Abstract: Stabilization of eastern wild turkey (Meleagris gallopavo silvestris; hereafter, turkey) populations over broad scales suggests density dependence is likely operating and continued population growth is not sustainable. Biologists across the midwestern United States are interested in maintaining recent levels of turkey harvest and understanding their sustainability. Yet, specific population and harvest targets are often unspecified and causes of density dependence have not been identified. Therefore, we conducted a deterministic simulation analysis to better understand implications of different harvest objectives and importance of unknown aspects of turkey ecology for harvest management. We developed 11 dynamic population and harvest models to simulate turkey populations in food rich habitat types of mixed agricultural–forest landscapes, and used these models to evaluate robustness of combined spring–fall harvest rates producing maximum equilibrium harvests to changes in model assumptions. We developed models with different levels of complexity (e.g., ageless versus stage-structured dynamics, equal versus differential harvest vulnerabilities by sex, stage, and season) and hypothesized forms of density dependence, including continuous and threshold hen-density feedbacks on per-capita recruitment. Our analyses demonstrated that changing assumptions had strong influences on fall harvest rates that maximized total annual harvest of turkeys over spring and fall seasons (range = 0 to 34%) or total harvest of turkeys in fall seasons (range = 6 to 34%). Harvest rates that maximized spring male harvest, or harvest of adult males during spring, were not sensitive to changes in density dependence assumptions. However, spring harvest rates that maximized harvest were sensitive to assumptions about stage-specific harvest vulnerabilities when adult male harvests were maximized (range = 33.75 to 55.75%). This research demonstrates that a lack of information on forms of density dependence in turkey populations will also be problematic if management objectives relate to harvest of adult males during spring seasons. We suggest that harvest rates should be identified that are robust to structural uncertainty in the form of density dependence and implementation uncertainty associated with relative harvest vulnerabilities.

Key words: density dependence, eastern wild turkey, harvest management, hunting, Meleagris gallopavo silvestris, population compensation, recruitment compensation, sustainable harvest.

Understanding limits to sustainable harvest is a fundamental goal of renewable resource management (Hilborn et al. 1995). Classical maximum-sustained-yield (MSY) theory has been an influential paradigm in harvest management since at least the 1950s (Ricker 1954, Schaefer 1954, McCullough 1984, Caughley and Sinclair 1994, Punt and Smith 2001). This theory assumes reducing
population density away from environmental carrying capacity ($K$) invokes a density dependent increase in population-level growth rate that occurs as a result of changes to survival, recruitment, or body growth of individuals, resulting in a harvestable surplus of individuals or biomass (Hilborn et al. 1995, Ludwig 2001, Sutherland 2001). In theory, these surpluses can subsequently be harvested to maintain densities at reduced but stable levels (Caughley and Sinclair 1994, Sutherland 2001). Classical applications of MSY define yield in terms of biomass (fisheries) or number of individuals (wildlife) harvested, where limits to sustainable exploitation are exceeded (i.e., population is overexploited) when equilibrium biomass ($B$) or abundance ($N$) is reduced below levels producing maximum harvestable surplus ($B_{\text{msy}} = N_{\text{msy}} = K/2$ for logistic models; Caughley and Sinclair 1994, Ludwig 2001, Punt and Smith 2001, Mills 2007). Deterministic population models were historically used to determine maximum sustainable yields, which were then harvested using a constant-quota policy (also referred to as constant-catch policy; Larkin 1977, McCullough 1984, Punt and Smith 2001). However, constant-quota policies are widely recognized as risky because they remove a constant number of individuals and thus do not respond to changes in abundance (McCullough 1984, Caughley and Sinclair 1994, Mills 2007). In contrast, harvest models developed for wild turkeys (*Meleagris gallopavo*; hereafter, turkeys) assumed a proportional harvest strategy, where a constant fraction of the population is removed annually, sometimes with variation in actual proportions removed each year (McGhee et al. 2008).

Population models are used to identify limits to sustainable harvesting, yet subtle changes to model assumptions can have strong implications for sustainable harvest management (Sutherland and Gill 2001, Williams 2013). Studies of density dependence for terrestrial wildlife often use simple models without population structure and with composite parameters representing all ecological processes affecting growth (e.g., logistic model and its nonlinear variants; Guthery and Shaw 2013, Williams 2013). Use of relatively simple models to assess wildlife harvests is likely due in part to uncertainty about how density dependence relates to specific mechanisms of population change (i.e., structural or model uncertainty; Williams 1997) and technical difficulties of assessing density dependence with time-series data from animal populations (McCullough 1990, Wolda and Dennis 1993, Lefebvre 2009, Lefebvre and Gimenez 2013). However, subtle changes to individual ecological processes are not captured by models with composite growth parameters, and these changes can affect inferences about sustainable harvests. For instance, many harvest models in aquatic systems rely on assumptions that density dependence operates specifically through recruitment processes (e.g., stock-recruitment models; Hilborn and Walters 1992). A number of such models exist, and small changes to model form or parameter values can have strong effects on sustainable maximization of harvest (Ricker 1954, 1958; Myers 2002).

Using population models to determine appropriate levels of harvest has a long history in turkey management (Lobdell et al. 1972, Suchy et al. 1983, Porter et al. 1990, Vangilder and Kurzejeski 1995, Alpizar-Jara et al. 2001). Early population models assumed density independent dynamics, which resulted in populations that could theoretically grow without bound because populations were small relative to available habitat (Suchy et al. 1983, 1990; Vangilder and Kurzejeski 1995; Alpizar-Jara et al. 2001). These models were generally developed for short-term use to determine harvests that would allow for continued population growth during the recovery phase of turkey management, and to approximate recovering populations thought to be far below carrying capacity. Stabilization of turkey populations (Tapley et al. 2011, Eriksen et al. 2015) and recent modeling efforts (McGhee and Berksen 2007b) provided evidence that density dependence is likely operating and should be explicitly included in turkey harvest models. McGhee et al. (2008) used a simple density dependent model with composite growth parameters to estimate maximum sustainable annual and fall harvests for turkeys assuming proportional spring harvest of males (gobblers) was 15%. This assumption may have been reasonable at the time, but spring male harvests in many areas now exceed 15% (Hubbard and Vangilder 2005, Wright and Vangilder 2005, Diefenbach et al. 2012). Moreover, specific mechanisms regulating turkey populations are poorly understood, and implications of structural uncertainty for turkey harvest management remain unclear (Healy 2011).

Although causes and consequences of density dependence in turkey populations are poorly understood, research from other ground-nesting birds can suggest plausible hypotheses for types of density dependence that may operate within turkey populations, and provide evidence of its likely importance for harvest management. For example, evidence of density dependent recruitment exists for waterfowl (Sheaffer 1998) and several species of Galliformes (e.g., Rands 1987, Dobson et al. 1988, Bro et al. 2003). Similarly, studies of northern bobwhite (*Colinus virginianus*) provided evidence for density dependence operating specifically on individual processes of reproduction and survival (reviewed by DeMaso et al. 2013). If density dependence in turkey populations is operating through specific demographic processes such as recruitment, then research from other systems suggests uncertainty in causes and forms of compensatory dynamics may have strong implications for attempting to sustain large turkey harvests (Hilborn and Walters 1992, Myers 2002).

Recent research (McGhee et al. 2008) and conversations with biologists across the midwestern United States suggested managers are interested in maintaining large turkey harvests and understanding their sustainability (C. J. Parent, Michigan State University, unpublished data). In addition to structural uncertainty surrounding population dynamics, there remains uncertainty about fundamental population objectives, and many states do not specify desirable levels of population abundance or other harvest-related metrics that can be used to directly measure management success (hereafter performance metrics; Healy and Powell 2000). Similarly, it remains unclear how management tradeoffs with performance metrics other than harvest (e.g., abundance, proportion of adults in the spring harvest) change when managers attempt to maximize different types of turkey harvest (e.g., spring, fall, or...
Therefore, our objectives were to: (1) determine robustness of harvest rates producing maximum-sustainable harvests among hypothesized models of population dynamics and (2) identify tradeoffs required among management performance metrics when maximizing different types of harvest. To accomplish these objectives, we followed previous convention and assumed proportional harvesting of turkey populations (e.g., McGhee et al. 2008) and determined harvest rates that produced maximum harvests of turkeys in a population at equilibrium.

**METHODS**

**General Approach**

We used deterministic population projections to identify how changes in population dynamics affected maximum sustainable harvests of turkeys. We simulated dynamics intended to mimic populations of turkeys in food-unlimited environments with density dependence mechanisms operating specifically through recruitment processes. We simulated populations in food-unlimited environments because our primary interest was turkeys inhabiting mixed agricultural–forest landscapes with abundant food resources that are common across northern areas of turkey range. Although we lack information about specific mechanisms causing density dependence, it is widely recognized that dynamics of turkey populations at northern latitudes are influenced by annual production and recruitment of poults into the fall population (Suchy et al. 1990, Roberts et al. 1995, Rolley et al. 1998). Turkey populations in agricultural landscapes at northern latitudes also tend to have strong overwinter survival (Porter et al. 1980, Vander Haegen et al. 1988, Porter 2005, Parent et al. 2011), suggesting increases in survival from reduced densities may be unlikely. Thus, we hypothesized that density dependence operating through per-capita recruitment is a plausible scenario in fragmented but food-rich landscapes commonly inhabited by turkeys. Although we emphasized population dynamics at northern latitudes because that is where we work, sensitivities of maximum sustainable harvests to model assumptions we demonstrate have broad implications for maximizing turkey harvests more generally, given current understanding of turkey population and harvesting dynamics.

