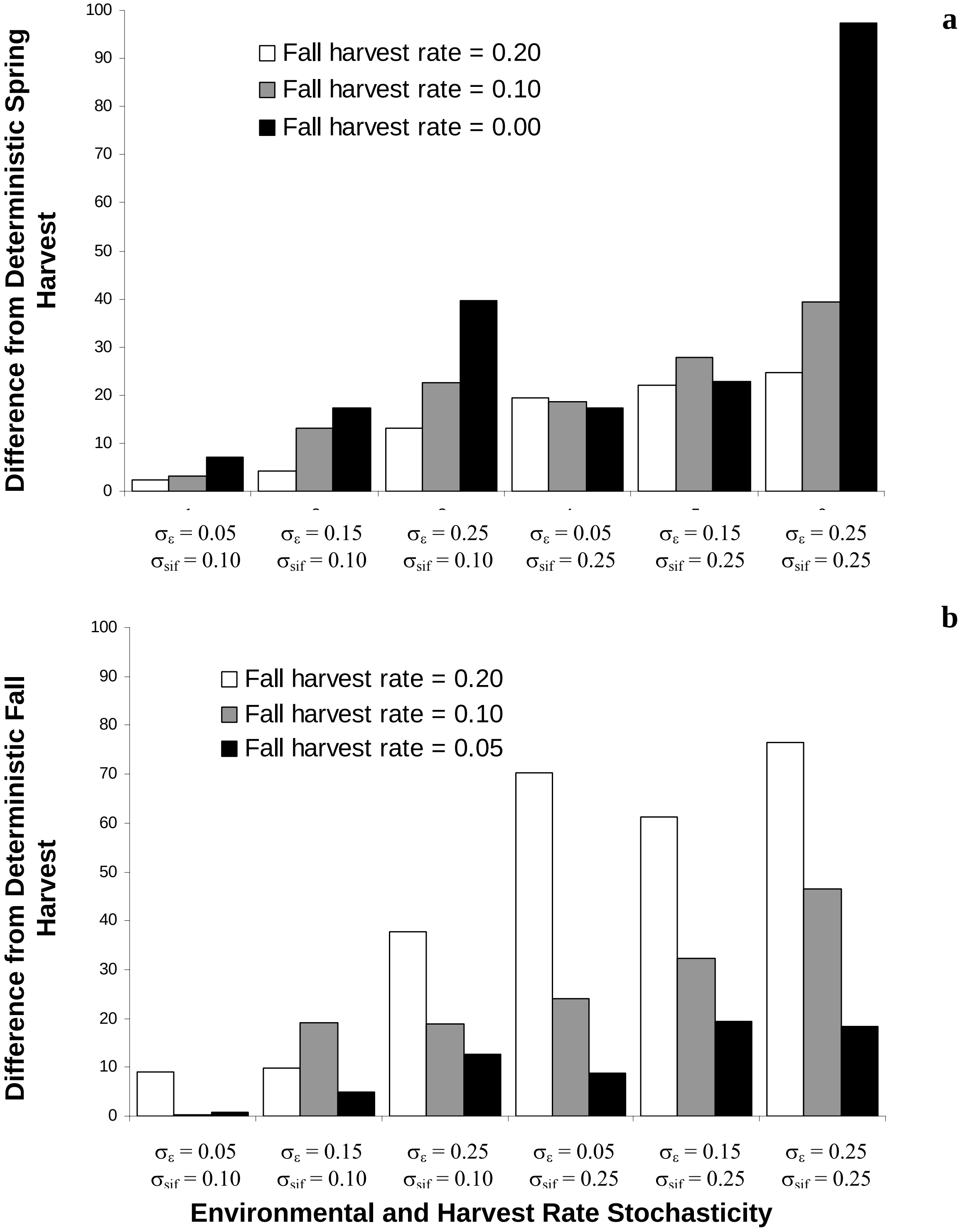

Figure 4.4. The difference in spring and fall harvests between the deterministic model and the stochastic model at different error treatments. As error increases, mean harvests are reduced from the expected. As fall harvest rate increases, the decrease in mean spring harvest due to stochasticity is reduced, while the decrease in mean fall harvest due to stochasticity increases.

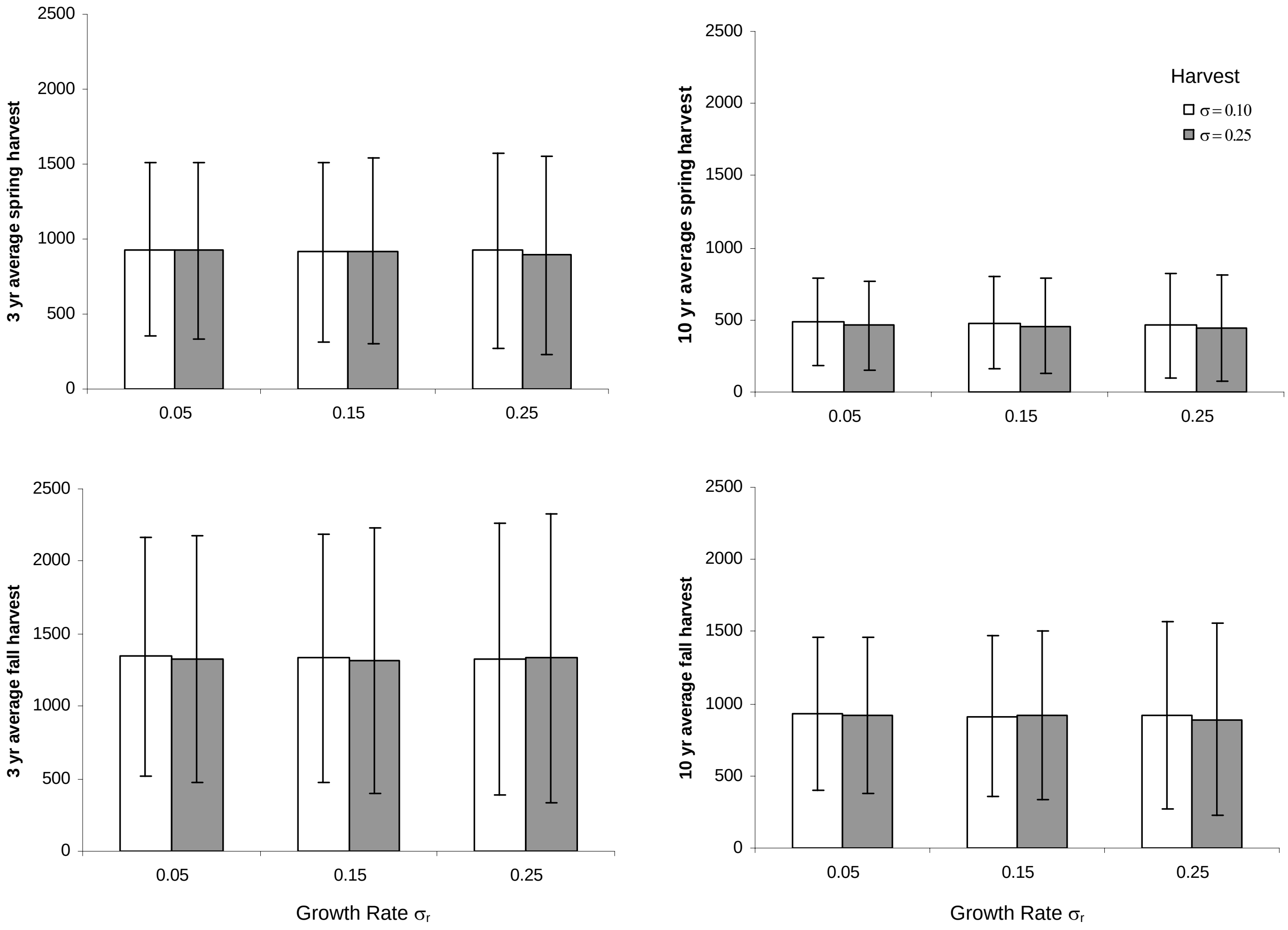

Figure 4.5. Short term (Year 3) and long-term (Year 10) spring and fall harvests are shown in relation to standard deviation in the harvest rate (0.10 – 0.25) and growth rate (0.05 – 0.25) for an average fall harvest of 0.10. Standard deviations are shown as error bars

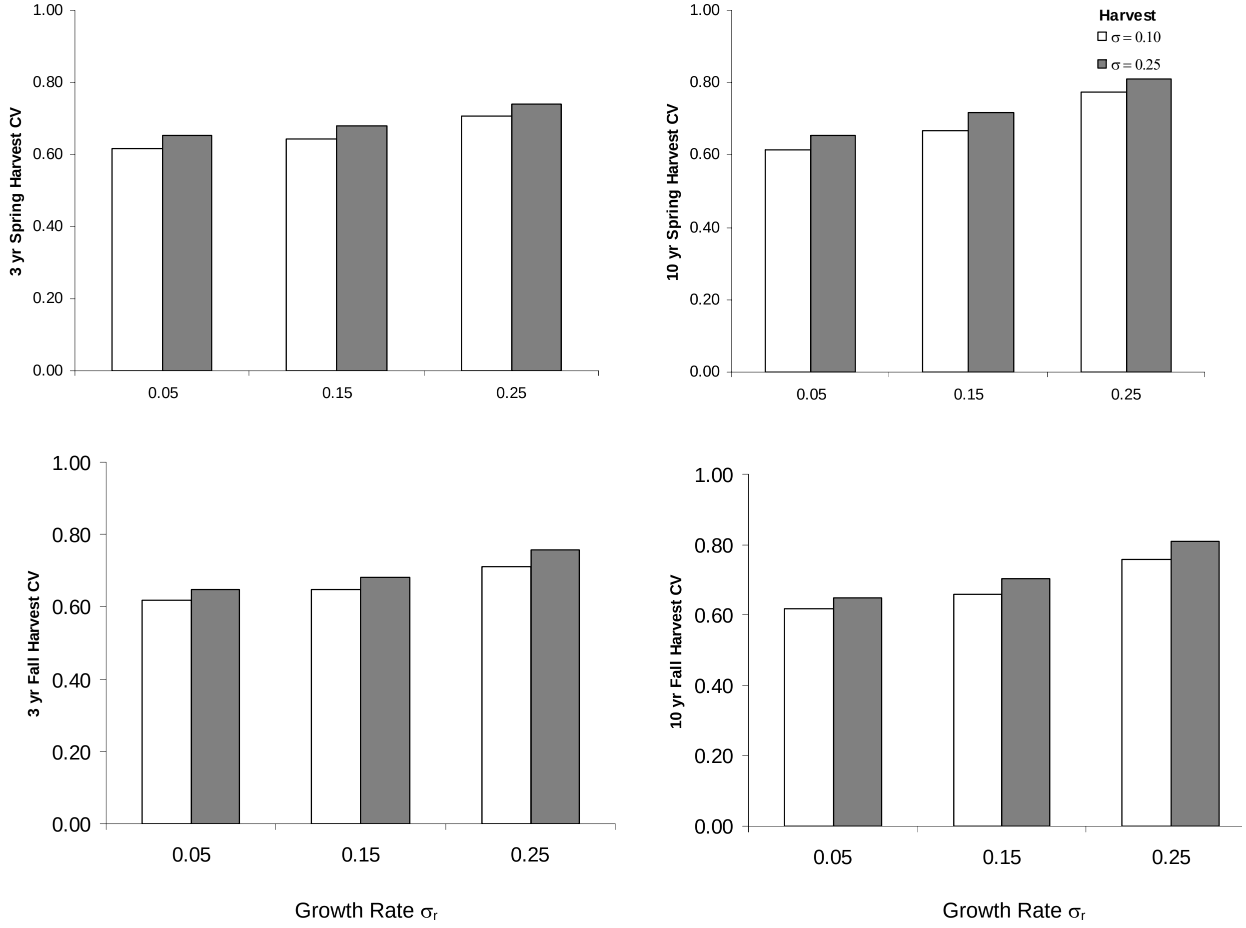

Figure 4.6. Short term (Year 3) and long-term (Year 10) coefficients of variation (cv) in the spring and fall harvests are shown in relation to standard deviation in the harvest rate (0.10, 0.25) and growth rate (0.05, 0.15, 0.25) for an average fall harvest of 0.10. CV varies little between short and long term harvests and increases primarily from environmental variation, rather than harvest variability.

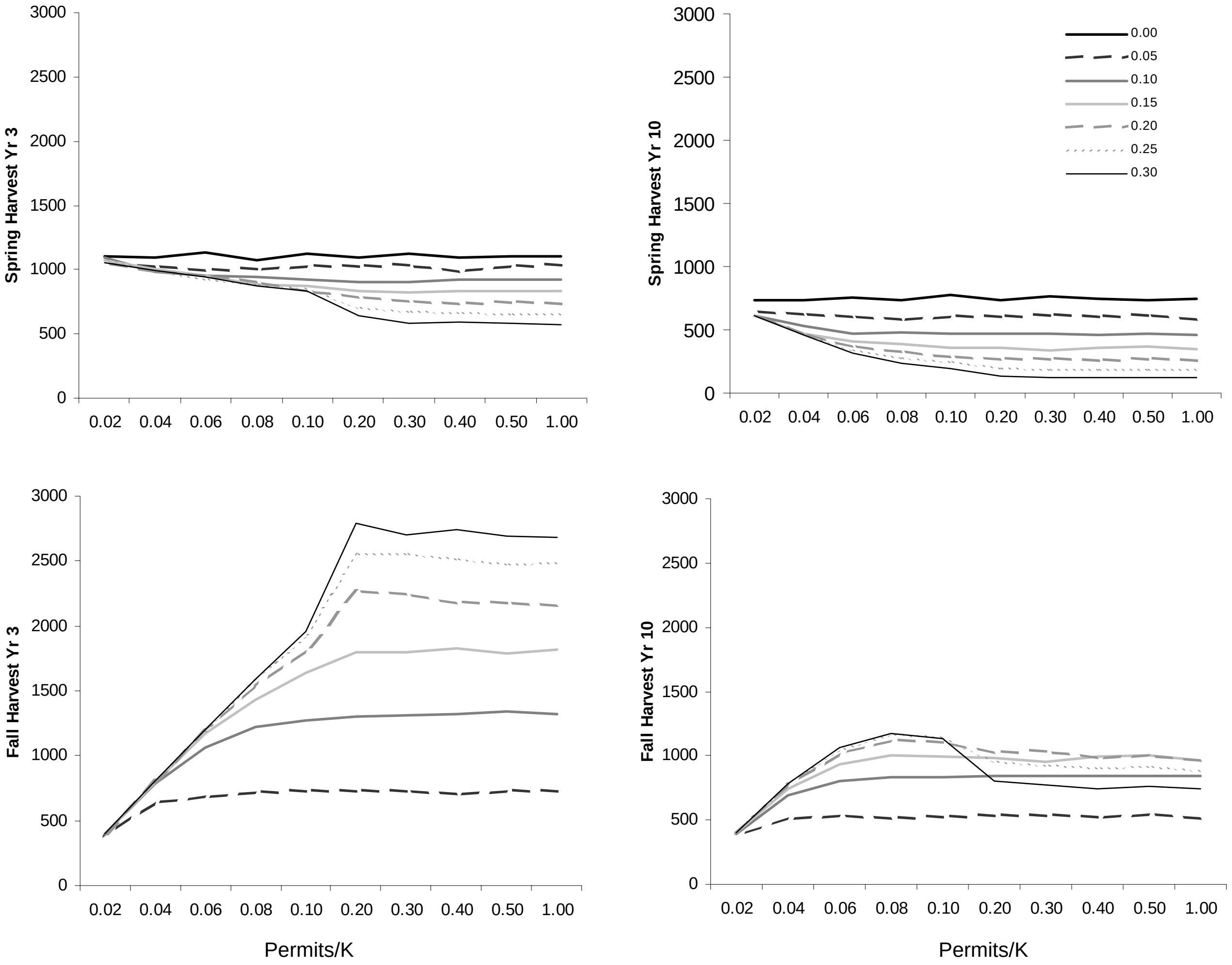

Figure 4.7. Short term (Year 3) and long-term (Year 10) mean spring and fall harvests are shown for fall permit levels expressed as a proportion of K in a restricted proportional harvest. At 1K, the harvest is entirely proportional. Each line represents the harvest at a different fall harvest rate (0.00 – 0.30).

