STRUCTURAL UNCERTAINTY AND THE MANAGEMENT OF MODERN WILD TURKEY HARVESTS

By

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ABSTRACT

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Wild turkey (*Meleagris gallopavo*; hereafter turkey) management has been in a state of transition since the turn of the 21st century, shifting away from restoration and towards a focus on sustainable harvest management. Several previous studies used mathematical models of population and harvest dynamics to understand performance of turkey management. However, increases to the number of hunters, changes to management objectives, and broad-scale shifts in demography (e.g., declining productivity) imply that many assumptions of previous studies may be untenable under modern conditions. More generally, the science informing sustainable harvest has progressed in recent years. These advancements include a more thorough understanding of uncertainty and increased use of decision-theory to inform management under uncertainty. Importantly, many of these developments are not captured by studies that used models to aide turkey harvest management, and as a consequence the performance of current harvest-management recommendations in the face of relevant uncertainties is only partially understood.

In this dissertation I attempt to bridge the gaps between turkey harvest models and more general developments in sustainable harvest management by addressing overlooked sources of uncertainty, and by linking simulation-modeling exercises to decision-theoretic methods that provide a rigorous foundation to decision making. Throughout I focus on the implications of structural uncertainty for modern management and the performance of existing harvest recommendations when structural uncertainty is acknowledged. Structural uncertainty refers to uncertainty about the dynamic processes of populations and harvesting, which creates uncertain

responses of populations to management activities. This can be represented as uncertainty about functional forms of system models (model uncertainty), uncertainty about values of specific model parameters (parameter uncertainty), or both. Structural uncertainty is thus directly relevant to modern management due to uncertainty about mechanisms of density regulation, causes of demographic changes, and segment-wise harvest rates resulting from hunting regulations.

I used simulation modeling and decision-analytic tools to demonstrate that structural uncertainty has important consequences for modern turkey management. Important findings include: 1) recommendations for maximizing turkey harvest are not robust to uncertainty, and depend on poorly understood aspects of turkey ecology and harvest; 2) currently accepted rules of thumb for fall harvest management are sensitive to uncertainty in turkey demography, and may perform poorly over a broad range of conditions; 3) existing fall harvest recommendations appear to only be optimal over a narrow range of the plausible parameter space for turkey populations; 4) the unknown causes of productivity declines directly affect risks imposed by fall harvest and the magnitude of harvest a population sustain; 5) target fall harvest rates of < 5% are more likely to achieve management objectives across a range of conditions than harvests ≥ 5%; 6) if reliable information about productivity, relative harvest vulnerabilities, and magnitude of spring harvest are not available, then 4% fall harvest of males should be viewed as the upper value likely to achieve modern objectives; and 7) if information about productivity, vulnerability, and magnitude of spring harvest are available, then my simulation results can be used to identify fall harvest targets that are tailored to characteristics of local populations and likely to accomplish objectives in the face of uncertainty. As such, I expect this research to be broadly useful to turkey management, and to facilitate continued advancement and adaptation of turkey harvest management systems into the future.

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CHAPTER 1: INTRODUCTION

The status of wild turkey (*Meleagris gallopavo*; hereafter turkey) management over the last twenty years has been one of transition. The restoration era of turkey management ended in the early 2000s when the rapid population growth observed during previous decades came to a close (Warnke and Rolley 2007, Porter et al. 2011, Tapley et al. 2011, Parent et al. 2016). Since the late 1990s, increased demand for hunting opportunities resulted in the liberalization of turkey harvest regulations, and subsequent growth of the number of hunters and number of turkeys harvested annually (Healy and Powell 2000, Healy and Powell 2001, Harris 2010). From 1996-2006 the total number of turkey hunters in the United States (US) increased by 15%, while the number of turkey hunters in the Midwest region increased by > 30% (Harris 2010). The number of turkey hunters in the US currently exceeds 2.6 million (fall 2013 and spring 2014 combined; Eriksen et al. 2016), and turkey hunting is second in popularity only to deer hunting (measured in number of participating hunters; Harris 2010). Consequently, recreational turkey hunting has developed into an activity that generates > $4 billion in annual output for the US economy (Harris 2010). While the number of turkey hunters has increased, there is also emerging evidence for broad-scale declines in recruitment of turkey poults into harvestable populations (Byrne et al. 2016, Casalena et al. 2016), and concerns over perceived local population declines in some areas (Porter et al. 2011, Ericksen et al. 2016).

A number of previous studies used population models to understand sustainability of turkey harvests (e.g., Lobdell et al. 1972, Vangilder 1992, Vangilder and Kurzejeski 1995, Alpizar-Jara et al. 2001), yet there is an ongoing need to study effectiveness of turkey management systems. Previous modeling studies often assessed performance of either-sex fall harvests (e.g., Vangilder and Kurzejeski 1995, Alpizar-Jara et al. 2001), but many models were parameterized using assumptions that appear untenable under present conditions. These assumptions often included highly productive turkey populations (e.g., 4.21 poults/hen; McGhee et al. 2008) and relatively light spring harvests (e.g., 15% of male population; Vangilder and Kurzejeski 1995, McGhee et al. 2008) that do not reflect reduced recruitment and high demand for hunting opportunities that exists currently in many areas. Despite the fact that turkey population change is known to be sensitive to the magnitudes of production and survival (Roberts and Porter 1996, Alpizar-Jara et al. 2001, McGhee et al. 2008), the precise implications of recent changes for sustainable harvest management are unclear.

More broadly, it has become evident that there are many exploitation rates that are biologically sustainable for any population (Rosenberg et al. 1993, Quinn and Collie 2005, Nichols et al. 2007). Thus, if scientific assessments of sustainable harvest are to be operational they must include clarification of fundamental objectives that relate to desirable levels of animals to harvest, and population sizes that are desirable to retain (Quinn and Collie 2005). Clarification of objectives related to both retention and harvest of a population forces managers and researchers to acknowledge the existence of management tradeoffs (between harvest and abundance) that are commonly induced by high levels of harvest (Quinn and Collie 2005, Bence et al. 2008). In the context of turkey management, harvest modeling studies conducted during the restoration era often implicitly assumed management objectives were to allow for continued population growth or population stability, while also meeting the demand for hunting opportunities (e.g., Vangilder 1992, Vangilder and Kurzejeski 1995, Rolley et al. 1998, Alpizar-Jara et al. 2001). Although maintaining populations at current levels may be possible, continued population growth appears to no longer be feasible. More recently, McGhee et al. (2008)

assumed the main objective of turkey management was to maximize annual harvest over both spring and fall hunting seasons, irrespective of population sizes resulting from harvest maximization. However, the implicit assumption underlying an objective of harvest maximization is that turkeys only provide value to stakeholders through their harvest, and not merely through their pursuit or through non-consumptive uses (e.g., wildlife viewing). Human dimensions evidence suggests, however, that even traditional turkey hunting stakeholder's value turkeys in more diverse ways than via harvest alone; for example, through interactions with gobbling males and the perception of abundant populations (Cartwright and Smith 1990, Little et al. 2000, Swanson et al. 2007). Thus, modern scientific assessments need to more closely align modeling outputs with modern management objectives to better inform turkey harvest management in the post-restoration era.

In addition to more closely aligning modeling studies with changing conditions, modern scientific assessments need to provide reliable, practical guidance to turkey management in the face of multiple uncertainties (Porter et al. 2011). The types of uncertainty most relevant to harvest management have been thoroughly described elsewhere (Francis and Shotton 1997, Williams 1997, Connelly et al. 2005), and include environmental, structural, implementation (also called partial controllability), and observation (also called partial observability) uncertainties. Environmental uncertainty refers to fluctuations in demographic processes that occur over time as a result of uncontrollable changes to environmental conditions (e.g., effects of spring weather on turkey recruitment; Roberts and Porter 1998). Structural uncertainty refers to the fact that dynamics of populations and their harvesting are only partially understood (e.g., causes of productivity declines, effects of density dependence, differential harvest vulnerabilities, etc.). Structural uncertainty can include uncertainty about the values of specific model parameters (parameter uncertainty; Francis and Shotton 1997, Fieberg 2004), or uncertainty about the correct functional or distributional forms describing system dynamics (Williams 1997, Runge and Johnson 2002). Structural uncertainty can also be reduced over time as we learn about the dynamics of managed populations, which is a cornerstone principle of adaptive management (Walters 1986, Johnson et al. 1997, Williams 1997, Irwin and Conroy 2013). Implementation uncertainty describes variation in realized harvest rates over time or space for a specific management action (i.e., for a set of hunting regulations), which exists because managers only have partial control of the actual number of turkeys harvested. Lastly, observation uncertainty refers to the imprecise information on population status before and after management decisions are made, which exists because population sizes are never known exactly (i.e., hunting regulations are set with imperfect knowledge of turkey abundance). These types of uncertainty are well established in the harvest management literature, but have been included inconsistently in turkey harvest models (Table 1.1).

Table 1.1 Review of turkey harvest modeling studies and their evaluation of different types of harvest policies (Policies) and inclusion of different types of uncertainty (Uncertainties).

	Policies		Uncertainties			
Study	Static[a]	State-dependent	Environmental[b]	Implementation	Structural	Observation
Lobdell et al. 1972	x	-	x	x	-	-
Suchy et al. 1983[c]	x	-	-	-	x	-
Vangilder 1992	x	-	x	-	-	-
Vangilder and Kurzejeski 1995[d]	x	-	x	-	-	-
Rolley et al. 1998[e]	x	-	-	-	x	-
Alpizar-Jara et al. 2001	x	-	x	-	-	-
Casalena et al. 2007	x	-	x	-	-	-
McGhee et al. 2008	x	-	x	x	-	-
McGhee and Berkson 2011[f]	x	x	x	x	-	-

[a] The most commonly assumed harvest strategy in turkey modeling studies was constant proportional harvesting.

[b] Not always termed environmental variation in literature, but refers annual fluctuations in demographic processes or parameter values that are usually assumed to be a function of changing environmental conditions.

[c] Suchy et al. (1983) considered structural uncertainty in the functional form of population responses to fall harvest (i.e., additive vs. compensatory mortality), but did so using deterministic models of population and harvest dynamics.

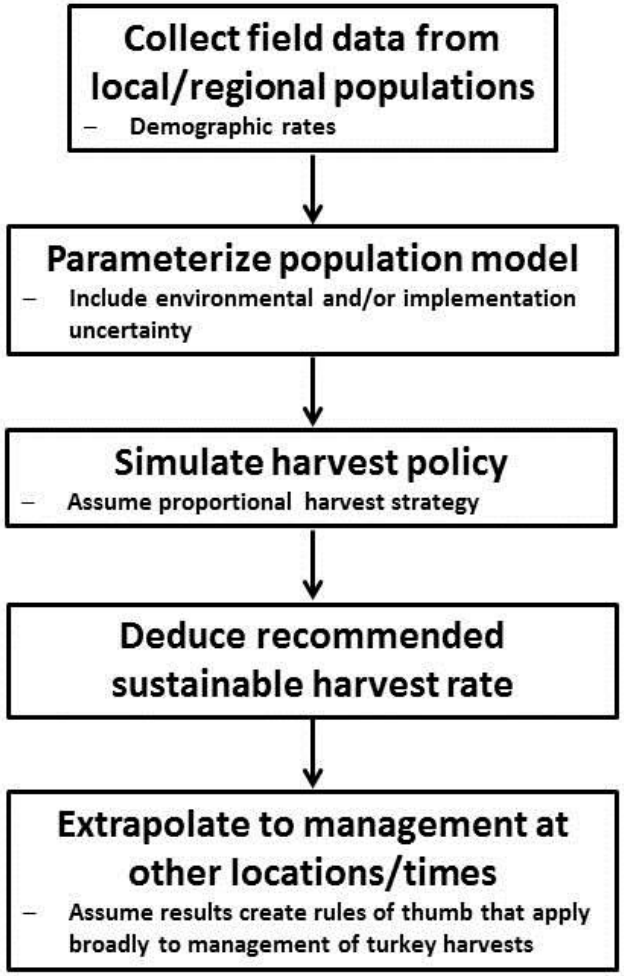
[d] Although structural uncertainty was not a focus of the manuscript, Vangilder and Kurzejeski (1995) did perform a simple sensitivity analysis to determine if changes to assumed values for several parameters affected performance of target harvests.

[e] Rolley et al. (1998) considered parameter uncertainty in recruitment and survival by generating random values of parameters across simulation replicates, but treated random realizations of demographic parameters as constant within simulation runs (i.e., no environmental uncertainty).

[f] McGhee and Berkson (2011) considered performance of state-dependent harvest policies that adjust target harvests using information updated annually, but did not acknowledge that information required is either not typically available to managers, or is estimated with observation uncertainty under a best case scenario.

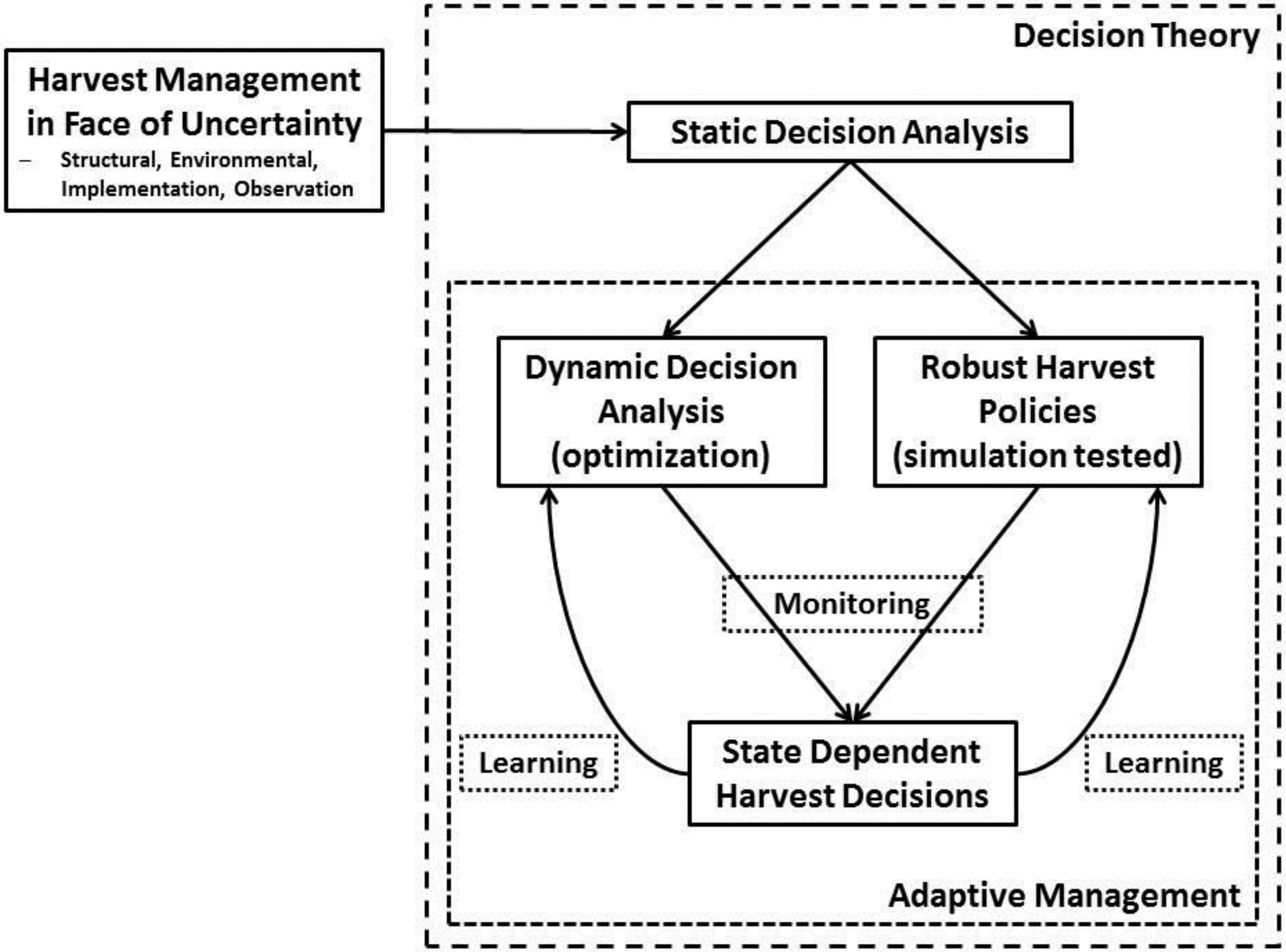
The traditional approach to deducing sustainable harvest recommendations for turkey management often considers several types of uncertainty (environmental, implementation), while uncommonly acknowledging others (structural, observation; Table 1.1). Development of recommendations often starts with collection of demographic data from a population in a spatially restricted area using field studies (Fig. 1.1). Such data are used to parameterize a mathematical model that is used to simulate population and harvest dynamics, which typically includes environmental and sometimes also implementation uncertainty to describe variation in demographic processes and realized harvest rates over time (Table 1.1). Simulation models are used to evaluate performance of different harvest policies, which allows for deduction of management recommendations for the area of interest (Fig. 1.1). However, results from earlier studies are often extrapolated through space-time to guide management at other locations-times, despite the fact that values of parameters (e.g., recruitment, survival) and functional forms of dynamics (e.g., different strengths and/or types of density dependence) for many populations are often unknown. Such extrapolation is by necessity, as decisions often must be made in the absence of detailed demographic information. What is potentially problematic, however, is when results of earlier studies are assumed to provide general rules of thumb for turkey management despite being developed without acknowledgement of important uncertainties (e.g., structural uncertainty; Runge and Johnson 2002). An example of this is the so-called “10% rule” adopted by many turkey managers in the Midwest (following results of Vangilder and Kurzejeski [1995] and further recommendations by Healy and Powel [2000]), suggesting fall harvests < 10% of the population are sustainable. An implicit assumption of such extrapolation is robustness of management recommendations to structural changes in population and harvest dynamics. Such robustness has often been assumed, but not adequately demonstrated.

Figure 1.1 Conceptual model of traditional approach commonly used to develop harvest management recommendations (i.e., rules of thumb) for sustainable management of wild turkey populations.