Models with density dependence operating through specific mechanisms, such as recruitment, have subtle but important differences from composite growth models like classical logistic models commonly used in wildlife management (Fig. 1). As such, model parameterizations and meaning of specific parameters associated with composite models change for models with density dependent recruitment or survival. For instance, classical logistic models specify that decreases in per-capita population growth occur as a direct result of increased density (Fig. 1), but do not indicate if these result from declining per-capita recruitment or survival rates (or both). In contrast, density dependent recruitment models assume declines in population growth with increased density are the specific result of decreasing per-capita recruitment (Ricker 1954; Fig. 1a), where subsequent natural survival is usually assumed constant, and implications for population growth patterns can be strong (Fig. 1b). As a result of these changes, many quantities of interest to managers are specified or identified in different ways. For example, environmental carrying capacity (K) is a specific parameter of classical logistic models, and MSY harvests (i.e., K/2) are determined easily by locating maximum points on plots of population-level growth against abundance. This simplistic definition of K as an input parameter is not generally the case for models with density dependence operating on individual processes of recruitment or survival (Newton 1998). Instead, K, which represents equilibrium population size in absence of harvest, is specified implicitly and located at the intersection point for total recruitment and total mortality curves (population level; Fig. 1a). Equivalently, K can be found as the population size at the intersection point for per-capita recruitment and mortality curves (individual level; Fig. 1a). Thus, K is specified indirectly through parameters of the recruitment and mortality functions (Ricker 1954), where specific details will vary with each model. Similarly, population abundance that results in maximum population growth (and thus MSY harvests) is identified as the abundance where difference between total recruitment and total mortality is maximized (Fig. 1; Ricker 1954), but this value will not necessarily equal K/2. Thus, for practical purposes, underlying assumptions and model parameters are fundamentally different when assuming density dependence is operating through a specific demographic process such as recruitment. However, changes to population growth from a composite model like the logistic growth model will depend on the specific model and values of its parameters (Fig. 1b).

We developed a set of 11 dynamic models to evaluate robustness of harvest rates maximizing equilibrium harvests to assumptions about turkey population dynamics and harvesting, including different forms of density dependence (Table 1). Models differed in functional forms of density dependence used and if they explicitly included stage-structured dynamics, stage-specific nesting rates, and differential harvest vulnerabilities by sex, stage, and hunting season. All models had the following characteristics: (1) they were discrete time, 2-sex population models with annual time steps; (2) harvest of males occurred during spring and fall seasons, whereas harvest of hens occurred during fall seasons, with additional poaching losses during spring (Kimmel and Kurzejeski 1985, Kurzejeski et al. 1987); (3) annual population sizes represented numbers of turkeys alive at the start of spring hunting seasons; (4) breeding occurred prior to spring male harvest, and thus harvesting males had no effect on poult production (except for theta-Ricker model; see Appendix A and McGhee et al. 2008); (5) poults produced in a given year were recruited into the
population at start of fall hunting seasons; and (6) harvest mortality was additive to natural mortality, and thus natural survival rates of remaining individuals were unaffected by harvesting. Additive mortality has been a common assumption for turkey harvest models (e.g., Vangilder and Kurzejeski 1995, Alpizar-Jara et al. 2001) with some empirical support in the literature (Little et al. 1990, Pack et al. 1999). This assumption would likely be further justified in agricultural landscapes, where populations are likely not limited by food availability. However, if populations were limited by available food supplies over winter, one might expect assumptions of additive mortality to be violated. If this was the case, seasonal, density dependent survival would likely affect population
Table 1. Descriptions of dynamic population models used to evaluate robustness of maximum harvests of wild turkeys to changes in forms of density dependence and model parameterizations.

<table>
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<tr>
<th>Modela</th>
<th>Model descriptions</th>
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<td>Ageless models</td>
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<td>0-R</td>
<td>Theta-Ricker model with composite growth and density dependence</td>
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<td>BH</td>
<td>Beverton–Holt model of density dependent recruitment</td>
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<td>TR</td>
<td>Threshold model of density dependent recruitment</td>
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<td>Stage-structured models</td>
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<td>BH1</td>
<td>Beverton–Holt recruitment, no stage-specific nesting, equal harvest vulnerability</td>
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<td>BH1-V</td>
<td>Beverton–Holt recruitment, no stage-specific nesting, differential harvest vulnerabilityb</td>
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<td>BH2</td>
<td>Beverton–Holt recruitment, stage-specific nesting, differential harvest vulnerability</td>
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<tr>
<td>BH2-V</td>
<td>Beverton–Holt recruitment, stage-specific nesting, differential harvest vulnerability</td>
</tr>
<tr>
<td>TR1</td>
<td>Threshold recruitment, no stage-specific nesting, equal harvest vulnerability</td>
</tr>
<tr>
<td>TR1-V</td>
<td>Threshold recruitment, no stage-specific nesting, differential harvest vulnerability</td>
</tr>
<tr>
<td>TR2</td>
<td>Threshold recruitment, stage-specific nesting, equal harvest vulnerability</td>
</tr>
<tr>
<td>TR2-V</td>
<td>Threshold recruitment, stage-specific nesting, differential harvest vulnerability</td>
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</table>

a Mathematical equations for all models of density dependence and different model parameterizations are in Methods and in Appendices A and B.
b Differential harvest vulnerabilities were defined proportional to adult male segment of the population during corresponding spring and fall hunting seasons following Vangilder and Kurzjeski (1995): juvenile male spring harvest = 0.5, juvenile male fall harvest = 2.33, juvenile hen fall harvest = 2.0, and adult hen fall harvest = 1.33 times more vulnerable than adult males.
c Stage-specific nesting assumed different nesting rates for juvenile (0.66) and adult (0.88) hen turkeys, where values for stage-specific nesting rates were generated from weighted averages of rates identified during literature review (Appendix C).

responses to harvesting because harvest could result in an increase in natural survival rates of remaining individuals overwinter (Ratikainen et al. 2008).

We modeled population dynamics and harvest for turkeys with 3 different functional forms of density dependence. We used one functional form with a composite growth parameter that did not specify density dependence as specifically affecting recruitment or survival (i.e., theta-Ricker, also called theta-logistic model in ecological literature; McGhee and Berkson 2007b). We used 2 functional forms of density dependence that assumed feedbacks on population dynamics operated specifically through recruitment of turkey poults into fall populations (Fig. 1). We modeled density dependent recruitment using 2 common stock-recruitment models from fisheries science (see chapter 7 of Hilborn and Walters 1992 for general information on stock-recruitment functions; Fig. 1). The Beverton–Holt model (Beverton and Holt 1957; hereafter BH model) represented continuous feedbacks on per-capita recruitment, whereas the hockey-stick model (Barrowman and Myers 2000) represented scenarios with threshold feedbacks on per-capita recruitment due to increased abundance of hens in the population. The BH recruitment model represented relatively strong density dependence because decreased per-capita recruitment occurs immediately at the smallest population size and acts continuously as populations grow. In contrast, the hockey-stick model assumed per-capita recruitment of poults into the fall population was constant until a threshold of hen density was reached, at which point increased density resulted in reduced per-capita recruitment. In this paper, we refer to the hockey-stick model as the TR model because it results in threshold responses for density dependent recruitment. We emphasize these models do not specify exact mechanisms of density dependence, only functional relationships. These patterns could be created by a variety of plausible mechanisms, including hen interference or spacing behavior during nesting, density dependent predation of nests or broods, and spatial heterogeneity in quality of nesting and brood-rearing habitat (Newton 1998). We discuss all mathematical details, biological meaning of all model parameters, and plausible mechanisms that could generate each model for a real turkey population in Appendices A–C.

We considered performance of a constant proportional harvest strategy, where a proportion of the population was removed each year during spring and fall seasons. We evaluated equilibrium harvests over a range of spring and fall harvest rates. Specifically, we used a grid search and varied spring and fall harvest rates for males (or adult males for models with stage-structure) from 0 to 1 in increments of 0.0025. For each combination of spring and fall harvest rates, we forward-projected population abundance until equilibrium conditions were reached. Harvest rates for other sex or stage categories were linear functions of male harvest rates. Because these simulation models were deterministic, we identified harvest rate combinations that resulted in maximum sustainable harvests to an accuracy of within 0.25% for each season. For this analysis, we calculated equilibrium harvest of all turkeys over both seasons (i.e., total annual harvest), equilibrium harvest of all males during spring seasons (i.e., spring gobbler harvest), and equilibrium harvest of adult males during spring seasons only. This allowed us to determine harvest rates resulting in maximum-sustainable harvest for the 3 different harvest objectives of total annual, total spring, and spring adult male harvests. Although not our primary interest, we also identified spring–fall harvest rates maximizing either-sex fall harvest for comparative purposes.

We calculated equilibrium values of the following population performance metrics at each of the maximum-sustainable harvest rates: abundance of turkeys at start of spring seasons, abundance of hens, and population sex ratio. We also monitored proportion of adult males in
spring harvest for models that included stage structure. We did not define specific objective functions that incorporated metrics other than harvests because management objectives will likely vary by location and resource agency. Rather, our modeling assumed fundamental objectives for a given population would be some unspecified function of harvest and the population performance metrics we monitored. This allowed comparison of relevant performance metrics when different types of harvest were maximized, and should facilitate further discussion and aid clarification of fundamental objectives for turkey management.