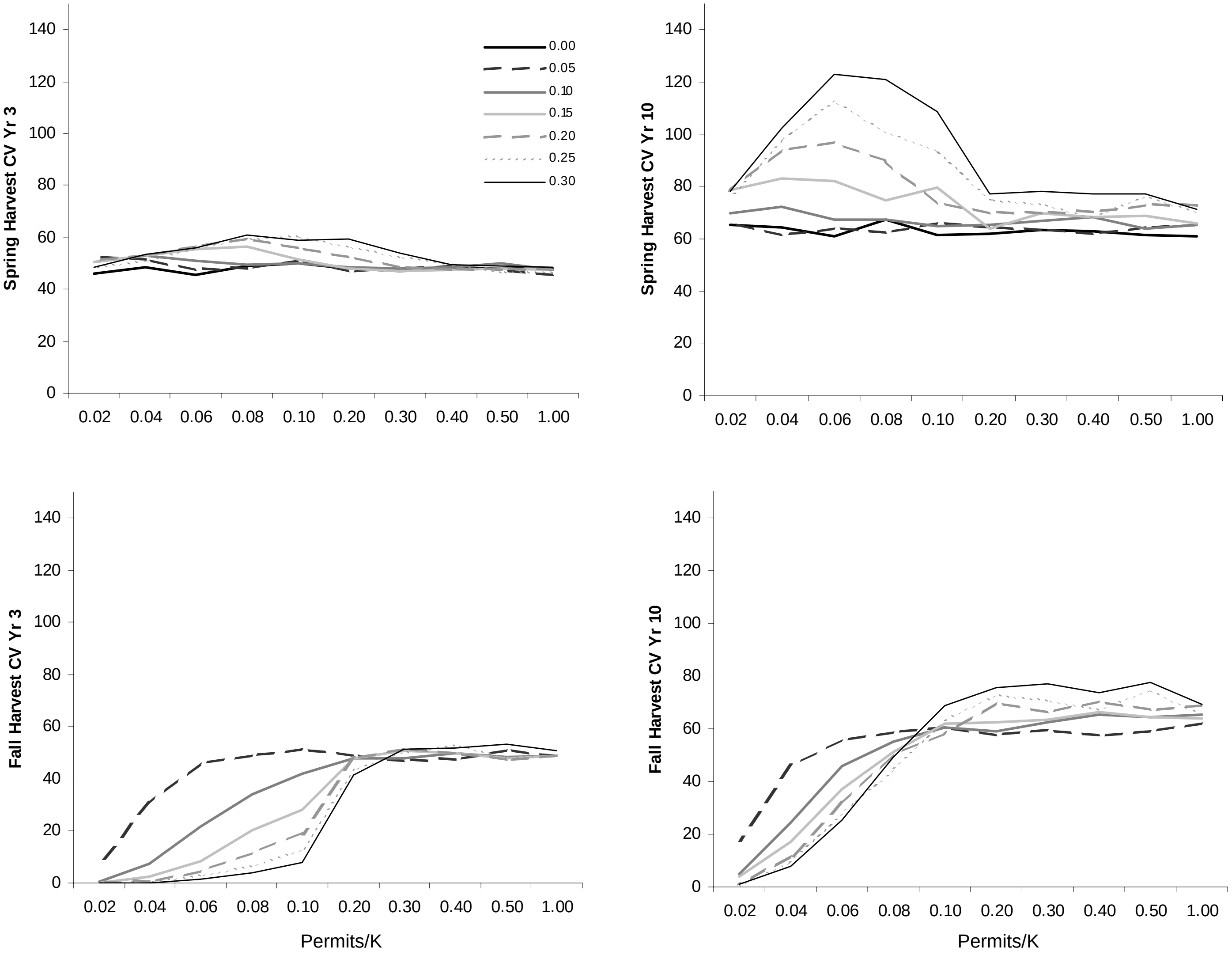

Figure 4.8. Short term (Year 3) and long-term (Year 10) coefficients of variation (cv) in the spring and fall harvests are shown fall permit levels expressed as a proportion of K in a restricted proportional harvest. At 1K, the harvest is entirely proportional. Each line represents the harvest at a different fall harvest rate (0.00 – 0.30).

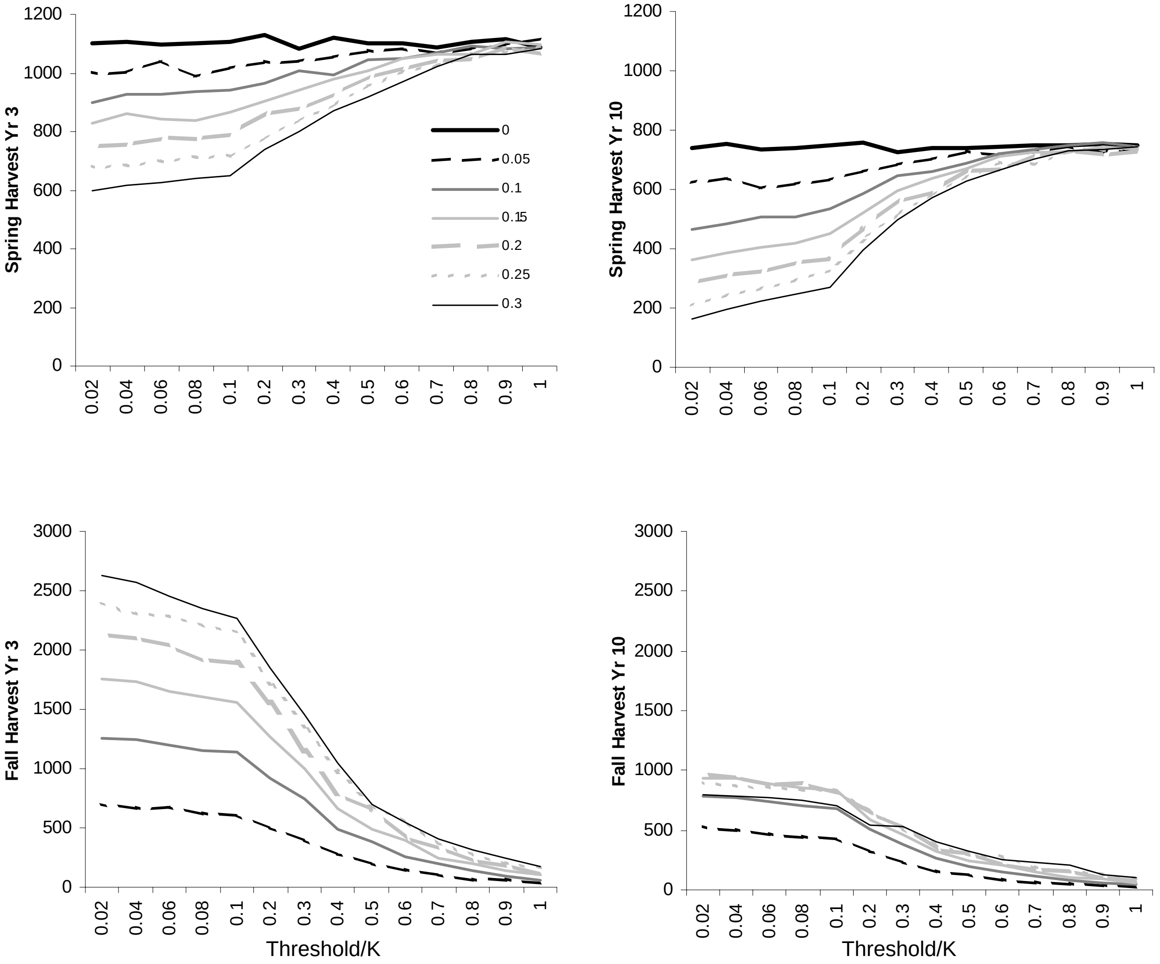

Figure 4.9. Short term (Year 3) and long-term (Year 10) mean spring and fall harvests are shown for population thresholds expressed as a proportion of K in a proportional threshold harvest. At 0.00K, the harvest is entirely proportional. Each line represents the harvest at a different fall harvest rate (0.00 – 0.30).

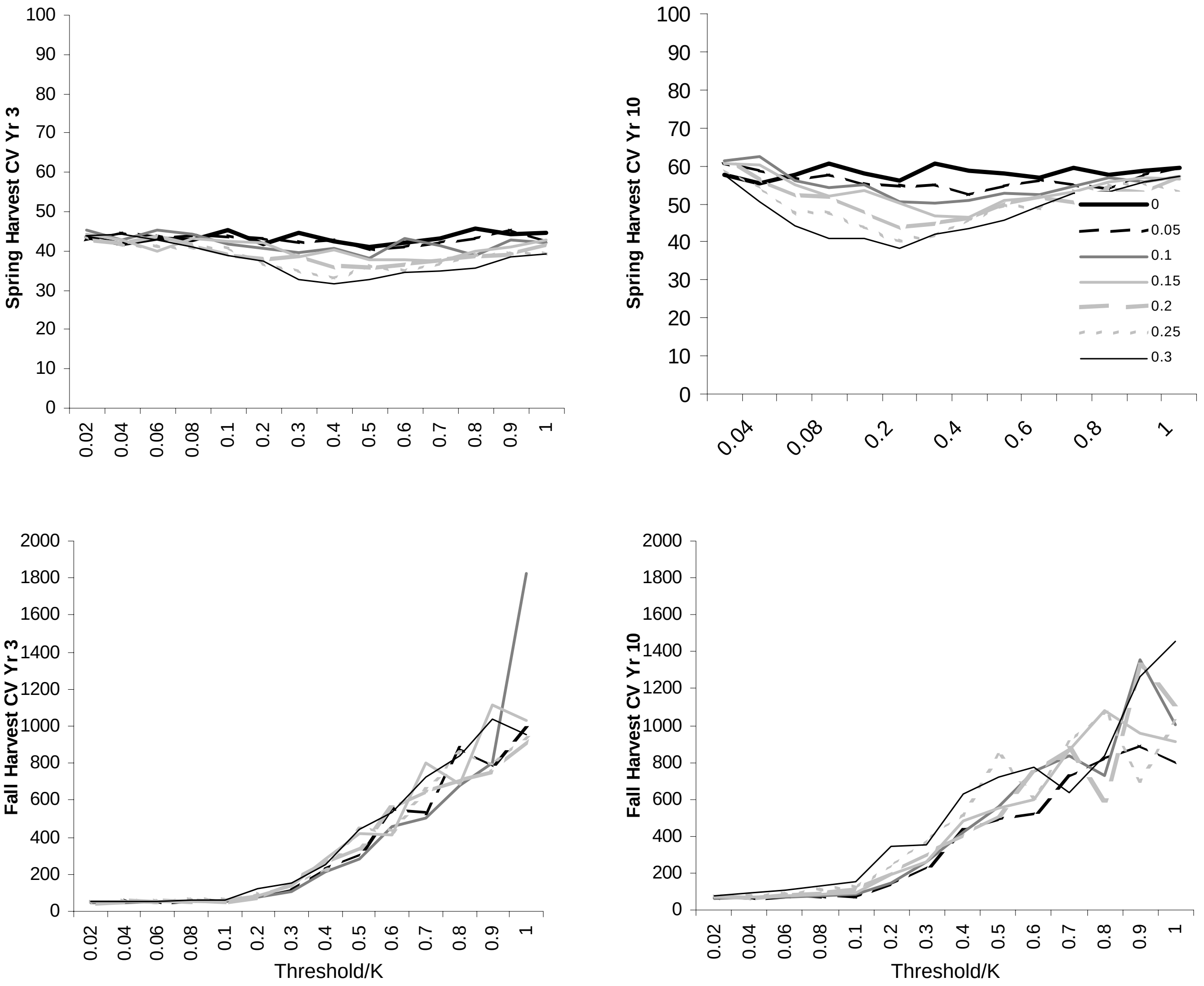

Figure 4.10. Short term (Year 3) and long-term (Year 10) coefficients of variation (cv) in the spring and fall harvests are shown for population thresholds expressed as a proportion of K in a proportional threshold harvest. At 0.00K, the harvest is entirely proportional. Each line represents the harvest at a different fall harvest rate (0.00 – 0.30).

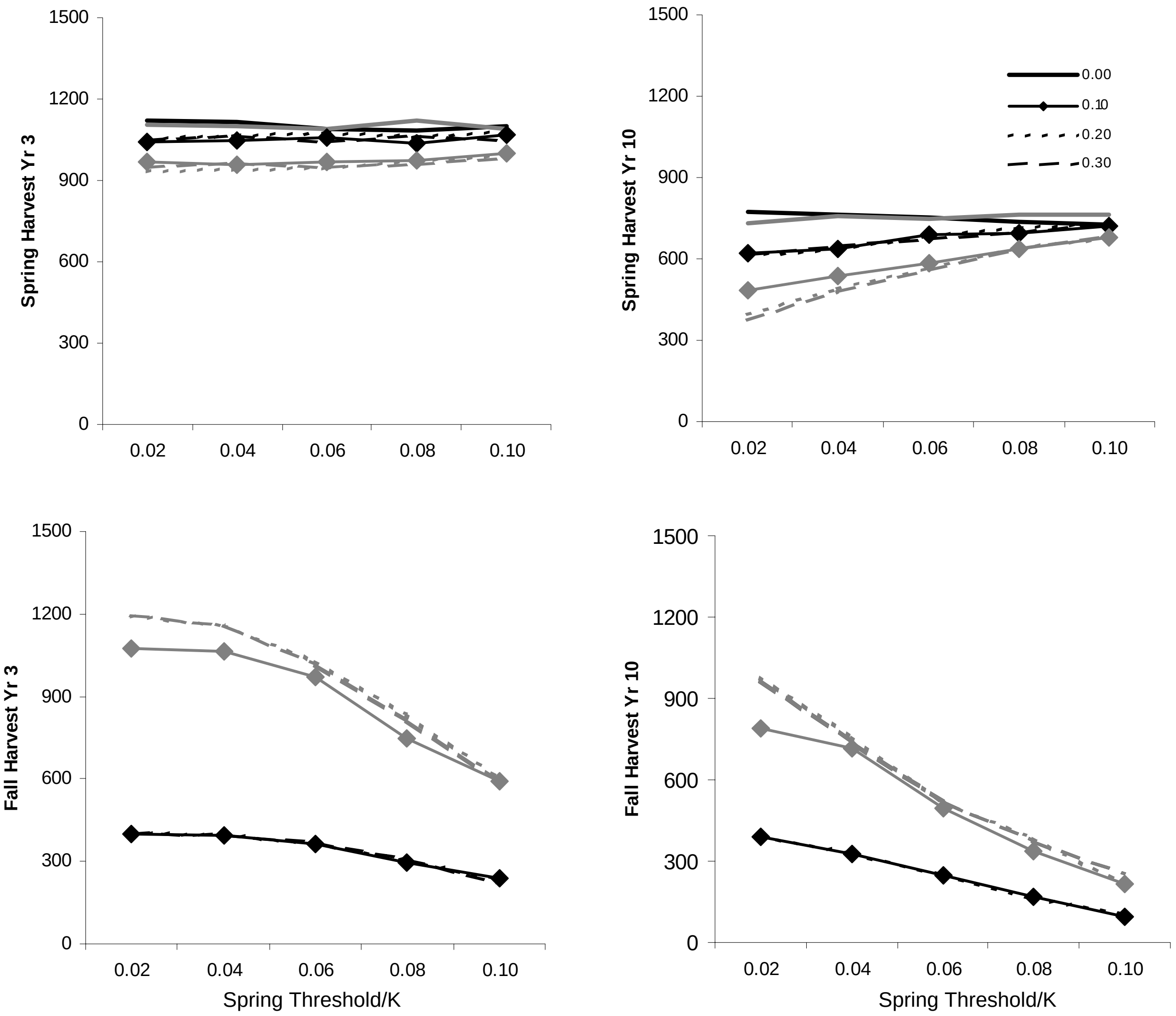

Figure 4.11. Short term (Year 3) and long-term (Year 10) mean spring and fall harvests are shown for spring harvest thresholds expressed as a proportion of K in a restricted proportional with spring threshold harvest. Black lines represent a permit level of 0.02K and gray lines represent a permit level of 0.06K. Each line represents the harvest at a different fall harvest rate (0.00 – 0.30).

