The Journal of Wildlife Management 81(4):617–628; 2017; DOI: 10.1002/jwmg.21228

Research Article

Structural Uncertainty Limits Generality of Fall Harvest Strategies for Wild Turkeys

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ABSTRACT Wild turkey (*Meleagris gallopavo*) populations are broadly distributed, occupy a variety of habitats, and have demographic rates that are heterogeneous through space and time. Dynamics of turkey populations are sensitive to the magnitude of fall either-sex harvest, yet there have been few attempts to study performance of fall harvests systematically across a range of plausible demographic scenarios. Thus robustness of existing recommendations to structural uncertainty in population dynamics is marginally understood. We used a stochastic, sex-specific theta-logistic model to simulate performance of fall harvests (0–15%) across scenarios representing uncertainty about current rates of population productivity (3 levels), female losses during spring hunting (2 levels), and spring male harvest (3 levels), with uncertainty in the strength of density dependence as a common attribute. We demonstrated that performance of previously recommended fall harvests was not robust to changes in demographic parameters that occur within and among populations, and thus previous management recommendations may not be appropriate for all regions. Fall harvest rates capable of maintaining large populations with high probability varied from 0–6% with changes to population productivity, when median male and female spring harvests were 30% and 5%, respectively. In general, risks and management tradeoffs accompanying fall harvests were tightly linked to assumed values of population parameters, where changes to productivity and female loss had particularly strong effects on management outcomes. Specifically, reduced productivity or increased female loss decreased the ability to maintain large populations for a given fall harvest rate. Thus, fall harvest recommendations deduced from models that considered only a small portion of the demographic parameter space may not meet modern management objectives over a broader range of conditions. Moreover, our results suggest that future management could be improved by reducing structural uncertainty about turkey demography to allow for region-specific harvest strategies, or by using decision-theoretic approaches to identify harvest strategies that are robust to uncertainty about population parameters. © 2017 The Wildlife Society.

KEY WORDS density dependence, harvest management, harvest models, *Meleagris gallopavo*, population management, sustainable harvest, turkey hunting.

Restoration of wild turkey (*Meleagris gallopavo*; turkey) populations and hunting opportunities was a substantial achievement of twentieth century wildlife management (Dickson 1992, Kennamer et al. 1992, Lewis 2001). Translocation efforts, habitat improvements, and the adaptability of turkeys to farmlands resulted in growth of populations from the 1970s through early 2000s (Kurzejeski and Vangilder 1992, Tapley et al. 2001, 2007). By 2004, nearly 7 million turkeys occupied a diversity of vegetation types across North America, including many found in areas outside their historical range (Tapley et al. 2007). Restoration of turkey populations was accompanied by increased demand for hunting opportunities, and consequently harvest regulations were liberalized in many areas as populations continued to grow and expand (Healy and Powell 2000, 2001, Harris 2010). The number of turkey hunters in the United States currently exceeds 2.6 million (fall 2013 and spring 2014 combined; Ericksen et al., 2016), and turkey hunting is second in popularity only to deer hunting (measured in no. participating hunters; Harris 2010). During the first decade of the twenty-first century, however, the period of rapid population growth ended (Tapley et al. 2007, Warnke and Rolley 2007, Porter et al. 2011, Parent et al. 2016). Moreover, there is emerging evidence for broad-scale declines in recruitment of turkey poults into harvestable

Received: 11 April 2016; Accepted: 23 November 2016

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populations (Byrne et al. 2016, Casalena et al. 2016) and concerns over perceived population declines in some areas (Porter et al. 2011, Ericksen et al. 2016).

Previous studies generally deduced harvest management recommendations for turkeys using models that assumed functional forms of dynamic equations and values of model parameters used to describe populations were known (Stevens 2016); thus, they did not typically account for uncertainty about demography that is common to regional turkey management. Turkey harvest models often allowed vital rates to vary over time from an assumed distribution (Vangilder and Kurzejeski 1995), and thus typically accounted for effects of annual environmental variation on population processes (i.e., environmental uncertainty; Williams 1997). Recent harvest models also incorporated variation in realized harvest over time (McGhee et al. 2008) to reflect the limited ability of management to control the number of turkeys removed through harvesting (i.e., partial controllability; Williams 1997). Yet few have studied the implications of uncertainty about mathematical models used to represent dynamics of turkey populations (but see Suchy et al. 1983, Stevens et al. 2016), which includes uncertainty about model form and the values of specific parameters that best represent population dynamics (Francis and Shotton 1997, Reagan et al. 2002, Fieberg 2004). This uncertainty is often collectively referred to as structural uncertainty in wildlife management (Williams 1997, Connelly et al. 2005) or model uncertainty in more general contexts (Reagan et al. 2002).

Recommendations deduced from previous turkey harvest models are often extrapolated through space and time to guide management, despite limited information about demographic parameters (e.g., recruitment, survival) and functional forms of dynamics (e.g., different strengths of density dependence) for populations in many areas. Such extrapolation is by necessity because decisions are commonly made in the absence of detailed information about populations being managed at regional scales. What is potentially problematic, however, is when recommendations from previous studies are assumed to provide general guidelines for turkey harvest management despite being developed without consideration of uncertainties that are relevant to current management. Input values for parameters of turkey harvest models were often generated from radio-telemetry studies conducted over short duration and at local geographic scales (Roberts et al. 1995, Vangilder and Kurzejeski 1995, Rolley et al. 1998). Such studies also provided direct evidence for heterogeneity of demographic rates that occurs within and among populations, and provided insight into limitations of the current understanding of turkey demography (Warnke and Rolley 2007). Mortality rates from legal and illegal harvest differ within and among populations (Vangilder 1992, Vangilder and Kurzejeski 1995, Rolley et al. 1998, Hubbard and Vangilder 2007, Wright and Vangilder 2007), for example, and the dynamics of turkey populations at high densities are poorly understood (Warnke and Rolley 2007, Healy 2011, Porter et al. 2011). Moreover, productivity (i.e., poults/F recruited into fall population) appears to be declining in many regions (Bond et al. 2012, Casalena et al. 2016), and there are multiple as yet untested hypotheses about the causes of these declines (Byrne et al. 2016, Stevens 2016, Stevens et al. 2016). Structural uncertainty in demography is thus a ubiquitous feature of modern management, but its implications for managing turkey harvests have received little focused study.