**Ageless Models**

We developed 3 models without specific designation of age classes to represent population dynamics with density dependence (Table 1, Appendix A). These models assumed no age structure in dynamics, equal production of male and female pouls, equal harvest vulnerability for all males during spring seasons, and equal harvest vulnerability for all turkeys during fall seasons. The theta-Ricker model included composite density dependence that modified population growth as a function of population size for each sex. We used the following general equations to simulate dynamics under the theta-Ricker model:

\[ N_{female,t+1} = N_{female,t}(1 - p) \times \text{growth}_{f,t} - H_{f,\text{fall},t} \]

\[ N_{male,t+1} = N_{male,t} \times \text{growth}_{m,t} - H_{m,\text{spring},t} - H_{m,\text{fall},t} \]

Where:

\[ H_{f,\text{fall},t} = N_{female,t}(1 - p) \times \text{growth}_{f,t} \times h_{f,\text{fall}} \]

\[ H_{m,\text{spring},t} = N_{male,t} \times h_{m,\text{spring}} \]

\[ H_{m,\text{fall},t} = [N_{male,t} \times \text{growth}_{m,t} - H_{m,\text{spring},t}] \times h_{m,\text{fall}}. \]

For this model, \( p \) represents hen poaching rate during spring male season, \( h_{i,j} \) represents proportional harvest rate for sex \( i \) in season \( j \), and \( H_{i,j,t} \) is number of harvested turkeys of sex \( i \) during season \( j \) at time \( t \). We assumed \( p = 0.05 \) for all models following McGhee et al. (2008); this value was also consistent with poaching rates reported by earlier studies (e.g., Vangilder and Kurzejeski 1995, Pack et al. 1999). We determined sex-specific functions representing new population growth at time \( t \) (i.e., \( \text{growth}_{i,t} \)) using nonlinear growth functions assumed by the theta-Ricker model (Appendix A). A theta-Ricker model for turkeys was originally developed and simulated by McGhee and Berkson (2007b) and McGhee et al. (2008). However, we made 2 corrections to model equations previously described to increase biological realism (see Appendix A for mathematical details): (1) we adjusted equations of McGhee et al. (2008) such that hens poached during spring seasons cannot contribute to reproduction or to the density dependent feedback term during the current time step (which occurs after reproduction), and (2) we defined per-capita birth rates that influence sex-specific population growth in terms of numbers of each individual sex, not numbers of turkeys in the entire population (e.g., hen birth rate = \((0.5 \times \text{births})/N_f \) instead of \((0.5 \times \text{births})/(N_f + N_m) \) presented originally by McGhee [2006]). We assumed all values for specific parameters of the theta-Ricker model were identical to those used by McGhee et al. (2008). Lastly, we arbitrarily set sex-specific environmental carrying capacities \( \left(K_i\right) \) for the theta-Ricker model equal to 10,000 individuals for both sexes, producing total equilibrium abundance in absence of harvest (i.e., so-called environmental carrying capacity) of 20,000 turkeys in the population. This determined overall scale of our results, but had no influence on relative values of population performance metrics.

We developed 2 ageless models to represent population and harvesting dynamics in absence of density dependent recruitment. These models used similar assumptions as the theta-Ricker model, with the following additional assumptions: (1) per-capita recruitment of pouls into the fall population decreased over some range of hen abundance (i.e., entire range for BH model, above threshold for TR model) and (2) equal survival for male and female pouls such that numbers of recruits of each sex into the population was half the number of fall recruits. The general form of ageless models with density dependent recruitment was:

\[ N_{female,t+1} = [N_{female,t}(1 - p) + 0.5R_t - H_{f,\text{fall},t}] \times s_f \]

\[ N_{male,t+1} = [N_{male,t} + 0.5R_t - H_{m,\text{spring},t} - H_{m,\text{fall},t}] \times s_m \]

where:

\[ H_{f,\text{fall},t} = [N_{female,t}(1 - p) + 0.5R_t] \times h_{f,\text{fall}} \]

\[ H_{m,\text{spring},t} = N_{male,t} \times h_{m,\text{spring}} \]

\[ H_{m,\text{fall},t} = [N_{male,t} + 0.5R_t - H_{m,\text{spring},t}] \times h_{m,\text{fall}}. \]

In this model \( R_t \) represents recruits into the fall population at time \( t \) and \( s_i \) represents natural survival for sex \( i \); all other parameters were defined above. For these models, recruitment into the fall population was a density dependent function of hen abundance (see Appendix A for details). We assumed natural survival rates were 0.74 for males and 0.64 for females (McGhee et al. 2008), and density independent recruitment rates were 3 pouls per hen (i.e., including males and females). However, we acknowledge this simulates dynamics for a very productive turkey population as many previous harvest studies assumed a smaller number of density independent recruits per female (but see Lobdell et al. 1972, McGhee et al. 2008). Although environmental carrying capacity is not an explicit parameter of these models, we calibrated values of individual parameters governing strength of density dependence for both recruitment models to
produce the same unharvested equilibrium abundance used in the theta-Ricker model where total $K=20,000$ turkeys. We started all ageless population simulations with 10,000 turkeys each for males and females, and we used a 1,000-year population projection to ensure we reached equilibrium conditions.

**Stage-Structured Models**

We developed 8 models of stage-structured populations for turkeys in presence of density dependent recruitment (Table 1, Appendix B). For all stage-structured models, abundance represented number of turkeys in each sex- and stage-class (i.e., juvenile $\leq 1$ year old; adult $>1$ year old) at the start of annual spring hunting, and all models had the general form:

$$N_{juv,f,t+1} = [0.5R_1 - H_{juv,f,fall,t}] \times s_{juv,f}$$

$$N_{juv,m,t+1} = [0.5R_1 - H_{juv,m,fall,t}] \times s_{juv,m}$$

$$N_{ad,f,t+1} = [(1-p)N_{ad,f,t} + (1-p)N_{juv,f,t} - H_{ad,f,fall,t}] \times s_{ad,f}$$

$$N_{ad,m,t+1} = [N_{ad,m,t} - H_{ad,m,spring,t} + N_{juv,m,t} - H_{juv,m,spring,t} - H_{ad,m,fall,t}] \times s_{ad,m}$$

where:

$$H_{juv,i,fall,t} = 0.5R_i h_{juv,i,fall,t}$$

$$H_{ad,f,fall,t} = \left((1-p)N_{ad,f,t} + (1-p)N_{juv,f,t}\right) h_{ad,f,fall,t}$$

$$H_{ad,m,spring,t} = N_{ad,m,t} h_{ad,m,spring,t}$$

$$H_{juv,m,spring,t} = N_{juv,m,t} h_{juv,m,spring,t}$$

$$H_{ad,m,fall,t} = [N_{ad,m,t} + N_{juv,m,t} - H_{ad,m,spring,t} - H_{juv,m,spring,t}] h_{ad,m,fall,t}.$$

These models make similar assumptions as ageless models unless otherwise indicated and also assume that 1-year-old turkeys transition from juvenile to adult stage after their first spring season, but prior to their second fall hunting season. We produced numbers of recruits ($R_i$) for stage-structured models according to either a BH or TR model (see Appendix B for mathematical details).

We developed 4 models each with BH and TR density dependent recruitment, where each model was parameterized to accommodate hypothesized differences in nesting rates and harvest vulnerabilities (Table 1). Specifically, we developed 2 parameterizations with stage-specific nesting rates for hens and 2 parameterizations with stage and sex-specific relative harvest vulnerabilities, resulting in 4 parameter combinations for each recruitment model. Nesting was either assumed to be equal across adult and juvenile hens with no explicit rate (BH1 and TR1 models), or explicitly defined and different between stages (BH2 and TR2 models). We reviewed the literature to obtain weighted average (weighted by sample sizes reported for each study) nesting rates for juveniles ($\bar{x} = 0.66, n = 10$ studies) and adults ($\bar{x} = 0.88, n = 13$ studies; Appendix C) for BH2 and TR2 models. We assumed relative harvest vulnerabilities were equal for all males during spring and all turkeys during fall (BH1, BH2, TR1, and TR2 models), or season-, stage-, and sex-specific harvest vulnerabilities (BH1-V, BH2-V, TR1-V, and TR2-V models). All differences in relative harvest vulnerabilities followed assumptions of Vangilder and Kurzejeski (1995) because few published estimates of these values exist (but see Diefenbach et al. 2012 for estimates of stage-specific harvest rates for males during spring). Specifically, we assumed juvenile male vulnerability during spring was 0.5 that of adult males; in fall seasons, juvenile males, juvenile hens, and adult hens were assumed to be 2.33, 2.0, and 1.33 times more vulnerable than adult males, respectively.

For stage-structured models, we assumed normal survival of adults was identical to values assumed in ageless models ($s_f = 0.64, s_m = 0.74$). Although some studies reported stage-specific differences in annual survival (Vander Haegen et al. 1988, Hubbard et al. 1999), few estimates of natural survival exist for juvenile turkeys without harvest. However, Little et al. (1990) reported natural survival rates of juvenile hens in Iowa were approximately 10% less than adult natural survival rates. Thus, we assumed juvenile natural survival for both sexes was 10% less than adults. Similar to ageless models, we assumed maximum per-capita recruitment at small population sizes (i.e., prior to onset of density dependent feedbacks) was 3 total poults per hen. Stage-structured models without differential nesting rates and harvest vulnerabilities (BH1 and TR1; Table 1) had similar functional forms of recruitment dynamics as their ageless counterparts (BH and TR; Table 1), yet they still retained unique (but constant) sex and stage-specific survival rates. We calibrated all parameters that determined strength of density dependent feedbacks on per-capita recruitment to produce unharvested equilibrium abundances of 20,000 turkeys for each model. We simulated all stage-structured dynamics for 1,000 years to reach equilibrium values of all performance metrics, and started simulations with 10,000 turkeys in each sex- and stage-class (i.e., 40,000 turkeys in the population).