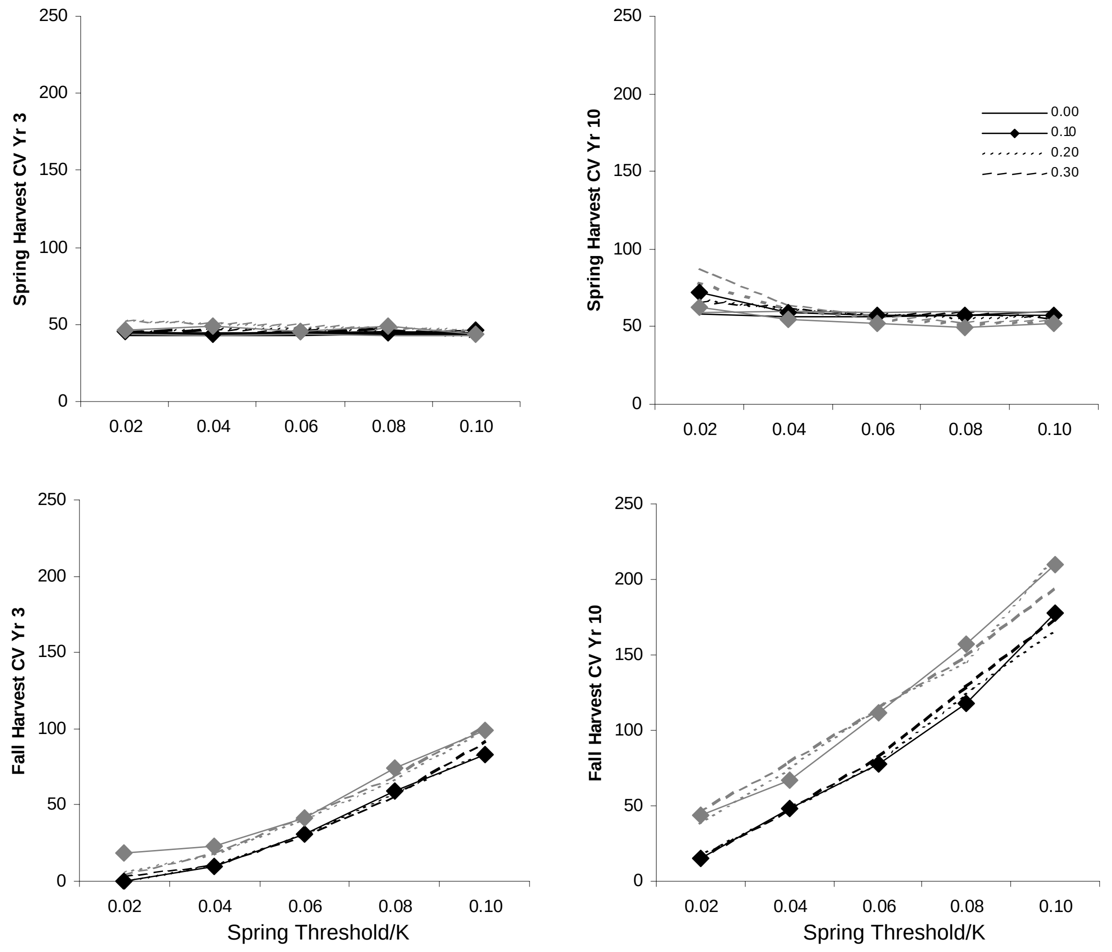

Figure 4.12. Short term (Year 3) and long-term (Year 10) coefficients of variation (cv) in the spring and fall harvests are shown for spring harvest thresholds expressed as a proportion of K in a restricted proportional with spring threshold harvest. Black lines represent a permit level of 0.02K and gray lines represent a permit level of 0.06K. Each line represents the harvest at a different fall harvest rate (0.00 – 0.30).

APPENDIX A. Environmental Correlates of Poult:Hen Ratios

Model selection to explain deviations in annual brood survey poult:hen ratios for Rhode Island, New York, New Jersey, Maryland. Models are compared using AIC_c. Results are presented in tables for regions. The coefficient of determination (r^2) and adjusted coefficient of determination (r^2_{adj}) estimate the amount of variation explained by models, n is the sample size, SSE is the sum of squared errors, and K is the number of parameters. AIC_c is the Akaike's Information Criterion corrected for small samples, with lower AIC_c values being assigned to the most parsimonious models. The Δ_i is the difference in AIC_c values from the best (lowest value) models and ω_i represents the relative likelihood of the model compared to all other models.

Table A1. Model selection by AICc explaining annual deviations in poult: hen ratios for Rhode Island. Departure from average precipitation in April (AprDP) performs best relative to the competing models.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
AprDP	0.7	0.66	9	1.17	3	17.98	0.00	0.89
MarDP, AprDP	0.75	0.66	9	1	4	23.77	5.79	0.05
AprDP, MayDP	0.71	0.61	9	1.15	4	25.02	7.04	0.03
JuneDP	0.29	0.18	9	2.83	3	25.93	7.95	0.02
AprHD	0.12	-0.01	9	3.49	3	27.81	9.84	0.01
MarHD	0.04	-0.1	9	3.82	3	28.63	10.65	0.00
MayDP	0.03	-0.11	9	3.86	3	28.72	10.74	0.00
MarDP	0.03	-0.11	9	3.86	3	28.72	10.74	0.00
MarHD, AprDP, JuneDP	0.80	0.68	9	0.78	5	33.53	15.55	0.00
AprHD,AprDP,JuneDP	0.79	0.67	9	0.82	5	33.98	16.00	0.00
MarHD, AprHD	0.16	-0.12	9	3.33	4	34.59	16.61	0.00
MarDP, AprDP, MayDP	0.75	0.6	9	0.98	5	35.58	17.61	0.00
MarDP, MayDP	0.05	-0.27	9	3.77	4	35.71	17.73	0.00
MarHD, MayDP, JuneDP	0.71	0.53	9	1.16	5	37.10	19.12	0.00
AprHD, MayDP, JuneDP	0.69	0.5	9	1.23	5	37.63	19.65	0.00
MarDP, AprDP, MayDP, JuneDP	0.85	0.71	9	0.58	6	54.86	36.88	0.00
MarHD, AprHD, MarDP, MayDP, JuneDP	0.82	0.51	9	0.72	8	128.81	110.83	0.00

Table A2. Model selection by AICc explaining annual deviations in poult: hen ratios for NY DEC region 3. Departure from average precipitation in May (MayDP) performs best relative to the competing models.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
MayDP	0.8	0.87	6	0.31	3	17.25	0.00	0.95
AprDP	0.24	0.05	6	0.91	3	23.71	6.46	0.04
MarDP	0.24	0.05	6	2.27	3	29.20	11.95	0.00
JuneDP	0.2	-0.01	6	2.41	3	29.55	12.30	0.00
AprHD	0.19	-0.02	6	2.44	3	29.63	12.38	0.00
MarHD	0.09	-0.13	6	2.72	3	30.28	13.03	0.00
AprDP, MayDP	0.92	0.86	6	0.25	4	45.96	28.71	0.00
MarDP, MayDP	0.91	0.85	6	0.27	4	46.42	29.17	0.00
MarDP, AprDP	0.79	0.66	6	0.61	4	51.31	34.06	0.00
MarHD, AprHD	0.19	-0.35	6	2.43	4	59.60	42.35	0.00

Table A3. Model selection by AICc explaining annual deviations in poult: hen ratios for NY DEC region 4. Departure from average precipitation in May (MayDP) performs best relative to the competing models.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
MayDP	0.74	0.68	6	0.77	3	22.71	0.00	0.69
JuneDP	0.61	0.52	6	1.16	3	25.17	2.46	0.20
MarHD	0.34	0.17	6	1.98	3	28.38	5.67	0.04
AprDP	0.2	-0.001	6	2.26	3	29.17	6.46	0.03
MarDP	0.16	-0.04	6	2.49	3	29.75	7.04	0.02
AprHD	0.07	-0.17	6	2.79	3	30.43	7.72	0.01
AprDP, MayDP	0.94	0.89	6	0.19	4	44.31	21.60	0.00
MarDP, MayDP	0.78	0.63	6	0.66	4	51.78	29.08	0.00
MarHD, AprHD	0.37	-0.05	6	1.88	4	58.06	35.36	0.00
MarDP, AprDP	0.25	-0.26	6	2.25	4	59.14	36.43	0.00

Table A4. Model selection by AICc explaining annual deviations in poult: hen ratios for NY DEC region 5. Departure from average precipitation in June (JuneDP) and March heating degree-days (MarHD) perform best relative to the competing models.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
JuneDP	0.33	0.17	6	0.71	3	22.22	0.00	0.28
MarHD	0.31	0.14	6	0.73	3	22.39	0.17	0.26
AprDP	0.01	-0.24	6	0.85	3	23.30	1.08	0.16
MayDP	0.15	-0.06	6	0.9	3	23.64	1.42	0.14
MarDP	0	-0.25	6	1.06	3	24.63	2.40	0.08
AprHD	0.01	-0.24	6	1.06	3	24.63	2.40	0.08
MarDP, AprDP	0.39	-0.02	6	0.65	4	51.69	29.47	0.00
MarHD, AprHD	0.32	-0.14	6	0.73	4	52.39	30.17	0.00
MarDP, MayDP	0.23	-0.28	6	0.82	4	53.09	30.86	0.00
AprDP, MayDP	0.2	-0.33	6	0.85	4	53.30	31.08	0.00

Table A5. Model selection by AICc explaining annual deviations in poult: hen ratios for NY DEC region 6. Departure from average precipitation in June (JuneDP) performs best relative to the competing models.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
JuneDP	0.87	0.84	6	0.14	3	12.48	0.00	0.96
AprHD	0.48	0.35	6	0.56	3	20.80	8.32	0.02
MarHD	0.46	0.33	6	0.58	3	21.01	8.53	0.01
MarDP	0.03	-0.21	6	1.05	3	24.57	12.09	0.00
AprDP	0.75	0.68	6	1.08	3	24.74	12.26	0.00
MayDP	0.01	-0.24	6	1.08	3	24.74	12.26	0.00
MarHD, AprHD	0.77	0.62	6	0.25	4	45.96	33.48	0.00
AprDP, MayDP	0.28	-0.2	6	0.78	4	52.79	40.31	0.00
MarDP, MayDP	0.07	-0.55	6	1.01	4	54.34	41.86	0.00
MarDP, AprDP	0.03	-0.61	6	1.05	4	54.57	42.09	0.00

Table A6. Model selection by AICc explaining annual deviations in poult: hen ratios for NY DEC region 7. Departure from average precipitation in April (AprDP) performs best relative to the competing models.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
AprDP	0.66	0.58	6	0.22	3	15.19	0.00	0.78
MayDP	0.47	0.34	6	0.46	3	19.62	4.43	0.09
MarDP	0.46	0.33	6	0.47	3	19.75	4.55	0.08
MarHD	0.16	-0.05	6	0.73	3	22.39	7.20	0.02
JuneDP	0.09	-0.14	6	0.8	3	22.94	7.75	0.02
AprHD	0.03	-0.21	6	0.84	3	23.23	8.04	0.01
MarDP, AprDP	0.92	0.87	6	0.07	4	38.32	23.13	0.00
AprDP, MayDP	0.78	0.64	6	0.19	4	44.31	29.12	0.00
MarDP, MayDP	0.49	0.15	6	0.44	4	49.35	34.16	0.00
MarHD, AprHD	0.21	-0.31	6	0.69	4	52.05	36.86	0.00

Table A7. Model selection by AICc explaining annual deviations in poult: hen ratios for NY DEC region 8. Departure from average precipitation in April (AprDP) performs best relative to the competing models.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
AprDP	0.60	0.5	6	0.50	3	20.12	0.00	0.47
JuneDP	0.53	0.41	6	0.71	3	22.22	2.10	0.17
MayDP	0.52	0.4	6	0.72	3	22.31	2.19	0.16
MarHD	0.44	0.3	6	0.83	3	23.16	3.04	0.10
MarDP	0.39	0.24	6	0.91	3	23.71	3.59	0.08
AprHD	0.04	-0.20	6	1.44	3	26.46	6.35	0.02
MarDP, AprDP	0.72	0.53	6	0.42	4	49.07	28.95	0.00
AprDP, MayDP	0.66	0.44	6	0.50	4	50.12	30.00	0.00
MarDP, MayDP	0.52	0.19	6	0.72	4	52.31	32.19	0.00
MarHD, AprHD	0.46	0.1	6	0.81	4	53.01	32.89	0.00

Table A8. Model selection by AICc explaining annual deviations in poult: hen ratios for NY DEC region 9. Departure from average precipitation in April (AprDP) performs best relative to the competing models.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
AprDP	0.70	0.62	6	0.19	3	14.31	0.00	0.60
MarDP	0.37	0.21	6	0.29	3	16.85	2.54	0.17
AprHD	0.27	0.08	6	0.34	3	17.80	3.49	0.10
JuneDP	0.04	-0.20	6	0.44	3	19.35	5.04	0.05
MayDP	0.00	-0.25	6	0.46	3	19.62	5.31	0.04
MarHD	0.00	-0.25	6	0.46	3	19.62	5.31	0.04
AprDP, MayDP	0.84	0.74	6	0.07	4	38.32	24.01	0.00
MarDP, AprDP	0.61	0.36	6	0.18	4	43.99	29.68	0.00
MarDP, MayDP	0.41	0.02	6	0.27	4	46.42	32.11	0.00
MarHD, AprHD	0.27	-0.22	6	0.34	4	47.80	33.49	0.00

Table A9. Model selection by AICc explaining annual deviations in poult: hen ratios for the NJ Appalachian region. Departure from average precipitation in May (MayDP), March (MarDP), and March and May perform best relative to the competing models.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
MayDP	0.21	0.15	15	65.56	3	72.87	0.00	0.28
MarDP, MayDP	0.36	0.25	15	53.06	4	73.52	0.65	0.20
MarDP	0.14	0.08	15	71.19	3	74.11	1.24	0.15
AprHD	0.05	-0.02	15	78.49	3	75.57	2.70	0.07
JuneDP	0.05	-0.02	15	78.95	3	75.66	2.79	0.07
AprDP	0.02	-0.06	15	81.53	3	76.14	3.27	0.05
MarHD	0.00	-0.07	15	82.63	3	76.34	3.47	0.05
AprDP, MayDP	0.21	0.08	15	65.44	4	76.66	3.79	0.04
MarDP, AprDP	0.18	0.05	15	67.63	4	77.16	4.28	0.03
MarDP, AprDP, MayDP	0.37	0.20	15	51.98	5	77.88	5.00	0.02
MarHD, AprHD	0.06	-0.10	15	78.40	4	79.37	6.50	0.01
AprHD, MayDP, JuneDP	0.26	0.06	15	61.16	5	80.32	7.45	0.01
MarHD, MayDP, JuneDP	0.25	0.04	15	62.29	5	80.59	7.72	0.01
AprHD, AprDP, JuneDP	0.09	-0.15	15	75.02	5	83.38	10.51	0.00
MarDP, AprDP, MayDP, JuneDP	0.38	0.13	15	51.56	6	83.59	10.71	0.00
MarHD, AprDP, JuneDP	0.06	-0.20	15	78.11	5	83.99	11.11	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP	0.38	-0.08	15	51.27	8	101.00	28.13	0.00

Table A10. Model selection by AICc explaining annual deviations in poult: hen ratios for the NJ Ridge and Valley region. All single variable models are equivalent.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
AprHD	0.13	0.07	17	40.97	3	71.04	0.00	0.27
MayDP	0.06	-0.01	17	44.23	3	72.35	1.30	0.14
JuneDP	0.04	-0.03	17	45.12	3	72.68	1.64	0.12
MarDP	0.04	-0.03	17	45.22	3	72.72	1.68	0.12
MarHD	0.02	-0.05	17	46.12	3	73.06	2.01	0.10
AprDP	0.00	-0.06	17	46.75	3	73.29	2.24	0.09
MarHD, AprHD	0.13	0.01	17	40.76	4	74.44	3.40	0.05
MarDP, MayDP	0.10	-0.03	17	42.36	4	75.10	4.05	0.04
AprDP, MayDP	0.06	-0.07	17	43.87	4	75.69	4.65	0.03
MarDP, AprDP	0.04	-0.1	17	45.16	4	76.19	5.14	0.02
AprHD, AprDP, JuneDP	0.16	-0.03	17	39.19	5	77.90	6.85	0.01
MarDP, AprDP, MayDP	0.10	-0.11	17	42.16	5	79.14	8.10	0.00
MarHD, AprDP, JuneDP	0.06	-0.16	17	44.19	5	79.94	8.89	0.00
AprHD, MayDP, JuneDP	0.19	0.003	17	37.99	5	80.32	9.27	0.00
MarHD, MayDP, JuneDP	0.11	-0.1	17	41.94	5	80.59	9.55	0.00
MarDP, AprDP, MayDP, JuneDP	0.14	-0.15	17	40.3	6	83.32	12.27	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP	0.23	-0.23	17	36.18	8	95.08	24.04	0.00

Table A11. Model selection by AICc explaining annual deviations in poult: hen ratios for the NJ Northeastern Highlands region. Heating degree-days in March (MarHD) performs best relative to the competing models. All single correlates represent competitive models.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
MarHD	0.25	0.15	10	42.26	3	52.79	0.00	0.35
AprHD	0.14	0.03	10	48.43	3	54.15	1.36	0.18
AprDP	0.08	-0.03	10	51.33	3	54.74	1.94	0.13
JuneDP	0.02	-0.1	10	54.73	3	55.38	2.59	0.10
MayDP	0.01	-0.11	10	55.44	3	55.51	2.71	0.09
MarDP	0.00	-0.12	10	55.97	3	55.60	2.81	0.09
MarHD, AprHD	0.36	0.18	10	35.78	4	57.13	4.34	0.04
MarDP, AprDP	0.09	-0.17	10	51.23	4	60.72	7.92	0.01
AprDP, MayDP	0.08	-0.18	10	51.29	4	60.73	7.94	0.01
MarDP, MayDP	0.02	-0.26	10	55.02	4	61.43	8.64	0.00
MarHD, AprDP, JuneDP	0.44	0.16	10	31.57	5	64.87	12.08	0.00
AprHD, AprDP, JuneDP	0.17	-0.24	10	46.46	5	68.74	15.95	0.00
MarDP, AprDP, MayDP	0.09	-0.37	10	51.23	5	69.72	16.92	0.00
AprHD, MayDP, JuneDP	0.15	-0.27	10	47.6	5	77.37	24.58	0.00
MarHD, MayDP, JuneDP	0.31	-0.03	10	38.46	5	79.05	26.26	0.00
MarDP, AprDP, MayDP, JuneDP	0.11	-0.60	10	49.77	6	84.43	31.64	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP	0.56	-0.31	10	24.57	8	197.40	144.61	0.00