There have been few attempts to systematically study performance of recommended harvest strategies across a range of plausible scenarios representing structural uncertainties relevant to modern turkey management (but see Rolley et al. 1998, Alpizar-Jara et al., 2001, McGhee et al. 2008 for basic sensitivity analyses). McGhee et al. (2008) recommended proportional harvest rates for maximizing turkey harvests based on results from a stochastic, density-dependent population model but generated recommendations using a single set of demographic parameters that did not account for the heterogeneity of demographic rates described by field studies. Stevens et al. (2016) assessed the implications of several hypothesized functional forms of density dependence for turkey harvest management but did so using deterministic models incapable of directly assessing risks to populations that accompany large either-sex fall harvests (Vangilder 1992, Vangilder and Kurzejeski 1995, Healy and Powell 2000, 2001). Yet, subtle changes to population model parameters or their stochastic distributions can have strong implications for quantitative assessment of risk that a harvest strategy will produce undesirable outcomes (Deroba and Bence 2008). Consequently, the generality and robustness of performance for existing fall harvest recommendations across plausible scenarios of turkey demography are not fully understood. Therefore, our objectives were to determine the generality of recent fall harvest recommendations across a range of plausible scenarios representing uncertainty in turkey population dynamics, and assess robustness of management performance over a range of fall harvest rates for these scenarios. Such assessments can aide the selection of appropriate harvest strategies when reliable estimates of population parameters are available (e.g., for a specific region), and the development of robust management strategies when they are not available.

METHODS

Population and Harvest Models

We evaluated performance of different proportional fall harvest rates using stochastic simulations. We simulated population dynamics using a sex-specific theta-logistic model with discrete annual time steps (Table 1). An analogous theta-Ricker model was first developed and applied to turkey harvest modeling by McGhee et al. (2008). The analyses of McGhee et al. (2008) focused on identifying harvest rates that maximized turkey harvests for a specific set of input parameters, and calculating the proportion of simulations that result in overharvest for a given year at different magnitudes of variation in annual population growth (environmental variation) and harvest rates (partial

Table 1. Model equations used to simulate population dynamics and fall harvest performance for wild turkeys.

Dynamic models and their equations[a]

Population model[b,c]

$$N_{m,t+1} = N_{m,t}\left(1 - h_{m,s,t}\right)e^{r_{m,t}\left(1-\left(\frac{N_{m,t}}{K_m}\right)^{\theta}\right)+\varepsilon_{p,t}} - H_{m,f,t}$$

$$N_{f,t+1} = N_{f,t}\left(1 - h_{f,s,t}\right)e^{r_{f,t}\left(1-\left(\frac{N_{f,t}}{K_f}\right)^{\theta}\right)+\varepsilon_{p,t}} - H_{f,f,t}$$

$$r_{m,t} = ln\left(\frac{0.5B_t}{N_{m,t}} + s_m\right)$$

$$r_{f,t} = ln\left(\frac{0.5B_t}{\left(1-h_{f,s,t}\right)N_{f,t}} + s_f\right)$$

$$B_t = \frac{2kN_{m,t}\left(1-h_{f,s,t}\right)N_{f,t}}{N_{m,t}+\frac{\left(1-h_{f,s,t}\right)N_{f,t}}{q}}$$

Harvest model[d,e]

$$H_{m,s,t} = N_{m,t}h_{m,s,t}$$

$$H_{m,f,t} = \left[N_{f,t}\left(1 - h_{m,s,t}\right)e^{r_{m,t}\left(1-\left(\frac{N_{m,t}}{K_m}\right)^{\theta}\right)+\varepsilon_{p,t}}\right]h_{m,f,t}$$

$$H_{f,f,t} = \left[N_{f,t}\left(1 - h_{f,s,t}\right)e^{r_{f,t}\left(1-\left(\frac{N_{f,t}}{K_f}\right)^{\theta}\right)+\varepsilon_{p,t}}\right]h_{f,f,t}$$

[a] Model symbols and their descriptions include: no. turkeys of sex *i* at the start of spring hunting in yr *t* ($N_{i,t}$), instantaneous growth rate for sex *i* in yr *t* ($r_{i,t}$), non-hunting survival rate for sex *i* (s_i), carrying capacity for sex *i* (K_i), parameter for nonlinearity in density dependence (θ), no. births in yr *t* (B_t), realized process deviation in population growth in yr *t* ($\varepsilon_{p,t}$), no. F recruits/ fertilized F (k), harem size (q), realized harvest rate for sex *i* in season *j* of yr *t* ($h_{i,j,t}$), and total harvest for sex *i* during season *j* of yr *t* ($H_{i,j,t}$).

[b] Values of annual process deviations in population growth were drawn from a normal distribution: $\varepsilon_{p,t} \sim N(0, \sigma_p = 0.15)$.

[c] Values of spring female losses were drawn from lognormal distributions with medians of 0.05 (low female loss scenario), or 0.15 (high female loss scenario).

[d] Values of spring male harvest rate were drawn from lognormal distributions with medians of 0.15 (low harvest scenario), 0.30 (medium harvest scenario), or 0.40 (high harvest scenario).

[e] Fall harvest rates were either set to zero or drawn from lognormal distributions with medians ranging from 1–15%.

controllability; Williams 1997). In contrast, we were motivated to understand robustness of previous fall harvest management recommendations. Thus, we used the theta-logistic model to evaluate dynamic consequences of a range of fall harvest rates, and repeated the analysis over a broader set of plausible scenarios. We determined a plausible set of scenarios based on a literature review and considered different spring harvest rates, different levels of population productivity (recruits/F), and different levels of female loss during spring hunting seasons.