We programmed population models in R statistical computing language (version 3.0.3, R Core Development Team 2014) and all analysis code is available from the lead author upon request. We emphasize that this analysis was deterministic and did not assess risks of attempting to maximize harvest for a given set of objectives under stochastic conditions. Rather, our goals were to demonstrate robustness of harvest rates that would produce maximum harvests of different types to meet different management objectives. In addition, we also sought to demonstrate robustness of these harvest rates among
Table 2. Combined spring–fall proportional harvest rates that maximized total annual harvest (Annual), spring male harvest (Spring gobbler), adult male harvest during spring (Adult spring), and fall either sex harvest for 11 density dependent models for wild turkeys. Numbers therein are expressed as percentages (i.e., proportional harvest rate×100).

<table>
<thead>
<tr>
<th>Modela</th>
<th>Harvest type by season</th>
<th>Spring</th>
<th>Fall</th>
<th>Spring</th>
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<td>Ageless models</td>
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<tr>
<td>0-R</td>
<td>Annual Spring gobbler</td>
<td>99.75</td>
<td>10.50</td>
<td>99.75</td>
<td>0.00</td>
<td>0.00</td>
<td>22.75</td>
<td>0.00</td>
<td>16.50</td>
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<tr>
<td>BH</td>
<td>Adult spring</td>
<td>100.00</td>
<td>6.75</td>
<td>100.00</td>
<td>0.00</td>
<td>0.00</td>
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a General descriptions of models are found in Table 1, whereas exact mathematical details of models and assumed parameter values are found in Methods and in Appendices A and B. 
b Harvest rates presented for stage-structured models with differential harvest vulnerabilities are those of the adult male segment of the population. Harvest rates of other stage- and sex-classes are linear functions of adult male rates (see Methods or Appendix B for details). Models without differential harvest vulnerabilities have shared harvest rates for all segments of the population.

different plausible population models, as precise functional relationships resulting from mechanisms of density dependence operating in turkey populations are poorly understood.

RESULTS

Ageless Models

Harvest rates that maximized harvest changed with the underlying form of density dependence (Table 2). Changes in harvest allocation between maximizing annual harvest and spring harvest were manifested through changes to fall harvest rates. Spring harvest was maximized by only harvesting males during spring, whereas maximizing annual harvest always involved fall harvesting. Fall harvest rates that maximized annual harvest were sensitive to the underlying form of density dependence (range = 6.75 to 34.0%; Table 2). The difference between fall harvest rates that maximized annual harvest between the theta-Ricker and BH models was <4%, but differences between these models and TR models were larger (range = 23.5 to 27.25%; Table 2). The exception was for the TR model, where maximizing annual harvest came from harvest of males during spring (i.e., similar annual and spring harvests; Table 3). The exception was for the TR model, where maximizing annual harvest resulted in a larger difference between annual harvest and spring harvest totals (difference of about 19% of K). Moreover, maximizing spring harvests resulted in more turkeys on the landscape than when maximizing annual harvests, irrespective of the model for density dependence. Two of the 3 models had equilibrium abundances of greater than K/2 when maximizing spring harvest (Table 3). Similar patterns existed for abundance of only hens, where maximizing spring harvest resulted in more turkeys than when maximizing annual harvest.

Annual harvest was a nonlinear function that peaked at non-zero values (Fig. 2a). Annual harvest for the TR model was maximized on a threshold, where small increases in fall harvest rate rapidly decreased annual harvest to 0, irrespective of spring harvest rate (Fig. 2a). In contrast, curves for total spring harvest versus harvest rate (Fig. 2b) showed a linearly decreasing effect on equilibrium spring harvest with increased fall harvest rate, at least for theta-Ricker and BH models. Maximum of the spring harvest curve for the TR model was moved away from the threshold on the fall harvest axis, but a threshold still existed where increased fall harvest suddenly reduced harvest rapidly to 0 (Fig. 2b). However, equilibrium spring harvest for the TR model decreased linearly with increases in fall harvest rates below the threshold (Fig. 2b).
Stage-Structured Models

Harvest rates that maximized annual harvest, fall harvest, and spring gobbler harvest for stage-structured models changed with assumptions about population dynamics and harvesting, including the form of density dependence (Table 2). Changes in harvest allocation between maximizing annual harvest or spring harvest were again manifested through changes to fall harvest rates (Table 2). For example, fall harvest rates needed to maximize harvest ranged from 0% for maximizing spring adult male harvest (all models) to 30% for maximizing annual harvest (TR1 model; Table 2). Total spring harvests were again maximized by harvesting only males during spring, whereas fall harvests were maximized by only harvesting during fall (range = 6.00–30.00% fall harvest; Table 2). Maximizing annual harvest required fall harvesting for all but the BH recruitment model with stage-specific nesting rates (BH2). Similar to ageless models, fall harvest rates that maximized annual harvest varied with the underlying form of density dependence (range = 0.00 to 30.00%; Table 2). Inclusion of stage-specific nesting rates reduced fall harvest rates required to maximize annual harvest, and this was true for all models of density dependence (e.g., changing from BH1 to BH2 reduced fall harvest rate from 5.25% to 0.00%; Table 2). Changing assumptions about relative harvest vulnerabilities had variable effects depending on types of harvest being maximized. Harvest vulnerability had no effect on harvest rates that maximized spring male harvest irrespective of stage, but directly changed spring harvest rates required to maximize harvest of adult males during spring (range = 33.75 to 55.75%). Similarly, inclusion of differential harvest vulnerability changed fall harvest rates required to maximize annual harvest, reducing fall harvest rate for all but 1 model of density dependence (i.e., changing from BH2 to BH2-V increased fall harvest rate from 0.00% to 1.25%; Table 2).

Harvest curves for stage-structured models changed with model assumptions and types of harvest being maximized (Fig. 3). General shapes of harvest curves for annual harvest (Fig. 3a) and spring harvest (Fig. 3b) were
similar to their ageless counterparts (Fig. 2). However, inclusion of stage-structure and differential harvest vulnerabilities produced subtle but distinct effects on shapes of these curves. On the fall harvest rate axis, inclusion of stage-specific nesting resulted in harvests declining towards 0 at smaller harvest rates, and this was true for all harvest curves (Fig. 3). Similarly, adding differential harvest vulnerability to annual (Fig. 3a) and spring (Fig. 3b) harvest curves resulted in smaller fall harvest rates required to drive harvest towards 0 than corresponding models assuming equal vulnerability. For example, harvest curves for models BH2 and BH2-V (Fig. 3a) represented BH recruitment with stage-specific nesting rates, both with (BH2-V) and without (BH2) differential harvest vulnerability. When compared to their corresponding BH1 models (Fig. 3a), ascending limbs of curves on the lesser end of fall harvest rate axes were reduced, with the overall result that harvest (both annual and spring) fell to 0 more quickly as fall harvest increased. Stage-structured TR model curves were not shown to conserve space (but are available from Stevens et al. 2015). However, inclusion of stage-specific nesting rates and differential harvest vulnerability produced an analogous effect on TR models. Specifically, thresholds shown for ageless models (Fig. 2) were simply moved along the fall harvest rate axis for stage-structured TR models, where both stage-specific nesting rates and differential vulnerability reduced fall harvest rates where harvests of all types declined precipitously towards 0.

Harvest curves for adult males during spring were distinctly shaped and maximized at smaller harvest rates (Fig. 3c) during spring than total spring harvest (Table 2), illustrating the tradeoff between maximizing spring or adult spring harvest. This was reflected via peaks in harvest curves at reduced spring harvest rates for adult males (Fig. 3c), compared to greater harvest rates to maximize spring harvest (Fig. 3b). Adding stage-specific nesting rates still resulted in reduced harvest at smaller harvest rates along the fall-harvest axis, but effects of differential harvest vulnerability were more pronounced (Fig. 3c). Specifically, adding differential vulnerability increased the spring harvest rate that maximized adult male harvest, and more generally increased adult male harvest at greater spring harvest rates. This was a direct result of assumed relative vulnerabilities. In this case, more juvenile turkeys would survive to be adults in subsequent years for a given adult male harvest rate when juvenile vulnerability is half that of adults.

Equilibrium values of performance metrics from stage-structured models provided information on both abundance and stage-related management tradeoffs required to maximize different types of harvest (Table 4). Differences in equilibrium annual harvest when maximizing annual, spring, and adult spring harvest depended on the model of density dependence (Table 4). Maximizing spring harvest provided nearly as much total harvest as maximizing annual harvest under BH recruitment models (harvest was actually identical for BH1 and BH2 models; Table 4). Similarly, when annual harvest was maximized, most of this harvest was composed of males harvested during spring for BH models. Differences in equilibrium annual harvest were more pronounced for TR models of density dependence (Table 4). For example, TR1-V was the only model where annual harvest was reduced by more than half when switching from an objective of maximizing annual harvest to one maximizing spring harvest.