Table A12. Model selection by AICc explaining annual deviations in poult: hen ratios for the NJ Piedmont region. Departure from average precipitation in March (MarDP) performs best relative to the competing models.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
MarDP	0.30	0.24	13	44.05	3	61.42	0.00	0.50
MarDP, MayDP	0.33	0.20	13	42.17	4	65.19	3.77	0.08
MarDP, AprDP	0.32	0.19	13	42.65	4	65.34	3.91	0.07
AprHD	0.04	-0.05	13	60.44	3	65.54	4.11	0.06
MayDP	0.02	-0.07	13	61.46	3	65.8	4.33	0.06
JuneDP	0.01	-0.08	13	62.21	3	65.90	4.49	0.05
MarHD	0.01	-0.08	13	62.32	3	65.93	4.51	0.05
AprDP	0.00	-0.09	13	62.72	3	66.02	4.59	0.05
MarHD, MayDP, JuneDP	0.04	-0.28	13	60.3	5	66.85	5.43	0.03
AprHD, MayDP, JuneDP	0.08	-0.22	13	57.58	5	68.98	7.56	0.01
MarHD, AprHD	0.05	-0.14	13	59.84	4	69.74	8.32	0.01
AprDP, MayDP	0.04	-0.15	13	60.12	4	69.80	8.38	0.01
MarDP, AprDP, MayDP	0.33	0.11	13	41.81	5	70.65	9.23	0.01
AprHD, AprDP, JuneDP	0.09	-0.21	13	57.13	5	74.71	13.28	0.00
MarHD, AprDP, JuneDP	0.03	-0.29	13	60.96	5	75.55	14.13	0.00
MarDP, AprDP, MayDP, JuneDP	0.40	0.1	13	37.75	6	76.75	15.33	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP	0.49	-0.03	13	32.36	8	100.7	39.28	0.00

Table A13. Model selection by AICc explaining annual deviations in poult: hen ratios for the NJ Pine Barrens region. Departure from average precipitation in May (MayDP) and heating degree-days in April, combined with departure from average precipitation in May (MayDP) and June (JuneDP) perform best relative to the competing models.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
MayDP	0.66	0.63	12	31.46	3	54.62	0.00	0.40
AprHD, MayDP, JuneDP	0.86	0.81	12	13.12	5	55.13	0.51	0.31
MarDP, AprDP, MayDP, JuneDP	0.91	0.87	12	7.94	6	57.90	3.28	0.08
AprDP, MayDP	0.69	0.62	12	28.74	4	58.25	3.63	0.07
MarDP, MayDP	0.68	0.61	12	29.55	4	58.58	3.96	0.06
MarHD, MayDP, JuneDP	0.85	0.8	12	17.74	5	58.75	4.13	0.05
MarDP	0.44	0.39	12	52.11	3	60.68	6.06	0.02
MarDP, AprDP, MayDP	0.72	0.62	12	26.17	5	63.41	8.79	0.00
MarDP, AprDP	0.51	0.40	12	45.70	4	63.82	9.19	0.00
MarHD	0.14	0.05	12	80.88	3	65.95	11.33	0.00
AprDP	0.06	-0.04	12	88.36	3	67.01	12.39	0.00
JuneDP	0.06	-0.04	12	88.51	3	67.03	12.41	0.00
AprHD	0.01	-0.09	12	92.70	3	67.59	12.97	0.00
MarHD, AprHD	0.14	-0.05	12	80.63	4	70.63	16.01	0.00
MarHD, AprDP, JuneDP	0.40	0.17	12	56.63	5	72.67	18.05	0.00
AprHD, AprDP, JuneDP	0.17	-0.14	12	78.03	5	76.52	21.90	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP	0.92	0.83	12	7.23	8	91.97	37.35	0.00

Table A14. Model selection by AICc explaining annual deviations in poult: hen ratios for the NJ Coastal Plains region. Departure from average precipitation in April (AprDP) performs best relative to the competing models.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
AprDP	0.34	0.28	12	46.01	3	59.18	0.00	0.51
MarDP, ApeDP	0.44	0.31	12	39.44	4	62.05	2.87	0.12
JuneDP	0.10	0.01	12	63.03	3	62.96	3.78	0.08
AprDP, MayDP	0.37	0.23	12	43.83	4	63.31	4.13	0.06
MarDP	0.07	-0.02	12	64.94	3	63.32	4.14	0.06
MayDP	0.03	-0.07	12	67.96	3	63.86	4.68	0.05
AprHD	0.00	-0.10	12	70.00	3	64.22	5.04	0.04
MarHD	0.00	-0.10	12	70.01	3	64.22	5.04	0.04
MarDP, AprDP, MayDP	0.49	0.30	12	35.48	5	67.06	7.88	0.01
MarDP, MayDP	0.12	-0.07	12	61.38	4	67.35	8.17	0.01
AprHD, AprDP, JuneDP	0.48	0.28	12	36.42	5	67.38	8.20	0.01
MarHD, AprDP, JuneDP	0.44	0.23	12	39.05	5	68.21	9.03	0.01
MarHD, AprHD	0.00	-0.22	12	69.98	4	68.93	9.75	0.00
MarDP, AprDP, MayDP, JuneDP	0.68	0.50	12	22.41	6	70.35	11.17	0.00
AprHD, MayDP, JuneDP	0.21	-0.08	12	55.09	5	72.34	13.16	0.00
MarHD, MayDP, JuneDP	0.20	-0.10	12	56.19	5	72.58	13.40	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP	0.71	0.36	12	20.43	8	104.40	45.22	0.00

Table A15. Model selection by AICc explaining annual deviations in poult: hen ratios for the MD Appalachian region. Heating degree-days in April (AprHD) performs best relative to the competing models. AprDP is removed from the global model because of small sample size and because its effects were similar to MayDP.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
AprHD	0.36	0.27	9	7.72	3	34.96	0.00	0.56
MarDP	0.06	-0.08	9	11.41	3	38.48	3.52	0.10
MayDP	0.03	-0.11	9	11.73	3	38.73	3.77	0.09
JuneDP	0.01	-0.13	9	11.96	3	38.90	3.94	0.08
MarHD	0.01	-0.13	9	12.02	3	38.95	3.98	0.08
AprDP	0.001	-0.14	9	12.1	3	39.00	4.04	0.07
MarHD, AprHD	0.38	0.17	9	7.55	4	41.96	7.00	0.02
MarDP, MayDP	0.08	-0.23	9	11.17	4	45.48	10.52	0.00
MarDP, ApeDP	0.06	-0.26	9	11.41	4	45.68	10.72	0.00
AprDP, MayDP	0.03	-0.29	9	11.7	4	45.90	10.94	0.00
AprHD, MayDP, JuneDP	0.45	0.12	9	6.64	5	52.80	17.84	0.00
AprHD, AprDP, JuneDP	0.39	0.02	9	7.39	5	53.77	18.81	0.00
MarDP, AprDP, MayDP	0.08	-0.47	9	11.11	5	57.44	22.48	0.00
MarHD, MayDP, JuneDP	0.04	-0.53	9	11.56	5	57.79	22.83	0.00
MarHD, AprDP, JuneDP	0.01	-0.58	9	11.94	5	58.08	23.12	0.00
MarDP, AprDP, MayDP, JuneDP	0.09	-0.83	9	11.06	6	81.40	46.44	0.00
MarHD, AprHD, MarDP, MayDP, JuneDP	0.5	-0.33	9	6.02	7	147.90	112.94	0.00

Table A16. Model selection by AICc explaining annual deviations in poult: hen ratios for the MD Piedmont region. Departure from average precipitation in Mar (MarDP) performs best relative to the competing models. AprDP is removed from the global model because of small sample size and because its effects were similar to MayDP.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
MarDP	0.44	0.36	9	1.64	3	21.02	0.00	0.59
MayDP	0.12	0.00	9	2.58	3	25.10	4.08	0.08
JuneDP	0.11	-0.02	9	2.62	3	25.23	4.22	0.07
MarDP, ApeDP	0.60	0.46	9	1.18	4	25.26	4.24	0.07
AprHD	0.09	-0.03	9	2.65	3	25.34	4.32	0.07
MarHD	0.01	-0.13	9	2.91	3	26.18	5.16	0.05
AprDP	0.00	-0.14	9	2.93	3	26.24	5.22	0.04
MarDP, MayDP	0.48	0.31	9	1.52	4	27.53	6.52	0.02
AprDP, MayDP	0.13	-0.16	9	2.55	4	32.19	11.17	0.00
MarHD, AprHD	0.09	-0.21	9	2.65	4	32.54	11.52	0.00
MarDP, AprDP, MayDP	0.66	0.45	9	1.00	5	35.77	14.75	0.00
AprHD, MayDP, JuneDP	0.38	0.00	9	1.83	5	41.20	20.19	0.00
MarHD, MayDP, JuneDP	0.21	-0.27	9	2.33	5	43.38	22.36	0.00
MarHD, AprDP, JuneDP	0.19	-0.30	9	2.38	5	43.57	22.55	0.00
AprHD, AprDP, JuneDP	0.19	-0.30	9	2.38	5	43.57	22.55	0.00
MarDP, AprDP, MayDP, JuneDP	0.68	0.36	9	0.93	6	59.11	38.09	0.00
MarHD, AprHD, MarDP, MayDP, JuneDP	0.51	-0.30	9	1.43	7	135.00	113.98	0.00

Table A17. Model selection by AICc explaining annual deviations in poult: hen ratios for the MD Ridge & Valley region. Heating degree-days in April (AprHD), and departure from average precipitation in June (JuneDP) perform best relative to the competing models. All single correlates represent competitive models. AprDP is removed from the global model because of small sample size and because its effects were similar to MayDP.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
AprHD	0.32	0.22	9	8.40	3	35.72	0.00	0.35
JuneDP	0.30	0.19	9	8.67	3	36.00	0.28	0.31
MarHD	0.08	-0.05	9	11.29	3	38.38	2.66	0.09
MarDP	0.05	-0.08	9	11.64	3	38.66	2.94	0.08
MayDP	0.04	-0.1	9	11.88	3	38.84	3.12	0.07
AprDP	0.01	-0.13	9	12.16	3	39.05	3.33	0.07
MarHD, AprHD	0.37	0.16	9	7.73	4	42.17	6.45	0.01
MarDP, MayDP	0.07	-0.24	9	11.46	4	45.72	10.00	0.00
MarDP, AprDP	0.05	-0.26	9	11.64	4	45.86	10.14	0.00
AprDP, MayDP	0.04	-0.28	9	11.86	4	46.02	10.30	0.00
AprHD, AprDP, JuneDP	0.59	0.34	9	5.10	5	50.43	14.71	0.00
AprHD, MayDP, JuneDP	0.57	0.31	9	5.34	5	50.84	15.12	0.00
MarHD, MayDP, JuneDP	0.36	-0.03	9	7.90	5	54.37	18.65	0.00
MarHD, AprDP, JuneDP	0.33	-0.07	9	8.26	5	54.77	19.05	0.00
MarDP, AprDP, MayDP	0.07	-0.48	9	11.41	5	57.68	21.96	0.00
MarDP, AprDP, MayDP, JuneDP	0.36	-0.28	9	7.87	6	78.33	42.61	0.00
MarHD, AprHD, MarDP, MayDP, JuneDP	0.63	0.01	9	4.57	7	145.4	109.68	0.00

Table A18. Model selection by AICc explaining annual deviations in poult: hen ratios for the MD Blue Ridge region. The Global model was omitted because of small sample size. Heating degree-days in April (AprHD) performs best relative to the competing models.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
AprHD	0.49	0.39	7	8.80	3	35.47	0.00	0.53
AprDP	0.21	0.06	7	13.55	3	38.49	3.02	0.12
JuneDP	0.21	0.05	7	13.68	3	38.56	3.09	0.11
MarHD	0.18	0.02	7	14.11	3	38.77	3.30	0.10
MarDP	0.01	-0.09	7	15.62	3	39.48	4.02	0.07
MayDP	0.09	-0.10	7	15.77	3	39.55	4.08	0.07
MarDP, AprDP	0.70	0.55	7	5.10	4	45.65	10.18	0.00
MarHD, AprHD	0.59	0.39	7	7.03	4	47.90	12.43	0.00
AprDP, MayDP	0.41	0.12	7	10.14	4	50.46	14.99	0.00
MarDP, MayDP	0.16	-0.26	7	14.45	4	52.94	17.47	0.00
MarDP, AprDP, MayDP	0.95	0.91	7	0.79	5	74.59	39.13	0.00
AprHD, MayDP, JuneDP	0.88	0.75	7	2.13	5	81.54	46.07	0.00
MarHD, AprDP, JuneDP	0.77	0.57	7	3.69	5	85.38	49.92	0.00
AprHD, AprDP, JuneDP	0.58	0.16	7	7.21	5	90.07	54.61	0.00
MarHD, MayDP, JuneDP	0.54	0.07	7	7.99	5	90.79	55.32	0.00

Table A19. Model selection by AICc explaining annual deviations in poult: hen ratios for the MD Coastal Plain region. Departure from average precipitation in April (AprDP) and heating degree-days in April (AprHD) perform best relative to competing models. Departure from average precipitation in March and April (MarDP, AprDP) and MarDP alone perform nearly as well. AprDP is removed from the global model because of small sample size and because its effects were similar to MayDP.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
AprDP	0.33	0.23	9	6.24	3	33.04	0.00	0.27
AprHD	0.32	0.22	9	6.37	3	33.23	0.19	0.25
MarDP, AprDP	0.67	0.56	9	3.09	4	33.92	0.87	0.17
MarDP	0.23	0.12	9	7.19	3	34.32	1.28	0.14
JuneDP	0.06	-0.07	9	8.77	3	36.11	3.06	0.06
MayDP	0.02	-0.12	9	9.13	3	36.47	3.43	0.05
MarHD	0.00	-0.14	9	9.28	3	36.62	3.57	0.05
MarHD, AprHD	0.32	0.10	9	6.32	4	40.36	7.31	0.01
AprDP, MayDP	0.35	0.13	9	6.68	4	40.86	7.81	0.01
MarDP, MayDP	0.23	-0.02	9	7.17	4	41.50	8.45	0.00
MarDP, AprDP, MayDP	0.68	0.49	9	2.96	5	45.53	12.49	0.00
AprHD, AprDP, JuneDP	0.48	0.17	9	4.85	5	49.98	16.93	0.00
MarHD, AprDP, JuneDP	0.35	-0.04	9	6.05	5	51.97	18.92	0.00
AprHD, MayDP, JuneDP	0.35	-0.04	9	6.08	5	52.01	18.97	0.00
MarHD, MayDP, JuneDP	0.07	-0.49	9	8.67	5	55.20	22.16	0.00
MarDP, AprDP, MayDP, JuneDP	0.74	0.47	9	2.46	6	67.87	34.82	0.00
MarHD, AprHD, MarDP, MayDP, JuneDP	0.45	-0.48	9	5.17	7	146.60	113.56	0.00

APPENDIX B. Environmental Correlates of Brood Abundance

Model selection to explain deviations in annual brood abundance estimates for West Virginia and Pennsylvania. Models are compared using AIC_c. Results are presented in tables for regions. The coefficient of determination (r^2) and adjusted coefficient of determination (r^2_{adj}) estimate the amount of variation explained by models, n is the sample size, SSE is the sum of squared errors, and K is the number of parameters. AIC_c is the Akaike's Information Criterion corrected for small samples, with lower AIC_c values being assigned to the most parsimonious models. The Δ_i is the difference in AIC_c values from the best (lowest value) models and ω_i represents the relative likelihood of the model compared to all other models.