Annual changes in abundance for the theta-logistic model depended upon a population growth rate calculated using an intrinsic rate of increase (r), adjustments due to density dependence, and a stochastic process error, where r was in turn calculated as a function of per-capita births and deaths that would occur in absence of density dependence or stochasticity (Table 1). During simulations we defined population size as the abundance at the beginning of the spring hunting season ($N_{i,t}$ for sex *i* in year *t*), and assumed all fertilization occurred prior to the onset of spring hunting. This assumption could be relaxed if loss of males via spring hunting prior to fertilization is thought to be problematic (similar to modeling losses of F by adjusting numbers in birth function; Table 1), but this would require information on the fraction of the male population removed before females are bred (or use of a continuous time model that allowed for simultaneous M losses and breeding). We calculated the number of annual births at time *t* (B_t) contributing to population growth before density-dependent or stochastic influences using a harmonic mean birth function that linked the sexes and accounted for skewed adult sex ratios caused by male-biased harvesting (i.e., does not assume there will always be enough M to fertilize all F; Caswell and Weeks 1986, McGhee et al. 2008; Table 1). This function has an input parameter (k) that explicitly defines the number of female recruits produced per fertilized female, providing a convenient way to explore effects of heterogeneous recruitment on risk of decrease in abundance due to fall harvest. This specific birth function was also developed for polygamous species, where an additional parameter (q) specifies the average number of females bred for each male in the population (referred to as harem size by Caswell and Weeks [1986]). We set q equal to 10 as in McGhee et al. (2008), which made the number of births a nonlinear function of the proportion of males in the population (Caswell and Weeks 1986: fig. 2). The practical importance of $q = 10$ was that the number of births did not fall towards zero until nearly all males were removed (Stevens et al. 2016: fig. 2).

We modeled population losses within the annual cycle associated with natural mortality and human harvest. We assumed constant *per capita* natural survival (i.e., survival in absence of harvest) for males ($S_m = 0.74$) and females ($S_f = 0.64$; McGhee et al. 2008), which implied that harvest mortality was additive to natural mortality. Additive harvest mortality is a nearly ubiquitous assumption in turkey harvest models (Vangilder and Kurzejeski 1995, Alpizar-Jara et al., 2001, McGhee et al. 2008) with some support from field research (Little et al. 1990, Godwin et al. 1991, Pack et al. 1999). We represented sex-specific instantaneous annual growth rates at time *t* ($r_{i,t}$) as the sum of *per capita* recruitment and survival rates on the natural log scale, where we assumed recruitment was equal between the sexes ($0.5 \times B_t$; Table 1). We modeled hunting and female losses as sex-specific and seasonal. Total hunting losses ($H_{i,j,t}$ for sex *i* in season *j* and year *t*) followed a proportional harvest strategy, where a fraction of the population was removed prior to (M only in spring; $H_{m,s,t}$) and after (both sexes in fall; $H_{m,f,t}$, $H_{f,f,t}$) new population growth within the annual cycle (Table 1). In addition to this legal removal, the model included losses of females in the spring, which were also removed from the birth function because females removed in the spring cannot produce young.

The theta-logistic model used to represent turkey population change did not assume density dependence operated through a specific population process such as recruitment or survival but rather represented population growth similar to a surplus-production model (Hilborn and Walters 1992) where density affects new growth through biologically unspecified mechanisms. Recent studies have hypothesized that density dependence in some turkey populations may operate through recruitment processes because of broad-scale evidence for declining *per capita* recruitment (Byrne et al. 2016, Stevens et al. 2016). However, regulatory mechanisms contributing to density-dependent dynamics are unknown (Schwertner 2005, Warnke and Rolley 2007, Healy 2011, Porter et al. 2011). Moreover, we are unaware of studies that have fit density-dependent recruitment models to data from any turkey population, or attempted to compare evidence for such models to alternative hypotheses about the causes of modern recruitment declines (e.g., reduced quantity or quality of nesting and brood rearing habitat; Stevens 2016). Thus, uncertainty about how specific population processes are affected by density is limiting the development of more biologically realistic models of turkey populations.

We incorporated uncertainty in the strength of density dependence and process variation in annual growth of turkey populations in our simulations. In this model the θ parameter encapsulates strength of density dependence (i.e., θ governs nonlinearity in the functional relationship between population growth and abundance; McGhee 2006, Clark et al. 2010). McGhee and Berkson (2007) estimated the θ parameter for turkeys using time series of harvest-based population indices from 11 states, assuming all populations shared the same demographic model and parameter values. More recently, others have documented the difficulty of accurately estimating θ from field data in the presence of measurement errors in time series of animal abundance estimates (Clark et al. 2010). We therefore accounted for uncertainty in θ by drawing its values for each forward population projection from a normal distribution with a mean and standard deviation equal to the estimated value and standard error reported by McGhee and Berkson (2007; $\theta \sim normal(\mu_\theta = 0.36, \quad \sigma_\theta = 0.09)$; Fig. S1, available online in Supporting Information). Annual growth of turkey populations is also affected by environmental conditions (e.g., spring weather; Roberts and Porter 1998, Rolley et al. 1998). Thus, we modeled process variation in annual population change as normally distributed environmental noise on the natural-log scale ($\varepsilon_{p,t} \sim normal\left(0, \sigma_p = 0.15\right)$), where standard deviation (σ_p) was set at 0.15, the midpoint between no environmental variation ($\sigma_p = 0$) and the largest value ($\sigma_p = 0.30$) considered by McGhee et al. (2008). This produces a lognormal distribution for population size in year $t + 1$ given the population size in year t. The environmental variation is not explicitly assumed to be associated with any specific process; however, within-year dynamics of this model assume this occurs between spring and fall hunting seasons (Table 1). Thus our model of environmental variation implies such variation affects the cumulative result of natural deaths and poult production during spring-summer, which is consistent with evidence that annual production (and consequently population growth) is affected by environmental conditions (Roberts and Porter 1998, Rolley et al. 1998).

We included additional stochasticity in harvest models to represent partial controllability (Williams 1997) of annual spring and fall harvest rates (Figs. S2–S3, available online in Supporting Information). We accounted for this uncertainty by modeling annual realizations of legal harvest (for M in spring and either sex in fall; $h_{m,s,t}$, $h_{i,f,t}$) and spring female loss rates ($h_{f,s,t}$) in year t as coming from lognormal distributions by exponentiating natural-log scale normal deviations ($\varepsilon_{i,j,t}$ for sex i in season j) and multiplying these by target proportional harvests (e.g., $h_{m,f,t} = target_{m,f} \times e^{\varepsilon_{m,f,t}}$, where $\varepsilon_{m,f,t} \sim normal\left(0, \sigma_{i,f}\right)$). This effectively set the target proportional harvest or female loss rate as the median of the realized distribution of harvest and female losses over time. We set the natural log-scale male spring and either-sex fall harvest standard deviations ($\sigma_{m,s}$, $\sigma_{i,f}$) equal to 0.175, corresponding to the midpoint of low (0.10) and high (0.25) values considered by McGhee et al. (2008). Distributions of realized harvests over time can be thought of as representing all harvest mortality (legal + illegal) for the corresponding hunting season, precluding the need for explicit parameters to account for additional illegal harvest. As such, inter-annual variation of illegal harvest during legal hunting seasons (for M in both seasons and F in fall) is viewed as one factor contributing to annual variation in realized harvest rates. Furthermore, this approach implicitly assumed managers could adjust for illegal harvest, on average, when implementing management actions to achieve a target harvest rate. We also increased annual variation in female losses during spring relative to variation in male harvests ($\sigma_{f,s} = 0.40$) because female losses can show a larger degree of variation through time (Vangilder and Kurzejeski 1995, Pack et al. 1999, Norman et al. 2007; Fig. S2).