For most density dependence models, spring harvest was minimally decreased when switching from a more liberal maximization of annual harvest to a more conservative objective of maximizing adult male harvest during spring (Table 4). This switch actually created gains in spring harvest for 3 of 4 models with differential harvest vulnerability. Similarly, equilibrium abundances always increased when switching from maximization of annual harvest to maximization of adult male harvest during spring, but magnitude of increases changed among models (greater change in abundance for TR models; Table 4). Moreover, switching from an objective function maximizing annual harvest to one maximizing spring harvest irrespective of stage usually resulted in larger abundances (but see model BH2; Table 4). Maximizing harvest of adult males during spring always resulted in largest proportion of adults in spring harvest for a given density dependence model, but magnitudes of differences among objectives depended on assumptions about harvest vulnerability. Specifically, when maximizing annual or spring harvest, including differential harvest vulnerability between adult and juvenile males always allowed for adult males in subsequent spring harvests, and thus differences in proportion of adults among harvest types

<table>
<thead>
<tr>
<th>Harvest type by model</th>
<th>Performance metrics</th>
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<td></td>
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\( a \) General descriptions of models are found in Table 1, whereas exact mathematical details of models and assumed parameter values are found in Methods and in Appendices A and B.

\( b \) Values of performance metrics are expressed as proportions of environmental carrying capacity for each model (i.e., proportion of 20,000).
Table 4. Equilibrium values of wild turkey management performance metrics when implementing proportional harvests that maximize harvest for density dependent population models with stage structure. Harvest types being maximized were annual, spring, or spring adult male harvests. Performance metrics include annual harvest of all turkeys (Annual harvest), harvest of males during spring (Spring harvest), population size (Abundance), and proportion of spring harvest that consisted of adults of each model (i.e., proportion of 20,000).

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<tr>
<th>Harvest type by model</th>
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<sup>a</sup> General descriptions of models are found in Table 1, whereas exact mathematical details of models and assumed parameter values are found in Methods and in Appendices A and B.

<sup>b</sup> Values of performance metrics other than proportion of adults in spring harvest are expressed as proportions of environmental carrying capacity for each model (i.e., proportion of 20,000).

being maximized were smaller when differential vulnerability was included.

**DISCUSSION**

**Harvest Maximization**

Our results demonstrated that harvest rates required to maximize turkey harvest were not robust across hypothesized forms of density dependence that may be operating in turkey populations. We also demonstrated that importance of these ecological assumptions were context-specific and depended on types of harvest being pursued. Changing the form of density dependence had larger effects on harvest rates when fall hunting was needed to maximize harvest. Harvest rates required to maximize annual harvest and fall harvest were affected by the form of density dependence, whereas rates that maximized spring male harvests were not. Moreover, fall harvest rates needed to maximize annual harvest varied among models. For example, a BH form of recruitment with stage-specific nesting rates (BH2) required no fall harvesting to maximize annual harvest, whereas a threshold recruitment model with no stage structure (TR) required a fall harvest rate of 34%. Similarly, fall harvest rates resulting in a maximum fall harvest varied among models. The variability in fall harvest rates that maximized annual harvest has important management implications because it is widely acknowledged that turkey population dynamics are sensitive to intensity of fall harvest. There seems to be a general agreement that fall harvest rates of <10% of the total population is sustainable (Suchy et al. 1990, Vangilder and Kurzejeski 1995, Alpizar-Jara et al. 2001, McGhee et al. 2008). However, McGhee (2006) proposed that corroboration of sustainable fall harvest results may simply be an artifact of models that mostly made identical assumptions about the form of density dependence (i.e., it did not exist). Indeed, relationships between per-capita production of young and population density are an influential determinant of levels of harvest a population can sustain (Hilborn et al. 1995). Thus, it is not surprising that previous studies reported similar sustainable fall harvests when most assumed no density dependence operating within turkey populations.

Sensitivity of fall harvest rates to structural uncertainty in the form of density dependence suggests that reliably maximizing total annual or fall harvest of turkeys will be difficult with existing information. The form of density dependence is important for maximizing annual and fall harvests, and compensation acting on specific ecological processes such as recruitment can result from multiple ecological mechanisms (Dobson et al. 1988, Newton 1998). We are not aware of any field-validated causes of density dependence that have been identified for turkeys (also see discussions by Healy and Powell [2000] and Healy [2011]), and therefore we cannot suggest insight into which population models most closely approximate reality for a given population. Although Bond et al. (2012) provided evidence for density dependence in recruitment over a 30-year period in Georgia, McGhee and Berkson (2007a) failed to detect such evidence using much shorter time series from 7 states (range = 6 to 14 years). Turkey demography and population drivers likely differ spatially among habitat types and landscapes (Vangilder 1996, Vangilder et al. 2001, Fleming and Porter 2007). Thus, it may not be
realistic to assume a single model or form of density dependence is applicable to all turkey populations. Similarly, use of a simple model to manage for MSY without knowledge of underlying causes of density dependence may not be a reliable approach to turkey harvest management. These findings reinforce suggestions by Healy and Powell (2000) that managers in most areas lack appropriate information necessary to reliably implement harvest strategies with an objective of maximizing fall harvest or annual harvest of turkeys over spring and fall seasons. Moreover, these objectives may become less relevant if fall turkey hunting effort declines over time. For instance, Tapley et al. (2011) reported a 20% decline in the number of fall hunters nationally from 2004 to 2009, but this increased somewhat (10.4%) between 2009 and 2014 (Eriksen et al. 2015).

Relative harvest vulnerabilities by stage, sex, and season also have important implications for maximizing turkey harvest. Inclusion of differential harvest vulnerability reduced fall harvest rates required to maximize an annual harvest, which was expected because our models with differential vulnerability assumed females were more vulnerable to fall harvests than males. Maximizing harvest of males during spring (irrespective of stage) was unaffected by harvest vulnerability assumptions, yet harvesting all, or nearly all, of the male population in a given spring season would clearly shift the population structure to mostly juveniles. Moreover, harvesting all of the males in a spring season could potentially cause
problems with future reproduction, as all breeders in subsequent years would be 1-year-old males. Technically, our models did not account for such effects, and it is unlikely that modern turkey hunting could remove even close to all of the male population (Lint et al. 1993). However, it is still useful to know that male harvest maximization was not affected by the model of density dependence, as spring gobbler hunting is more popular than fall hunting in many states (Eriksen et al. 2015). Furthermore, when juvenile males have reduced harvest rates in spring relative to adults (Diefenbach et al. 2012), adult males would still remain in years subsequent to large removals, and thus adult harvest could still be maintained in presence of large spring harvest rates. Indeed, including differential harvest vulnerability in our models resulted in a 65% increase in spring male harvest rate (from 33.75% to 55.75%) when the objective was to maximize adult male harvest, irrespective of the population model used. Once again, this was a function of our vulnerability assumptions where juvenile vulnerabilities to spring harvest were less than those of adult males, and thus more juveniles could survive harvest during their first spring at a given harvest rate. Clearly, information on harvest vulnerability by stage-class is necessary if managers want to maximize spring harvest constrained by maintaining a desired stage structure.

There is a paucity of published information on relative harvest vulnerabilities and causes of heterogeneity in vulnerability in different areas or through time. We assumed harvest vulnerabilities followed assumptions made by Vangilder and Kurzejeski (1995). However, they did not describe how these estimates were obtained. Diefenbach et al. (2012) used tag-recovery models to estimate harvest rates for adult and juvenile males during spring hunting in New York, Pennsylvania, and Ohio, and state-specific harvest rates for juvenile males averaged approximately half the rate of adult males. Managers in Mississippi, intentionally reduced juvenile male vulnerability during spring hunting by implementing harvest regulations severely limiting juvenile take so as to shift the age structure of harvest towards adult males (i.e., Jake harvest is only allowed for youth hunters [Butler et al. 2015]). Norman and Steffen (2003) suggested vulnerability during fall seasons may vary stochastically on an annual basis with oak (Quercus spp.) mast crops in Virginia. Roberts et al. (1995) hypothesized fall harvest vulnerability for adult females may be reduced in years of good recruitment due to an abundance of more vulnerable juveniles in the population. Moreover, some managers have suggested anecdotal observations indicate fall harvest vulnerabilities may have shifted in recent years due to an increase in archery deer hunters and their corresponding selectivity for males. Although we are unaware of published evidence of changes to fall turkey hunter selectivity patterns, these would almost certainly affect sustainability of fall turkey harvests for a given level of hunter effort because hen harvest rates could be reduced. Irrespective of vulnerability patterns for a specific region or season, more general evaluation of factors that influence vulnerability is uncommon. Indeed, many studies combined juveniles and adults when estimating harvest rates, although this was likely due to limited sample sizes with radiotagged turkeys (e.g., Vangilder and Kurzejeski 1995, Vangilder 1996, Pack et al. 1999; except see Godwin et al. 1991). Regardless, a limited understanding of relative harvest vulnerabilities by stage, sex, or season will likely complicate efforts to maximize total annual harvest or spring harvest with stage-specific constraints (i.e., in absence of specific regulations limiting juvenile harvest [Butler et al. 2015]).