Table B1. Model selection by AICc explaining annual deviations in brood abundance for the WV Eastern Panhandle region. Hard mast crop from the previous autumn (Mast) performs best relative to competing models.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
Mast	0.59	0.56	15	1786.56	3	122.45	0.00	0.36
MayDP, Mast	0.66	0.60	15	1505.5	4	123.70	1.25	0.19
MarDP, Mast	0.65	0.59	15	1538.82	4	124.03	1.58	0.16
AprDP, Mast	0.62	0.56	15	1676.65	4	125.32	2.87	0.09
JuneDP, Mast	0.61	0.55	15	1694.98	4	125.48	3.03	0.08
AprHD, Mast	0.60	0.53	15	1767.02	4	126.10	3.65	0.06
MarHD, Mast	0.60	0.53	15	1771.32	4	126.14	3.69	0.06
MarHD, AprHD, Mast	0.60	0.49	15	1756.07	5	130.68	8.23	0.01
MarDP, AprDP	0.16	0.02	15	3716.06	4	133.44	10.99	0.00
MarDP	0.12	0.05	15	3902.94	3	134.17	11.72	0.00
MarHD	0.09	0.02	15	4009.04	3	134.57	12.12	0.00
AprDP, MayDP	0.07	-0.09	15	4124.4	4	135.00	12.55	0.00
AprDP	0.05	-0.02	15	4177.56	3	135.19	12.74	0.00
AprHD	0.03	-0.04	15	4282.31	3	135.56	13.11	0.00
JuneDP	0.01	-0.06	15	4361.08	3	135.84	13.39	0.00
MayDP	0.00	-0.08	15	4411.88	3	136.01	13.56	0.00
MarDP, MayDP	0.14	0.00	15	3775.64	4	137.49	15.04	0.00
MarHD, AprHD	0.11	-0.04	15	3943.65	4	138.15	15.70	0.00
MarDP, AprDP. MayDP	0.22	0.01	15	3445.04	5	140.78	18.33	0.00
MarHD, AprDP, JuneDP	0.20	-0.02	15	3544.19	5	141.21	18.76	0.00
MarHD, MayDP, JuneDP	0.12	-0.12	15	3875.65	5	142.55	20.10	0.00
AprHD, AprDP, JuneDP	0.08	-0.16	15	4036.92	5	143.16	20.71	0.00
AprHD, MayDP, JuneDP	0.04	-0.23	15	4253.45	5	143.95	21.50	0.00
MarDP, AprDP, MayDP, JuneDP	0.22	-0.09	15	3429.93	6	146.55	24.10	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP	0.59	0.28	15	1811.93	8	154.48	32.03	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP, Mast	0.74	0.49	15	1127.5	9	161.36	38.91	0.00

Table B2. Model selection by AICc explaining annual deviations in brood abundance for the WV Mountain region. Heating degree-days in March (MarHD),combined with departure from average precipitation in April (AprDP) and June (JuneDP) performs best relative to competing models.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
MarHD, AprDP, JuneDP	0.60	0.49	15	6129.92	5	144.76	0.00	0.39
JuneDP	0.45	0.40	15	8528.13	3	145.90	1.14	0.22
JuneDP, Mast	0.53	0.45	15	7290.02	4	147.36	2.60	0.11
MarHD, Mast	0.47	0.38	15	8128.72	4	148.99	4.23	0.05
Mast	0.30	0.24	15	10836.00	3	149.49	4.73	0.04
MarDP, AprDP, MayDP, JuneDP	0.45	0.23	15	8481.39	6	149.63	4.87	0.03
MarHD, MayDP, JuneDP	0.60	0.48	15	6232.74	5	149.68	4.92	0.03
MarHD	0.26	0.20	15	11399.00	3	150.25	5.49	0.03
AprHD, Mast	0.40	0.30	15	9182.56	4	150.82	6.06	0.02
MayDP, Mast	0.38	0.27	15	9590.96	4	151.48	6.72	0.01
AprHD, AprDP, JuneDP	0.53	0.40	15	7261.38	5	151.97	7.21	0.01
AprHD, MayDP, JuneDP	0.53	0.40	15	7261.37	5	151.97	7.21	0.01
MarHD, AprHD, Mast	0.51	0.38	15	7539.98	5	152.53	7.77	0.01
MarDP, Mast	0.32	0.21	15	10440.00	4	152.75	7.99	0.01
AprHD	0.11	0.05	15	13658.00	3	152.96	8.20	0.01
AprDP	0.10	0.03	15	13832.00	3	153.15	8.39	0.01
AprDP, Mast	0.30	0.18	15	10764.00	4	153.21	8.45	0.01
MarHD, AprHD	0.29	0.17	15	10935.00	4	153.44	8.68	0.01
MayDP	0.03	-0.04	15	14933.00	3	154.30	9.54	0.00
MarDP	0.00	-0.07	15	15349.00	3	154.71	9.95	0.00
AprDP, MayDP	0.16	0.02	15	12983.00	4	156.02	11.26	0.00
MarDP, AprDP	0.10	-0.05	15	13817.00	4	156.95	12.19	0.00
MarDP, MayDP	0.03	-0.13	15	14912.00	4	158.10	13.34	0.00
MarDP, AprDP. MayDP	0.16	-0.06	15	12878.00	5	160.56	15.80	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP	0.64	0.36	15	5608.67	8	171.43	26.67	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP, Mast	0.76	0.52	15	3680.56	9	179.11	34.35	0.00

Table B3. Model selection by AICc explaining annual deviations in brood abundance for the WV Southern region. Heating degree-days in April (AprHD) and March (MarHD) perform best relative to competing models.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
AprHD	0.24	0.19	16	4462	3	143.50	0.00	0.22
MarHD	0.22	0.17	16	4572.26	3	143.89	0.39	0.18
MarHD, AprHD	0.34	0.24	16	3858.41	4	144.81	1.31	0.12
JuneDP	0.14	0.08	16	5046.56	3	145.47	1.97	0.08
MayDP	0.10	0.03	16	5310.33	3	146.28	2.78	0.06
MarDP	0.10	0.03	16	5315.27	3	146.30	2.80	0.06
MarHD, Mast	0.25	0.14	16	4402.36	4	146.92	3.42	0.04
AprDP	0.05	-0.02	16	5585.25	3	147.09	3.59	0.04
MarDP, AprDP, MayDP, JuneDP	0.27	0.00	16	3482.68	6	147.53	4.04	0.03
Mast	0.01	-0.06	16	5836.63	3	147.80	4.30	0.03
AprDP, MayDP	0.19	0.06	16	4770.94	4	148.21	4.71	0.02
JuneDP, Mast	0.17	0.05	16	4860.27	4	148.50	5.00	0.02
MarHD, AprHD, Mast	0.37	0.21	16	3706.73	5	148.53	5.03	0.02
MayDP	0.16	0.03	16	4943.09	4	148.77	5.27	0.02
AprHD, MayDP, JuneDP	0.34	0.18	16	3858.91	5	149.17	5.68	0.01
MarDP, AprDP	0.13	-0.01	16	5131.27	4	149.37	5.87	0.01
MayDP, Mast	0.10	-0.04	16	5304.79	4	149.90	6.40	0.01
MarDP, Mast	0.10	-0.04	16	5315.01	4	149.93	6.44	0.01
AprDP, Mast	0.09	-0.05	16	5368.48	4	150.09	6.60	0.01
AprHD, AprDP, JuneDP	0.30	0.12	16	4136.82	5	150.29	6.79	0.01
MarHD, MayDP, JuneDP	0.41	0.26	16	4182.4	5	150.46	6.96	0.01
MarDP, AprDP. MayDP	0.22	0.03	16	4563.54	5	151.86	8.36	0.00
MarHD, AprDP, JuneDP	0.29	0.11	16	4293.15	5	156.21	12.72	0.00
AprHD, Mast	0.25	0.14	16	9398.41	4	159.05	15.56	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP	0.52	0.19	16	2848.95	8	164.89	21.39	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP, Mast	0.51	0.09	16	2847.97	9	176.31	32.81	0.00

Table B4. Model selection by AICc explaining annual deviations in brood abundance for the WV Western region. Heating degree-days in April (AprHD) performs best relative to competing models.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
AprHD	0.36	0.31	15	52420.00	3	173.13	0.00	0.29
JuneDP	0.26	0.20	15	60490.00	3	175.28	2.15	0.10
MarHD, AprHD	0.42	0.33	15	46991.00	4	175.31	2.18	0.10
AprHD, Mast	0.41	0.31	15	48321.00	4	175.73	2.60	0.08
MarDP, AprDP, MayDP, JuneDP	0.41	0.17	15	48402.00	6	175.76	2.63	0.08
MarHD, AprDP, JuneDP	0.39	0.23	15	49253.00	5	176.02	2.89	0.07
MarHD	0.20	0.13	15	65585.00	3	176.50	3.36	0.05
AprHD, MayDP, JuneDP	0.52	0.39	15	38972.00	5	177.17	4.04	0.04
AprHD, AprDP, JuneDP	0.52	0.39	15	39271.00	5	177.29	4.16	0.04
MayDP	0.26	0.20	15	69870.00	3	177.45	4.31	0.03
MarDP	0.00	-0.07	15	75168.00	3	178.54	5.41	0.02
JuneDP, Mast	0.28	0.16	15	58609.00	4	178.63	5.49	0.02
MayDP, Mast	0.28	0.16	15	58895.00	4	178.70	5.57	0.02
MarDP, MayDP	0.27	0.15	15	59495.00	4	178.85	5.72	0.02
Mast	0.04	-0.03	15	78123.00	3	179.12	5.98	0.01
MarHD, AprHD, Mast	0.43	0.28	15	46020.00	5	179.67	6.53	0.01
AprDP	0.14	0.08	15	81363.00	3	179.73	6.59	0.01
MarHD, MayDP, JuneDP	0.41	0.25	15	47903.00	5	180.27	7.14	0.01
MarHD, Mast	0.20	0.06	15	65585.00	4	180.31	7.18	0.01
AprDP, MayDP	0.14	0.00	15	69867.00	4	181.26	8.13	0.00
MarDP, Mast	0.09	-0.06	15	74027.00	4	182.13	9.00	0.00
MarDP, AprDP, MayDP, JuneDP	0.08	-0.08	15	75090.00	4	182.34	9.21	0.00
AprDP, Mast	0.07	-0.08	15	75814.00	4	182.49	9.35	0.00
MarDP, AprDP. MayDP	0.27	0.07	15	59487.00	5	183.52	10.39	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP	0.62	0.34	15	30556.00	8	196.86	23.73	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP, Mast	0.63	0.26	15	30146.00	9	210.65	37.52	0.00

Table B5. Model selection by AICc explaining annual deviations in brood abundance for PA TMA 1. Heating degree-days in April (AprHD) performs best relative to competing models.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
AprHD	0.40	0.34	11	81.11	3	62.62	0.00	0.63
MarHD, AprHD	0.50	0.38	11	67.17	4	65.79	3.16	0.13
AprDP	0.16	0.06	11	114.3	3	66.40	3.77	0.10
MarDP	0.01	-0.1	11	133.88	3	68.13	5.51	0.04
MayDP	0.01	-0.1	11	134.48	3	68.18	5.56	0.04
JuneDP	0.00	-0.11	11	135.34	3	68.25	5.63	0.04
MarDP, AprDP	0.17	-0.04	11	113.11	4	71.52	8.90	0.01
AprDP, MayDP	0.16	-0.05	11	114.29	4	71.63	9.01	0.01
AprHD, MayDP, JuneDP	0.52	0.32	11	64.90	5	72.74	10.12	0.00
MarDP, MayDP	0.03	-0.21	11	130.7	4	73.11	10.49	0.00
AprHD, AprDP, JuneDP	0.49	0.27	11	69.09	5	73.43	10.81	0.00
MarHD, AprDP, JuneDP	0.28	-0.02	11	97.25	5	77.19	14.57	0.00
MarDP, AprDP, MayDP	0.17	-0.19	11	112.88	5	78.83	16.21	0.00
MarHD, MayDP, JuneDP	0.06	-0.34	11	127.23	5	80.15	17.52	0.00
MarHD	0.04	-0.07	11	130.63	3	88.44	25.81	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP	0.63	0.07	11	50.17	8	135.91	73.29	0.00

Table B6. Model selection by AICc explaining annual deviations in brood abundance for PA TMA 2. Departure from average precipitation in May (MayDP) and June (JuneDP) perform best relative to competing models.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
MayDP	0.17	0.08	11	473.78	3	82.04	0.00	0.26
JuneDP	0.16	0.07	11	479.22	3	82.16	0.13	0.24
MarHD	0.02	-0.09	11	559.81	3	83.87	1.84	0.10
MarDP	0.00	-0.11	11	567.80	3	84.03	1.99	0.10
AprDP	0.00	-0.11	11	569.82	3	84.07	2.03	0.09
AprHD	0.00	-0.11	11	570.30	3	84.08	2.04	0.09
MarDP, MayDP	0.36	0.19	11	367.51	4	84.48	2.44	0.08
AprDP, MayDP	0.18	-0.03	11	469.37	4	87.17	5.14	0.02
MarHD, AprHD	0.02	-0.23	11	559.80	4	89.11	7.07	0.01
MarDP, AprDP	0.01	-0.24	11	566.50	4	89.24	7.20	0.01
MarDP, AprDP, MayDP	0.36	0.09	11	364.90	5	91.74	9.70	0.00
AprHD, MayDP, JuneDP	0.23	-0.09	11	436.37	5	93.70	11.67	0.00
MarHD, MayDP, JuneDP	0.23	-0.09	11	436.73	5	93.71	11.68	0.00
MarHD, AprDP, JuneDP	0.21	-0.13	11	451.06	5	94.07	12.03	0.00
AprHD, AprDP, JuneDP	0.20	-0.15	11	458.12	5	94.24	12.20	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP	0.47	-0.33	11	302.48	8	155.67	73.63	0.00

Table B7. Model selection by AICc explaining annual deviations in brood abundance for PA TMA 3. Model uncertainty is high and models are uninformative. All single correlate models are equally competitive.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
AprHD	0.05	-0.06	11	269.07	3	75.81	0.00	0.19
MarHD	0.01	-0.10	11	279.30	3	76.22	0.41	0.16
AprDP	0.01	-0.10	11	280.79	3	76.28	0.47	0.15
JuneDP	0.01	-0.10	11	281.13	3	76.30	0.48	0.15
MarDP	0.00	-0.11	11	282.46	3	76.35	0.53	0.15
MayDP	0.00	-0.11	11	282.92	3	76.37	0.55	0.15
MarHD, AprHD	0.06	-0.17	11	264.60	4	80.87	5.05	0.02
MarDP, AprDP	0.01	-0.24	11	280.49	4	81.51	5.70	0.01
AprDP, MayDP	0.01	-0.24	11	280.78	4	81.52	5.71	0.01
MarDP, MayDP	0.00	-0.25	11	282.01	4	81.57	5.75	0.01
AprHD, AprDP, JuneDP	0.11	-0.27	11	250.61	5	87.60	11.79	0.00
AprHD, MayDP, JuneDP	0.09	-0.30	11	256.77	5	87.87	12.06	0.00
MarHD, MayDP, JuneDP	0.03	-0.38	11	274.22	5	88.59	12.78	0.00
MarHD, AprDP, JuneDP	0.03	-0.39	11	275.59	5	88.65	12.83	0.00
MarDP, AprDP, MayDP	0.01	-0.42	11	280.43	5	88.84	13.03	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP	0.14	-1.15	11	243.81	8	153.3	77.49	0.00

B8. Model selection by AICc explaining annual deviations in brood abundance for PA TMA 4. Departure from average precipitation in May (MayDP) and June (JuneDP) perform best relative to competing models.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
MayDP	0.25	0.17	11	75.22	3	61.79	0.00	0.37
MarDP, MayDP	0.44	0.30	11	56.76	4	63.93	2.14	0.13
AprDP	0.08	-0.02	11	92.8	3	64.10	2.31	0.12
MarDP	0.04	-0.06	11	96.68	3	64.55	2.76	0.09
MarHD	0.03	-0.07	11	97.45	3	64.64	2.85	0.09
JuneDP	0.00	-0.11	11	100.87	3	65.02	3.23	0.07
AprHD	0.00	-0.11	11	100.91	3	65.02	3.23	0.07
AprDP, MayDP	0.32	0.14	11	69.14	4	66.10	4.31	0.04
MarDP, AprDP	0.09	-0.14	11	92.00	4	69.25	7.45	0.01
MarHD, AprHD	0.03	-0.21	11	97.45	4	69.88	8.09	0.01
MarDP, AprDP, MayDP	0.44	0.20	11	56.67	5	71.25	9.46	0.00
AprHD, MayDP, JuneDP	0.29	-0.01	11	71.39	5	73.79	12.00	0.00
MarHD, MayDP, JuneDP	0.29	-0.01	11	71.48	5	73.80	12.01	0.00
MarHD, AprDP, JuneDP	0.15	-0.22	11	86.19	5	75.86	14.07	0.00
AprHD, AprDP, JuneDP	0.09	-0.30	11	92.10	5	76.59	14.80	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP	0.67	0.17	11	33.63	8	131.51	69.72	0.00

Table B9. Model selection by AICc explaining annual deviations in brood abundance for PA TMA 5. Departure from average precipitation in June (JuneDP) performs best relative to competing models.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
JuneDP	0.52	0.47	11	89.54	3	63.71	0.00	0.80
MayDP	0.27	0.19	11	136.42	3	68.34	4.63	0.08
AprDP, MayDP	0.44	0.30	11	104.11	4	70.61	6.90	0.03
AprDP	0.06	-0.04	11	174.46	3	71.05	7.34	0.02
AprHD	0.02	-0.09	11	183.31	3	71.59	7.88	0.02
MarDP	0.01	-0.10	11	185.11	3	71.70	7.99	0.01
MarHD	0.00	-0.11	11	185.98	3	71.75	8.04	0.01
MarDP, MayDP	0.31	0.14	11	127.50	4	72.84	9.13	0.01
AprHD, MayDP, JuneDP	0.64	0.48	11	67.41	5	73.16	9.45	0.01
AprHD, AprDP, JuneDP	0.61	0.44	11	73.30	5	74.08	10.37	0.00
MarHD, MayDP, JuneDP	0.59	0.42	11	76.14	5	74.50	10.79	0.00
MarDP, AprDP	0.14	-0.08	11	160.93	4	75.40	11.69	0.00
MarHD, AprDP, JuneDP	0.55	0.35	11	84.56	5	75.65	11.94	0.00
MarHD, AprHD	0.02	-0.23	11	183.00	4	76.81	13.10	0.00
MarDP, AprDP, MayDP	0.44	0.20	11	104.09	5	77.94	14.23	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP	0.70	0.26	11	55.16	8	136.95	73.24	0.00