More generally, decision theory has provided a conceptual framework for substantial advancement in the development of approaches to managing harvests in the face of uncertainty (Fig. 1.2; Hilborn and Ludwig 1993, Shae et al. 1998). Development of such programs often starts with a static decision analysis (Clemen and Reilly 2001), which provides a framework for evaluating performance of management options at a single point in time, or performance of a static harvest policy (i.e., policy does not respond to changes in system-state variables) over a relevant time horizon. Iterative, state-dependent harvest policies can also be developed that update management decisions at regular intervals (e.g., annually) conditional on updated estimates of important system-state variables (e.g., animal abundance, environmental conditions, etc.). For example, adaptive harvest management of North American waterfowl is based on a dynamic decision analysis framework that uses optimization algorithms (stochastic dynamic programming; Lubow 1996) to determine optimal hunting regulations annually, conditional on estimates of waterfowl abundance and the number of ponds in the prairie-pothole region during the spring breeding season (Nichols et al. 1995, Johnson et al. 1997, Nichols et al. 2007). The emphasis of this approach is optimality, and on identifying the optimal decision at each point in time given the information at hand. Moreover, optimality is typically defined via a mathematical function describing how decision makers value different outcomes relative to underlying management objectives (called a utility or objective function; Runge and Walshe 2014). Thus, harvest decisions that are most likely to meet management objectives can be identified at regular intervals, and decisions are updated to reflect changing conditions.

Figure 1.2 Conceptual model of state-of-the-art decision-theoretic approaches to decision making for management of harvests of renewable natural resources in the presence of realistic uncertainties.



Another decision-analytic modeling framework has emerged in quantitative fisheries science to facilitate development of robust harvest policies that are effectively simulation-tested, state-dependent decision rules (Butterworth and Punt 1999, Punt 2006, Bence et al. 2008, Hilborn et al. 2012; Fig. 1.2). These decision rules modify target harvests annually, conditional on updated estimates of abundance or spawning-stock biomass. The simulation framework typically focuses on development of harvest policies (also called harvest control rules) that are robust to realistic uncertainties, rather than policies that are strictly optimal. As such, this approach often does not involve use of explicit objective functions, but instead focuses on visualizing tradeoffs among competing objectives (i.e., harvest vs. abundance) directly for each harvest policy under consideration (Bence et al. 2008, Irwin et al. 2011). This framework also commonly integrates management stakeholders directly into the process of harvest policy development through a sequence of workshops (Irwin et al. 2011). Thus, a robust harvest policy whose performance is acceptable to diverse groups of stakeholders can be identified without assuming a priori that all stakeholders must agree specifically on how to value different outcomes of harvest management.

Importantly, monitoring programs that permit estimation of important state variables like population size at regular intervals are a necessary component of state-dependent decision making in harvest management (Fig. 1.2). Both dynamic decision analysis and robust harvest policy approaches generally require estimates of abundance, for example, which is used to update harvest regulations at regular intervals. Dynamic decision analyses often do not incorporate observation uncertainty directly into modeling, but instead assume abundance estimates are unbiased and reasonable precise such that partial observability does not affect optimal decision-making (see additional discussions in Williams and Brown 2015). In contrast, development of robust harvest policies generally builds observation uncertainty into simulation testing, such that decision rules can be evaluated in the presence of imperfect information (Butterworth and Punt 1999, Punt 2006). Moreover, application of both dynamic decision analysis and robust harvest policies can be conducted in a manner consistent with adaptive management (Walters 1986) if monitoring programs are designed in a way that permits reduction of key structural uncertainties over time through learning (Fig. 1.2). When formal monitoring programs are not linked to explicit population assessment and decision frameworks (e.g., as in turkey harvest management), scientific assessments often focus on evaluating static policies that do not adjust target harvests in response to changing conditions, or assume perfect availability of information that is not actually present at the time decisions are made (Table 1.1). These result in possible disconnects between harvest management decisions and the science that provides guidance to those decisions.

Although substantial advancement has been made applying decision-analytic methods to the development of harvest management systems, application of such methods to develop rigorous approaches to managing turkey harvests is in its infancy. The general approach for deducing harvest recommendations common in turkey management (Fig. 1.1) is conceptually similar to the simulation framework used to identify robust harvest policies (Fig. 1.2); however, there are some stark differences. First, it should be clear that the range of uncertainties considered in past modeling studies (Table 1.1) was inadequate to ensure that existing turkey management recommendations are robust in the face of common management uncertainties. Moreover, abundance of turkey populations is typically not estimated regularly at scales relevant for harvest regulation using statistically rigorous estimation procedures, with a few notable and recent exceptions (Diefenbach et al. 2012, Gast et al. 2013, Clawsen et al. 2015). Employment of simulation-tested, state-dependent policies for harvest management (typical emphasis of robust policy development; Fig. 1.2) is therefore not feasible for most turkey populations. This is probably the reason why scientific evaluations have mostly assessed performance of static harvest policies for turkeys (Table 1.1). Several studies have described state-dependent decision rules for use in turkey management (e.g., Kimmel 2001, Bellamy and Pollard 2007); however, performance of these rules in the presence of realistic uncertainties has not been ascertained.

A first step towards more formally linking turkey harvest management with decision-theoretic methods is to address the need to better understand implications of structural uncertainty for turkey harvest management, as well as performance of existing recommendations in the presence of structural uncertainty. The reduction of structural uncertainty and development of tools needed to employ rigorous, state-dependent harvest policies is likely to take considerable time and effort. Thus, modern management is also in need of a viable path forward for developing management guidelines that are scientifically defensible in the face of current uncertainties, while also practically acknowledging that rigorous abundance estimates are typically not available to guide decision making in most areas. This research was pursued to address such needs and provide guidance to modern turkey management in the face of structural uncertainties in the dynamics of turkey populations and their harvesting. In this research I attempted to answer 3 general questions related to turkey harvest management: 1) How reliable are recently recommended strategies for maximizing turkey harvests to existing structural uncertainties in the form of both population and harvest models? 2) Are existing sustainable fall harvest recommendations robust to uncertainty about demographic parameters and harvest rates that is prevalent in the modern era of management? 3) Can I develop reliable harvest recommendations that are indicative of satisfactory management performance relative to modern objectives in the face of structural uncertainty?

This study used population modeling and simulation techniques to study the implications of structural uncertainty for modern turkey harvest management. In chapter 2 I describe a deterministic, heuristic modeling study used to evaluate sensitivity of proportional harvests that maximize different types of turkey harvest (annual, fall, spring, adult males during spring) to plausible functional forms of population and harvest models. I developed a set of 11 models representing hypothesized density-dependent dynamics and differential harvest vulnerabilities (among segments of the turkey population), and used these models to determine sensitivity of proportional harvests maximizing turkey harvests to incomplete information about system dynamics. I used stochastic simulation in chapter 3 to test robustness of performance for proportional fall harvests across a range of scenarios representing values of demographic and harvest parameters. Specifically, I developed 18 scenarios representing a plausible range of parameter space for 3 model parameters (population productivity, hen poaching during spring, spring male-only harvest), and used simulation to evaluate performance of fall harvests (0–15%) under each scenario. In chapter 4 I used a combination of stochastic simulation, static optimization, and static decision analysis to demonstrate an approach for developing target harvest rates in the presence of strong structural uncertainties, using fall turkey harvesting as a case study. Specifically, I developed 1,392 scenarios representing combinations of demographic and harvest parameters (population productivity, differential harvest vulnerability, spring male-only harvest), and used simulation to evaluate performance of fall harvests (0–15%) under each scenario. I identified fall harvest rates that were optimal for meeting modern objectives under each scenario using static optimization, and therefore described how optimal harvests change as a function of harvest and demographic parameters that may vary locally among turkey populations. I also used decision analysis to develop recommendations for target fall harvests in the face of limited information about productivity, differential vulnerability, and the strength of density-dependent feedbacks to population growth. Lastly, I finish the dissertation in chapter 5 by providing general conclusions and management recommendations, as well as discussion of steps needed to develop rigorous, state-dependent harvest policies for turkey management, and discussion of passive and active adaptive management options for learning about turkey population dynamics.

CHAPTER 2: SENSITIVITY OF MAXIMUM WILD TURKEY HARVESTS TO UNCERTAIN POPULATION AND HARVEST DYNAMICS

INTRODUCTION

Understanding limits to sustainable harvest is a fundamental goal of renewable resource management (Hilborn et al. 1995). Towards this end, 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 a population's density away from environmental carrying capacity (*K*) invokes a density-dependent increase in population growth that occurs as a result of changes to survival, recruitment, or body growth of individual animals, thus resulting in a surplus of animals that can be harvested (Hilborn et al. 1995, Ludwig 2001, Sutherland 2001). In theory these surpluses can be harvested to maintain population densities at reduced but stable levels relative to *K* (Caughley and Sinclair 1994, Sutherland 2001). Classical applications of MSY define yield in terms of biomass (fisheries) or number of individuals (wildlife) harvested, where overexploitation is achieved, and thus limits to sustainable exploitation are exceeded, when equilibrium biomass (B) or abundance (N) is reduced below values producing maximum population growth and harvestable surpluses (e.g., $B_{msy} = N_{msy} = K/2$ for logistic models; Caughley and Sinclair 1994, Mills 2007, Ludwig 2001, Punt and Smith 2001). Historically, maximum sustainable yields have often been identified using mathematical models of dynamics for the species and population of interest (Larkin 1977, McCullough 1984, Caughley and Sinclair 1994, Punt and Smith 2001). For example, McGhee et al. (2008) identified proportional either-sex fall harvest rates resulting in maximum sustainable harvests of wild turkeys (*Meleagris gallopavo*; hereafter, turkeys) using a sex-specific, density-dependent population model.

Mathematical models are used to determine maximum sustainable harvests, yet uncertainty affects the ability to identify and implement appropriate harvest strategies in fisheries and wildlife (Williams 1997, Sutherland 2001, Harwood and Stokes 2003, Bence et al. 2008). Williams (1997) categorized four types of uncertainty in the context of terrestrial wildlife harvest management: environmental, observation (also called partial observability), implementation (also called partial controllability), and structural. Although not the only characterization of uncertainties relevant for conservation and natural resource management (e.g., Francis and Shotton 1997, Regan et al. 2002), these categories provide a simple conceptual framework for studying implications of different types of uncertainty for wildlife harvest management. Environmental uncertainty exists because variation in environmental conditions creates variation in population processes (e.g., survival and reproduction) over time. Observation uncertainty refers to the fact that at best only estimates of population size are available to inform management decisions, and thus the number of animals in the population is likely known imprecisely prior to and after harvest. Implementation uncertainty exists because managers have a limited ability to control the number of animals removed by harvesters, as the processes underlying harvest have multiple dimensions (e.g., social, economic, environmental) that are not under management control. Specifically, implementation uncertainty refers to variation of actual harvests about their management targets due to these uncontrollable factors. Structural uncertainty occurs when there are multiple plausible models of ecological dynamics that are hypothesized, and thus responses of a population to harvest may be poorly understood. In reality, however, there can also be substantial uncertainty as to the most appropriate stochastic distributions needed to represent each type of uncertainty described by Williams (1997). Thus a more nuanced definition of structural uncertainty incorporates uncertain central tendencies and distributional forms for environmental, observation, and implementation uncertainty, respectively. Here I use this broader definition of structural uncertainty when referring to uncertain functional forms and parameters for models of population and harvest dynamics.

Use of population models to determine appropriate harvest strategies has a long history in turkey management (Lobdell et al. 1972, Porter et al. 1990, Vangilder and Kurzejeski 1995, Alpizar-Jara et al. 2001), yet consideration of structural uncertainty in population and harvest dynamics has received little attention (chapter 1). Many turkey harvest models included variation of population parameters or growth over time; implicitly assuming this variation was as a function of uncontrollable environmental conditions (e.g., Lobdell et al. 1972, Vangilder and Kurzejeski 1995, Alpizar-Jara et al. 2001, McGhee et al. 2008, McGhee and Berkson 2011). However, previous studies mostly assumed dynamics of turkey populations were precisely understood when evaluating harvest policies. Suchy et al. (1983) is the only study of which I am aware that acknowledged multiple hypotheses for the structural form of population dynamics; this study examined deterministic responses of turkey populations to fall harvest under multiple hypothesized models of survival compensation. Moreover, previous modeling studies have individually assumed different functional forms of realized segment-wise turkey harvest (e.g., harvest rates shared among population segments vs. sex- and stage-specific harvest rates), and the implications of these assumptions for management are poorly understood.

Recent research (McGhee et al. 2008) and conversations with biologists across the Midwestern United States (U.S.) suggested managers are interested in maintaining large turkey harvests and understanding their sustainability. Although McGhee et al. (2008) recommended combined fall proportional harvest rates for achieving maximum sustained harvests of turkey populations, these recommendations were deduced from models that did not adequately characterize structural uncertainty that exists in modern turkey management. For example, dynamics of high-density turkey populations and specific mechanisms regulating such populations are poorly understood (Healy 2011, Porter et al. 2011). Moreover, estimates of sex- and stage-specific harvest rates are unavailable for most populations, thus it remains unclear how best to represent expected segment-wise harvest resulting from hunting regulations in management models for turkeys. While early studies often assumed differential vulnerability to harvest among segments of the turkey population (e.g., Vangilder 1992, Vangilder and Kurzejeski 1995), recent studies assumed all turkeys share the same harvest rate during each hunting season (e.g., McGhee et al. 2008, McGhee and Berkson 2011). It remains unclear if recently recommended strategies for maximizing harvests generalize across a more plausible set of turkey management models. Therefore, my objective was to determine sensitivity of harvest rates producing maximum-sustainable harvests among models representing modern hypotheses for population and harvest dynamics of wild turkeys. I took this approach because if harvest rates producing maximum-sustainable harvests are sensitive to structural assumptions, this implies sensitivity of management recommendations to uncertainty in dynamics of turkey populations and their harvesting.

METHODS

General Approach

I used deterministic population projections to identify how changes in structural dynamics of turkey populations affected maximum sustainable harvests of turkeys. I simulated dynamics intended to mimic populations of turkeys in food-rich environments with density dependence mechanisms operating specifically through recruitment processes. I simulated populations in food-rich environments because my primary interest was turkeys inhabiting mixed agricultural–forest landscapes with abundant food resources that are common across northern areas of turkey range. Although causes and consequences of density dependence in turkey populations are poorly understood, research from other ground-nesting birds suggests recruitment compensation is a plausible hypotheses for the type of density dependence that may operate within turkey populations. 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). Some preliminary evidence for density-dependent recruitment in turkey populations has also recently emerged (e.g., Bond et al. 2012). Moreover, my conversations with turkey biologists from across the U.S. suggested density-dependent recruitment as a dominant hypothesis regarding the regulation of modern turkey populations. It is also widely recognized that dynamics of turkey populations at northern latitudes are strongly influenced by annual production and recruitment of poults into the fall population (Suchy et al. 1990, Roberts and Porter 1996, Rolley et al. 1998). Also, turkey populations in agricultural landscapes at northern latitudes often to have high overwinter survival (Porter et al. 1980, Vander Haegen et al. 1988, Porter 2007, Parent et al. 2011), suggesting increases in survival at this stage from reduced densities may be unlikely. Thus, I hypothesize that density dependence operating through per-capita recruitment is a plausible scenario in fragmented but food-rich landscapes commonly inhabited by turkeys.

I developed a set of 11 dynamic models to evaluate robustness of harvest rates maximizing equilibrium harvests to assumptions about turkey population dynamics and harvesting. Models differed in functional forms of density dependence and whether they explicitly included stage-structured dynamics, stage-specific nesting rates, and differential harvest vulnerabilities by sex, stage, and hunting season (Table 2.1). 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 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 non-hunting survival rates of remaining individuals were unaffected by harvest. Additive mortality is a common assumption for turkey harvest models (e.g., Vangilder and Kurzejeski 1995, Alpizar-Jara et al. 2001, McGhee et al. 2008) 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 food resources are abundant, but could be violated if seasonally density-dependent survival is present (Ratikainen et al. 2008).

Table 2.1 Descriptions of population models used to evaluate robustness of maximum harvests of wild turkeys to changes in forms of density dependence and model parameterizations.

Model[a]	Model descriptions
Ageless models	
θ-R	Theta-Ricker model with composite growth and density dependence
BH	Beverton-Holt model of density-dependent recruitment
TR	Threshold model of density-dependent recruitment
Stage-structured models	
BH1	Beverton-Holt recruitment, no stage-specific nesting, equal harvest vulnerability
BH1-V	Beverton-Holt recruitment, no stage-specific nesting, differential harvest vulnerability[b]
BH2	Beverton-Holt recruitment, stage-specific nesting[c], equal harvest vulnerability
BH2-V	Beverton-Holt recruitment, stage-specific nesting, differential harvest vulnerability
TR1	Threshold recruitment, no stage-specific nesting, equal harvest vulnerability
TR1-V	Threshold recruitment, no stage-specific nesting, differential harvest vulnerability
TR2	Threshold recruitment, stage-specific nesting, equal harvest vulnerability
TR2-V	Threshold recruitment, stage-specific nesting, differential harvest vulnerability

[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 Kurzejeski (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 (Table 2.2).

I modeled population dynamics and harvest for turkeys with 3 different functional forms of density dependence (Table 2.1). I used 1 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 2007a). I used 2 functional forms of density dependence that assumed feedbacks on population dynamics operated specifically through recruitment of turkey poults into fall populations (Fig. 2.1). I 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. 2.1). 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, I refer to the hockey-stick model as the TR model because it results in threshold responses for density-dependent recruitment. 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). Mathematical details for all models, biological meaning of all model parameters, and plausible mechanisms that could generate each model for a real turkey population are discussed in Appendices A–B.