Simulation Study Design

We evaluated performance of different fall harvest rates across population scenarios intended to represent a broad range of plausible conditions. Specifically, we simulated performance of fall harvest for all combinations of 3 levels of productivity (k), 2 levels of female losses during spring ($h_{f,s,t}$), and 3 levels of spring male harvest ($h_{m,s,t}$; 18 simulation scenarios). We manipulated levels of population productivity by changing the parameter representing number of female recruits per fertilized female (k), which we set to the lowest (0.775; Vangilder 1992) and highest (2.105; McGhee et al. 2008) values assumed by previous turkey harvest studies and the midpoint between these extremes (1.440). Although our model and the model of McGhee et al. (2008) assumed density-dependent dynamics, the k parameter provided a convenient means of manipulating population productivity in a manner that was comparable with parameters of earlier models. Prior to McGhee et al. (2008), turkey harvest models generally assumed density-independent dynamics, and thus assumed *per capita* recruitment was unaffected by changes to density of turkeys. The theta-logistic model makes identical assumptions about *per capita* recruitment at low population densities as did earlier models (i.e., unaffected by density). The difference comes in that the rate of population increase declines with density in the theta logistic through an unspecified combination of mechanisms (e.g., reduced *per capita* production of poults and-or survival). Thus, the *per capita* recruitment parameters of earlier modeling studies are informative about and comparable to k from our model because neither assumes that density affects recruitment explicitly. However McGhee et al. (2008) set k to the highest value that we are aware of for a published turkey harvest model, and thus implicitly assumed changes to the rate of population increase associated with density would result from reduced recruitment, and that the maximal production of young would occur at low densities. Although this may reflect dynamics and productive capacity of turkey populations in some localities, it may not apply to populations in all vegetation types and regions, and as previously described the mechanisms causing density dependence in real turkey populations are poorly understood (Healy 2011, Porter et al. 2011).

We also manipulated levels of spring harvest losses for males and females. We set the 2 levels of female losses during spring hunting through the median fraction removed, which included a lower value commonly described (0.05; Vangilder and Kurzejeski 1995, Pack et al. 1999, McGhee et al. 2008) and a value consistent with the highest female poaching rates we found reported in the literature (0.15; Norman et al. 2007; Fig. S3). We set spring male harvest rates at 3 levels by changing the medians of their lognormal distributions: a low value assumed by previous studies (0.15; McGhee et al. 2008), a higher value previously recommended as the maximum spring harvest rate for avoiding shifts in age structure towards juveniles (0.30; Vangilder and Kurzejeski 1995, Hubbard and Vangilder 2007), and a yet higher value consistent with the largest estimates of spring harvest reported in literature (0.40; Hubbard and Vangilder 2007, Wright and Vangilder 2007; Fig. S2).

We simulated performance of fall harvests by manipulating target fall harvest rates from 0–15% at 1% increments for each combination of factors described above. Fifteen percent is the maximum fall harvest rate recommended as sustainable by previous harvest simulation studies (Alpizar-Jara et al., 2001). Moreover, this range encompassed common management recommendations for sustainable fall harvest in the Midwest (e.g., ≤10%; Vangilder and Kurzejeski 1995) and more recently recommended fall harvest rates for maximizing annual turkey harvest across spring and fall seasons (9%; McGhee et al. 2008). During simulations we assumed that fall harvest rates were shared for males and females during fall hunting seasons ($target_{m,f} = target_{f,f}$ and $\varepsilon_{m,f,t} = \varepsilon_{f,f,t}$), and thus equal vulnerability to fall harvest. Equal fall harvest vulnerability has been assumed by many (Alpizar-Jara et al., 2001, McGhee et al. 2008), but not all (Vangilder and Kurzejeski 1995, Schwertner 2005) turkey harvest models. However, there is little published information on sex-specific differences in harvest vulnerability from the post-restoration era of turkey management.

We conducted 10,000 replications of a 200-year forward population projection at each target fall harvest rate to evaluate long-term performance harvest management. We initialized population projections assuming sex-specific population sizes started from their environmental carrying capacities ($K_m = K_f = 10,000$). Although we acknowledge that management will not realistically be held consistent over such long time horizons, we simulated long-term dynamics to characterize the stationary distributions of performance metrics of management interest. Stationary stochastic distributions are time-invariant and independent of initial conditions, which is not the case for simulated distributions during the transient period of stochastic dynamics (Figs. S4–S7, available online in Supporting Information). We focused on comparison of stationary distributions because our primary interest was in testing generality of existing recommendations, not developing short-term recommendations for a specific population. We also monitored performance metrics related to the temporal consistency of harvest and abundance over time, and thus long-term projections allowed us to better characterize their stationary distributions while reducing Monte Carlo error and minimizing effects of trivial assumptions about starting population sizes, which result in different short-term dynamics prior to converging to their stationary distributions (Figs. S4–S5). To describe short-term dynamics of management performance, we also provide summaries of abundance at shorter time intervals and for different starting population sizes (Figs. S4–S7). We programmed all simulations in the R statistical computing language (version 3.1.1; R Core Development Team, 2014), and the simulation script is provided (Supplemental Materials 2).