Given proportional harvest rates that maximized turkey harvest were not robust to changes in assumptions about density dependence and harvest vulnerability, management efforts may be better served by focusing on developing harvest strategies that are robust to uncertainty rather than on objectives of harvest maximization. Maximum harvest rates were sensitive to our limited understanding of population dynamics and harvest vulnerabilities, yet it is likely possible to identify proportional harvest rates that do not maximize harvest but still perform well relative to management objectives under a variety of conditions. For instance, all of our spring harvest curves suggested harvest that was not strictly maximized, but that was very close to the maximum, can be achieved at spring harvest rates around half of the rate that maximizes spring harvest (Fig. 2 and 3b). If this information is combined with assumptions of greater vulnerability for adult males than juveniles during spring, then one would expect that both large spring harvest and adequate age structure can be maintained at intermediate spring harvest rates for adult males. We caution, however, that a thorough understanding of harvesting risks and tradeoffs among competing objectives (e.g., total spring versus adult spring harvest) as a function of different harvest rates would be better accomplished with a stochastic risk assessment than by our deterministic modeling. Previous harvest-policy assessments for turkeys have pursued the goal of identifying harvest rates that perform well under uncertainty (e.g., Vangilder and Kurzejeski 1995). However, our analyses demonstrate that type of uncertainties considered were likely too narrow to ensure identification of robust harvest rates. Specifically, our results suggest that structural uncertainty in the form of population dynamics and implementation uncertainty regarding harvest vulnerabilities can have implications for management that depend on harvest objectives. Modern stochastic risk-assessment methods embrace uncertainty while seeking robust approaches to harvesting (Francis and Shotton 1997, Bence et al. 2008) and future research would benefit turkey management by a more thorough assessment of harvesting risks in stochastic environments. Ideally, this would facilitate identifying proportional harvest rates that are robust to critical uncertainties identified in this study (i.e., forms of density dependence, harvest vulnerabilities).
Harvest Tradeoffs

Our modeling illustrates importance of identifying clear population and harvest objectives for turkey management as tradeoffs exist when allocating harvest between spring and fall seasons and for maximizing different types of harvest. In general, tradeoffs existed between spring and fall harvesting, where increasing fall harvest rates decreased equilibrium harvest of males during spring. For most models, equilibrium spring harvest was decreased proportionally to fall harvest rates (Fig. 2 and Fig. 3b). Thus, smaller fall harvests may not reduce spring harvests noticeably. The exception was for models with a threshold in recruitment density dependence, where decreases in equilibrium spring harvest associated with increased fall harvest rates were nonlinear (Fig. 2b). Plausibility of such thresholds will thus have a direct bearing on expected tradeoffs between fall and spring harvesting. If threshold models are plausible for turkeys, then managers should consider that there could be nonlinear thresholds where small increases in fall harvest rate result in precipitous declines in abundance. However, precise fall harvest rates where thresholds occurred depended on model details and population characteristics, and thus would probably be difficult to estimate with field data in most areas. More generally, identifying tradeoffs between fall and spring harvest is a common result in turkey harvest simulations (Alpizar-Jara et al. 2001, McGhee et al. 2008), and reflects the assumption of additive harvest mortality and the fact that a male harvested in the fall cannot be harvested again the following spring.

Although maximizing annual harvests generally resulted in largest equilibrium harvests, our analyses indicated that shifting the objective toward spring harvest maximization can result in nearly the same level of total harvest (Table 4). Most harvest was comprised of males during spring even when annual harvest was maximized. Thus, for most models, we did not observe much loss to total harvest by shifting emphasis toward maximizing harvest in spring. The exceptions were again models with thresholds in recruitment, where equilibrium annual harvest was larger when maximizing annual harvest than when maximizing spring harvest (Table 4). Thus, precise tradeoffs in total harvest and abilities to maintain nearly the same total harvest by only hunting during spring may depend on plausibility of thresholds in density dependence.

Regardless of potential changes to total harvest, increased abundance of turkeys may be a desirable outcome of focusing on spring hunting over annual harvest. Our results support previous research that suggested increased annual harvest via fall harvest is accomplished at the expense of fewer turkeys in populations during spring hunting and breeding activities (Vangilder and Kurzejeski 1995, Pack et al. 1999, Alpizar-Jara et al. 2001). Thus, harvests more heavily weighted towards spring gobble hunting are favored if maintenance of large populations is a management objective (Little et al. 1990, Suchy et al. 1990, Kurzejeski and Vangilder 1992). Similarly, our results indicate that shifting harvests even more conservatively to emphasize harvesting of adult males would further increase equilibrium population abundance. This approach would provide greater abundances and more harvest of adult males during spring, typically at the expense of smaller annual and spring harvests. Moreover, this approach to harvest management could likely be implemented via regulatory changes limiting juvenile male harvest during spring (e.g., similar to Mississippi [Butler et al. 2015]). In contrast, more liberal spring harvests may reduce male age structures to levels that may be undesirable for managers and turkey hunters (Kurzejeski and Vangilder 1992, Vangilder and Kurzejeski 1995, Paisley et al. 1996). Clarification of population objectives is therefore necessary to understand desirability of different types and magnitudes of harvest, irrespective of whether management is attempting to maximize harvest or implement harvest policies that are designed to be robust to uncertainty.

MANAGEMENT IMPLICATIONS

Our analyses demonstrated that changes to ecological assumptions affected combined spring–fall proportional harvest rates that resulted in maximum sustainable harvest for turkeys. Attempts at maximizing total annual harvest across spring and fall seasons, or maximizing fall-only harvests, are ill-advised because fall harvest rates maximizing these types of harvest were very sensitive to changes in assumptions about poorly understood attributes of population dynamics and harvest. Although including fall hunting generally only resulted in marginal increases in annual harvest, it could contribute to other management objectives, such as providing additional hunting opportunities. However, seeking to maximize annual or fall harvest, or achieving large fall harvest, may be less relevant in states where fall hunting participation has already declined and definitely where fall hunting is not legal. In these states, more emphasis will likely be placed on spring harvest. Although harvest rates that maximize spring male harvest were less sensitive to changes in population-dynamics assumptions, a precise understanding of relative harvest vulnerabilities is still necessary when management objectives relate to stage structure of male populations. This demonstrates that more data on stage-specific harvest vulnerabilities and harvest simulations that include stage structure are needed if managers seek to optimize harvest while accounting for stage composition of male harvest. Similarly, if stage-related harvest is desirable, then population models without stage structure are incapable of providing information necessary for management and, in this case, ageless models should be abandoned during harvest policy assessments for turkeys. Regardless of types of harvest being pursued, clarifying fundamental management objectives that relate to harvest and desirable levels of population abundance is warranted. Future work would benefit management by pairing carefully articulated population and harvest objectives with risk assessments.
that evaluate harvest in stochastic environments and thus attempt to identify harvest regulations that produce desirable outcomes for specific sets of objectives in the presence of critical uncertainties we identified in this study (i.e., form and magnitude of density dependence and differential harvest vulnerabilities).

ACKNOWLEDGMENTS

Funding for this work was provided by Boone and Crockett Endowment and the Quantitative Fisheries Center at Michigan State University, and the Michigan Department of Natural Resources. We thank all state agency biologists involved in the Midwest Wild Turkey Consortium for preliminary conversations about turkey harvest maximization and management. Lastly, we thank 2 anonymous reviewers for comments that improved the clarity of this manuscript substantially. This is publication number 2015-10 of the Quantitative Fisheries Center at Michigan State University.

LITERATURE CITED


the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 47:170–175.


APPENDIX A

Descriptions and mathematical details of all ageless population models developed to simulate density dependent dynamics and harvesting of wild turkey populations.

Theta-Ricker Model

The theta-Ricker model included composite density dependence that modifies growth rates as population size changes for each sex. We used the following general equation to simulate dynamics under the theta-Ricker model:

\[
N_{female,t+1} = N_{female,t}(1 - p) \times Growth_{t} - H_{female,fall,t}
\]

\[
N_{male,t+1} = N_{male,t} \times Growth_{t} - H_{male,fall,t}
\]

where:

\[
H_{female,fall,t} = N_{female,t}(1 - p) \times Growth_{t} \times h_{female,fall}
\]

\[
H_{male,fall,t} = N_{male,t} \times h_{male,fall}
\]

\[
H_{male,spring,t} = \frac{[N_{male,t} \times Growth_{t} - H_{male,spring,t}] \times h_{male,spring}}{N_{male,t} \times Growth_{t}}
\]

\[
p = \text{hen poaching rate}
\]

\[
h_{i,j} = \text{harvest rate for sex } i \text{ in season } j
\]

\[
H_{i,j,t} = \text{total harvest for sex } i \text{ in season } j \text{ at time } t.
\]

This model assumes sex-specific abundance at time \(t+1\) is a function of abundance at time \(t\). However, population compensation (i.e., density dependent feedback) is not specifically affecting recruitment or survival. Rather, the population growth term includes a density dependent feedback that modifies a sex-specific intrinsic rate of increase. A theta-Ricker model for wild turkey population dynamics was originally developed and fit by McGhee and Berkson (2007), and was used to simulate harvest dynamics by McGhee et al. (2008). The sex-specific growth term in the dynamic model equations (i.e., \(Growth_{i,t}\)) was presented by McGhee et al. (2008) as

\[
Growth_{female} = e^{r_{female} \left(1 - \left(\frac{N_{female}}{K_{female}}\right)^{\theta}\right)}
\]

\[
Growth_{male} = e^{r_{male} \left(1 - \left(\frac{N_{male}}{K_{male}}\right)^{\theta}\right)}
\]

where:

\[
\theta = \text{nonlinear density dependent feedback parameter} = 0.37
\]

\[
K_{i} = \text{environmental carrying capacity for sex } i = 10,000
\]

\(r_{i,t}\) = intrinsic rate of increase for sex \(i\) at time \(t\).