Figure 2.1 Total (a) and per-capita (b) recruitment for functional forms of recruitment density dependence used to model population and harvest dynamics for wild turkeys. The density-independent mortality process is represented by the dashed line, and thus total mortality is proportional to abundance. Note that recruitment models demonstrated here are of the same form but slightly different than actual parameterizations used for turkey population and harvest models. These examples are simplified by ignoring sex structure and stage structure and are used for demonstrating basic concepts. A full description of model parameterizations used for sex-specific and density-dependent turkey population models are described in the Methods and in Appendices A and B.

a)

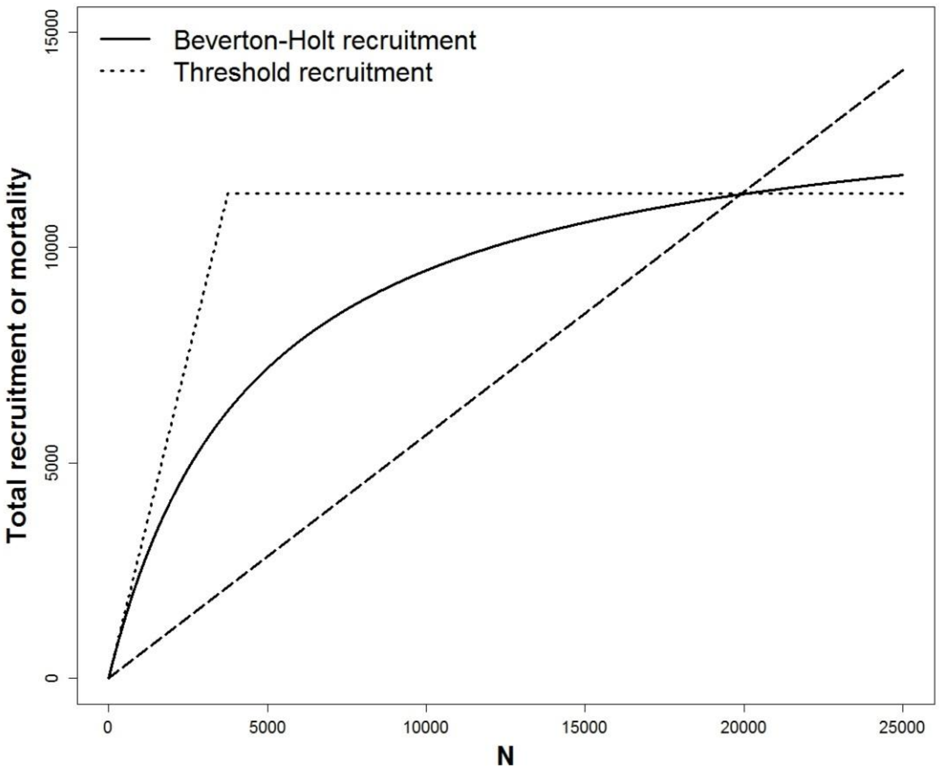
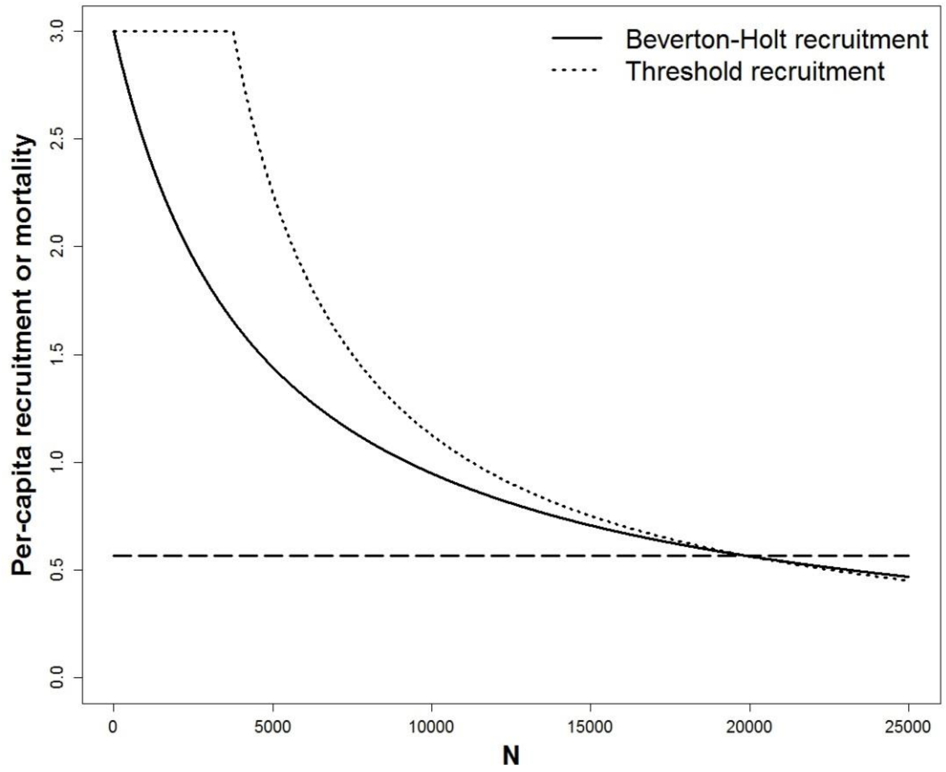


Figure 2.1 (cont'd)
b)



I considered performance of a constant proportional harvest strategy, where a proportion of the population was removed each year during spring and fall seasons. I evaluated equilibrium harvests over a range of spring and fall harvest rates to identify combined proportional harvests maximizing different types of turkey harvest on an annual basis. Specifically, I used a grid search and varied spring and fall proportional harvest rates for males (or adult males for models with stage-structure) from 0 to 1 in increments of 0.0025. I forward-projected population abundance until equilibrium was reached for each combination of spring and fall harvest rates. Harvest rates for other sex or stage categories were linear functions of male harvest rates. Because these simulation models were deterministic, I identified harvest rate combinations that resulted in maximum sustainable harvests to an accuracy of within 0.25% for each hunting season. For this analysis I calculated equilibrium harvest of all turkeys over both seasons (i.e., total annual harvest), equilibrium harvest of all turkeys during fall hunting seasons (i.e., total fall 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 me to determine harvest rates resulting in maximum-sustainable harvest for the 4 different harvest objectives of total annual, total fall, total spring, and spring adult male harvest.

Production Models

I developed 3 models without specific designation of age classes to represent population dynamics with density dependence (Table 2.1, Appendix A). These models assumed no age structure in dynamics, equal production of male and female poults, 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 population size changed for each sex. I used the following general equations to simulate dynamics under the theta-Ricker model:

$$N_{female,t+1} = N_{female,t}(1-p) \times growth_{f,t} - H_{f,fall,t}$$
$$N_{male,t+1} = N_{male,t} \times growth_{m,t} - H_{m,spring,t} - H_{m,fall,t}$$

Where:

$$H_{f,fall,t} = N_{female,t}(1-p) \times growth_{f,t} \times h_{f,fall}$$
$$H_{m,spring,t} = N_{male,t} \times h_{m,spring}$$
$$H_{m,fall,t} = \left[N_{male,t} \times growth_{m,t} - H_{m,spring,t}\right] \times h_{m,fall}.$$

For this model, p represents hen poaching rate during spring hunting 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. I assumed $p = 0.05$ for all models following McGhee et al. (2008); this value was also consistent with poaching rates reported by several earlier studies (e.g., Vangilder and Kurzejeski 1995, Pack et al. 1999). I determined sex-specific functions representing new population growth at time t (i.e., $growth_{i,t}$) 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 (2007a) and McGhee et al. (2008). However, I made 2 changes to model equations previously described to increase biological realism (see Appendix A for mathematical details): (1) I 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) I 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×births)/N_f instead of (0.5×births)/($N_f + N_m$) presented originally by McGhee [2006]). I assumed all values for specific parameters of the theta-Ricker model were identical to those used by McGhee et al. (2008). Lastly, I arbitrarily set sex-specific environmental carrying capacities (K_i) 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. This determined the overall scale of results, but had no influence on harvest rates resulting in maximum proportional harvests.

I developed 2 production models to represent population and harvesting dynamics in presence of density-dependent recruitment. These models used similar assumptions as the theta-Ricker model, with the following additional assumptions: (1) per-capita recruitment of poults 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 poults such that numbers of recruits of each sex into the population was half the number of total fall recruits. The general form of production models with density-dependent recruitment was:

$$N_{female,t+1} = \left[N_{female,t}(1-p) + 0.5R_t - H_{f,fall,t}\right] \times s_f$$
$$N_{male,t+1} = \left[N_{male,t} + 0.5R_t - H_{m,spring,t} - H_{m,fall,t}\right] \times s_m$$

where:

$$H_{f,fall,t} = \left[N_{female,t}(1-p) + 0.5R_t\right] \times h_{f,fall}$$
$$H_{m,spring,t} = N_{male,t} \times h_{m,spring}$$
$$H_{m,fall,t} = \left[N_{male,t} + 0.5R_t - H_{m,spring,t}\right] \times h_{m,fall}.$$

In this model R_t represents total recruits into the fall population at time *t* and s_i represents survival during the non-hunting period 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). I assumed non-hunting survival rates were 0.74 for males and 0.64 for females (McGhee et al. 2008), and density-independent recruitment rates were 3 poults per hen (i.e., including males and females). However, I acknowledge this simulates dynamics for a very productive turkey population as many previous harvest simulation 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, I 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. I started all population simulations with 10,000 turkeys each for males and females, and used a 1,000-year population projection to ensure equilibrium conditions were reached.

Stage-Structured Models

I developed 8 models of stage-structured populations for turkeys in presence of density dependent recruitment (Table 2.1, Appendix B). For all stage-structured models, abundance represented number of turkeys in each sex- and stage-class (i.e., juvenile ≤1 year old; adult >1 year old) at the start of annual spring hunting seasons, and all models had the general form:

$$
\begin{aligned}
N_{juv,f,t+1} &= \left[0.5R_t - H_{juv,f,fall,t}\right] \times s_{juv,f} \\
N_{juv,m,t+1} &= \left[0.5R_t - H_{juv,m,fall,t}\right] \times s_{juv,m} \\
N_{ad,f,t+1} &= \left[(1-p)N_{ad,f,t} + (1-p)N_{juv,f,t} - H_{ad,f,fall,t}\right] \times s_{ad,f} \\
N_{ad,m,t+1} &= \left[N_{ad,m,t} - H_{ad,m,spring,t} + N_{juv,m,t} - H_{juv,m,spring,t} - H_{ad,m,fall,t}\right] \times s_{ad,m}
\end{aligned}
$$

where:

$$
\begin{aligned}
H_{juv,i,fall,t} &= 0.5R_t h_{juv,i,fall} \\
H_{ad,f,fall,t} &= \left((1-p)N_{ad,f,t} + (1-p)N_{juv,f,t}\right)h_{ad,f,fall} \\
H_{ad,m,spring,t} &= N_{ad,m,t}h_{ad,m,spring} \\
H_{juv,m,spring,t} &= N_{juv,m,t}h_{juv,m,spring} \\
H_{ad,m,fall,t} &= \left[N_{ad,m,t} + N_{juv,m,t} - H_{ad,m,spring,t} - H_{juv,m,spring,t}\right]h_{ad,m,fall}.
\end{aligned}
$$

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

I developed 4 models each with BH and TR density-dependent recruitment, where each model was parameterized to accommodate hypothesized differences in nesting rates (i.e., proportion of hens nesting) and harvest vulnerabilities (Table 2.1). Specifically, I 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). I reviewed 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; Table 2.2) for BH2 and TR2 models. I 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, I 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.

Table 2.2 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 ($\bar{x}$ = 0.66) than adult hens ($\bar{x}$ = 0.88). I attempted to emphasize studies from northern latitudes, although the VA and WV studies were admitted primarily because they reported nesting rates by stage. I assumed all birds were adults for studies that failed to report the stage-structure of their samples (n = 4 studies).

		Juveniles		Adults	
Source	Location	Nesting rate	n	Nesting rate	n
Glidden and Austin 1975[a]	NY	1	51.57[b]	0.9	118.45[b]
Hayden 1980[a]	PA	0.42	51.57[b]	0.98	118.45[b]
Porter et al. 1983	MN	0.88	48	0.96	27
Vangilder et al. 1987	MO	-	-	1	127
Vander Haegen et al. 1988	MA	0.81	16	1	20
Roberts et al. 1995	NY	0.89	52	0.99	136
Paisley et al. 1996	WI	0.79	56	0.98	164
Godfrey and Norman 2001	VA	0.54	28	0.78	68
Vangilder et al. 2001[c]	MO	-	-	0.74	100
Vangilder et al. 2001[c]	MO	-	-	0.83	101
Norman et al. 2001	VA/WV	0.49	156	0.8	536
Nguyen et al. 2003	ON	0.42	5	0.68	15
Jackson et al. Unpublished[a]	IA	0.56	51.57[b]	0.97	118.45[b]
Little and Varland 1981	IA	-	-	0.89	9

[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.

[c] Vangilder et al. (2001) reported nesting rates separately for populations in 2 distinct regions of MO.

For stage-structured models, I assumed non-hunting survival of adults was identical to values assumed in production 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 survival exist for juvenile turkeys in the absence of harvest. However, Little et al. (1990) reported non-hunting survival rates of juvenile hens in Iowa, U.S., were approximately 10% less than adult survival rates. Thus, I assumed juvenile survival for both sexes was 10% less than adults. Similar to production models, I assumed maximum per-capita recruitment at small population sizes was 3 total poults per hen. Stage-structured models without differential nesting rates and harvest vulnerabilities (BH1 and TR1; Table 2.1) had similar functional forms of recruitment dynamics as their ageless counterparts (BH and TR; Table 2.1), yet they retained unique (but constant) sex and stage-specific survival rates. I 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. I simulated all stage-structured dynamics for 1,000 years to reach equilibrium conditions, and started simulations with 10,000 turkeys in each sex- and stage-class (i.e., 40,000 turkeys in the population). I programmed all population models in R statistical computing language (version 3.03, R Core Development Team 2014). This analysis was deterministic and did not assess risks of attempting to maximize harvest for a given set of objectives under stochastic conditions. Rather, the goal was to demonstrate robustness (or lack thereof) of harvest rates that would produce maximum harvests of different types to meet different management objectives.

RESULTS

Production Models

Harvest rates that maximized harvest changed with the underlying form of density dependence (Table 2.3). 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 = 6.75–34.0%; Table 2.3). 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 = 23.5–27.25%; Table 2.3). Fall harvest was maximized by only harvesting during fall seasons, and harvest rates maximizing fall harvest more than doubled across models of density dependence (range = 16.50–34.00%; Table 2.3).

Table 2.3 Combined spring–fall proportional harvest rates that maximized total annual harvest (Annual), spring gobbler harvest (Spring gobbler), adult male harvest during spring (Adult spring), and fall either sex harvest for density-dependent models for wild turkeys. Numbers are expressed as percentages (i.e., proportional harvest rate×100).

	Harvest type by season							
	Annual		Spring gobbler		Adult spring		Fall either sex	
Model[a]	Spring	Fall	Spring	Fall	Spring	Fall	Spring	Fall
Ageless models								
θ-R	99.75	10.50	99.75	0.00	-	-	0.00	22.75
BH	100.00	6.75	100.00	0.00	-	-	0.00	16.50
TR	100.00	34.00	100.00	0.00	-	-	0.00	34.00
Stage-structured models[b]								
BH1	100.00	5.25	100.00	0.00	33.75	0.00	0.00	14.50
BH1-V	100.00	4.50	100.00	0.00	55.75	0.00	0.00	9.00
BH2	100.00	0.00	100.00	0.00	33.75	0.00	0.00	9.25
BH2-V	100.00	1.25	100.00	0.00	55.75	0.00	0.00	6.00
TR1	100.00	30.00	100.00	0.00	33.75	0.00	0.00	30.00
TR1-V	100.00	17.50	100.00	0.00	55.75	0.00	0.00	17.50
TR2	100.00	19.00	100.00	0.00	33.75	0.00	0.00	19.25
TR2-V	100.00	11.50	100.00	0.00	55.75	0.00	0.00	11.50

[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.

Harvest curves changed in subtle ways with changes to underlying forms of density dependence and types of harvest being maximized (Fig. 2.2). Despite being maximized at a different combination of spring–fall harvest rates, harvest curves were similarly shaped for theta-

Ricker and BH models (Fig. 2.2). On the fall harvest axis, annual harvest was a nonlinear function that peaked at non-zero values (Fig. 2.2a). 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. 2.2a). In contrast, curves for spring harvest versus harvest rate (Fig. 2.2b) showed a linearly decreasing effect on equilibrium spring harvest with increased fall harvest rate, at least for theta-Ricker and BH models. The 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 reduced harvest rapidly to 0 (Fig. 2.2b). However, the equilibrium spring harvest for the TR model decreased linearly with increases in fall harvest rates below the threshold (Fig. 2.2b).