During simulations, we monitored population and harvest performance metrics relevant to modern management objectives to determine risks of undesirable outcomes for each level of fall harvest. Although explicit population objectives are often not defined in turkey management (Healy and Powell 2000), maintenance of large populations is desirable to ensure management stakeholders remain satisfied. Thus, we monitored metrics describing the ability to maintain large population sizes over time for each simulation. Specifically, we monitored the proportion of years between years 100–200 where starting population abundance in the spring ($N_{Total,t} = N_{m,t} + N_{f,t}$) was greater than half of the environmental carrying capacity (i.e., $K/2$, where $K = K_m + K_f$). Within a simulated population projection a population is either above or below $K/2$ at the start of each spring hunting season (binary outcome), and thus we calculated the proportion of the simulation years where this condition was satisfied. This proportion has a stochastic distribution across the simulation trials, and this distribution was summarized for each harvest rate under each scenario.

We used $K/2$ in a manner analogous to a utility threshold (Nichols et al. 2014) to define desirable population size in this analysis. Importantly, thresholds of this nature reflect management objectives, and therefore how stakeholders and managers value outcomes of management, not biological attributes of populations (Nichols et al. 2014, Runge and Walshe 2014). Thus, our performance metric implies that populations $> K/2$ confer some benefit to stakeholders above that achieved by merely harvesting a turkey; for example, by providing increased satisfaction through direct interaction with more turkeys or perceiving larger populations of turkeys on the landscape (Cartwright and Smith 1990, Little et al. 2000, Swanson et al. 2007). We are aware of no research attempting to quantify the precise location of such utility thresholds for turkey populations, or the degree to which specific population objectives change among regions. The threshold of $K/2$ provides a useful starting point for such discussions and is rooted in harvest theory; $K/2$ is the abundance maximizing harvest yield for a simple logistic population model (Schaefer 1954). If obtaining larger harvests are an objective that is more important than maintaining larger populations, then thresholds $< K/2$ (or no threshold at all; McGhee et al. 2008) could be used to reflect differences in the valuation of outcomes of turkey harvest management, and simulations could be used to assess performance of fall harvests relative to different objectives. Previous turkey harvest models often included such value judgements about desired population status implicitly (e.g., we have enough turkeys, we want more turkeys, or we primarily value turkeys through harvest; Vangilder 1992, Vangilder and Kurzejeski 1995, McGhee et al. 2008), whereas we allow for valuation of management outcomes that underlies scientific assessment of fall harvests to be made explicit. However, because population objectives may vary among regions, we also summarize distributions of total abundance after a variety of time periods (Figs. S4–S7).

To monitor size and variation of total annual harvest across both hunting seasons, we retained the distribution of total harvest on the last year of population projections ($H_{Total,200}$). Because consistency of harvests over time is often considered desirable, we also monitored the standard deviation of total annual harvest through time over simulation years 100–200 (σ_{H_T}) for each population projection, and summarized the simulated distribution of σ_{H_T} across all simulation replicates.

RESULTS

Generality of Previous Harvest Recommendations

Performance of the 9% fall harvest rate previously recommended for maximizing annual turkey harvest (McGhee et al. 2008) was not robust to changes in demographic parameters, and risk to populations at this fall harvest rate varied among scenarios (Fig. 1). Distributions of the proportion of years with large abundances (i.e., $N > K/2$) at the start of spring hunting were right skewed for many scenarios, with medians concentrated around small values and distribution tails extending towards larger values (Fig. 1). Increased productivity and decreased female loss during spring allowed for abundance to remain large for more years during simulations (Fig. 1). The medians for proportion of years with large abundance were nearly all <0.5 under low female loss scenarios, as were most interquartile ranges (Fig. 1). When productivity was low, the proportion of years with large abundance was frequently near 0 at a 9% target fall harvest rate. These proportions shifted to larger values under medium and high productivity scenarios with low female loss, where the medians for high productivity scenarios were 8.7 times greater on average (range = 2.7–18 times greater, $n = 3$; Fig. 1) than medians for corresponding scenarios with medium productivity. Maintaining large populations was rarely attainable under high female loss; the median proportion of years with large abundance was 0.12 under the best-case scenario (i.e., high productivity, low spring male harvest; Fig. 1). In general, increased spring harvest rate also reduced the proportion of years with large abundance by shifting the distributions to reduced values (Fig. 1). Importantly, the same general patterns held when summarizing distributions of total abundance after a range of short- and long-term time intervals (Figs. S4–S7). Moreover, median abundance was usually $<0.4K$, and frequently $<0.3K$ when implementing 9% fall harvests, except for scenarios with high productivity and low female loss (Figs. S6–S7).

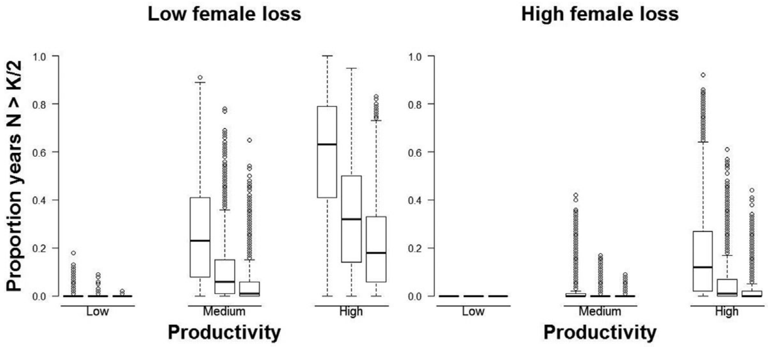

Figure 1. Evaluation of population risks for 9% target fall harvest across changing demographic scenarios for simulated wild turkey populations. Scenarios represent combinations of low ($k = 0.775$), medium ($k = 1.440$), and high ($k = 2.105$) productivity; low (left; median = 0.05) and high (right; median = 0.15) rates of female loss during the spring hunting season; and low (median = 0.15), medium (median = 0.30), and high (median = 0.40) spring male harvest rates (moving left to right within a productivity scenario). Boxplots represent the simulated distribution of the proportion of years where turkey population abundance was greater than half of the environmental carrying capacity at the start of spring hunting seasons (proportion years $N > K/2$). Solid horizontal lines represent medians, boxes delineate the interquartile ranges (IQR), and boxplot whiskers delineate IQR boundaries values $\pm 1.5 \times$ IQR. Individual points represent simulated metrics whose absolute values were greater than $1.5 \times$ IQR.