Thus, a sex-specific, density dependent feedback on population growth is induced by proportion of sex-specific carrying capacity currently alive, and a nonlinear relationship between \(r_{i,t}\) and abundance is induced by the shared theta parameter. However, the above growth equation for females allows for females poached during spring to induce density dependent reductions in population growth after they are killed, which is probably not a biologically reasonable assumption. Thus we replaced \(\frac{N_{female}}{K_{female}}\) in the female growth equation with \(\frac{B_{i}}{2(N_{male,t} + N_{female,t})}\), where \(p\) represents poaching rate as a proportion of the female population size. McGhee et al. (2008) did not present equations used for sex-specific intrinsic rates of increase \((r_{i,j})\). Rather, they stated these were natural log-scale sums of sex-specific birth and natural survival rates. However, McGhee (2006; pgs. 99–101) presented equations for sex-specific rates of increase as

\[
r_{i,j} = \ln\left(\frac{B_{i}}{2(N_{male,t} + N_{female,t}) + s_{i}}\right),
\]

where:

\[
s_{m} = \text{male natural survival rate} = 0.74
\]

\[
s_{f} = \text{female natural survival rate} = 0.64
\]

\[
B_{i} = \frac{2aN_{male,t}N_{female,t}}{N_{male,t} + N_{female,t}} = \text{number of births at time } t
\]
The equation for number of births \( B_i \) accounts for effects of skewed sex-ratio on fertilization of hens that is caused by male-biased harvesting (McGhee et al. 2008). However, parameter values used ensure there is very little effect of male-biased harvesting on future population growth until virtually all males are harvested each spring (Fig. 1 of text). In the formula for sex-specific per capita rate of increase \( r_{ij} \), number of births \( B_i \) is divided by 2 assuming an equal sex ratio at birth. However, sex-specific number of births is also divided by number of males and females in the population, precluding any interpretation as a sex-specific per capita rate and further reducing population growth associated with producing young turkeys. Thus, the above equation divides number of births by 2 to get number of births for sex \( i \) at time \( t \), but then divides number of births for sex \( i \) by number of turkeys at time \( t \) instead of the sex-specific population size at time \( t \). This makes the resulting per capita rate incorrect as it is applied to the population of a specific sex, not to total population. To correct this problem, we modified the above equations to use sex-specific per capita birth rates:

\[
\begin{align*}
    r_{f,t} &= \ln \left( \frac{0.5B_t}{(1-p)N_{f,t} + s_f} \right) \\
    r_{m,t} &= \ln \left( \frac{0.5B_t}{N_{m,t} + s_m} \right),
\end{align*}
\]

where multiplying \( N_{f,t} \) by \( 1-p \) ensures that poached hens cannot contribute to births or birth rates in the current year.

The density dependent recruitment model assumes per-capita recruitment is unaffected by number of hens until a threshold number is reached:

\[
B_i = \frac{2aN_{m,t}(1-p)N_{f,t}}{N_{m,t} + (1-p)N_{f,t}}.
\]

All other model equations and parameters values remained unchanged.

### Density Dependent Recruitment Models

We used the following general equation to simulate ageless population models for wild turkeys with density dependence specifically operating through recruitment of pullets into the fall population:

\[
\begin{align*}
N_{female,t+1} &= [N_{female,t}(1-p) + 0.5R_t - H_{f,fall,t}] \times s_f \\
N_{male,t+1} &= [N_{male,t} + 0.5R_t - H_{m,fall,t} - H_{m,spring,t}] \times s_m
\end{align*}
\]

where:

- \( s_i \) = natural survival rate for sex \( i \)
- \( R_t \) = recruits into the fall population at time \( t \)
- \( H_{f,fall,t} = [N_{female,t}(1-p) + 0.5R_t] \times h_{f,fall} \)
- \( H_{m,fall,t} = [N_{male,t} + 0.5R_t - H_{m,spring,t}] \times h_{m,fall} \)

\[
H_{m,spring,t} = N_{male,t} \times h_{m,spring}
\]

\[
H_{m,fall,t} = [N_{male,t} + 0.5R_t - H_{m,spring,t}] \times h_{m,fall}.
\]

These models assume recruitment of turkeys into the male and female segments of the population follows either a Beverton–Holt or Threshold stock-recruitment model. The Beverton–Holt model induces population compensation through recruitment via the following equation:

\[
R_t = \frac{a(1-p)N_{f,t}}{1 + b(1-p)N_{f,t}} = \text{total number of recruits at time } t
\]

- \( a \) = density independent per-capita recruitment at low \( N_{f,t} \)
- \( b \) = strength of density dependent reductions in recruitment
- \( \frac{a}{b} \) = maximum number of total recruits produced for population

We assumed the density independent number of recruits \( (a) \) was 3 turkeys per female, whereas we calibrated the density dependence parameter to produce an unharvested environmental carrying capacity of 20,000 turkeys for consistency across models \( (b = 0.0002167) \). The threshold recruitment model assumes per-capita recruitment is unaffected by number of hens until a threshold number is reached:

\[
\begin{align*}
R_t &= \begin{cases} 
    a(1-p)N_{f,t} & \text{if } (1-p)N_{f,t} < N_f^* \\
    aN_f^* & \text{if } (1-p)N_{f,t} \geq N_f^*
\end{cases}
\end{align*}
\]

- \( a \) = density independent recruits per female
- \( N_f^* \) = threshold female abundance for density dependent production

We again calibrated the parameter affecting density dependence to produce an unharvested environmental carrying capacity of 20,000 turkeys \( (N_f^* = 2883.55) \). All other simulation details are described in Methods.

### APPENDIX B

Descriptions and mathematical details of all stage-structured population models developed to simulate density dependent recruitment and harvest dynamics for wild turkeys.

### General Form of Stage-Structured Models

All stage-structured models developed took the following general form:

\[
N_{juv,f,t+1} = [0.5R_t - H_{juv,f,fall,t}] \times s_{juv,f}
\]

\[
N_{juv,m,t+1} = [0.5R_t - H_{juv,m,fall,t}] \times s_{juv,m}
\]
Maximum Sustainable Harvests of Wild Turkeys • Stevens et al.

\[ N_{ad,f,t+1} = [(1 - p)N_{ad,f,t} + (1 - p)N_{juv,f,t} - H_{ad,f,fall,t}] \times s_{ad,f} \]

\[ N_{ad,m,t+1} = [N_{ad,m,t} - H_{ad,m,spring,t} + N_{juv,m,t} - H_{juv,m,spring,t} - H_{ad,m,fall,t}] \times s_{ad,m} \]

Where:

\( R_t \) = total number of recruits into the fall population at time \( t \)

\( s_{ij} \) = natural survival rate for stage \( l \) and sex \( i \)

\( H_{l,i,j,t} \) = total harvest of stage \( l \) and sex \( i \) in season \( j \)

\( h_{l,i,j} \) = proportional harvest rate for stage \( l \) and sex \( i \) in season \( j \)

\( H_{juv,f,fall,t} = 0.5R_t h_{juv,f,fall} \)

\( H_{ad,f,fall,t} = \left( (1 - p)N_{ad,f,t} + (1 - p)N_{juv,f,t} \right) h_{ad,f,fall} \)

\( H_{ad,m,spring,t} = N_{ad,m} h_{ad,m,spring} \)

\( H_{juv,m,spring,t} = N_{juv,m} h_{juv,m,spring} \)

\[ H_{ad,m,fall,t} = [N_{ad,m,t} + N_{juv,m,t} - H_{ad,m,spring,t} - H_{juv,m,spring,t}] h_{ad,m,fall} \]

Specific models varied in their parameterizations and functional forms of density dependent recruitment, and mathematical details are described below. All density dependence parameters were calibrated to produce an environmental carrying capacity (i.e., unharvested equilibrium abundance) of 20,000 turkeys for consistency, and all models were initiated with 10,000 turkeys in each sex- and stage-class and ran for 1,000 years to ensure equilibrium conditions were obtained.

**Model BH1 – Beverton–Holt Recruitment Without Stage-Specific Nesting Rates**

This model assumed increases in number of hens during nesting results in decreased per-capita recruitment into the fall population. A number of mechanisms could result in this pattern, where one example would be interference behaviors of hens during the nesting season.

\[ R_t = \frac{aN_{f,t}}{1 + bN_{f,t}} = \text{total number of recruits at time } t \]

\( a \) = density independent per-capita recruitment at low \( N_{f,t} = 3 \)

\( b \) = density dependent feedback parameter

\( \frac{a}{b} \) = maximum number of total recruits produced for population

\[ N_{f,t} = (1 - p)N_{ad,f,t} + (1 - p)N_{juv,f,t} \]

\( N_{f,t} \) = total number of hens at time \( t \)

**Model BH2 – Beverton–Holt Recruitment With Stage-Specific Nesting Rates**

For this model, the “stock” size in the density dependent stock-recruitment relationship is defined in terms of number of nests, not number of hens. Thus, density dependent feedbacks are invoked by density of actual nests, which is a function of number of hens in the population and the stage structure. This is a biologically reasonable assumption for plausible mechanisms resulting in density dependent recruitment. For example, this could occur if density dependent nest predation resulted as a function of generalist predators encountering more nests as density increases, or if populations inhabited a landscape with strong spatial heterogeneity in quality of nesting habitat (Newton 1998). Note that stage-structured stock-recruitment models used in fisheries management commonly assume stock is defined in terms of number of eggs produced, where number of eggs per female is related to body size of an individual, and therefore the stage structure of the population influences number of eggs (and subsequently number of potential recruits, see Hilborn and Walters 1992 chapter 7). Clutch sizes reported for turkeys do not suggest that number of eggs is stage-dependent. However, stage-specific nesting rates are sometimes reported in the literature (see Appendix C for examples). Thus, our stage-specific nesting models assumed stage-structure influenced production of recruits through number of hens that initiate nesting (which dictates number of potential recruits), a more biologically realistic assumption for turkeys than feedbacks through number of total eggs.