Figure 2.2 Equilibrium harvest of wild turkeys generated from models of population and harvest dynamics under different forms of recruitment density dependence. Equilibrium harvest is presented as a proportion of the un-harvested equilibrium (i.e., environmental carrying capacity) on vertical axes for spring–fall proportional harvest rates for the following harvest types: a) total annual harvest and b) total spring harvest for the theta-Ricker, Beverton-Holt recruitment, and threshold recruitment models of density dependence (moving from left to right).

a)

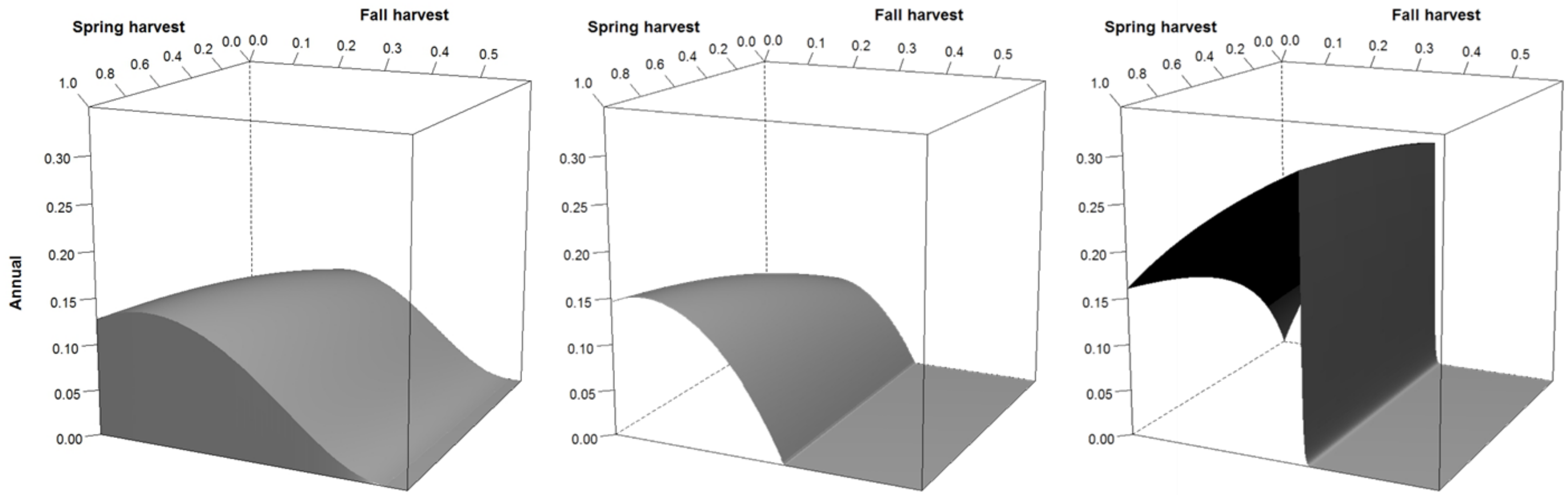
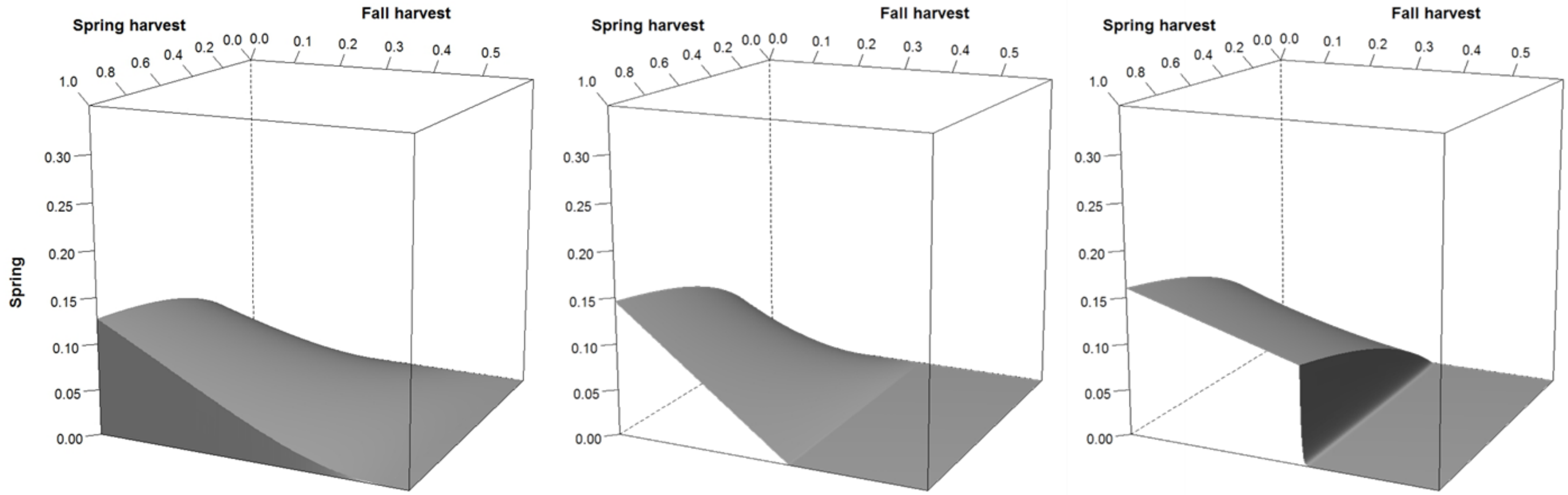


Figure 2.2 (cont'd)
b)



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 2.3). Changes in harvest allocation between maximizing annual harvest or spring harvest were again manifested through changes to fall harvests rates (Table 2.3). 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 2.3). 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 2.3). 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 = 0.00–30.0%; Table 2.3). 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 2.3). 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 = 33.75–55.75%). 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 2.3).

Harvest curves for stage-structured models changed with model assumptions and types of harvest being maximized (Figs. 2.3–2.5). General shapes of harvest curves for annual harvest (Fig. 2.3) and spring harvest (Fig. 2.4) were similar to their ageless counterparts (Fig. 2.2). 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 zero at smaller harvest rates, and this was true for all harvest curves. Similarly, adding differential harvest vulnerability to annual (Fig. 2.3) and spring (Fig. 2.4) harvest curves resulted in smaller fall harvest rates required to drive harvest towards zero than corresponding models assuming equal vulnerability. For example, harvest curves for models BH2 and BH2-V (Fig. 2.3) 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. 2.3), ascending limbs of curves on the low end of fall harvest rate axes were reduced, with the overall result that harvest (both annual and spring) fell to zero more quickly as fall harvest increased. Stage-structured TR model curves were not shown to conserve space (but are available at www.figshare.com; 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. 2.2) 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 zero.

Figure 2.3 Equilibrium total annual harvest (annual) of wild turkeys generated from stage-structured models of population and harvest dynamics under different forms of recruitment density dependence. Equilibrium harvest is presented as a proportion of the un-harvested equilibrium (i.e., environmental carrying capacity) on vertical axes for combinations of spring–fall proportional harvest rates. Results are presented for the Beverton-Holt recruitment model with the following parameterizations: a) no stage-specific nesting and equal harvest vulnerability (BH1), no stage-specific nesting but differential harvest vulnerability by sex, stage, and season (BH1-V), and b) stage-specific nesting and equal harvest vulnerability (BH2), and stage-specific nesting rates with differential harvest vulnerability by sex, stage, and season (BH2-V).

a)

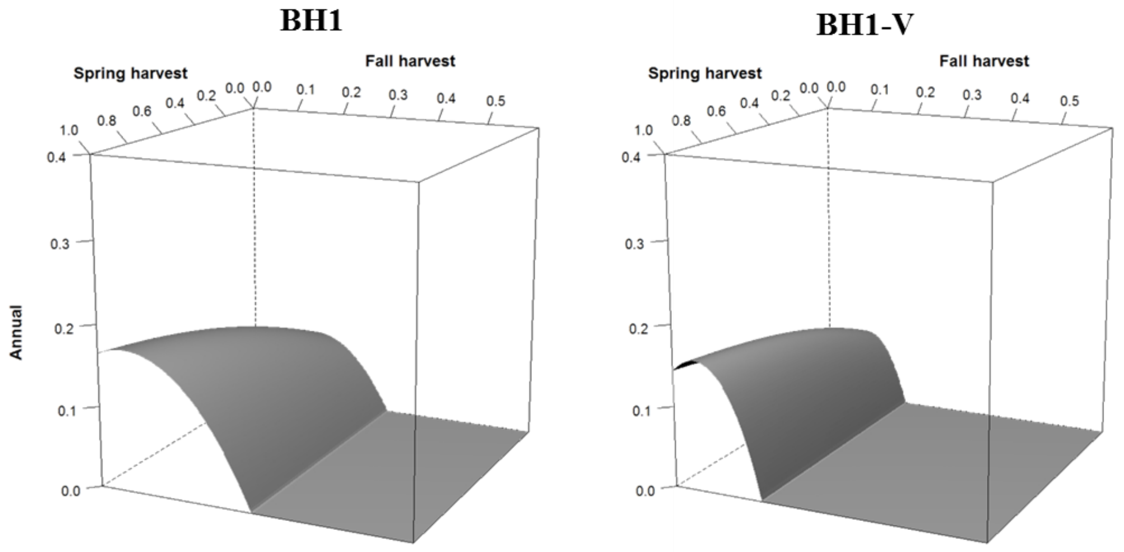
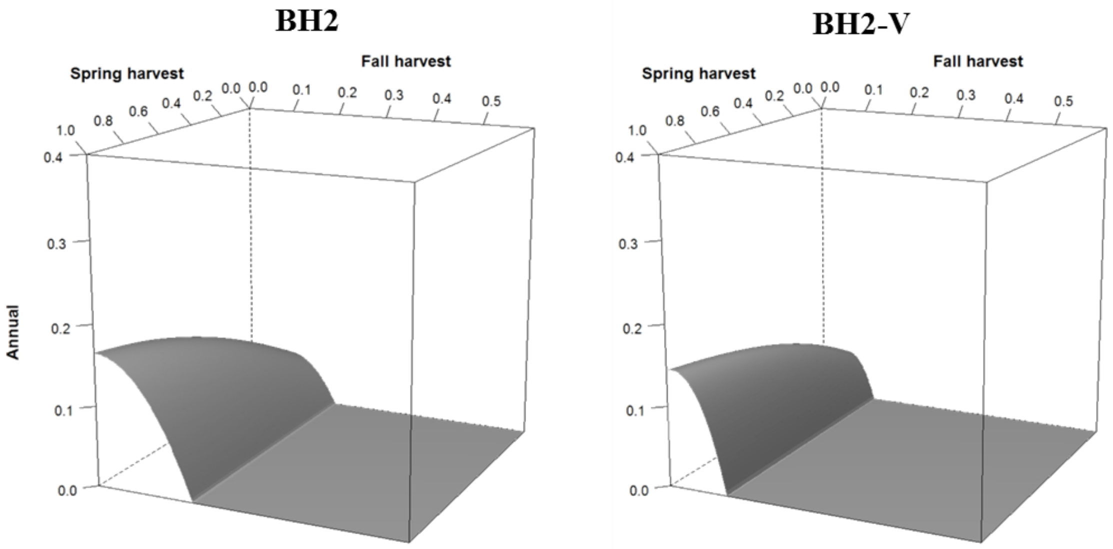


Figure 2.3 (cont'd)
b)


BH2

BH2-V

Figure 2.4 Equilibrium total spring harvests (spring) of wild turkeys generated from stage-structured models of population and harvest dynamics under different forms of recruitment density dependence. Equilibrium harvest is presented as a proportion of the un-harvested equilibrium (i.e., environmental carrying capacity) on vertical axes for combinations of spring–fall proportional harvest rates. Results are presented for the Beverton-Holt recruitment model with the following parameterizations: a) no stage-specific nesting and equal harvest vulnerability (BH1), no stage-specific nesting but differential harvest vulnerability by sex, stage, and season (BH1-V), and b) stage-specific nesting and equal harvest vulnerability (BH2), and stage-specific nesting rates with differential harvest vulnerability by sex, stage, and season (BH2-V).

a)

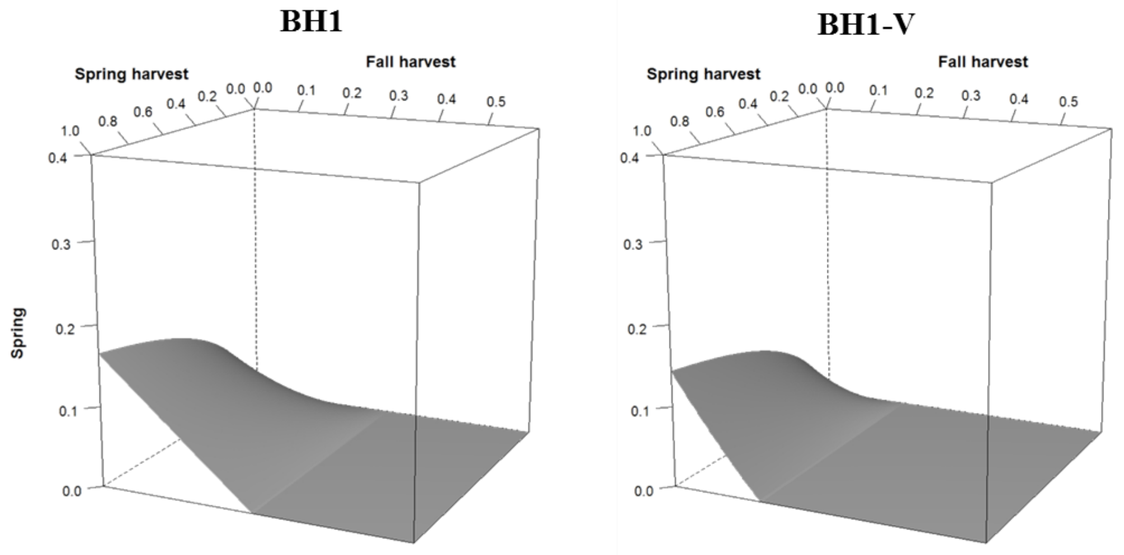


Figure 2.4 (cont’d)
b)

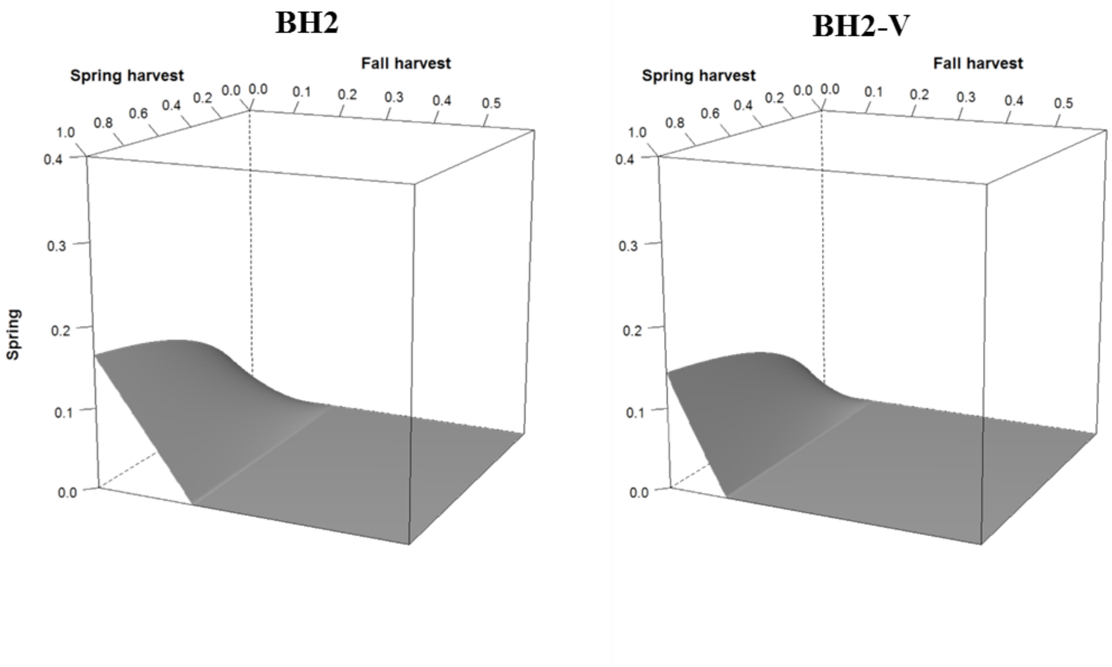
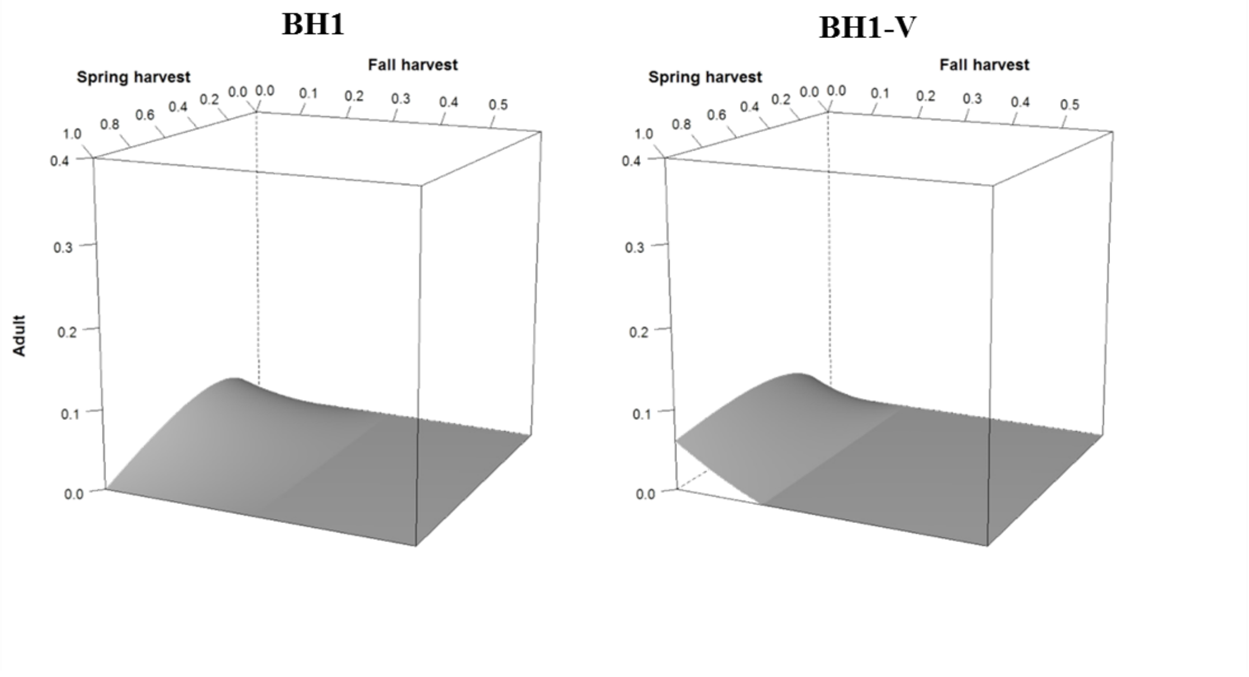


Figure 2.5 Equilibrium harvest of adult male wild turkeys during spring (adult) generated from stage-structured models of population and harvest dynamics under different forms of recruitment density dependence. Equilibrium harvest is presented as a proportion of the un-harvested equilibrium (i.e., environmental carrying capacity) on vertical axes for combinations of spring–fall proportional harvest rates. Results are presented for the Beverton-Holt recruitment model with the following parameterizations: a) no stage-specific nesting and equal harvest vulnerability (BH1), no stage-specific nesting but differential harvest vulnerability by sex, stage, and season (BH1-V), and b) stage-specific nesting and equal harvest vulnerability (BH2), and stage-specific nesting rates with differential harvest vulnerability by sex, stage, and season (BH2-V).