Table B10. Model selection by AICc explaining annual deviations in brood abundance for PA TMA 6. All single correlate models are competitive.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
AprHD	0.10	0.00	11	101.26	3	65.06	0.00	0.23
JuneDP	0.04	-0.07	11	108.62	3	65.83	0.77	0.16
MarDP	0.03	-0.07	11	108.96	3	65.87	0.81	0.16
AprDP	0.01	-0.10	11	111.93	3	66.16	1.10	0.13
MarHD	0.01	-0.10	11	112.19	3	66.19	1.13	0.13
MayDP	0.00	-0.11	11	112.41	3	66.21	1.15	0.13
MarHD, AprHD	0.12	-0.10	11	98.98	4	70.05	4.99	0.02
MarDP, AprDP	0.05	-0.18	11	106.61	4	70.87	5.80	0.01
MarDP, MayDP	0.03	-0.21	11	108.82	4	71.09	6.03	0.01
AprDP, MayDP	0.02	-0.22	11	110.58	4	71.27	6.21	0.01
AprHD, MayDP, JuneDP	0.15	-0.21	11	95.76	5	77.02	11.96	0.00
AprHD, AprDP, JuneDP	0.11	-0.28	11	100.81	5	77.59	12.52	0.00
MarHD, AprDP, JuneDP	0.07	-0.33	11	104.63	5	77.99	12.93	0.00
MarHD, MayDP, JuneDP	0.07	-0.33	11	105.12	5	78.05	12.98	0.00
MarDP, AprDP, MayDP	0.06	-0.35	11	106.55	5	78.19	13.13	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP	0.27	-0.82	11	82.16	8	141.33	76.27	0.00

Table B11. Model selection by AICc explaining annual deviations in brood abundance for PA TMA 7. Departure from average precipitation in March (MarDP) and April (AprDP) combined performs best relative to competing models.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
MarDP, AprDP	0.86	0.82	11	4.30	4	35.55	0.00	0.73
MarDP	0.71	0.68	11	8.71	3	38.08	2.53	0.21
MarDP, AprDP, MayDP	0.88	0.83	11	3.63	5	41.02	5.47	0.05
MarDP, MayDP	0.71	0.64	11	8.54	4	43.10	7.55	0.02
MarHD	0.38	0.31	11	18.66	3	46.46	10.91	0.00
AprHD	0.09	-0.01	11	27.33	3	50.66	15.10	0.00
MayDP	0.07	-0.03	11	27.76	3	50.83	15.28	0.00
MarHD, AprHD	0.42	0.28	11	17.28	4	50.85	15.30	0.00
JuneDP	0.03	-0.08	11	29.01	3	51.31	15.76	0.00
AprDP	0.03	-0.08	11	29.10	3	51.35	15.80	0.00
AprDP, MayDP	0.09	-0.13	11	27.14	4	55.82	20.27	0.00
MarHD, MayDP, JuneDP	0.43	0.19	11	17.05	5	58.04	22.49	0.00
MarHD, AprDP, JuneDP	0.43	0.19	11	17.07	5	58.05	22.50	0.00
AprHD, MayDP, JuneDP	0.21	-0.13	11	23.65	5	61.64	26.09	0.00
AprHD, AprDP, JuneDP	0.14	-0.22	11	25.65	5	62.53	26.98	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP	0.91	0.78	11	2.67	8	103.64	68.09	0.00

Table B12. Model selection by AICc explaining annual deviations in brood abundance for PA TMA 8. All single correlate models are competitive.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
MarDP	0.16	0.07	11	67.15	3	60.54	0.00	0.27
AprHD	0.11	0.01	11	71.35	3	61.21	0.67	0.19
JuneDP	0.06	-0.04	11	75.01	3	61.76	1.22	0.14
AprDP	0.05	-0.06	11	76.18	3	61.93	1.39	0.13
MarHD	0.00	-0.11	11	80.02	3	62.47	1.93	0.10
MayDP	0.00	-0.11	11	80.03	3	62.47	1.93	0.10
MarDP, MayDP	0.17	-0.04	11	66.48	4	65.67	5.13	0.02
MarDP, AprDP	0.16	-0.05	11	67.14	4	65.78	5.24	0.02
MarHD, AprHD	0.11	-0.11	11	71.32	4	66.45	5.90	0.01
AprDP, MayDP	0.05	-0.19	11	76.13	4	67.16	6.62	0.01
MarDP, AprDP, MayDP	0.17	-0.19	11	66.48	5	73.01	12.46	0.00
AprHD, MayDP, JuneDP	0.17	-0.19	11	66.76	5	73.05	12.51	0.00
AprHD, AprDP, JuneDP	0.16	-0.2	11	67.40	5	73.16	12.61	0.00
MarHD, AprDP, JuneDP	0.10	-0.29	11	72.34	5	73.93	13.39	0.00
MarHD, MayDP, JuneDP	0.07	-0.33	11	74.34	5	74.23	13.69	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP	0.23	-0.92	11	61.33	8	138.12	77.58	0.00

Table B13. Model selection by AICc explaining annual deviations in brood abundance for PA TMA 9. Heating degree-days in March (MarHD) performs best relative to competing models.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
MarHD	0.16	0.07	11	45.92	3	56.36	0.00	0.29
JuneDP	0.06	-0.05	11	51.61	3	57.65	1.28	0.15
AprHD	0.03	-0.08	11	53.21	3	57.99	1.62	0.13
MarDP	0.03	-0.08	11	53.3	3	58.00	1.64	0.13
MayDP	0.02	-0.09	11	53.47	3	58.04	1.67	0.12
AprDP	0.01	-0.10	11	53.99	3	58.15	1.78	0.12
MarHD, AprHD	0.18	-0.02	11	44.87	4	61.35	4.98	0.02
MarDP, MayDP	0.12	-0.10	11	48.21	4	62.14	5.77	0.02
MarDP, AprDp	0.09	-0.14	11	49.9	4	62.52	6.15	0.01
AprDP, MayDP	0.03	-0.22	11	53.27	4	63.24	6.87	0.01
MarHD, MayDP, JuneDP	0.22	-0.11	11	42.57	5	68.10	11.74	0.00
MarHD, AprDP, JuneDP	0.21	-0.13	11	43.24	5	68.27	11.91	0.00
MarDP, AprDP, MayDP	0.17	-0.18	11	45.31	5	68.79	12.42	0.00
AprHD, AprDP, JuneDP	0.15	-0.21	11	46.41	5	69.05	12.69	0.00
AprHD, MayDP, JuneDP	0.12	-0.25	11	47.89	5	69.40	13.03	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP	0.37	-0.56	11	34.2	8	131.69	75.33	0.00

APPENDIX C. Environmental Correlates of Fall Harvest Juvenile:Hen Ratios

Model selection to explain deviations in fall harvest juvenile:hen ratios for New York,Virginia, and West Virginia. Models are compared using AIC_c. Results are presented in tables for regions. The coefficient of determination (r^2) and adjusted coefficient of determination (r^2_{adj}) estimate the amount of variation explained by models, n is the sample size, SSE is the sum of squared errors, and K is the number of parameters. AIC_c is the Akaike's Information Criterion corrected for small samples, with lower AIC_c values being assigned to the most parsimonious models. The Δ_i is the difference in AIC_c values from the best (lowest value) models and ω_i represents the relative likelihood of the model compared to all other models.

Table C1. Model selection by AICc explaining annual deviations in fall harvest juvenile:hen ratios for NY DEC region 3. Departure from average precipitation in May (MayDP) and April (AprDP) performs best relative to competing models.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
MayDP	0.35	0.31	19	4.33	3	33.42	0.00	0.44
MarDP, MayDP	0.41	0.34	19	3.91	4	34.74	1.32	0.23
AprDP, MayDP	0.36	0.28	19	4.25	4	36.32	2.90	0.10
MarHD, MayDP, JuneDP	0.45	0.33	19	3.69	5	37.40	3.98	0.06
MarDP, AprDP, MayDP	0.42	0.30	19	3.86	5	38.25	4.83	0.04
AprHD, MayDP, JuneDP	0.41	0.29	19	3.92	5	38.55	5.13	0.03
JuneDP	0.13	0.07	19	5.84	3	39.11	5.68	0.03
MarDP	0.07	0.01	19	6.20	3	40.24	6.82	0.01
AprDP	0.06	0.00	19	6.26	3	40.42	7.00	0.01
MarHD	0.01	-0.05	19	6.63	3	41.52	8.09	0.01
AprHD	0.00	-0.06	19	6.68	3	41.66	8.24	0.01
MarDP, AprDP, MayDP, JuneDP	0.44	0.27	19	3.75	6	42.09	8.67	0.01
MarDP, AprDP	0.12	0.01	19	5.87	4	42.46	9.04	0.00
MarHD, AprHD	0.09	-0.03	19	6.09	4	43.16	9.74	0.00
MarHD, AprDP, JuneDP	0.23	0.06	19	5.17	5	43.81	10.38	0.00
AprHD, AprDP, JuneDP	0.19	0.02	19	5.41	5	44.67	11.25	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP	0.53	0.27	19	3.16	8	50.24	16.82	0.00

Table C2. Model selection by AICc explaining annual deviations in fall harvest juvenile:hen ratios for NY DEC region 4. Departure from average precipitation in March (MarDP) and May (MayDP) combined; MarDP; MarDP, MayDP, and April (AprDP); and MarDP and AprDP combined perform best relative to competing models.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
MarDP, MayDP	0.4	0.33	18	7.2	4	45.67	0.00	0.28
MarDP	0.28	0.23	18	8.76	3	45.83	0.17	0.26
MarDP, AprDP, MayDP	0.50	0.40	18	6.02	5	46.37	0.70	0.20
MarDP, AprDP	0.30	0.22	18	8.40	4	48.44	2.77	0.07
MayDP	0.11	0.06	18	10.72	3	49.47	3.80	0.04
AprDP, MayDP	0.24	0.15	18	9.16	4	50.00	4.33	0.03
MarDP, AprDP, MayDP, JuneDP	0.52	0.39	18	5.73	6	50.11	4.44	0.03
AprDP	0.05	-0.01	18	11.49	3	50.72	5.05	0.02
JuneDP	0.05	-0.01	18	11.50	3	50.73	5.07	0.02
AprHD	0.02	-0.03	18	11.81	3	51.21	5.54	0.02
MarHD	0.00	-0.06	18	12.07	3	51.60	5.94	0.01
MarHD, AprHD	0.02	-0.10	18	11.81	4	54.57	8.91	0.00
AprHD, MayDP, JuneDP	0.14	-0.03	18	10.34	5	56.10	10.44	0.00
MarHD, MayDP, JuneDP	0.13	-0.04	18	10.47	5	56.33	10.66	0.00
AprHD, AprDP, JuneDP	0.13	-0.04	18	10.48	5	56.35	10.68	0.00
MarHD, AprDP, JuneDP	0.11	-0.07	18	10.74	5	56.79	11.12	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP	0.54	0.31	18	5.57	8	61.97	16.30	0.00

Table C3. Model selection by AICc explaining annual deviations in fall harvest juvenile:hen ratios for NY DEC region 5. Departure from average precipitation in May (MayDP), April (AprDP), and AprDP and MayDP combined perform best relative to competing models.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
MayDP	0.19	0.15	19	13.63	3	55.21	0.00	0.32
AprDP	0.15	0.10	19	14.28	3	56.09	0.89	0.21
AprDP, MayDP	0.25	0.15	19	12.76	4	57.21	2.00	0.12
MarDP, MayDP	0.19	0.09	19	13.60	4	58.42	3.22	0.06
MarDP, AprDP	0.17	0.07	19	13.97	4	58.93	3.73	0.05
AprHD	0.01	-0.05	19	16.74	3	59.11	3.91	0.05
JuneDP	0.00	-0.06	19	16.86	3	59.25	4.04	0.04
MarDP	0.00	-0.06	19	16.91	3	59.31	4.10	0.04
MarHD	0.00	-0.06	19	16.91	3	59.31	4.10	0.04
MarDP, AprDP, MayDP	0.26	0.11	19	12.52	5	60.61	5.40	0.02
AprHD, MayDP, JuneDP	0.20	0.04	19	13.49	5	62.03	6.82	0.01
MarHD, MayDP, JuneDP	0.20	0.04	19	13.52	5	62.07	6.86	0.01
MarHD, AprHD	0.01	-0.11	19	16.74	4	62.37	7.16	0.01
MarHD, AprDP, JuneDP	0.16	-0.01	19	14.22	5	63.03	7.82	0.01
AprHD, AprDP, JuneDP	0.16	-0.01	19	14.26	5	63.08	7.87	0.01
MarDP, AprDP, MayDP, JuneDP	0.26	0.05	19	12.44	6	64.87	9.66	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP	0.27	-0.10	19	12.42	8	76.24	21.03	0.00

Table C4. Model selection by AICc explaining annual deviations in fall harvest juvenile:hen ratios for NY DEC region 6. Departure from average precipitation in June (JuneDP) performs best relative to competing models. Heating degree-days in April (AprHD), combined with departure from average precipitation in April (AprDP) and June (JuneDP), or heating degree-days in April (AprHD), combined MayDP and JuneDP perform nearly as well.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
JuneDP	0.22	0.16	19	16.71	3	59.08	0.00	0.36
AprHD, AprDP, JuneDP	0.42	0.26	19	12.37	5	60.38	1.30	0.19
AprHD, MayDP, JuneDP	0.42	0.26	19	12.40	5	60.43	1.35	0.18
AprHD	0.04	-0.04	19	20.60	3	63.06	3.98	0.05
MarDP	0.02	-0.05	19	20.91	3	63.34	4.26	0.04
MayDP	0.02	-0.06	19	21.01	3	63.43	4.35	0.04
AprDP	0.00	-0.08	19	21.35	3	63.74	4.66	0.04
MarHD	0.00	-0.08	19	21.38	3	63.76	4.68	0.03
MarHD, MayDP, JuneDP	0.23	0.02	19	16.46	5	65.81	6.73	0.01
MarHD, AprDP, JuneDP	0.22	0.01	19	16.61	5	65.98	6.90	0.01
MarHD, AprHD	0.04	-0.12	19	20.54	4	66.26	7.18	0.01
MarDP, AprDP	0.03	-0.13	19	20.67	4	66.38	7.30	0.01
MarDP, MayDP	0.03	-0.13	19	20.67	4	66.38	7.30	0.01
AprDP, MayDP	0.03	-0.13	19	20.69	4	66.40	7.32	0.01
MarDP, AprDP, MayDP, JuneDP	0.27	-0.03	19	15.69	6	69.28	10.20	0.00
MarDP, AprDP, MayDP	0.07	-0.19	19	19.99	5	69.50	10.42	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP	0.44	0.02	19	12.03	8	75.64	16.56	0.00

Table C5. Model selection by AICc explaining annual deviations in fall harvest juvenile:hen ratios for NY DEC region 7. Heating degree-days in April (AprHD) performs best relative to competing models. AprHD, combined with departure from average rainfall in May (MayDP) and June (JuneDP) performs nearly as well.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
AprHD	0.38	0.35	16	6.36	3	38.65	0.00	0.48
AprHD, MayDP, JuneDP	0.57	0.48	16	4.49	5	41.07	2.43	0.14
MayDP	0.27	0.23	16	7.50	3	41.28	2.64	0.13
MarHD, AprHD	0.40	0.33	16	6.17	4	41.80	3.15	0.10
AprDP, MayDP	0.31	0.22	16	7.18	4	44.22	5.58	0.03
AprHD, AprDP, JuneDP	0.46	0.36	16	5.54	5	44.44	5.79	0.03
MarDP, MayDP	0.28	0.19	16	7.49	4	44.90	6.25	0.02
MarHD	0.07	0.02	16	9.62	3	45.27	6.62	0.02
JuneDP	0.03	-0.03	16	10.03	3	45.93	7.29	0.01
MarDP	0.01	-0.05	16	10.23	3	46.25	7.60	0.01
AprDP	0.00	-0.05	16	10.32	3	46.39	7.74	0.01
MarHD, MayDP, JuneDP	0.35	0.22	16	6.71	5	47.50	8.86	0.01
MarDP, AprDP, MayDP	0.31	0.17	16	7.18	5	48.59	9.94	0.00
MarDP, AprDP, MayDP, JuneDP	0.02	-0.10	16	10.17	4	49.79	11.15	0.00
MarHD, AprDP, JuneDP	0.12	-0.06	16	9.13	5	52.43	13.78	0.00
MarDP, AprDP, MayDP, JuneDP	0.33	0.14	16	6.93	6	53.35	14.70	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP	0.60	0.40	16	4.11	8	60.23	21.59	0.00