Performance of Fall Harvest Rates

Risk of not maintaining large turkey populations varied among simulation scenarios and target fall harvest rates (Fig. 2). In general both productivity and female loss had strong effects on assessments of population risk. Populations with low productivity showed little ability to maintain large abundances for any fall harvest rate under levels of spring male harvest and female loss considered (Fig. 2a; Table S1, available online in Supporting Information). The median proportion of years with large abundance decreased nonlinearly with increasing fall harvest rates for most scenarios (Fig. 2), and risk to populations for a given fall harvest rate was reduced as productivity was increased (Fig. 2). The median proportion of years with large abundance at 5% target fall harvest rate increased from 0 to 0.27 to 0.60 as productivity increased from low to medium to high values, under low female loss and medium spring harvest conditions (Fig. 2). Risk of not maintaining large populations increased considerably as female loss increased from low to high scenarios, for corresponding fall harvest rates and productivity scenarios (Fig. 2). With the exception of low spring male harvest scenarios, median proportions of years with large abundance were never >0.5 when female losses during spring were high, even under high productivity scenarios (Table S1).

Relationships between annual harvest and target fall harvest rate varied among simulation scenarios. Specifically, losses or gains to the median of distributions of annual harvest were inconsistent as fall harvest rates were increased (Fig. S8, available online in Supporting Information), and fall harvest rates resulting in a maximum median for the distribution of annual harvest also changed among scenarios (Table 2). Increases to annual harvest with increased fall harvest rate occurred for scenarios with medium-high productivity (Table 2; Fig. S8). In contrast, annual harvest increased minimally or decreased with increasing fall harvest rate under low productivity scenarios because fall harvest reduced harvests the subsequent spring (Table 2; Fig. S8). Thus, when productivity was low the annual

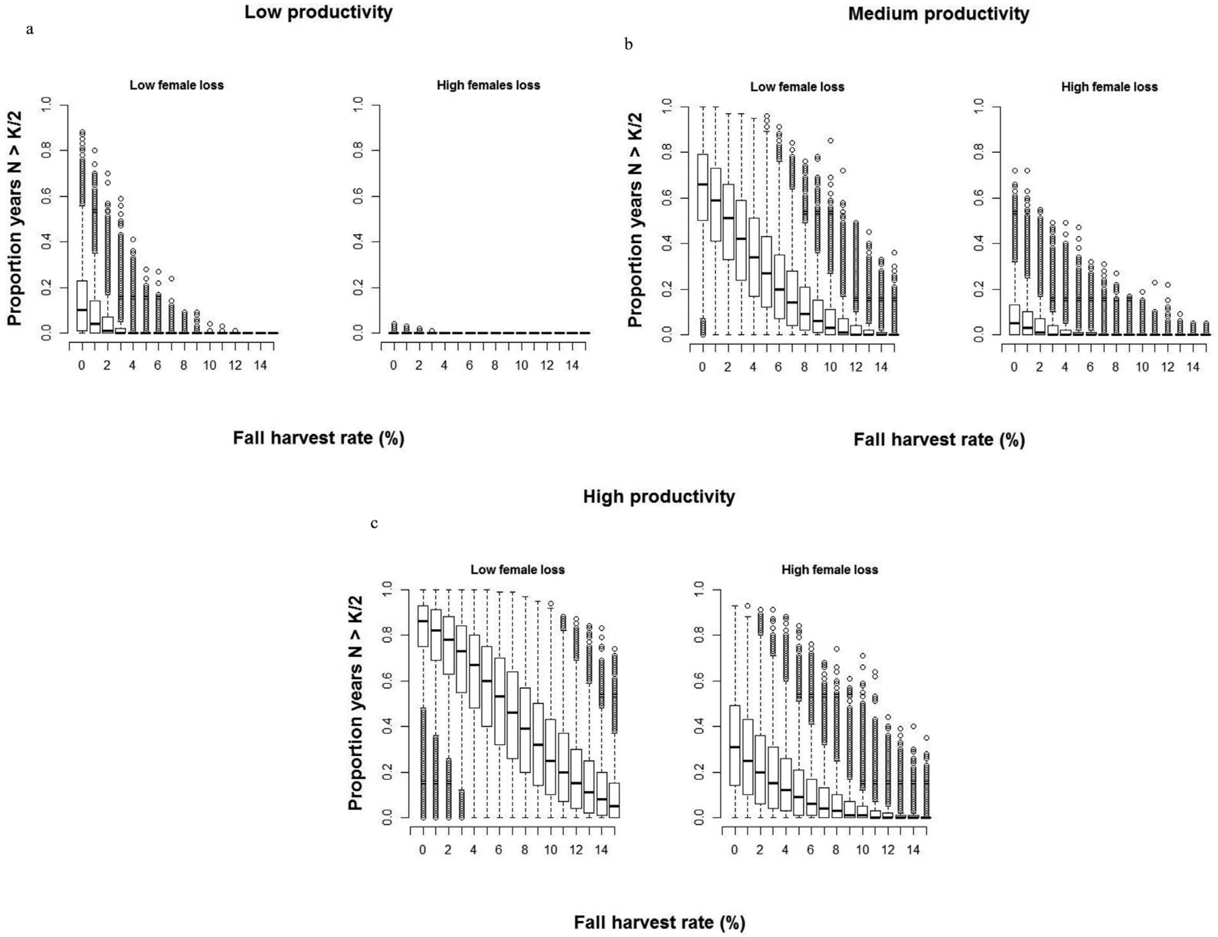

Figure 2. Evaluation of population risks for target fall harvest rates of 0–15% across changing demographic scenarios for simulated wild turkey populations. Scenarios represent combinations of low (a; $k = 0.775$), medium (b; $k = 1.440$), and high (c; $k = 2.105$) productivity, with low (left; median = 0.05) and high (right; median = 0.15) rates of female loss during the spring hunting season, at medium spring male harvest rates (median = 0.30). Boxplots represent the simulated distribution of the proportion of years where turkey population abundance was greater than half of the environmental carrying capacity at the start of spring hunting seasons (proportion years $N > K/2$). Solid horizontal lines represent medians, boxes delineate the interquartile ranges (IQR), and boxplot whiskers delineate IQR boundaries values ± 1.5 × IQR. Individual points represent simulated metrics whose absolute values were greater than 1.5 × IQR.

harvest was maximized by harvesting at very low levels in fall or by harvesting only during spring hunting seasons (Table 2; Fig. S8). Increased female loss flattened the relationship between the median of annual harvest and fall harvest rate for medium-high productivity scenarios (Fig. S8b,c), and shifted distributions of annual harvest to lower values for corresponding fall harvest rates, irrespective of productivity (Fig. S8). Similarly, fall harvest rates that maximized the median of annual harvest varied among scenarios from the lowest (0%) to highest (15%) values considered, and these harvest rates were reduced by increased losses of females and decreased productivity (Table 2). The relationship between fall harvest rate and the variation of annual harvests over time was also inconsistent among scenarios (Fig. S9, available online in Supporting Information). Specifically, variation of annual harvest typically increased with fall harvest rates (Fig. S9), except for low productivity and high female loss scenarios (Fig. S9a, b) where increased fall harvest decreased the temporal variation of annual harvest because it was consistently driven to smaller values (Figs. S8–S9).