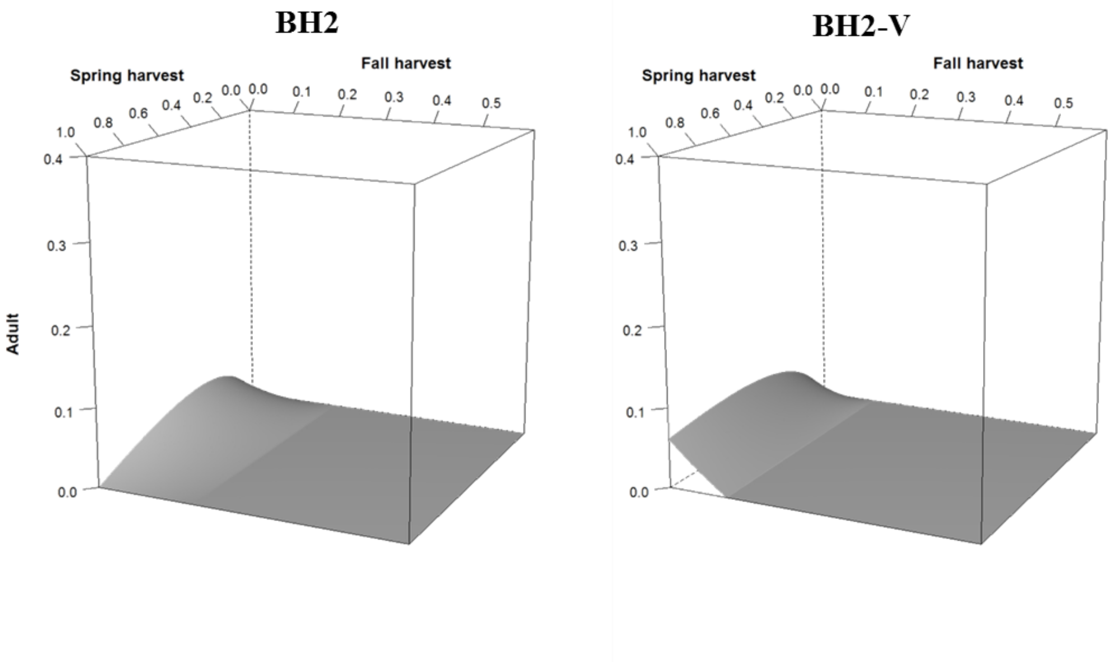
a)



BH1

BH1-V

Figure 2.5 (cont'd)
b)



Harvest curves for adult males during spring were distinctly shaped and maximized at smaller harvest rates (Fig. 2.5) during spring than total spring harvest (Table 2.2), illustrating the tradeoff between maximizing spring-male or adult-spring harvest. This was reflected via peaks in harvest curves at reduced spring harvest rates for adult males (Fig. 2.5), compared to greater harvest rates to maximize spring harvest (Fig. 2.4). 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. 2.5). 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.

DISCUSSION

My results demonstrate that proportional harvests required to maximize turkey harvest were not robust across alternative plausible models of population and harvest dynamics. This strongly suggests such harvest rates are sensitive to structural uncertainty surrounding appropriate model forms for the dynamics of turkey populations and their harvest. I also demonstrate that the importance of assumptions about ecological and harvest processes were context-specific and depended on the types of harvest being maximized. 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 and fall harvests varied among models. For example, a BH form of recruitment with stage-specific nesting rates (BH2) required no fall harvest to maximize annual harvest of turkeys over spring and fall hunting seasons, whereas a threshold recruitment model with no stage structure (TR) required a fall harvest rate of 34%. Sensitivity of fall harvest rates that maximized annual harvest has important management implications because turkey populations are sensitive to intensity of fall harvest (Vangilder 1992, Vangilder and Kurzejeski 1995, Alpizar-Jara et al. 2001). The relationship between per-capita production of young and population density is an influential determinant of the amount of harvest a population can sustain, which is widely known in the stock-recruitment literature (Ricker 1954, Hilborn and Walters 1992, Hilborn et al. 1995). My results corroborate this idea and show that if hypothesized density-dependent recruitment is plausible for wild turkeys it will directly affect maximum sustainable harvests.

Sensitivity of proportional fall harvests to structural form of the population model suggests that reliably maximizing total annual or fall harvest of turkeys will be difficult with existing information. Compensation acting on specific ecological processes such as recruitment can result from multiple ecological mechanisms (Dobson et al. 1988, Newton 1998), and I am 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]). Therefore I 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 (2007b) failed to detect such evidence using much shorter time series from 7 states (range = 6–14 years). Turkey demography and population drivers also differ spatially and among habitat types and landscapes (Vangilder 1996, Vangilder et al. 2001, Fleming and Porter 2007). Thus, it may not be realistic to envision a single model or form of density dependence is applicable to all turkey populations. My results therefore suggest attempting to manage for MSY without knowledge of underlying causes of density dependence may not be a reliable approach to turkey harvest management, as decision makers would lack robust harvest targets to guide management. In fisheries science it has been recognized for nearly 40 years that uncertainty about biological dynamics can make MSY an unattainable management goal (Larkin 1977), although recognition of these limitations was not acknowledged by studies recommending harvest rates to achieve MSY for turkeys (McGhee et al. 2008). Furthermore, my results reinforce suggestions by Healy and Powell (2000) that managers in most areas lack appropriate information necessary to maximize annual or fall harvest of turkeys, even though they were primarily referring to inadequate knowledge of population sizes.

Sensitivity of proportional harvest rates to structural form of harvest models also has important implications for harvest that change with underlying management objectives. Inclusion of differential harvest vulnerability reduced proportional fall harvests required to maximize annual turkey harvest, which was expected because 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. This would cause unknown problems for future reproduction, but could be problematic as all breeders in subsequent years would be 1-year-old males. Technically my models did not account for such effects, but it is unlikely that modern turkey hunting could remove even close to all of the male population in most areas (Lint et al. 1993). Yet 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. 2016). Moreover, if juvenile males have reduced harvest rates in spring relative to adults due to differential vulnerability to harvest (e.g., Diefenbach et al. 2012), more juvenile birds would survive to be adults in subsequent years for a given adult male harvest rate. Thus, adult males would still exist in the population in years subsequent to large spring removals, and adult harvest could be maintained in presence of large spring harvests. Indeed, including differential harvest vulnerability in my 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. This was a function of vulnerability assumptions, where juvenile vulnerability to spring harvest was less than that of adult males and thus more juveniles could survive harvest during their first spring at a given rate of adult harvest.

Clearly, more information on harvest vulnerability by stage-class is necessary in many areas if managers want to maximize spring harvest constrained by maintaining a desired population structure.

There is a paucity of recent published information on relative harvest vulnerabilities and causes of heterogeneity in vulnerability in different areas or through time. I assumed harvest vulnerabilities followed assumptions made by Vangilder and Kurzejeski (1995). However, this may not reflect modern turkey hunting and hunter behavior. 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 reduce juvenile male vulnerability during spring hunting by implementing harvest regulations severely limiting juvenile take (Butler et al. 2016). Such regulations shift the age structure of harvest towards adults because jake harvest is only allowed for youth hunters (Butler et al. 2016). However, even in the absence of specific regulations, changes to harvest vulnerability may occur through time. For example, Norman and Steffen (2003) suggested vulnerability to fall hunting may vary annually with oak (*Quercus* spp.) mast crops in Virginia. Others have 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 (Roberts et al. 1995).

Despite a lack of current information for most turkey populations, some managers have suggested anecdotal observations indicate fall harvest vulnerabilities may have shifted in recent years due to a changing hunter preference towards harvesting males. Although I am unaware of published evidence of changes to fall turkey hunter selectivity patterns, these would almost certainly affect sustainability of fall harvests for a given level of hunter effort because hen harvest could be reduced. Irrespective of vulnerability patterns for a specific region or season, however, 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 radio-marked turkeys (Vangilder and Kurzejeski 1995, Vangilder 1996, Pack et al. 1999; except see Godwin et al. [1991]). Regardless, a limited understanding of current harvest vulnerabilities by stage, sex, or season will likely complicate efforts to maximize total annual harvest or spring harvest with stage-specific constraints in the absence of specific harvest regulations limiting stage-specific take (e.g., Butler et al. 2016).

Given harvest rates maximizing turkey harvests were not robust to structural form of population and harvest models, management efforts may be better served by focusing on development of harvest strategies that are robust to uncertainty rather than on attempting to maximize harvest. Maximum proportional harvests were sensitive to a limited understanding of the dynamics of turkey populations and their harvest, yet it is likely possible to identify harvest strategies that do not maximize harvest but still perform reasonably well relative to management objectives under a variety of plausible conditions. For instance, all of the equilibrium 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 (Figs. 2.2b and 2.3b). 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 proportional spring harvests of adult males.

Although my analyses suggest potential pathways to robust harvest strategies, a more thorough understanding of harvesting risks and tradeoffs among competing objectives (e.g., total spring versus adult spring harvest) would be better accomplished with a stochastic simulation analysis than by 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, my analyses demonstrate that the types of uncertainties considered were too narrow to ensure identification of turkey harvest strategies that are robust across plausible scenarios of population and harvest dynamics. Specifically, my results strongly suggest that structural form of models for population dynamics and relative harvest vulnerabilities can have implications for management that depend on harvest objectives, and therefore structural uncertainty should be more explicitly accounted for in turkey harvest models. Explicit incorporation of structural uncertainty could be accomplished by assigning probabilities to each hypothesized model and identifying harvest rates that meet management objectives in the presence of uncertainty in the models themselves. It is highly unlikely that identifying target harvest rates using a single model would produce the same results as formally weighting multiple models, given the sensitivity of harvest rates achieving MSY turkey harvests identified in this study. Modern stochastic-simulation methods embrace uncertainty while seeking harvest strategies that are robust across plausible scenarios (Francis and Shotton 1997, Punt 2006, Punt and Donovan 2007, Bence et al. 2008), and future research would benefit turkey management by a more thorough assessment of harvest performance in stochastic environments.

MANAGEMENT IMPLICATIONS

My analyses demonstrate that changes to ecological and harvest model assumptions affect combined spring–fall proportional harvests that maximize sustainable harvest of turkeys. Attempts at maximizing total annual harvest across spring and fall seasons, or maximizing fall-only harvests, are ill-advised because fall harvests maximizing these types of harvest were very sensitive to changes in assumptions about poorly understood attributes of population dynamics and harvest. Although the magnitude of fall harvest required varied with harvest-maximization objectives, fall hunting could contribute to other management objectives, such as providing additional hunting opportunities. Moreover, seeking to maximize annual or fall harvest, or achieving a large fall harvest in general, may be less relevant in areas where fall hunting participation has already declined and certainly where fall hunting is not legal. In these regions more emphasis will likely be placed on spring harvest. Although harvest rates that maximize spring male harvest were less sensitive to structural changes in population dynamics, a precise understanding of implementation uncertainty is still necessary when management objectives relate to stage-specific harvest. 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 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 research 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 regulations that produce desirable outcomes for specific objectives in the presence of uncertainties discussed in this study.

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CHAPTER 3: STRUCTURAL UNCERTAINTY LIMITS GENERALITY OF FALL HARVEST STRATEGIES FOR WILD TURKEYS

INTRODUCTION

Restoration of wild turkey (*Meleagris gallopavo*; hereafter turkey) populations and hunting opportunities was a substantial achievement of 20th century wildlife management (Dickson 1992, Kennamer et al. 1992, Lewis 2001). Translocation efforts, habitat improvements, and the adaptability of turkeys to farmland habitats resulted in rapid growth of populations from the 1970s through early 2000s (Kurzejeski and Vangilder 1992, Tapley et al. 2001, Tapley et al. 2007). By 2004, nearly 7 million turkeys were believed to occupy a diversity of habitats across North America, including many 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, Healy and Powell 2001, Harris 2010). By 2006, an estimated 2.6 million hunters made turkey hunting second in popularity only to deer hunting in the United States (U.S.; Harris 2010). During the first decade of the 21st century, however, the period of rapid population growth came to a close (Warnke and Rolley 2007, Porter et al. 2011, Tapley et al. 2011, Parent et al. 2016). More recently managers have voiced concerns over perceived local declines for populations in many areas (Rudolf et al. 2011, Porter et al. 2011, Ericksen et al. 2016).

The end of rapid turkey population growth over large spatial scales resulted in changes to population models used to inform turkey harvest management, as well as the objectives of harvest-modeling studies. Early models assumed density-independent dynamics and were intended to reflect the rapid growth observed for many turkey populations (e.g., Lobdell et al. 1972, Suchy et al. 1990, Vangilder and Kurzejeski 1995, Alpizar-Jara et al. 2001). Demographic processes contributing to population growth were known to be influenced by annual environmental variation (e.g., production of poults and spring weather; Markley 1967, Healy 1992, Roberts and Porter 1998), and sustained growth suggested populations were well below any habitat-induced carrying capacity. Simulation studies thus focused on effects of harvest on rate of increase in the absence of density-induced feedbacks to population growth (Suchy et al 1990, Vangilder and Kurzejeski 1995, Rolley et al. 1998, Alpizar-Jara 2001). Moreover, restoration efforts were still in progress and a common objective of harvest modeling was to identify fall either-sex harvest rates that allowed for continued growth of turkey populations (Porter et al. 1990, Vangilder 1992, Alpizar-Jara et al. 2001). Evidence for density-dependent dynamics began to emerge as population growth declined and populations over large scales appeared to be approaching equilibrium levels, suggesting population growth and possibly production of young declined as densities of turkeys increased through time (McGhee and Berkson 2007a, Bond et al. 2012, Byrne et al. 2016). Consequently, the objectives of modeling studies have changed. Sustained population growth appears to no longer be realistic; therefore the emphasis of harvest models has shifted towards understanding risks and sustainability of harvests over longer time horizons (McGhee et al. 2008, McGhee and Berkson 2011).

Previous studies often deduced harvest management recommendations under the assumption that the correct form of population dynamics and values of demographic parameters were known, thus not accounting for structural uncertainty in turkey demographic processes (sensu Williams 1997). Turkey harvest models often allowed demographic rates to vary over time from an assumed stochastic distribution (e.g., Vangilder and Kurzejeski 1995), and thus typically accounted for effects of annual environmental variation on population processes (i.e., environmental uncertainty; Williams 1997). Yet few have studied the implications for harvest management of uncertainty in the specific form of turkey population models or the specific values of their parameters (see Suchy et al. 1983 and chapter 2 for deterministic exceptions). Consequently, the implicit assumption has been that structural uncertainty (Williams 1997, Connelly et al. 2005) surrounding demographic parameter values (i.e., parameter uncertainty; Francis and Shotton 1997, Fieberg 2004) or the appropriate population model form (i.e., model uncertainty; Runge and Johnson 2002) for local turkey populations is inconsequential to management. Input values for demographic parameters of most turkey harvest models were generated from radio-telemetry studies conducted over relatively short duration and at small geographic scales (Suchy et al. 1983, Roberts et al. 1995, Vangilder and Kurzejeski 1995, Rolley et al. 1998). Importantly, field studies also provided direct evidence for systematic heterogeneity of demographic rates that occurs among turkey populations. For instance, mortality rates from legal and illegal harvest differ among populations through space and time (Vangilder 1992, Vangilder and Kurzejeski 1995, Rolley et al. 1998, Hubbard and Vangilder 2007, Wright and Vangilder 2007). Moreover, it has recently been recognized that dynamics of turkey populations at high densities are poorly understood (Healy 2011, Porter et al. 2011), and productivity (i.e., poults/hen recruited into fall population) appear to be declining across broad scales in some regions (Bond et al. 2012, Byrne et al. 2016). Structural uncertainty in demography is thus ubiquitous in modern turkey management, but its implications for managing harvests have received very little 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 Alpizar-Jara et al. [2001] and McGhee et al. [2008] for sensitivity of population growth to changes in individual parameters). For instance, McGhee et al. (2008) recommended proportional harvest rates for maximizing annual turkey harvest across spring and fall seasons based on results from a stochastic, density-dependent population model but generated recommendations using a single set of demographic parameters. In chapter 1 I 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 are known to accompany large either-sex fall harvests (e.g., Vangilder 1992, Vangilder and Kurzejeski 1995). Yet, subtle changes to population model parameters or their stochastic distributions can have strong implications for resulting assessment of risks that a harvest strategy will produce undesirable outcomes (Deroba and Bence 2008). Consequently, the generality and robustness of harvest rates resulting in appropriate fall harvests of turkeys is poorly understood. Therefore, my objectives were to: 1) determine the generality of previous fall harvest recommendations across a range of plausible scenarios representing structural uncertainty in turkey population dynamics, 2) assess performance of fall harvest over a range of harvest rates for these scenarios, and 3) determine management tradeoffs between potentially conflicting objectives of maintaining large annual harvests and large populations of turkeys. A more general goal of this study is to provide a thorough assessment of the implications of structural uncertainty for modern turkey management.

METHODS

Population and Harvest Models

I evaluated performance of different proportional fall harvest rates using stochastic simulations. I simulated population dynamics using a sex-specific theta-logistic model with discrete annual time steps (Tables 3.1 and 3.2). 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 fall harvest rates that maximized annual turkey harvest over spring and fall seasons for a specific set of input parameters, and calculating the proportion of simulations that result in overharvest (i.e., harvest > equilibrium maximum sustainable harvest) for different magnitudes of variation in annual population growth (environmental variation) and harvest rates (partial controllability; Williams 1997). In contrast, I was motivated by a desire to understand robustness of previous fall harvest management recommendations. Thus I 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 population scenarios. I determined a plausible range of scenarios based on a review of literature and considered different spring harvest rates, different levels of population productivity (recruits per hen), and different levels of hen poaching during spring hunting seasons (Table 3.1).

Table 3.1 Symbols, descriptions of symbols, and values of described quantities used for simulating population dynamics and harvest-policy performance for wild turkeys.