Table C6. Model selection by AICc explaining annual deviations in fall harvest juvenile:hen ratios for NY DEC region 8. All single variable models are equivalent based on Δ_i.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
JuneDP	0.07	0.02	19	13.94	3	55.64	0.00	0.17
AprHD	0.07	0.02	19	13.98	3	55.69	0.05	0.17
MarDP	0.06	0.01	19	14.13	3	55.89	0.26	0.15
MarHD	0.05	0.00	19	14.24	3	56.04	0.40	0.14
MayDP	0.00	-0.06	19	15.02	3	57.05	1.42	0.08
AprDP	0.00	-0.06	19	15.05	3	57.09	1.46	0.08
MarHD, AprHD	0.14	0.03	19	12.92	4	57.45	1.81	0.07
MarDP, MayDP	0.07	-0.05	19	13.98	4	58.95	3.31	0.03
MarDP, AprDP, MayDP, JuneDP	0.07	-0.05	19	14.05	4	59.04	3.41	0.03
AprHD, MayDP, JuneDP	0.19	0.02	19	12.23	5	60.16	4.53	0.02
AprDP, MayDP	0.00	-0.12	19	15.02	4	60.31	4.67	0.02
AprHD, AprDP, JuneDP	0.14	-0.03	19	12.87	5	61.13	5.50	0.01
MarHD, MayDP, JuneDP	0.12	-0.05	19	13.21	5	61.63	5.99	0.01
MarHD, AprDP, JuneDP	0.11	-0.06	19	13.31	5	61.77	6.14	0.01
MarDP, AprDP, MayDP	0.07	-0.11	19	13.92	5	62.62	6.99	0.01
MarDP, AprDP, MayDP, JuneDP	0.15	-0.09	19	12.74	6	65.33	9.69	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP	0.25	-0.12	19	11.28	8	74.41	18.78	0.00

Table C7. Model selection by AICc explaining annual deviations in fall harvest juvenile:hen ratios for NY DEC region 9. Heating degree-days in April (AprHD) performs best relative to competing models.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
AprHD	0.41	0.38	19	5.72	3	38.71	0.00	0.55
AprHD, MayDP, JuneDP	0.53	0.43	19	4.63	5	41.71	3.00	0.12
MarHD, AprHD	0.42	0.35	19	5.66	4	41.77	3.06	0.12
MayDP	0.29	0.24	19	6.98	3	42.49	3.78	0.08
AprHD, AprDP, JuneDP	0.5	0.39	19	4.94	5	42.94	4.23	0.07
AprDP, MayDP	0.29	0.2	19	6.92	4	45.59	6.88	0.02
MarDP, MayDP	0.29	0.2	19	6.95	4	45.67	6.96	0.02
JuneDP	0.12	0.07	19	8.64	3	46.55	7.84	0.01
MarHD, MayDP, JuneDP	0.32	0.19	19	6.64	5	48.56	9.85	0.00
AprDP	0.01	-0.05	19	9.73	3	48.80	10.09	0.00
MarDP	0	-0.05	19	9.75	3	48.84	10.13	0.00
MarHD	0	-0.06	19	9.78	3	48.90	10.19	0.00
MarDP, AprDP, MayDP	0.29	0.15	19	6.91	5	49.32	10.61	0.00
MarDP, AprDP, MayDP, JuneDP	0.01	-0.11	19	9.66	4	51.92	13.21	0.00
MarDP, AprDP, MayDP, JuneDP	0.31	0.11	19	6.79	6	53.37	14.66	0.00
MarHD, AprDP, JuneDP	0.13	-0.05	19	8.56	5	53.39	14.67	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP	0.56	0.34	19	4.29	8	56.04	17.33	0.00

Table C8. Model selection by AICc explaining annual deviations in fall harvest juvenile:hen ratios for the VA Northern Mountains region. All single correlate models are competitive. Heating degree-days in April (AprHD) combined with departure from average precipitation in April (AprDP) or May (MayDP) and June (JuneDP); and heating degree-days in March (MarHD) and AprHD are considered competitive as well.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
AprHD	0.13	0.09	25	36.16	3	87.32	0.00	0.25
AprHD, MayDP, JuneDP	0.29	0.19	25	29.29	5	88.06	0.75	0.17
MarDP	0.04	0.00	25	39.67	3	89.63	2.32	0.08
AprHD, AprDP, JuneDP	0.25	0.14	25	31.23	5	89.67	2.35	0.08
JuneDP	0.04	0.00	25	39.83	3	89.73	2.42	0.07
MarHD, AprHD	0.14	0.06	25	35.66	4	89.83	2.51	0.07
MarHD	0.03	0.01	25	40.16	3	89.94	2.62	0.07
MayDP	0.02	-0.02	25	40.54	3	90.18	2.86	0.06
AprDP	0.01	-0.03	25	40.83	3	90.35	3.04	0.05
MarDP, AprDP, MayDP, JuneDP	0.07	-0.01	25	38.48	4	91.73	4.41	0.03
MarDP, MayDP	0.04	-0.04	25	39.57	4	92.43	5.11	0.02
AprDP, MayDP	0.04	-0.05	25	39.81	4	92.58	5.26	0.02
MarHD, MayDP, JuneDP	0.14	0.02	25	35.70	5	93.01	5.69	0.01
MarHD, AprDP, JuneDP	0.10	-0.03	25	37.27	5	94.09	6.77	0.01
MarDP, AprDP, MayDP	0.07	-0.06	25	38.40	5	94.83	7.52	0.01
MarDP, AprDP, MayDP, JuneDP	0.11	-0.06	25	36.70	6	97.21	9.89	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP	0.35	0.13	25	27.08	8	97.94	10.62	0.00

Table C9. Model selection by AICc explaining annual deviations in fall harvest juvenile:hen ratios for the VA Northern Mountains region when the previous year's mast crop is included. Heating degree-days in April (AprHD) performs best relative to competing models. AprHD combined with the previous fall's hard mast crop (Mast), and departure from average precipitation in April (AprDP) are considered competitive as well.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
AprHD	0.33	0.25	6	8.19	3	36.38	0.00	0.40
AprHD, Mast	0.55	0.42	6	5.49	4	38.38	2.00	0.15
AprDP	0.13	0.03	6	10.58	3	38.94	2.56	0.11
MarDP	0.06	-0.06	6	11.50	3	39.78	3.39	0.07
MayDP	0.04	-0.08	6	11.78	3	40.02	3.63	0.07
MarHD	0.02	-0.11	6	12.05	3	40.24	3.86	0.06
JuneDP	0.00	-0.12	6	12.17	3	40.34	3.96	0.06
Mast	0.00	-0.12	6	12.23	3	40.39	4.01	0.05
AprDP, Mast	0.25	0.04	6	9.15	4	43.49	7.11	0.01
MarDP, Mast	0.08	-0.18	6	11.27	4	45.57	9.19	0.00
MayDP, Mast	0.04	-0.24	6	11.77	4	46.01	9.63	0.00
MarHD, Mast	0.02	-0.26	6	12.03	4	46.23	9.84	0.00
JuneDP, Mast	0.01	-0.27	6	12.13	4	46.31	9.93	0.00

Table C10a. Model selection by AICc explaining annual deviations in fall harvest juvenile:hen ratios for the VA Southern Mountains region when the previous year's mast crop is excluded. All single correlate models are competitive. Departure from average precipitation in April (AprDP) and May (MayDP), and heating degree-days in March (MarHD) and April (AprHD) are considered competitive as well.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
MarHD	0.09	0.05	25	37.73	3	88.38	0.00	0.23
AprDP	0.06	0.02	25	39.01	3	89.21	0.83	0.15
JuneDP	0.04	0.00	25	39.78	3	89.70	1.32	0.12
AprHD	0.01	-0.03	25	40.88	3	90.38	2.00	0.08
MayDP	0.01	-0.03	25	40.92	3	90.41	2.03	0.08
MarDP	0.00	-0.04	25	41.43	3	90.72	2.34	0.07
AprDP, MayDP	0.10	0.02	25	37.25	4	90.92	2.54	0.06
MarHD, AprHD	0.09	0.01	25	37.61	4	91.16	2.78	0.06
MarDP, AprDP, MayDP, JuneDP	0.07	-0.02	25	38.67	4	91.85	3.47	0.04
MarHD, AprDP, JuneDP	0.15	0.03	25	34.99	5	92.51	4.13	0.03
MarDP, MayDP	0.01	-0.08	25	40.91	4	93.26	4.88	0.02
MarHD, MayDP, JuneDP	0.12	0.00	25	36.43	5	93.52	5.14	0.02
AprHD, AprDP, JuneDP	0.10	-0.02	25	37.16	5	94.01	5.63	0.01
MarDP, AprDP, MayDP	0.10	-0.02	25	37.17	5	94.02	5.64	0.01
AprHD, MayDP, JuneDP	0.06	-0.08	25	39.06	5	95.26	6.88	0.01
MarDP, AprDP, MayDP, JuneDP	0.14	-0.04	25	35.84	6	96.62	8.24	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP	0.21	-0.05	25	32.67	8	102.64	14.26	0.00

Table C10b. Model selection by AICc explaining annual deviations in fall harvest juvenile:hen ratios for the VA Southern Mountains region when the previous year's mast crop is included. All single correlate models are competitive, as is departure from average precipitation in March (MarDP) combined with Mast.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
Mast	0.23	0.14	10	2.37	3	23.98	0.00	0.25
MarDP	0.16	0.07	10	2.59	3	24.87	0.89	0.16
MarHD	0.10	-0.01	10	2.77	3	25.54	1.56	0.12
AprDP	0.09	-0.02	10	2.8	3	25.65	1.67	0.11
AprHD	0.04	-0.08	10	2.96	3	26.20	2.22	0.08
MayDP	0.00	-0.12	10	3.08	3	26.60	2.62	0.07
JuneDP	0.00	-0.12	10	3.09	3	26.63	2.65	0.07
MarDP, Mast	0.44	0.28	10	1.73	4	26.83	2.85	0.06
MarHD, Mast	0.34	0.16	10	2.03	4	28.43	4.45	0.03
MayDP, Mast	0.28	-0.07	10	2.23	4	29.37	5.39	0.02
AprHD, Mast	0.27	0.07	10	2.24	4	29.42	5.44	0.02
AprDP, Mast	0.23	0.01	10	2.37	4	29.98	6.00	0.01
JuneDP, Mast	0.23	0.01	10	2.37	4	29.98	6.00	0.01

Table C11a. Model selection by AICc explaining annual deviations in fall harvest juvenile:hen ratios for the VA Northern Piedmont region when the previous year's mast crop is excluded. All single correlate models are competitive.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
JuneDP	0.07	0.03	25	4.9	3	37.35	0.00	0.24
MayDP	0.02	-0.03	25	5.19	3	38.79	1.44	0.12
AprDP	0.01	-0.03	25	5.21	3	38.88	1.53	0.11
MarHD	0.01	-0.04	25	5.24	3	39.03	1.68	0.10
MarDP	0.00	-0.04	25	5.26	3	39.12	1.77	0.10
AprHD	0.00	-0.04	25	5.26	3	39.12	1.77	0.10
MarHD, MayDP, JuneDP	0.14	0.02	25	4.51	5	41.29	3.94	0.03
AprDP, MayDP	0.03	-0.06	25	5.13	4	41.35	4.00	0.03
MarDP, AprDP	0.02	-0.07	25	5.16	4	41.50	4.15	0.03
MarDP, MayDP	0.02	-0.07	25	5.16	4	41.50	4.15	0.03
MarHD, AprHD	0.01	-0.08	25	5.22	4	41.79	4.44	0.03
AprHD, MayDP, JuneDP	0.12	-0.01	25	4.66	5	42.11	4.76	0.02
MarHD, AprDP, JuneDP	0.11	-0.02	25	4.70	5	42.32	4.97	0.02
AprHD, AprDP, JuneDP	0.10	-0.03	25	4.76	5	42.64	5.29	0.02
MarDP, AprDP, MayDP	0.04	-0.10	25	5.06	5	44.17	6.82	0.01
MarDP, AprDP, MayDP, JuneDP	0.15	-0.02	25	4.51	6	44.80	7.45	0.01
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP	0.23	-0.03	25	4.08	8	50.63	13.28	0.00

Table C11b. Model selection by AICc explaining annual deviations in fall harvest juvenile:hen ratios for the VA Northern Piedmont region.when the previous year's mast crop is included. All single correlate models are competitive.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
JuneDP	0.10	-0.02	10	1.78	3	21.12	0.00	0.17
Mast	0.09	-0.03	10	1.81	3	21.29	0.17	0.16
MayDP	0.07	-0.05	10	1.84	3	21.45	0.33	0.14
MarHD	0.06	-0.06	10	1.86	3	21.56	0.44	0.14
MarDP	0.04	-0.08	10	1.91	3	21.82	0.70	0.12
AprHD	0.02	-0.11	10	1.94	3	21.98	0.86	0.11
AprDP	0.00	-0.12	10	1.98	3	22.18	1.06	0.10
MarHD, Mast	0.18	-0.05	10	1.62	4	26.18	5.06	0.01
AprHD, Mast	0.14	-0.10	10	1.70	4	26.66	5.54	0.01
MayDP, Mast	0.12	-0.14	10	1.75	4	26.95	5.83	0.01
JuneDP, Mast	0.12	-0.14	10	1.75	4	26.95	5.83	0.01
MarDP, Mast	0.10	-0.15	10	1.77	4	27.06	5.94	0.01
AprDP, Mast	0.10	-0.16	10	1.79	4	27.17	6.06	0.01

Table C12a. Model selection by AICc explaining annual deviations in fall harvest juvenile:hen ratios for the VA Southern Piedmont region when the previous year's mast crop is excluded. Departure from average precipitation in June (JuneDP); and heating degree-days in March (MarHD) or April (AprHD), combined with MayDP and JuneDP perform best relative to competing models.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
JuneDP	0.16	0.12	25	16.2	3	67.24	0.00	0.26
MarHD, MayDP, JuneDP	0.33	0.23	25	12.95	5	67.66	0.42	0.21
AprHD, MayDP, JuneDP	0.33	0.23	25	12.95	5	67.66	0.42	0.21
MayDP	0.06	0.02	25	18.07	3	69.97	2.73	0.07
MarHD	0.04	0.00	25	18.49	3	70.55	3.31	0.05
MarDP, AprDP, MayDP, JuneDP	0.33	0.20	25	12.89	6	71.05	3.81	0.04
MarDP	0.00	-0.04	25	19.17	3	71.45	4.21	0.03
AprHD	0.00	-0.04	25	19.2	3	71.49	4.25	0.03
AprDP	0.00	-0.04	25	19.26	3	71.57	4.33	0.03
MarDP, MayDP	0.07	-0.02	25	17.99	4	72.72	5.48	0.02
AprDP, MayDP	0.06	-0.02	25	18.07	4	72.83	5.59	0.02
MarHD, AprDP, JuneDP	0.17	0.05	25	16.04	5	73.01	5.77	0.01
AprHD, AprDP, JuneDP	0.16	0.04	25	16.13	5	73.15	5.91	0.01
MarHD, AprHD	0.04	-0.04	25	18.45	4	73.35	6.11	0.01
MarDP, AprDP	0.01	-0.09	25	19.16	4	74.29	7.05	0.01
MarDP, AprDP, MayDP	0.07	-0.07	25	17.97	5	75.85	8.61	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP	0.35	0.13	25	12.5	8	78.62	11.38	0.00

Table C12b. Model selection by AICc explaining annual deviations in fall harvest juvenile:hen ratios for the VA Southern Piedmont region.when the previous year's mast crop is included. All single correlate models are competitive.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
Mast	0.17	0.07	10	3.22	3	27.05	0.00	0.20
JuneDP	0.16	0.06	10	3.25	3	27.14	0.09	0.19
MarHD	0.16	0.06	10	3.25	3	27.14	0.09	0.19
AprHD	0.02	-0.10	10	3.81	3	28.73	1.68	0.09
MayDP	0.01	-0.11	10	3.83	3	28.78	1.73	0.08
MarDP	0.01	-0.12	10	3.86	3	28.86	1.81	0.08
AprDP	0.00	-0.12	10	3.87	3	28.88	1.84	0.08
MarHD, Mast	0.27	0.06	10	2.83	4	31.75	4.71	0.02
AprHD, Mast	0.24	0.03	10	2.93	4	32.10	5.06	0.02
MayDP, Mast	0.23	0.01	10	3.00	4	32.34	5.29	0.01
JuneDP, Mast	0.20	-0.03	10	3.12	4	32.73	5.68	0.01
AprDP, Mast	0.18	-0.06	10	3.19	4	32.95	5.91	0.01
MarDP, Mast	0.17	-0.07	10	3.22	4	33.047	6.00	0.01