DISCUSSION

Management Consequences of Uncertain Population Processes

Characterizing management risks is a first step towards decision making that formally acknowledges and accounts for uncertainty (Walters 1986, Sethi 2010). Our modeling suggests that risks and tradeoffs accompanying management of fall turkey harvests depend on values of population and harvest parameters that are often imprecisely estimated or unavailable for regional decision making. We demonstrate that a proportional harvest strategy using a target fall either-sex harvest consistent with previous recommendations (Vangilder and Kurzejeski 1995, Alpizar-Jara et al., 2001, McGhee et al. 2008) will likely not sustain populations at desirably large levels unless productivity is high and female losses and male harvest rates during spring are low. Absent reliable estimates of these parameters for a region of interest, harvesting at previously recommended levels risks undesirable management outcomes. We assumed population objectives were to maintain turkey abundance at levels at least half those that could be supported in the absence of harvest ($K/2$), but specific optimal harvest rates will depend on clear objectives and therefore the population sizes that are desirable to maintain (Stevens 2016). However, our simulations suggest that previously recommended fall harvest rates often would not succeed in sustaining populations at desirably large levels unless the lower bound on desirable abundance was below $K/2$ (e.g., $0.3K$ or $0.4K$ depending on scenario; Figs. S6–S7). Moreover, the 9% fall harvest rate rarely resulted in the highest possible total annual harvest over both spring and fall hunting seasons. Thus recent fall harvest recommendations have not produced generalizable management targets for either maintaining large turkey populations or maximizing total annual harvest with high probability.

Our results demonstrate performance of fall harvests relative to population and harvest objectives is not robust but will depend on the suite of factors affecting local recruitment and mortality of turkeys (Roberts and Porter 1996, Rolley et al. 1998, Schwertner 2005, Warnke and Rolley 2007). In some areas fall harvest management seeks to ensure turkey populations remain protected under worst-case conditions (Healy and Powell 2000:24). We show that under worst-case scenarios for recruitment and spring female losses, in particular, harvesting turkey populations at currently recommended levels may incur considerable risk that populations would not be maintained at desirable levels. Unfortunately the relative frequency of turkey populations whose dynamics are represented by each of our scenarios is unknown because many populations lack estimates of important population parameters. However, fall harvesting risks are reduced in areas that support highly productive turkey populations (e.g., areas with high quality nesting and brood-rearing habitats), which is an anticipated result given sensitivity of turkey populations to annual production and recruitment of poults (Vangilder and Kurzejeski 1995, Roberts and Porter 1996, Rolley et al. 1998, Warnke and Rolley 2007, McGhee et al. 2008).

Uncertain causes of productivity change have strong implications for modern turkey harvest management. Contemporary, broad-scale assessments suggested turkey production is declining in many areas (Bond et al. 2012, Bowling et al. 2016, Byrne et al. 2016, Casalena et al. 2016), whereas the causes of these declines are currently unknown. The sources of such declines have direct relevance to interpretation of our results in the context of modern management. Because our parameter k can be thought of as productivity prior to the onset of density-dependent feedbacks, the different values of k we used in low to high productivity scenarios are reflective of changes that might

Table 2. Target fall harvest rate (% harvest) resulting in maximum median annual harvest across changing population scenarios for a simulated population of wild turkeys.

	Low productivity[a]		Medium productivity[a]		High productivity[a]	
Spring harvest[c]	Low F loss[b]	High F loss[b]	Low F loss	High F loss	Low F loss	High F loss
Low	2	0	11	8	15	14
Medium	1	0	9	6	15	12
High	0	0	8	5	15	10

[a] Productivity was manipulated by changing the number of *per capita* female recruits (k) to low (0.775), medium (1.440), and high (2.105) values.

[b] Values of spring female losses were drawn from lognormal distributions with medians of 0.05 (low) or 0.15 (high).

[c] Values of spring male harvest rate were drawn from lognormal distributions with medians of 0.15 (low), 0.30 (medium), or 0.40 (high).

occur as a result of changes in habitat or other regional conditions that could reduce average recruitment irrespective of density. Thus, if productivity declines are due solely or in part to degrading quality or quantity of nesting and brood-rearing habitats, then our results suggest fall harvests needed to achieve modern management objectives may be <9–15%, and possibly even the 5–10%, recommended by earlier studies (Vangilder and Kurzejeski 1995, Healy and Powell 2000, Alpizar-Jara et al., 2001, McGhee et al. 2008). If production declines are the result of density dependence alone, however, we would expect reduction of densities through harvest to increase *per capita* recruitment towards larger values (Stevens et al. 2016). The unknown causes of recent productivity declines therefore contribute heavily to existing uncertainty about turkey population dynamics and have direct implications for modern harvest management.

Dealing With Uncertainty in Wild Turkey Harvest Management

Lack of robustness of fall turkey harvests suggests management strategies could be tailored to dynamics of regional populations to the extent possible; however, existing uncertainties create challenges for customizing management recommendations. Uncertainty about the value of vital rates is relevant to turkey management at regional scales because rigorous estimates of population parameters are often not available. Demographic rates can be heterogeneous among turkey populations at management scales and also systematically shift over time (Vangilder et al. 2001, Norman et al. 2007, Bowling et al. 2016, Byrne et al. 2016), and little is known about mechanisms of density dependence that may be regulating turkey populations (Warnke and Rolley 2007, Healy 2011, Porter et al. 2011). This creates uncertainty about the strength of density-induced feedbacks to population growth and the appropriate underlying forms of mathematical models used to represent dynamics of turkey populations, and it remains unclear if current models (McGhee et al. 2008, this study) generalize across populations in different habitats and regions.