Symbol	Description	Value
Population model		
$N_{i,t}$	No. of turkeys of sex *i* in yr. *t*	-
$r_{i,t}$	Instantaneous growth rate for sex *i* in yr. *t*	-
s_i	Non-hunting survival rate for sex *i*	0.74, 0.64
K_i	Carrying capacity for sex *i*	10,000
θ	Parameter for nonlinearity in density dependence	$N(0.36, \sigma_\theta)$
B_t	No. of births at yr. *t*	-
$\varepsilon_{p,t}$	Realized process deviation in population growth in yr. *t*	$N(0, \sigma_p)$
k	No. of female recruits per fertilized hen	0.775, 1.440, 2.105
q	Harem size	10
σ_θ	SD of θ across population projections, representing parameter uncertainty in estimated value of θ	0.09
σ_p	SD of annual process variation in population growth	0.15
Harvest model[a,b]		
$h_{m,s,t}$	Realized Gobbler harvest rate during spring season in yr. *t*	$0.15e^{\varepsilon_{s,t}}$, $0.30e^{\varepsilon_{s,t}}$, $0.40e^{\varepsilon_{s,t}}$
$h_{f,s,t}$	Realized hen poaching rate during the spring season in yr. *t*	$0.05e^{\varepsilon_{i,t}}$, $0.15e^{\varepsilon_{i,t}}$
$h_{i,f,t}$	Realized fall harvest rate in yr. t	$target \times e^{\varepsilon_{f,t}}$
$H_{i,j,t}$	Total harvest for sex *i* during season j of yr. *t*	-
$\varepsilon_{s,t}$	Realized variation in spring harvest rate in yr. *t*	$N(0, \sigma_s)$
$\varepsilon_{i,t}$	Realized variation in hen poaching rate in yr. *t*	$N(0, \sigma_i)$
$\varepsilon_{f,t}$	Realized variation in fall harvest rate in yr. *t*	$N(0, \sigma_f)$
σ_s	SD of annual variation in spring harvest rates	0.175
σ_i	SD of annual variation in hen poaching rates	0.400
σ_f	SD of annual variation in fall harvest rates	0.175
Performance metrics		
$N_{>K/2}$	Percentage of simulation years 100–200 where population size at start of year was > K/2	-
$H_{Total,t}$	Total annual legal harvest of all birds in yr. *t*	-
σ_{H_T}	SD of total harvest over simulation years 100-200	-

[a] Common harvest rate values were used for both male and female turkeys during fall, thus simulations assumed equal harvest vulnerability between the sexes during fall hunting seasons.

[b] Target fall harvest rates were systematically varied from 0–15% by manipulating the medians (target) for the lognormal distributions of realized fall harvest rates.

Table 3.2 Model equations used to simulate population dynamics and fall harvest performance for wild turkeys.

Dynamic models and their equations

Population model[a,b]

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

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

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

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

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

Harvest model[c,d]

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

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

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

[a] Values of annual process deviations in population growth were drawn from a normal distribution: $\varepsilon_{p,t} \sim N(\mu = 0, \sigma_p = 0.15)$ (Table 3.1).

[b] Values of spring hen poaching rate were drawn from lognormal distributions with medians of 0.05 (low poaching scenario), or 0.15 (high poaching scenario; Table 3.1).

[c] Values of spring gobbler 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; Table 3.1).

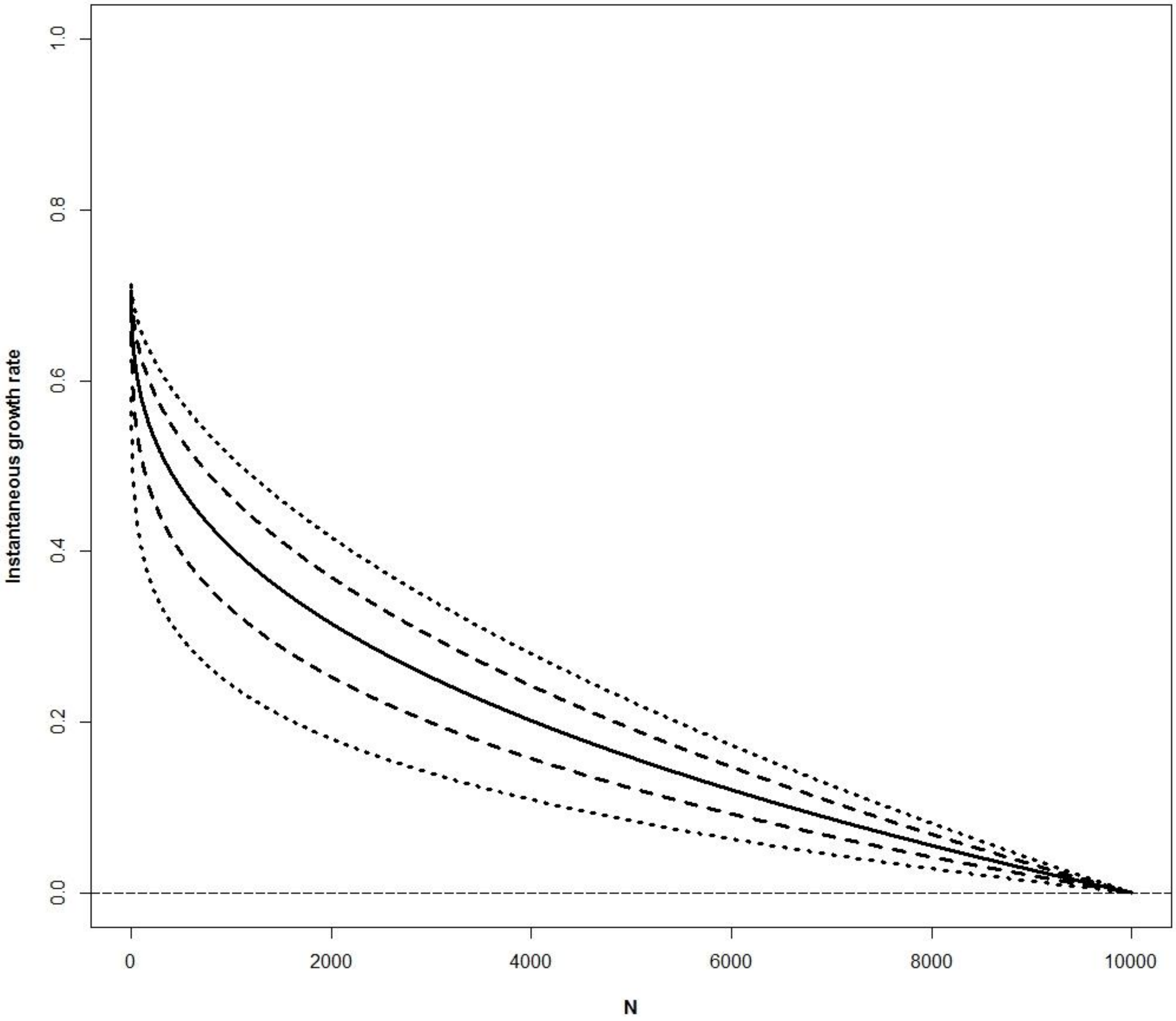
[d] Fall harvest rates were either set to zero or drawn from lognormal distributions with medians ranging from 1–15% (Table 3.1).

Annual changes in the theta-logistic model depended upon a population growth rate calculated using an intrinsic rate of increase (*r*) and adjustments due to density dependence, and *r* is in turn calculated as a function of number of births (Table 3.2). During simulations I defined population size as the abundance at the beginning of spring gobbler hunting seasons, and assumed all fertilization occurred prior to the onset of spring hunting. The number of births was calculated 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 males to fertilize all females; Caswell and Weeks 1986, McGhee et al. 2008; Table 3.2). This function has an input parameter (*k*) that explicitly defines the number of female recruits produced per fertilized hen, providing a convenient way to explore effects of heterogeneous recruitment on risks 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]). I 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 (see Fig. 2 of Caswell and Weeks [1986]). The practical importance of $q = 10$ is that the number of births did not fall towards zero until nearly all males were removed (chapter 1).

I modeled population losses within the annual cycle associated with natural mortality and human harvest. I assumed constant per-capita natural survival rates (i.e., survival in absence of harvest) for males (0.74) and females (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 (e.g., Suchy et al. 1990, 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). However, this assumption could be violated if populations were limited by available food supplies over winter (e.g., populations in areas without agriculture at northern latitudes: Austin and DeGraff 1975, Wunz and Hayden 1975, Porter et al. 1980, Kimmel and Krueger 2007, Porter 2007) and seasonally density-dependent survival was present (Kokko and Lindström 1998, Boyce et al 1999, Kokko 2001, Ratikainen et al. 2008). Sex-specific instantaneous annual growth rates were represented as the sum of per-capita recruitment and survival rates on the natural log scale, where recruitment was assumed equal between the sexes ($0.5\times B_t$; Table 3.2). Hunting and poaching losses were modeled as sex-specific, and seasonal. Hunting losses followed a proportional harvest strategy, where a fraction of the population was removed prior to (males only in spring) and after (both sexes in fall) new population growth within the annual cycle (Table 3.2). In addition to this legal removal, the model included poaching of females in the spring, which were removed from the birth function such that these individuals could not contribute to production of young (Table 3.2).

I incorporated structural uncertainty in the strength of density dependence and process variation in annual growth of turkey populations in my simulations. In theta-logistic models, the θ parameter encapsulates the strength of density dependence in population dynamics (i.e., θ governs nonlinearity in the functional relationship between per-capita population growth and abundance; McGhee 2006, Clark et al. 2010). McGhee and Berkson (2007a) 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 (Clark et al. 2010). I therefore accounted for parameter uncertainty in θ by drawing θ values for each forward population projection from a Normal distribution with a mean and standard deviation equal to the estimated value and standard error of θ reported by McGhee and Berkson (2007a; $\theta \sim Normal(\mu = 0.36, \sigma_\theta = 0.09)$; Table 3.1; Fig. 3.1). Annual growth of turkey populations is also widely acknowledged to be affected by environmental conditions (e.g., spring weather, Roberts and Porter 1998, Rolley et al. 1998). Thus, I modeled process variation in population growth as normally distributed environmental noise on the natural-log scale ($\varepsilon_{p,t} \sim Normal(\mu = 0, \sigma_p = 0.15)$; Table 3.1), where process standard deviation (σ_p) was set at the midpoint between the smallest (σ_p = 0.05) and largest (σ_p = 0.30) values considered by McGhee et al. (2008).

Figure 3.1 Illustration of how different θ values influenced assumed relationships between instantaneous population growth and abundance for the male segment of turkey populations. Plotted relationships were generated assuming a balanced sex ratio and per-capita female recruits (k) equal to 1.440 (i.e., medium productivity scenario; Table 3.1). Results are shown for θ values selected at specific points from the normal distribution used to introduce parameter uncertainty in θ , namely the average θ (solid line), as well as for θ values ± 1 (dashed lines) and 2 (dotted lines) standard deviations from average.



I included additional stochasticity in harvest models to represent implementation uncertainty (also called partial controllability; Williams 1997) in annual spring and fall harvest rates (Figs. C1–C2). I accounted for implementation uncertainty by modeling annual realizations of legal harvest and hen poaching rates as coming from lognormal distributions by exponentiating natural-log scale normal deviations and multiplying these by target proportional harvests (Table 3.1). This effectively set the target harvest or poaching rate as the median of the realized distribution of harvest and hen poaching. I set the natural log-scale spring and fall harvest standard deviations (σ_s, σ_f) equal to 0.175, again corresponding to the midpoint of low (0.10) and high (0.25) values of variation in harvest considered by McGhee et al. (2008). Distributions of realized annual spring and fall harvest can be thought of as representing all harvest mortality (legal + illegal) for the corresponding hunting season, precluding the need for explicit poaching parameters to account for additional illegal harvest during legal hunting seasons (i.e., males in spring and either sex in fall). As such, illegal harvest during legal hunting seasons is viewed as one factor contributing to variation in realized harvest rates on an annual basis (i.e., implementation uncertainty). This simulation approach thus implicitly assumed managers could adjust for this uncertainty, on average, when implementing management actions to achieve a target hunting rate. I increased variation in annual female poaching rates during spring hunting seasons relative to annual variation in legal harvest in simulation models ($\sigma_i = 0.40$; Table 3.1) because female poaching rates can show a larger degree of variation through time (e.g., Vangilder and Kurzejeski 1995, Pack et al. 1999, Norman et al. 2007). The larger magnitude of σ_i, relative to σ_s and σ_f, produces annual variation in female poaching rates consistent with estimates from field studies (Fig. C2).

Simulation Study Design

I evaluated performance of different fall harvest rates across population scenarios intended to represent a broad range of plausible conditions. Specifically, I simulated performance of fall harvest for all combinations of 3 levels of productivity, 2 levels of female poaching during spring hunting, and 3 levels of spring gobbler harvest (18 total simulation scenarios; Table 3.1). I manipulated levels of population productivity by changing the input parameter representing number of female recruits per fertilized hen (*k*), which I set to the lowest (Vangilder 1992) and highest (McGhee et al. 2008) values assumed by previous turkey harvest simulations, as well as the midpoint between these extremes (Table 3.1). I set the two levels of hen poaching during spring hunting through the median poaching rate, which included a lower value commonly described (Vangilder and Kurzejeski 1995, Pack et al. 1999, McGhee et al. 2008) and a value consistent with the highest hen poaching rates I found reported in the turkey literature (Norman et al. 2007; Fig. C2). I set spring gobbler harvest rates via the medians of their distributions, and used a low value assumed by McGhee et al. (2008), a higher value that was previously recommended as the maximum spring harvest rate for avoiding shifts in gobbler age structure towards juveniles (Vangilder and Kurzejeski 1995, Hubbard and Vangilder 2007), and a yet higher value consistent with the largest estimates of spring harvest rates I found reported in the literature (Hubbard and Vangilder 2007, Wright and Vangilder 2007; Fig. C1).

I simulated performance of fall harvests by manipulating target fall harvest rates from 0–15% at 1% increments for each combination of the 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 both common management rules of thumb for sustainable fall harvesting 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 I assumed that the fall harvest rates were shared for males and females during fall hunting seasons, and thus equal vulnerability to fall harvest. Equal fall harvest vulnerability has been assumed by most previously published turkey harvest models (e.g., Alpizar-Jara et al. 2001, McGhee et al. 2008). I conducted 10,000 replications of a 200-year forward population projection at each target fall harvest rate to evaluate long-term performance of harvests. I initialized population projections assuming sex-specific population sizes started from their environmental carrying capacities ($K_m = K_f = 10{,}000$). I also explicitly tested the effects of including structural uncertainty in strength of density dependence by replicating all simulations without uncertainty in the form of density-dependent feedbacks, assuming θ was constant at the mean used in the stochastic simulations (but retaining process variation in population growth, $\varepsilon_{p,t}$). I programmed all simulations in the R computing language (version 3.1.1, R Core Development Team 2014).

I monitored attributes of turkey populations and harvest relevant to common management objectives (hereafter performance metrics) during simulations to determine risks of undesirable outcomes and likely management tradeoffs across heterogeneous conditions. Although explicit target population and harvest levels for turkey management are commonly not defined (Healy and Powell 2001), maintenance of large populations is desirable to ensure management stakeholders remain satisfied. Thus, I monitored performance metrics describing the ability to maintain large population sizes through time for each simulation scenario (Table 3.1). Specifically, I monitored the proportion of simulation 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 combined environmental carrying capacity (i.e., $K/2$, where $K = K_m + K_f$). Thus, I used $K/2$ in a manner analogous to a utility threshold (sensu Nichols et al. 2014) to define minimum desirable population size in my analysis. McGhee et al. (2008) showed that a deterministic version of this model will have an annual harvest curve that peaks at abundances around $0.4K$ for spring harvest and hen poaching rates of 15% and 5%, respectively. Thus, my abundance-threshold performance metric implies that populations > $K/2$ confer some benefit to management 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). I am aware of no research attempting to quantify desirable abundance thresholds for turkey populations. However, the threshold of $K/2$ provides a useful starting point that is rooted in harvest theory, as $K/2$ is the abundance maximizing harvest yield for a simple logistic population model (Schaefer 1954).

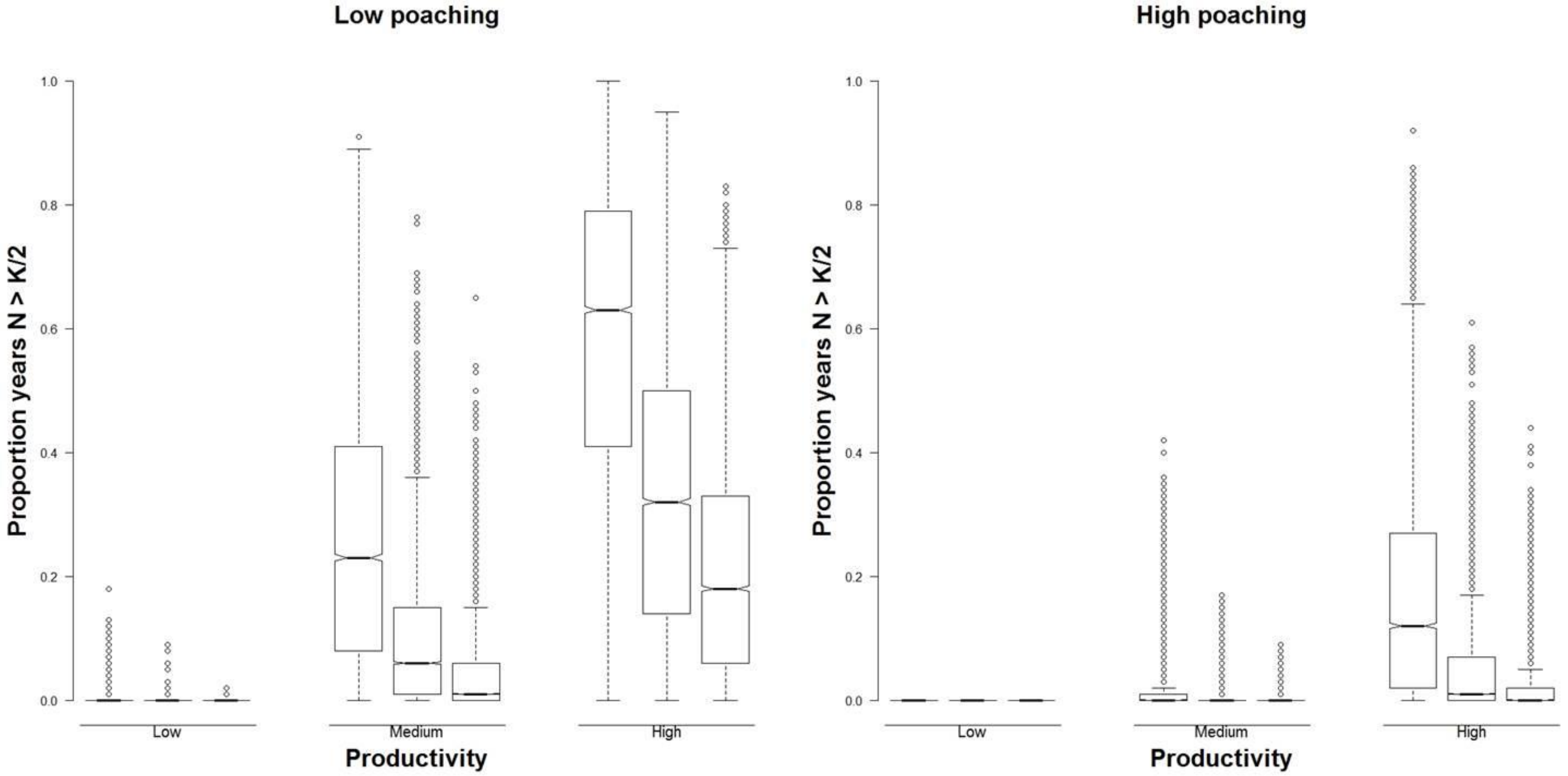
To monitor size and variation of total annual harvest across spring and fall seasons in any given year I retained the distribution of total harvest on the last year of population projections ($H_{Total,200}$; Table 3.1). Because consistency of harvest through time is often considered desirable, I also monitored the standard deviation of total annual harvest through time over simulation years 100–200 (σ_{H_T}; Table 3.1). For this analysis I was interested in understanding long-term performance of fall harvests under a variety of demographic scenarios, thus I retained metrics within simulation years 100–200 to avoid the transient period of stochastic dynamics. As such, these results avoided reliance on arbitrary assumptions about starting population characteristics when summarizing the distributions of management performance metrics.