Table C13a. Model selection by AICc explaining annual deviations in fall harvest juvenile:hen ratios for the VA Tidewater region when the previous year's mast crop is excluded. All single correlate models are competitive.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
AprHD	0.34	0.31	24	16.25	3	65.95	0.00	0.58
MarHD, AprHD	0.36	0.30	24	15.64	4	67.94	1.99	0.21
AprHD, AprDP, JuneDP	0.40	0.31	24	14.66	5	69.61	3.66	0.09
AprHD, MayDP, JuneDP	0.40	0.31	24	14.82	5	69.87	3.92	0.08
AprDP	0.06	0.00	24	23.44	3	74.74	8.79	0.01
MayDP	0.02	-0.02	24	24.02	3	75.33	9.38	0.01
MarHD	0.02	-0.02	24	24.10	3	75.41	9.46	0.01
JuneDP	0.02	-0.02	24	24.11	3	75.42	9.47	0.01
MarDP	0.01	-0.04	24	24.42	3	75.72	9.78	0.00
AprDP, MayDP	0.05	-0.03	24	23.26	4	77.46	11.51	0.00
MarDP, AprDP	0.05	-0.04	24	23.44	4	77.65	11.70	0.00
MarDP, MayDP	0.03	-0.06	24	23.90	4	78.11	12.16	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP	0.47	0.28	24	13.11	8	79.20	13.25	0.00
MarHD, AprDP, JuneDP	0.10	-0.03	24	22.03	5	79.39	13.44	0.00
MarHD, MayDP, JuneDP	0.06	-0.07	24	23.01	5	80.43	14.48	0.00
MarDP, AprDP, MayDP	0.05	-0.09	24	23.26	5	80.69	14.74	0.00
MarDP, AprDP, MayDP, JuneDP	0.08	-0.11	24	22.50	6	83.50	17.55	0.00

Table C13b. Model selection by AICc explaining annual deviations in fall harvest juvenile:hen ratios for the VA Tidewater region when the previous year’s mast crop is included. Heating degree-days in April (AprHD) performs best relative to competing models.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
AprHD	0.40	0.32	10	2.20	3	23.66	0.00	0.46
MarDP	0.29	0.19	10	2.61	3	25.20	1.54	0.21
Mast	0.17	0.06	9	3.18	3	26.92	3.26	0.09
MarHD	0.03	-0.10	10	3.56	3	27.99	4.33	0.05
JuneDP	0.02	-0.12	10	3.62	3	28.14	4.48	0.05
MayDP	0.01	-0.13	10	3.64	3	28.19	4.53	0.05
AprDP	0.00	-0.14	10	3.68	3	28.29	4.63	0.05
AprHD, Mast	0.44	0.25	10	2.08	4	30.36	6.70	0.02
MarDP, Mast	0.37	0.16	10	2.32	4	31.34	7.68	0.01
MarHD, Mast	0.22	-0.03	10	2.86	4	33.22	9.56	0.00
AprDP, Mast	0.19	-0.07	10	2.97	4	33.56	9.90	0.00
JuneDP, Mast	0.19	-0.08	10	2.99	4	33.62	9.96	0.00
MayDP, Mast	0.17	-0.11	10	3.06	4	33.83	10.17	0.00

Table C14. Model selection by AICc explaining annual deviations in fall harvest juvenile:hen ratios for the WV Eastern Panhandle region. All single correlate models are competitive.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
JuneDP	0.10	0.05	19	69.64	3	86.20	0.00	0.21
AprDP	0.07	0.02	19	71.53	3	86.71	0.51	0.16
MarHD	0.04	-0.02	19	74.25	3	87.42	1.22	0.11
AprHD	0.03	-0.03	19	74.83	3	87.56	1.37	0.11
MarDP	0.01	-0.05	19	76.75	3	88.04	1.85	0.08
MayDP	0.00	-0.05	19	76.95	3	88.09	1.90	0.08
MarDP, AprDp	0.10	-0.02	19	69.92	4	89.53	3.33	0.04
AprDP, MayDP	0.07	-0.04	19	71.53	4	89.96	3.77	0.03
MarHD, AprHD	0.05	-0.06	19	73.11	4	90.38	4.18	0.03
JuneDP, Mast	0.16	0.08	19	75.80	4	91.07	4.87	0.02
MarDP, MayDP	0.02	-0.10	19	75.92	4	91.10	4.90	0.02
AprHD, MayDP, JuneDP	0.19	0.03	19	62.72	5	91.22	5.03	0.02
Mast	0.01	-0.04	19	90.92	3	91.26	5.06	0.02
MarHD, AprDP, JuneDP	0.18	0.02	19	63.07	5	91.33	5.13	0.02
AprHD, AprDP, JuneDP	0.18	0.02	19	63.20	5	91.37	5.17	0.02
MarHD, MayDP, JuneDP	0.17	0.01	19	63.79	5	91.55	5.35	0.01
MarDP, AprDP, MayDP	0.10	-0.08	19	69.80	5	93.26	7.06	0.01
MarHD, Mast	0.06	-0.04	19	86.18	4	93.50	7.31	0.01
AprDP, Mast	0.02	-0.09	19	90.28	4	94.39	8.19	0.00
AprHD, Mast	0.02	-0.09	19	90.30	4	94.39	8.19	0.00
MayDP, Mast	0.02	-0.09	19	90.30	4	94.39	8.19	0.00
MarDP, Mast	0.01	-0.10	19	90.89	4	94.52	8.32	0.00
MarHD, MayDP, JuneDP, Mast	0.28	0.10	19	66.35	6	96.68	10.48	0.00
MarHD, AprDP, JuneDP, Mast	0.26	0.07	19	68.06	6	97.16	10.96	0.00
MarHD, AprDP, Mast	0.06	-0.10	19	86.08	5	97.24	11.04	0.00
AprHD, MayDP, JuneDP, Mast	0.23	0.04	19	70.86	6	97.93	11.73	0.00
AprDP, MayDP, Mast	0.02	-0.15	19	89.90	5	98.07	11.87	0.00
MarDP, MayDP, Mast	0.02	-0.15	19	90.02	5	98.09	11.89	0.00
MarDP, AprDP, Mast	0.02	-0.15	19	90.21	5	98.13	11.93	0.00
AprHD, AprDP, JunedDP, Mast	0.21	0.02	19	72.35	6	98.32	12.12	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP	0.38	0.06	19	48.26	8	102.03	15.83	0.00
MarDP, AprDP, MayDP, Mast	0.03	-0.22	19	89.59	6	102.38	16.18	0.00
MarDP, AprDP, MayDP, JuneDP, Mast	0.19	-0.08	19	74.21	7	103.99	17.79	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP, Mast	0.44	0.14	19	51.64	9	110.92	24.72	0.00

Table C15. Model selection by AICc explaining annual deviations in fall harvest juvenile:hen ratios for the WV Mountains region. All single correlate models are competitive; as is the combination of AprHD and Mast; MarHD and AprHD; AprHD, MayDP and JuneDP; MarDp and AprDP; and AprDP and MayDP.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
AprHD	0.13	0.08	22	27.18	3	74.42	0.00	0.15
AprDP	0.08	0.03	22	28.61	3	75.55	1.13	0.09
MarDP	0.07	0.02	22	28.88	3	75.75	1.33	0.08
AprHD, Mast	0.17	0.09	22	25.70	4	76.21	1.79	0.06
MayDP	0.04	0.00	22	29.74	3	76.40	1.98	0.06
MarHD, AprHD	0.16	0.07	22	26.25	4	76.67	2.25	0.05
Mast	0.03	-0.02	22	30.23	3	76.76	2.34	0.05
MarDP, MayDP	0.15	0.06	22	26.37	4	76.77	2.35	0.05
JuneDP	0.03	-0.02	22	30.28	3	76.79	2.38	0.05
AprHD, MayDP, JuneDP	0.27	0.15	22	22.70	5	76.87	2.45	0.05
MarHD	0.02	-0.03	22	30.53	3	76.98	2.56	0.04
MarDP, AprDP	0.14	0.05	22	26.73	4	77.07	2.65	0.04
AprDP, MayDP	0.13	0.04	22	27.04	4	77.32	2.91	0.04
MarDP, Mast	0.12	0.03	22	27.38	4	77.60	3.18	0.03
AprDP, Mast	0.10	0.00	22	28.06	4	78.14	3.72	0.02
MarDP, AprDP, MayDP	0.23	0.10	22	24.07	5	78.16	3.74	0.02
AprHD, AprDP, JuneDP	0.20	0.07	22	24.81	5	78.83	4.41	0.02
MarHD, AprHD, Mast	0.19	0.06	22	25.11	5	79.09	4.67	0.01
MayDP, Mast	0.06	-0.04	22	29.34	4	79.12	4.70	0.01
JuneDP, Mast	0.04	-0.06	22	29.74	4	79.42	5.00	0.01
MarHD, Mast	0.04	-0.06	22	29.88	4	79.52	5.10	0.01
MarDP, MayDP, Mast	0.17	0.04	22	25.65	5	79.56	5.14	0.01
MarDP, AprDP, Mast	0.17	0.04	22	25.68	5	79.59	5.17	0.01
AprHD, MayDP, JuneDP, Mast	0.27	0.10	22	22.59	6	80.62	6.20	0.01
MarHD, AprDP, JuneDP	0.12	-0.03	22	27.44	5	81.044	6.63	0.01
MarHD, MayDP, JuneDP	0.11	-0.04	22	27.67	5	81.23	6.81	0.01
MarDP, AprDP, MayDP, Mast	0.24	0.06	22	23.69	6	81.66	7.24	0.00
AprHD, AprDP, JuneDP, Mast	0.22	0.04	22	24.09	6	82.03	7.61	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP	0.47	0.26	22	16.43	8	83.09	8.67	0.00
MarHD, AprDP, JuneDP, Mast	0.13	-0.08	22	27.22	6	84.72	10.30	0.00
MarHD, MayDP, JuneDP, Mast	0.11	-0.10	22	27.67	6	85.08	10.66	0.00
MarDP, AprDP, MayDP, JuneDP, Mast	0.27	0.04	22	22.73	7	85.15	10.73	0.00
AprDP, MayDP, Mast	0.14	0.00	22	26.89	5	85.33	10.91	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP, Mast	0.49	0.23	22	15.96	9	88.37	13.95	0.00

Table C16. Model selection by AICc explaining annual deviations in fall harvest juvenile:hen ratios for the WV Southern region. Heating degree-days in April (AprHD) performs best relative to competing models.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
AprHD	0.44	0.40	14	68.87	3	70.43	0.00	0.58
AprHD, AprDP, JuneDP	0.64	0.53	14	44.89	5	73.54	3.11	0.12
AprHD, Mast	0.44	0.34	14	68.81	4	74.47	4.03	0.08
MarHD, AprHD	0.44	0.34	14	69.51	4	74.61	4.17	0.07
AprDP	0.12	0.04	14	109.03	3	76.87	6.43	0.02
AprHD, MayDP, JuneDP	0.51	0.37	14	60.15	5	77.64	7.20	0.02
MarDP	0.06	-0.01	14	115.50	3	77.67	7.24	0.02
MayDP	0.03	-0.06	14	120.34	3	78.25	7.81	0.01
JuneDP	0.01	-0.07	14	122.18	3	78.46	8.03	0.01
Mast	0.01	-0.07	14	122.48	3	78.49	8.06	0.01
MarHD	0.00	-0.08	14	123.52	3	78.61	8.18	0.01
MarDP, AprDP	0.24	0.11	14	93.37	4	78.74	8.31	0.01
MarHD, AprHD, Mast	0.45	0.28	14	68.38	5	79.43	9.00	0.01
AprHD, AprDP, JuneDP, Mast	0.64	0.48	14	44.38	6	79.88	9.45	0.01
AprDP, Mast	0.14	-0.01	14	106.04	4	80.52	10.09	0.00
AprDP, MayDP, Mast	0.16	-0.10	14	104.16	5	80.60	10.17	0.00
AprDP, MayDP	0.13	-0.03	14	107.80	4	80.75	10.32	0.00
MarDP, Mast	0.08	-0.08	14	113.23	4	81.44	11.01	0.00
MarDP, MayDP	0.07	-0.10	14	114.76	4	81.63	11.19	0.00
MayDP, Mast	0.04	-0.13	14	118.50	4	82.08	11.64	0.00
JuneDP, Mast	0.02	-0.16	14	120.84	4	82.35	11.92	0.00
MarHD, Mast	0.01	-0.17	14	122.39	4	82.53	12.09	0.00
MarDP, AprDP, Mast	0.30	0.09	14	86.29	5	82.69	12.26	0.00
MarDP, AprDP, MayDP	0.25	0.02	14	93.03	5	83.74	13.31	0.00
AprHD, MayDP, JuneDP, Mast	0.51	0.30	14	60.09	6	84.13	13.70	0.00
MarHD, AprDP, JuneDP	0.13	-0.13	14	106.97	5	85.70	15.26	0.00
MarDP, MayDP, Mast	0.09	-0.19	14	112.11	5	86.36	15.93	0.00
MarHD, MayDP, JuneDP	0.04	-0.25	14	118.86	5	87.17	16.74	0.00
MarDP, AprDP, MayDP, Mast	0.30	-0.01	14	86.11	6	89.16	18.73	0.00
MarHD, AprDP, JuneDP, Mast	0.17	-0.20	14	102.71	6	91.63	21.20	0.00
MarHD< MayDP, JuneDP, Mast	0.06	-0.36	14	116.53	6	93.40	22.97	0.00
MarDP, AprDP, MayDP, JuneDP, Mast	0.36	-0.03	14	78.44	7	96.52	26.09	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP	0.65	0.35	14	43.19	8	100.30	29.87	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP, Mast	0.67	0.28	14	41.01	9	117.78	47.35	0.00

Table C17. Model selection by AICc explaining annual deviations in fall harvest juvenile:hen ratios for the WV Central region. Departure from normal precipitation in March (MarDP), and Mast combined with MarDP perform best relative to competing models.

Model	r^2	r^2_{adj}	n	SSE	K	AIC_c	Δ_{AIC}	ωi
MarDP	0.29	0.23	14	68.24	3	70.31	0.00	0.38
MarDP, Mast	0.38	0.26	14	59.87	4	72.52	2.21	0.13
MarDP, MayDP	0.33	0.20	14	64.66	4	73.60	3.29	0.07
MarDP, AprDP	0.32	0.20	14	65.09	4	73.69	3.38	0.07
JuneDP	0.06	-0.01	14	89.91	3	74.17	3.86	0.05
MayDP	0.05	-0.02	14	90.94	3	74.33	4.02	0.05
Mast	0.04	-0.03	14	91.73	3	74.45	4.14	0.05
MarHD	0.01	-0.07	14	95.17	3	74.96	4.66	0.04
AprDP	0.01	-0.07	14	95.29	3	74.98	4.67	0.04
AprHD	0.00	-0.08	14	96.08	3	75.10	4.79	0.03
JuneDP, Mast	0.12	-0.04	14	84.37	4	77.32	7.01	0.01
MarDP, MayDP, Mast	0.38	0.20	14	59.20	5	77.42	7.11	0.01
MarDP, AprDP, Mast	0.38	0.20	14	59.26	5	77.43	7.12	0.01
MarDP, AprDP, MayDP	0.36	0.17	14	61.43	5	77.93	7.63	0.01
AprDP, MayDP, Mast	0.07	-0.20	14	88.98	5	78.07	7.76	0.01
MayDP, Mast	0.07	-0.10	14	89.17	4	78.10	7.79	0.01
MarHD, Mast	0.06	-0.11	14	89.99	4	78.22	7.92	0.01
AprDP, MayDP, Mast	0.06	-0.11	14	90.04	4	78.23	7.93	0.01
AprHD, Mast	0.05	-0.13	14	91.62	4	78.48	8.17	0.01
AprDP, Mast	0.04	-0.13	14	91.72	4	78.49	8.18	0.01
MarHD, AprHD	0.01	-0.17	14	95.17	4	79.01	8.70	0.00
MarHD, MayDP, JuneDP	0.14	-0.12	14	82.79	5	82.11	11.81	0.00
AprHD, MayDP, JuneDP	0.12	-0.14	14	84.16	5	82.34	12.04	0.00
MarHD, AprDP, JuneDP	0.09	-0.19	14	87.78	5	82.93	12.63	0.00
AprHD, AprDP, JuneDP	0.08	-0.20	14	88.54	5	83.05	12.75	0.00
MarHD, AprHD, Mast	0.07	-0.21	14	89.62	5	83.22	12.91	0.00
MarDP, AprDP, MayDP, Mast	0.39	0.12	14	58.31	6	83.70	13.39	0.00
MarDP, AprDP, MayDP, JuneDP, Mast	0.58	0.31	14	40.82	7	87.38	17.07	0.00
MarHD, MayDP, JuneDP, Mast	0.17	-0.20	14	79.76	6	88.09	17.78	0.00
AprHD, MayDP, JuneDP, Mast	0.15	-0.23	14	81.91	6	88.46	18.15	0.00
MarHD, AprDP, JuneDPMast	0.14	-0.24	14	82.68	6	88.59	18.28	0.00
AprHD, AprDP, JuneDP, Mast	0.12	-0.26	14	84.20	6	88.85	18.54	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP	0.62	0.30	14	36.34	8	97.88	27.58	0.00
MarHD, AprHD, MarDP, AprDP, MayDP, JuneDP, Mast	0.69	0.34	14	29.73	9	113.04	42.73	0.00

VITA

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