\( f_l \) = nesting rate for stage \( l \)

\[ Nest_t = f_{juv}(1 - p)N_{juv,f,t} + f_{ad}(1 - p)N_{ad,f,t} \]

\( Nest_t \) = total number of nests at time \( t \)

\[ R_t = \frac{aN_{f,t}}{1 + bN_{f,t}} \]

\( a \) = density independent number of recruits per initiated nest = 3

\( b \) = density dependent feedback parameter

\( \frac{a}{b} \) = maximum number of total recruits produced for population.
Model TR1 – Threshold Recruitment Without Stage-Specific Nesting Rate

This model assumes density independent recruitment persists until number of hens in the population increases above a threshold number, above which per-capita number of recruits into the fall population decreases. This could happen, for example, if quality of nesting and brood-rearing habitat was relatively homogenous but spatially limited, or if there existed thresholds of hen density above which density dependent predation of nests or broods commenced.

\[ R_{t} = \begin{cases}aN_{f, t} & \text{if } N_{f, t} < N_{f}^c \\ aN_{f}^c & \text{if } N_{f, t} \geq N_{f}^c \end{cases} \]

\[ N_{f, t} = (1 - p)N_{ad, f, t} + (1 - p)N_{juv, f, t} \]

\[ a = \text{density independent number of recruits per female} \]

\[ a = 3 \]

\[ N_{f}^c = \text{threshold female abundance for density dependent recruitment} = 3307.76 \]

Model TR2 – Threshold Recruitment With Stage-Specific Nesting Rates

This model once again used number of nests to define stock size that dictates density dependence, where number of nests is a function of stage-specific nesting rates and there is a threshold density of nests above which density dependent recruitment begins. Strictly speaking, this form of density dependent recruitment could be caused by similar factors as the TR1 model, but with triggering mechanisms (i.e., spatial limitation or density dependent predation) initiated by number of nests instead of number of females in the population. For example, mechanisms whereby hens exhibit spacing behavior during nesting in a landscape with limited nesting habitat, or where density dependent nest predation is triggered by a threshold number of nests, could cause this relationship.

\[ f_{l} = \text{nesting rate of stage } l \]

\[ Nest_{t} = f_{juv}(1 - p)N_{juv, f, t} + f_{ad}(1 - p)N_{ad, f, t} \]

\[ Nest^* = \text{threshold nest abundance for density dependent recruitment} = 3307.76 \]

\[ R_{t} = \begin{cases}aNest_{t} & \text{if } Nest_{t} < Nest^* \\ aNest^* & \text{if } Nest_{t} \geq Nest^* \end{cases} \]

\[ a = \text{density independent number of recruits produced per initiated nest} = 3 \]

Models BH1-V, BH2-V, TR1-V, and TR2-V

These models are identical to the corresponding stage-structured density dependent recruitment models described above, but differ in their specific inclusion of stage- and season-specific harvest vulnerabilities. Note that all harvest vulnerabilities are defined relative to the adult male segment of the population for the corresponding season following Vangilder and Kurzejeski (1995):

\[ h_{juv, \text{spring}} = 0.5h_{ad, \text{spring}} \]

\[ h_{juv, \text{fall}} = 2.33h_{ad, \text{fall}} \]

\[ h_{juv, f, \text{fall}} = 2h_{ad, \text{fall}} \]

\[ h_{ad, f, \text{fall}} = 1.33h_{ad, \text{fall}}. \]
APPENDIX C. List of literature sources (Source), study locations by state (USA) or province (Canada; Location), juvenile and adult nesting rates, and sample sizes (n) used for weighted average and stage-specific nesting rates assumed for wild turkey population and harvest simulation models. All stage-structured models that were parameterized using stage-specific nesting rates assumed juvenile hens nested at a lower rate ($\tau = 0.66$) than adult hens ($\tau = 0.88$). We attempted to emphasize studies from northern latitudes, although the VA and WV studies were admitted primarily because they reported nesting rates by stage. We assumed all turkeys were adults for studies that failed to report the stage-structure of their samples ($n = 4$ studies).

<table>
<thead>
<tr>
<th>Source</th>
<th>Location</th>
<th>Nesting rate</th>
<th>n</th>
<th>Nesting rate</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Glidden and Austin 1975</td>
<td>NY</td>
<td>1</td>
<td>51.57</td>
<td>0.9</td>
<td>118.45</td>
</tr>
<tr>
<td>Hayden 1980</td>
<td>PA</td>
<td>0.42</td>
<td>51.57</td>
<td>0.98</td>
<td>118.45</td>
</tr>
<tr>
<td>Little and Varland 1981</td>
<td>IA</td>
<td>0.89</td>
<td>9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Porter et al. 1983</td>
<td>MN</td>
<td>0.88</td>
<td>48</td>
<td>0.96</td>
<td>27</td>
</tr>
<tr>
<td>Vangilder et al. 1987</td>
<td>MO</td>
<td>1</td>
<td>127</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vander Haegen et al. 1988</td>
<td>MA</td>
<td>0.81</td>
<td>16</td>
<td>1</td>
<td>20</td>
</tr>
<tr>
<td>Roberts et al. 1995</td>
<td>NY</td>
<td>0.89</td>
<td>52</td>
<td>0.99</td>
<td>136</td>
</tr>
<tr>
<td>Paisley et al. 1996</td>
<td>WI</td>
<td>0.79</td>
<td>56</td>
<td>0.98</td>
<td>164</td>
</tr>
<tr>
<td>Godfrey and Norman 2001</td>
<td>VA</td>
<td>0.54</td>
<td>28</td>
<td>0.78</td>
<td>68</td>
</tr>
<tr>
<td>Vangilder et al. 2001</td>
<td>MO</td>
<td>0.74</td>
<td>100</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Vangilder et al. 2001</td>
<td>MO</td>
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<td></td>
</tr>
<tr>
<td>Norman et al. 2001</td>
<td>VA–WV</td>
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<td>156</td>
<td>0.8</td>
<td>536</td>
</tr>
<tr>
<td>Nguyen et al. 2003</td>
<td>ON</td>
<td>0.42</td>
<td>5</td>
<td>0.68</td>
<td>15</td>
</tr>
<tr>
<td>Jackson et al. Unpublished</td>
<td>IA</td>
<td>0.56</td>
<td>51.57</td>
<td>0.97</td>
<td>118.45</td>
</tr>
</tbody>
</table>

$a$ Numbers obtained and cited from within Vangilder (1992).

$b$ Exact sample sizes not provided and thus average sample sizes for each category were used to avoid giving these numbers undue weight when calculating weighted average nesting rates.

Appendix C.

$c$ Vangilder et al. (2001) reported nesting rates separately for populations in 2 distinct regions of Missouri.

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**James R. Bence** is co-Director of the Quantitative Fisheries Center (QFC) and the William E. Ricker Professor of Fisheries Management in the Department of Fisheries and Wildlife at Michigan State University, where he has been on the faculty since 1994. Prior to arriving at MSU, he held a position with the National Marine Fisheries Service in Tiburon California, and received a Ph.D. in Ecology and a M.A. degree in Statistics from the University of California at Santa Barbara. Jim’s research program emphasizes population dynamics, stock assessment, and model-based evaluation of management strategies. He teaches graduate courses in fish population dynamics and non-credit courses in quantitative methods. He also works closely with management agencies, as part of the Partnership for Ecosystem Research and Management (PERM) that involves the Michigan Department of Natural Resources, the Great Lakes Fishery Commission and the Environment, USGS, and Michigan State University.
William F. Porter is the Boone and Crockett Chair of Wildlife Conservation at Michigan State University. He spent more than 30 years in Syracuse, where he and his students explored the behavior and population dynamics of wild turkeys in relation to weather and habitat. Bill is also Director of the Boone and Crockett Quantitative Wildlife Center, a group of graduate students and postdoctoral research associates dedicated to promoting the growth of science and future leadership to face the coming challenges in wildlife conservation.

Chad J. Parent is a research associate in the Boone and Crockett Quantitative Wildlife Center. Chad’s research is influenced by his experiences working with diverse landowners and natural resource agency personnel. He applies these perspectives to research to enable users of wildlife knowledge to more easily understand and adopt complex quantitative methodologies. The focus of his research integrates landscape and ecological modeling to make informed decisions about management and conservation. Currently, Chad coordinates the Midwest Wild Turkey Consortium (MWTC). The MWTC is a collaborative effort by natural resource agencies and the QWC to develop proactive conservation strategies for wild turkeys by coalescing agency perspectives with quantitative methodologies. Chad received a Ph.D. in Wildlife Science from the Caesar Kleberg Wildlife Research Institute at Texas A&M in Kingsville, and a M.S. and B.S. in Biology from the University of North Dakota.