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 of population declines at this fall harvest rate varied among population scenarios. Distributions of the proportion of years (calculated over time for each simulation replicate) with large abundances (i.e., $N > K/2$) at the start of spring hunting season were right skewed for many scenarios, where medians were concentrated around small values with distribution tails extending towards larger values (Fig. 3.2). Increased productivity and decreased hen poaching shifted these proportions to larger values (Fig. 3.2), indicating that abundance remained large for more years during simulations. Medians of these proportions were nearly all < 0.5 under low poaching scenarios, as were most interquartile ranges (Fig. 3.2). When productivity was low, the proportion of years with large abundance was nearly always zero at a 9% median fall harvest rate. These proportions were shifted to larger values under medium and high productivity scenarios with low poaching, where the medians for high productivity scenarios were 8.7 times greater on average (*range* = 2.7–18 times greater, $n = 3$; Fig. 3.2) than medians for corresponding scenarios with medium productivity. Maintaining large populations was rarely attainable under high poaching; the median proportion of years with large abundance was 0.12 under the best-case scenario (i.e., high productivity, low spring gobbler harvest; Fig. 3.2). In general, increased spring harvest rate also reduced the proportion of years with large abundance by shifting the distributions to reduced values (Fig. 3.2). For example, increasing median spring harvest rate from 0.15 to 0.3 and 0.4 reduced the median proportion by 49% and 71%, respectively, under low poaching-high productivity scenarios.

Figure 3.2 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 hen poaching during the spring hunting season, and low (median = 0.15), medium (median = 0.30), and high (median = 0.40) spring gobbler 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, boxplot notches represent an approximate 95% confidence intervals for medians ($\pm 1.58 * \frac{IQR}{\sqrt{n}}$; Chambers et al. 1983), and boxplot whiskers delineate IQR boundaries values ±1.5×IQR. Individual points represent metrics whose absolute values were greater than 1.5×IQR.



Performance of 9% fall harvest rates at attaining large annual harvests (total over spring and fall seasons) also varied among scenarios. When productivity was at medium–high values, implementing a target 9% fall harvest rate achieved nearly the same median annual harvest as the target harvest rates resulting in maximum annual harvest for the corresponding scenario (Table 3.3). Under these conditions the ratios of median annual harvest to the maximum median annual harvest were > 0.9, except when both hen poaching and spring gobbler harvests were at their lowest values. In contrast, when productivity was low the fraction of maximum annual harvest attained was reduced (≤ 0.61) and more directly related to spring harvest and hen poaching (Table 3.3). When productivity was low and hen poaching high, 9% fall harvests reduced median annual harvest to very low values (< 0.05 of the maximum annual harvest). Similarly, increased spring harvest rates reduced the relative annual harvest attained when both productivity and hen poaching were at low values (Table 3.3).

Table 3.3 Ratio of median annual harvest at 9% fall harvest rate to the maximum median annual harvest achieved for the corresponding population scenario.

	Productivity[a]					
	Low		Medium		High	
	Poaching[b]					
Spring harvest[c]	Low	High	Low	High	Low	High
Low	0.61	0.05	0.99	0.97	0.88	0.95
Medium	0.44	0.01	1.00	0.96	0.94	0.98
High	0.30	0.00	0.99	0.93	0.95	0.98

[a] Productivity was manipulated by changing the input number of per-capita number female recruits (*k*) to low (0.775), medium (1.440), and high (2.105) values (Table 3.1).

[b] Values of spring hen poaching rate were drawn from lognormal distributions with medians of 0.05 (low), or 0.15 (high; Table 3.1).

[c] Values of spring gobbler harvest rate were drawn from lognormal distributions with medians of 0.15 (low), 0.30 (medium), or 0.40 (high; Table 3.1).

Performance of Fall Harvest Rates

Risks of not maintaining large turkey populations through time varied widely among simulation scenarios and target fall harvest rates (Fig. 3.3). In general both productivity and hen poaching 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 medium levels of spring gobbler harvest (Fig. 3.3a). The median proportion of years with large abundance decreased nonlinearly with increasing fall harvest rates for most scenarios (Fig 3.3). Risks to populations for a given fall harvest rate and level of poaching were reduced as productivity was increased (i.e., the proportion of years with large abundance increased; Fig. 3.3). For instance, the median proportion 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, respectively, under low poaching and medium spring harvest conditions (Fig. 3.3). Moreover, as productivity increased from medium to high values, the largest fall harvest rate resulting in a median proportion > 0.5 (i.e., > 50% of the simulations had a population above $K/2$ for more than 50% of years) increased from 2% to 6%, respectively (for low poaching with medium spring gobbler harvests; Fig. 3.3b, c). Risks of not maintaining large populations increased considerably as poaching levels increased from low to high scenarios, for corresponding fall harvest rates and productivity scenarios (Fig. 3.3). Increased poaching had a particularly large impact on risk assessments for low and medium productivity scenarios. For instance, the median proportion of years with large abundance decreased from 0.1 to 0, and 0.66 to 0.05, for low and medium productivity scenarios with no fall harvest (for medium spring gobbler harvests; Fig. 3.3a, b). However poaching also impacted risk assessments under high productivity conditions. With the exception of low spring gobbler harvest scenarios, median proportions of years with large abundance were never > 0.5 when poaching levels were high.

Figure 3.3 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 hen poaching during the spring hunting season, at medium spring gobbler 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, boxplot notches represent an approximate 95% confidence intervals for medians ($\pm 1.58 * \frac{IQR}{\sqrt{n}}$; Chambers et al. 1983), and boxplot wiskers delineate IQR boundaries values $\pm$1.5×IQR. Individual points represent metrics whose absolute values were greater than 1.5×IQR.

Figure 3.3 (cont'd)
a)

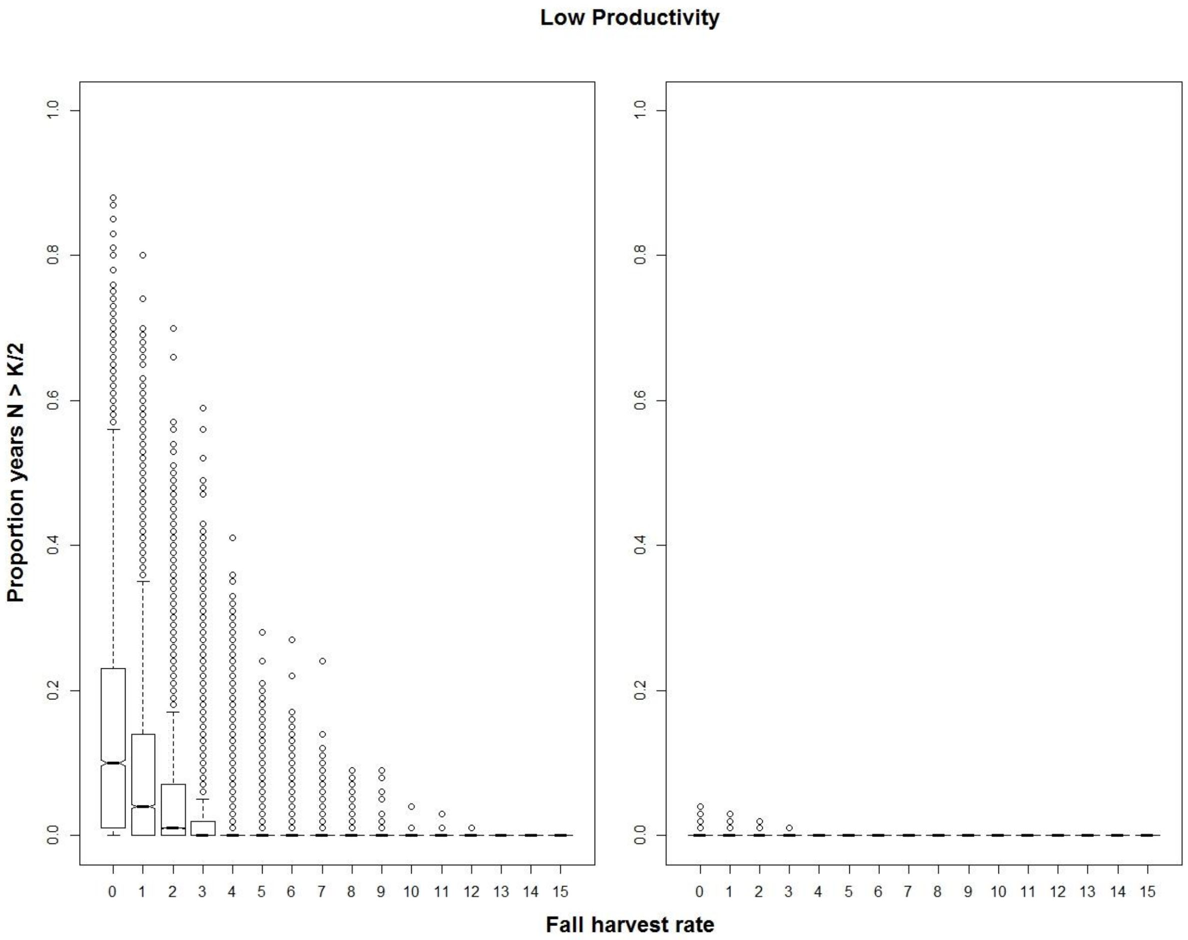


Figure 3.3 (cont'd)
b)

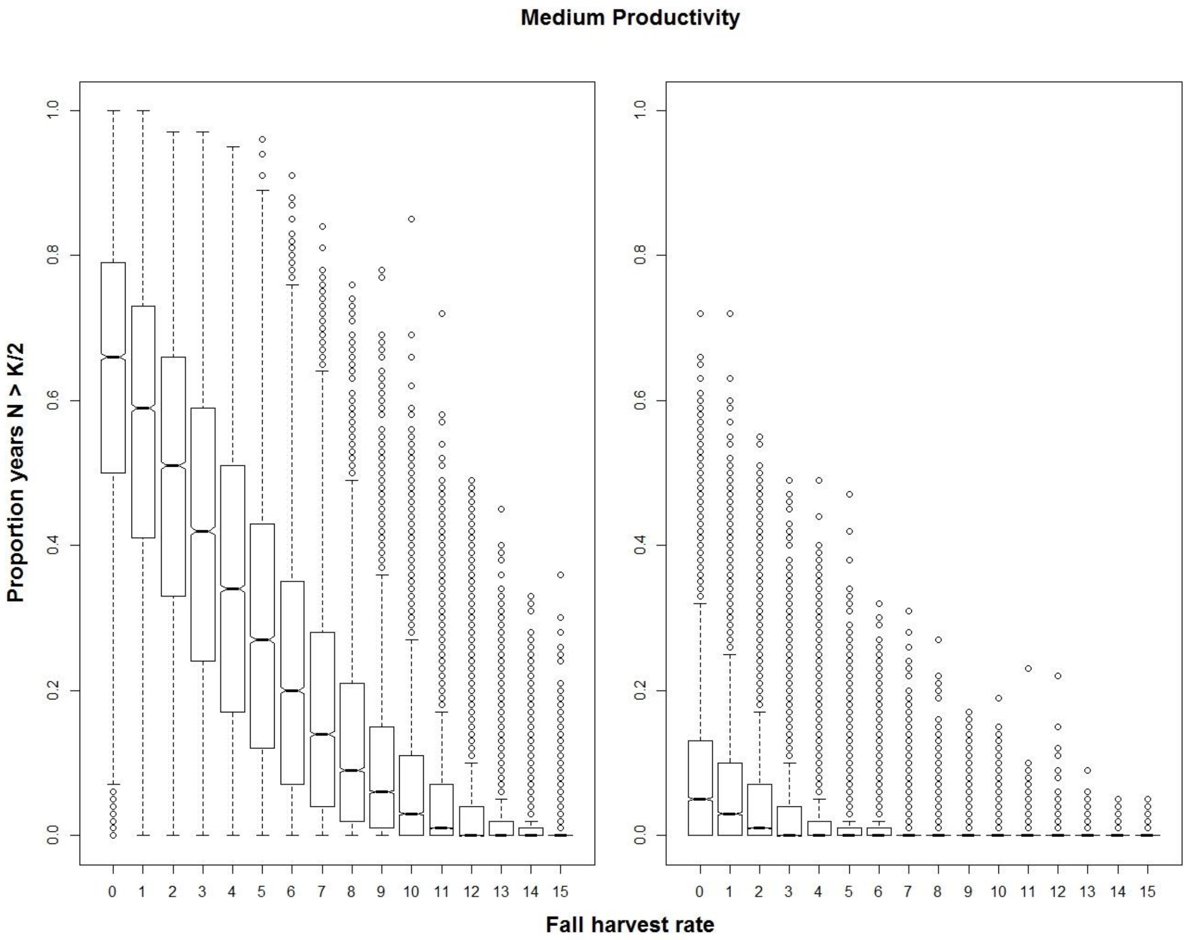
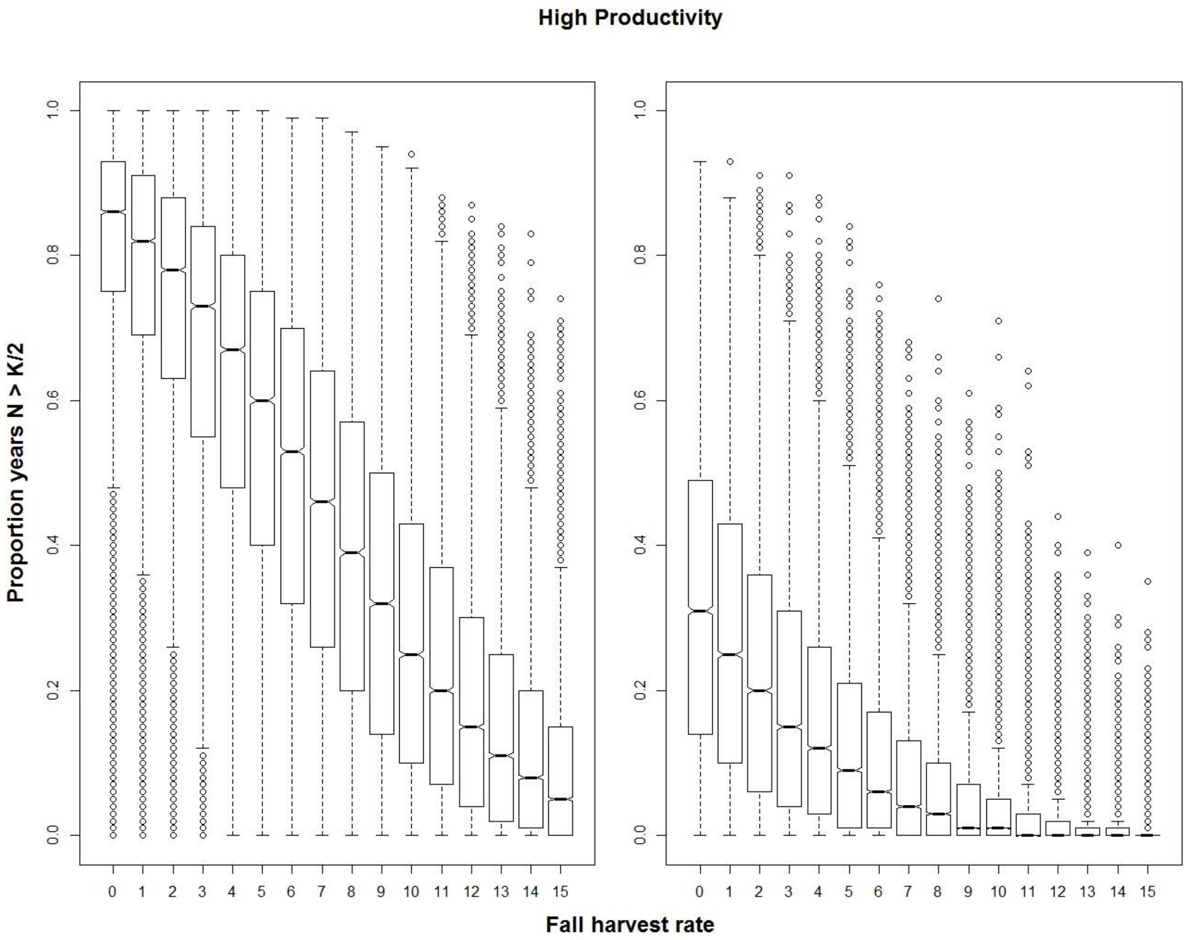


Figure 3.3 (cont'd)
c)



Relationships between annual harvest and target fall harvest rate varied among simulation scenarios. Differences among scenarios included losses or gains to median annual harvest with increased fall harvest rates (Fig. 3.4), fall harvest rates maximizing median annual harvest (Table 3.4), and the relationship between fall harvest rate and variation of annual harvest over time (Fig. 3.5). Increases to annual harvest with increased fall harvest rate occurred for scenarios with medium-high productivity (Fig. 3.4b, c). For example, median annual harvest increased by approximately 30% and 47% when target fall harvests were increased from 0% to 9% for medium and high productivity scenarios, respectively, when poaching rates were low (for medium spring gobbler harvest; Fig. 3.4b, c). 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. Thus, when productivity was low the annual harvest was maximized by either harvesting at very low levels in fall, or by only harvesting during spring hunting seasons (Fig. 3.4a; Table 3.4). Increased hen poaching flattened the relationship between median annual harvest and fall harvest rate for medium-high productivity scenarios (Fig. 3.4b, c). Increased hen poaching also shifted distributions of annual harvest to lower values for corresponding fall harvest rates, irrespective of productivity (Fig. 3.4). Similarly, fall harvest rates that maximized median annual harvest varied among scenarios from the lowest (0%) to highest (15%) values considered, and these harvest rates were reduced by increased poaching and decreased productivity (Table 3.4). Increased spring harvest rates also decreased fall harvest rates that maximized annual harvest for most simulation scenarios (Table 3.4). Moreover, variation of annual harvest increased with fall harvest rates under most scenarios (Fig. 3.5). Exceptions to this pattern were low productivity scenarios (Fig. 3.5a), where increased fall harvest rate decreased variation of annual harvest because harvests were driven towards small values (Figs. 3.4–3.5).