Sensitivity of performance of fall harvest management suggests a need to explicitly consider structural uncertainty when developing turkey harvest policies. There are 2 general, but not necessarily mutually exclusive approaches for dealing with the effects of structural uncertainty in management decision making: reduce uncertainty to facilitate better management decisions, or identify decisions with adequate performance in the face of existing uncertainties. The first approach focuses on reduction of critical uncertainties through targeted research and monitoring efforts, and possibly through learning via formal adaptive management. A traditional approach would focus on eliminating uncertainty by conducting research to directly estimate demographic parameters at the scales at which local populations are managed. Conducting field studies to estimate demographic parameters for turkey populations that exist in different regions or vegetation communities is certainly possible (Pack et al. 1999, Norman et al. 2001, Hubbard and Vangilder 2007, Diefenbach et al. 2012). Field-intensive studies are time consuming and costly to implement over broad scales, however, and thus may not be realistic for many populations. Uncertainty about regional dynamics will therefore probably remain for many populations in the face of changing environmental conditions and limited agency budgets (Porter et al. 2011).

Although vital rates could be estimated using traditional research methods, additional tools would be needed to reduce uncertainty surrounding density-dependent processes operating within turkey populations. Estimating vital rates by itself does not necessarily reduce uncertainty surrounding the values of θ or interpretation of productivity declines in the face of multiple hypothesized causes. Formal adaptive harvest management can be used to reduce structural uncertainty through time by intentionally making management decisions that enable learning about hypothesized system dynamics (Walters 1986, Nichols et al. 2007). Importantly though, adaptive approaches that formally integrate learning into management require linkage of targeted monitoring data with tools to assess population responses to harvest (Nichols and Williams 2006, Nichols et al. 2007). It would not be useful for management experiments to intentionally manipulate turkey densities, for example, without the ability to precisely monitor population responses. In turkey management the development of practical methods to rigorously assess populations at management scales using widely available data is in progress (e.g., Gast et al. 2013, Clawsen et al. 2015), and such techniques are not yet widely used to guide management programs in most states. Thus formal adaptive management of turkey harvests may only become feasible as rigorous methods are more widely adopted to assess abundance and dynamics of populations at appropriate management scales (Stevens 2016).

The second approach to explicitly dealing with uncertainty in management decision making incorporates structural uncertainty directly into the analysis of management options by using decision-analytic tools to identify decisions that are likely to meet objectives in spite of existing uncertainties (Peterman and Peters 1999, Harwood 2000, Gilboa 2011). This approach acknowledges decision makers will never know the true values of population parameters, and uncertainty is embraced (but not necessarily reduced) in the evaluation of management options. Specifically, a decision analysis would view unknown values of demographic parameters as representing different plausible hypotheses about system dynamics (Peterman and Peters 1999), and assign probability distributions to these parameters to describe likely values using expert opinion or data. Harvest policies likely to meet objectives could then be identified visually from the simulated marginal distributions of management performance measures (Bence et al. 2008), or by using optimization techniques after combining performance measures into an explicit utility function (Runge and Walshe 2014, Williams and Nichols 2014). This approach is intuitively appealing for turkey management because appropriate harvest strategies can be identified in the face of uncertainty while efforts to formally reduce uncertainty in the region of interest are being developed. Moreover, dynamic optimization methods commonly used in adaptive management (Nichols et al. 2007, Williams and Nichols 2014) are iterative extensions of decision analysis used to integrate monitoring, assessment, and decision making to identify optimal decisions in the face of uncertainty, while also reducing uncertainty and improving management decisions over time.

A final but important challenge to development of turkey harvest strategies that embrace uncertainty is elaboration of population objectives for the post-restoration era of turkey management. Modeling studies conducted during restoration often assumed an objective was to maintain or grow turkey populations while also providing hunting opportunities (Vangilder 1992, Vangilder and Kurzejeski 1995, Alpizar-Jara et al., 2001). More recently, McGhee et al. (2008) assumed management objectives were to maximize sustainable turkey harvests irrespective of the resulting abundances that are maintained, and thus assumed turkeys are primarily valued through harvest. However, turkey populations have likely plateaued in many areas (Warnke and Rolley 2007, Ericksen et al. 2016, Parent et al. 2016), and modern management objectives appear more complex than merely maximizing harvest. Our interactions with turkey managers and management stakeholders suggest fundamental objectives often relate to hunter satisfaction, which is related to harvest but also the ability of hunters to interact with large numbers of gobbling birds in spring (Cartwright and Smith 1990, Little et al. 2000, Swanson et al. 2007). Yet specific population objectives likely vary and may need to be refined regionally. Regardless of such region-specific objectives, our work suggests maintenance of larger turkey populations may be challenging under some conditions (e.g., low productivity, high female loss during spring) when managing fall harvest as recommended by previous studies.

MANAGEMENT IMPLICATIONS

Our results imply performance of fall harvest recommendations deduced from modeling studies that only considered a small fraction of the population parameter space may not be robust over a broader range of conditions experienced by turkey populations. If reliable estimates of population parameters were available for a region, our simulation results could be used directly to guide development of regional management strategies. This would require identifying scenarios that closely resemble the set of local demographic rates, and determining a level of acceptable risk to regional turkey populations. If regional differences in objectives necessitate different thresholds for the desirable abundance of turkeys than we considered, our approach could be replicated easily using a different population threshold. If reliable region-specific population parameters were not available, fall harvests that are robust to uncertainty could be identified using decision-analytic tools. Our results suggest, however, that fall harvest rates that best achieve objectives in the absence of information about population parameters will likely be lower than previously recommended. In the absence of such decision analyses and in light of regional productivity declines, our results suggest cautious implementation of fall harvests when reliable estimates of population parameters are not available.

ACKNOWLEDGMENTS

We thank biologists involved in the Midwest Wild Turkey Consortium, and especially C. A. Stewart and D. R. Luukkonen, for conversations and insight about turkey hunting and harvest management that informed this project. We also thank M. L. Jones, B. A. Collier, and anonymous reviewers whose constructive feedback improved the clarity and focus of this manuscript. Funding for this work was provided by the Boone and Crockett Endowment and the Quantitative Fisheries Center at Michigan State University, and Michigan Department of Natural Resources. This is publication number 2017-03 of the Quantitative Fisheries Center at Michigan State University.

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Associate Editor: Bret Collier.

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