Table 3.4 Target fall harvest rate (percent harvest) resulting in maximum median annual harvest across changing population scenarios.

	Productivity[a]					
	Low		Medium		High	
	Poaching[b]					
Spring harvest[c]	Low	High	Low	High	Low	High
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 input number of per-capita number female recruits (k) to low (0.775), medium (1.440), and high (2.105) values (Table 3.1).

[b] Values of spring hen poaching rate were drawn from lognormal distributions with medians of 0.05 (low), or 0.15 (high; Table 3.1).

[c] Values of spring gobbler harvest rate were drawn from lognormal distributions with medians of 0.15 (low), 0.30 (medium), or 0.40 (high; Table 3.1).

Figure 3.4 Distributions of total annual harvest (sum of spring and fall hunting seasons) from simulations of wild turkey populations for target fall harvest rates of 0–15% for a range of demographic scenarios. 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 hen poaching during the spring hunting season, at medium spring gobbler harvest rates (median = 0.30). Boxplots represent the simulated distribution of annual harvest on the last year of stochastic population projection ($H_{Total,200}$). Solid horizontal lines represent median annual harvests, boxes delineate the interquartile ranges, boxplot notches represent an approximate 95% confidence intervals for medians ($\pm 1.58 * \frac{IQR}{\sqrt{n}}$; Chambers et al. 1983), and boxplot whiskers delineate IQR boundaries values $\pm$1.5×IQR. Individual points represent metrics whose absolute values were greater than 1.5×IQR.

Figure 3.4 (cont’d)
a)

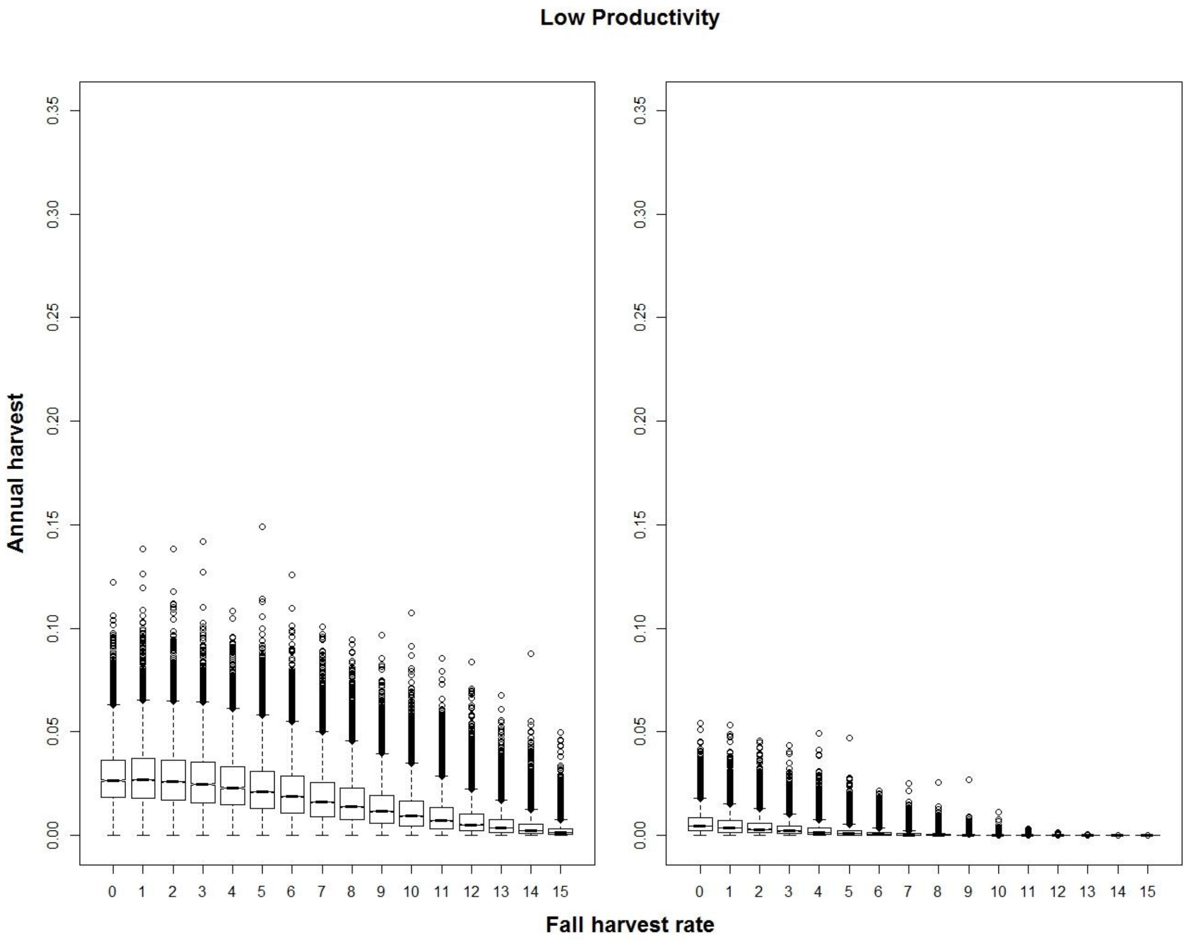


Figure 3.4 (cont'd)
b)

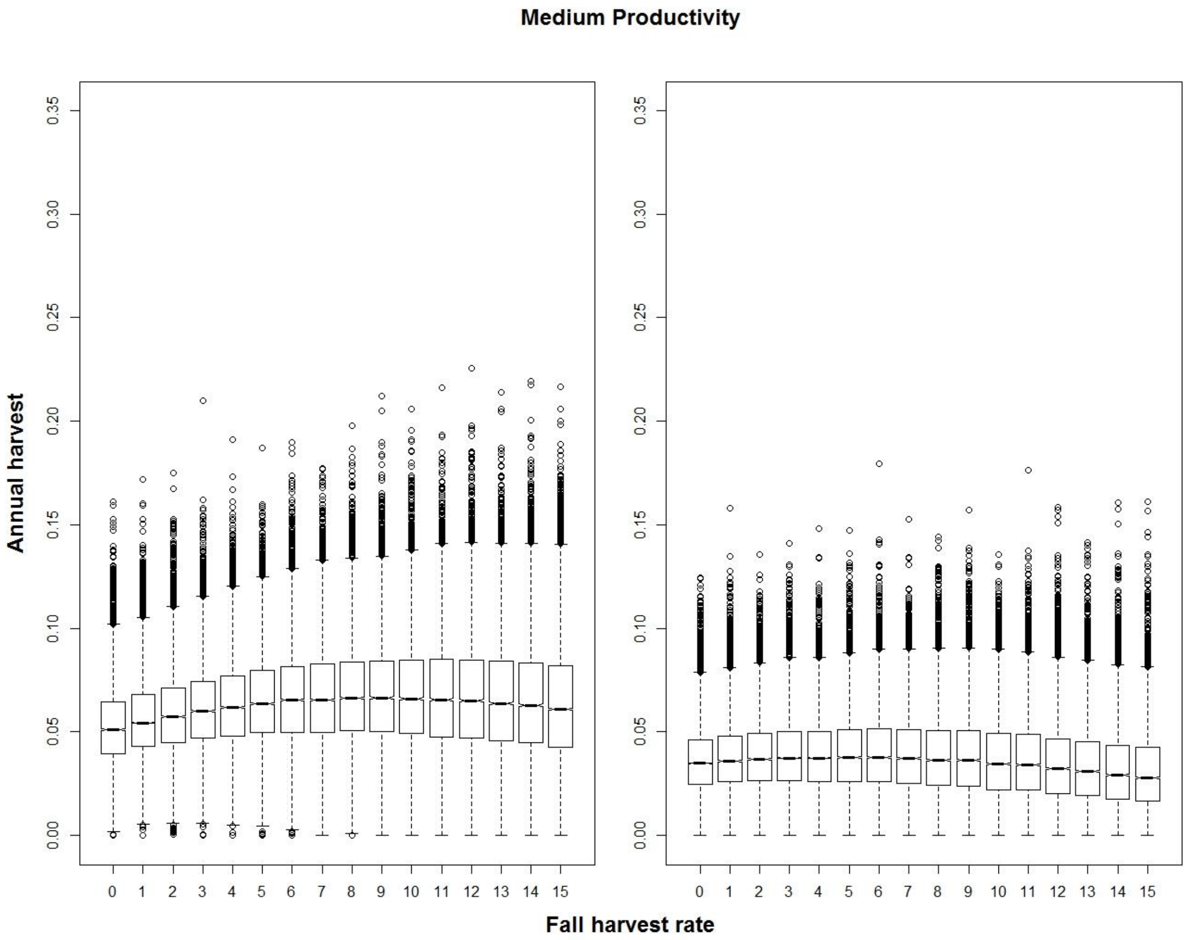


Figure 3.4 (cont'd)
c)

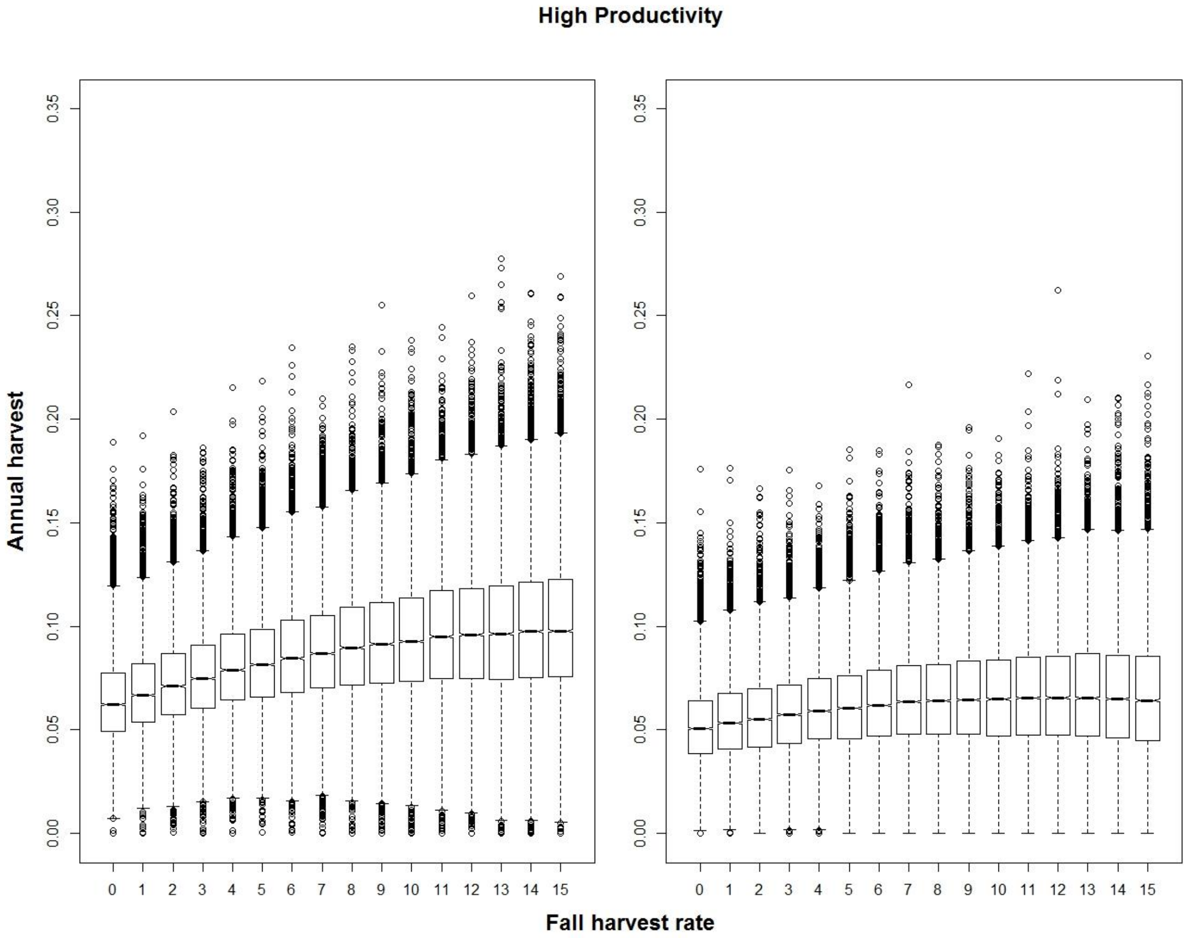


Figure 3.5 Distributions of standard deviation of total annual harvest across spring and fall hunting seasons for target fall harvest rates of 0–15% across changing demographic scenarios for simulated wild turkey populations. Scenarios represent combinations of low (a; k = 0.775), medium (b; k = 1.440), and high (c; k = 2.105) productivity, with low (left; median = 0.05) and high (right; median = 0.15) rates of hen poaching during the spring hunting season, at medium spring gobbler harvest rates (median = 0.30). Boxplots represent the distributions of standard deviation of annual harvest from years 100-200 of stochastic population projections (θ_{H_T}). Solid horizontal lines represent median standard deviations, boxes delineate the interquartile ranges, boxplot notches represent an approximate 95% confidence intervals for medians ($\pm\ 1.58 * \frac{IQR}{\sqrt{n}}$; Chambers et al. 1983), and boxplot wiskers delineate IQR boundaries values $\pm$1.5×IQR. Individual points represent values greater than IQR boundaries $\pm$1.5×IQR.

Figure 3.5 (cont'd)
a)

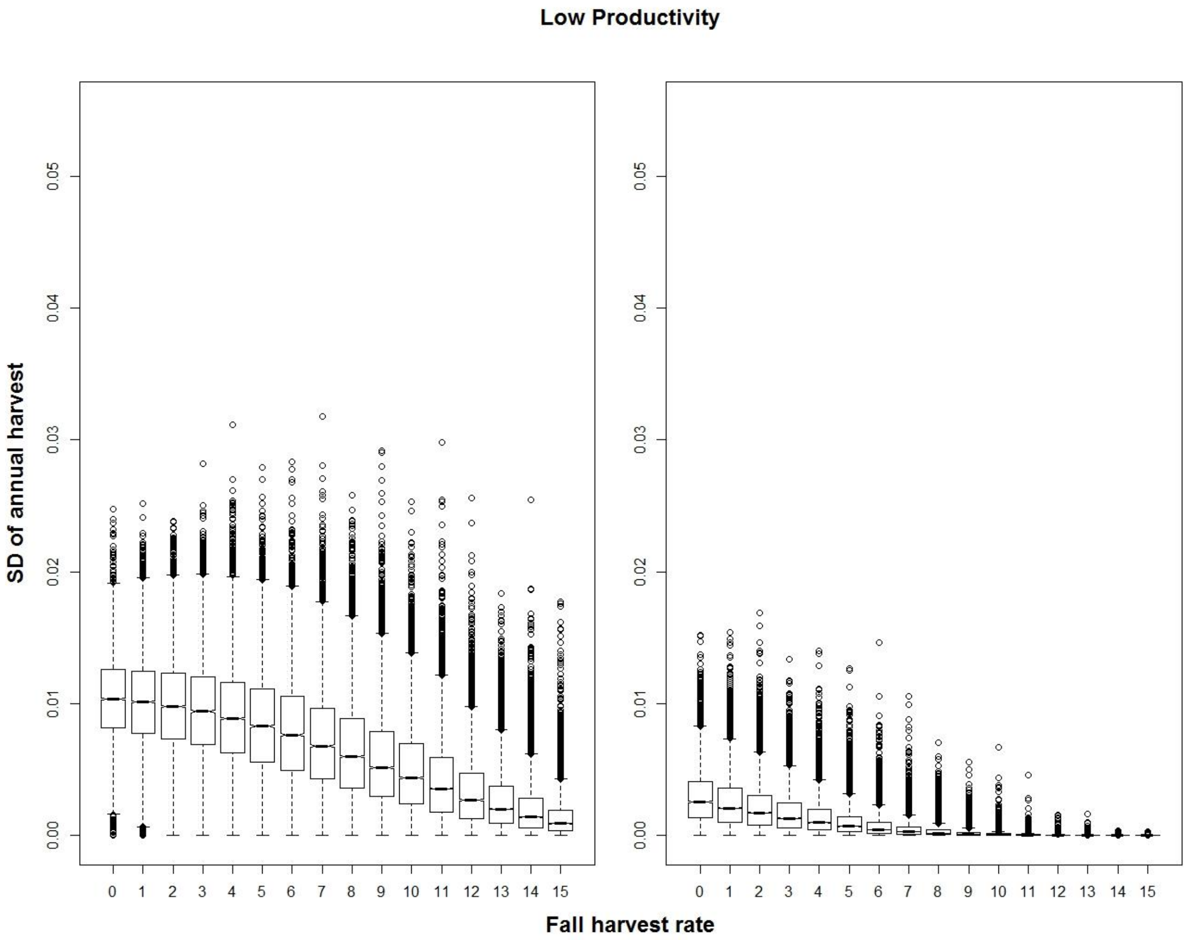


Figure 3.5 (cont'd)
b)

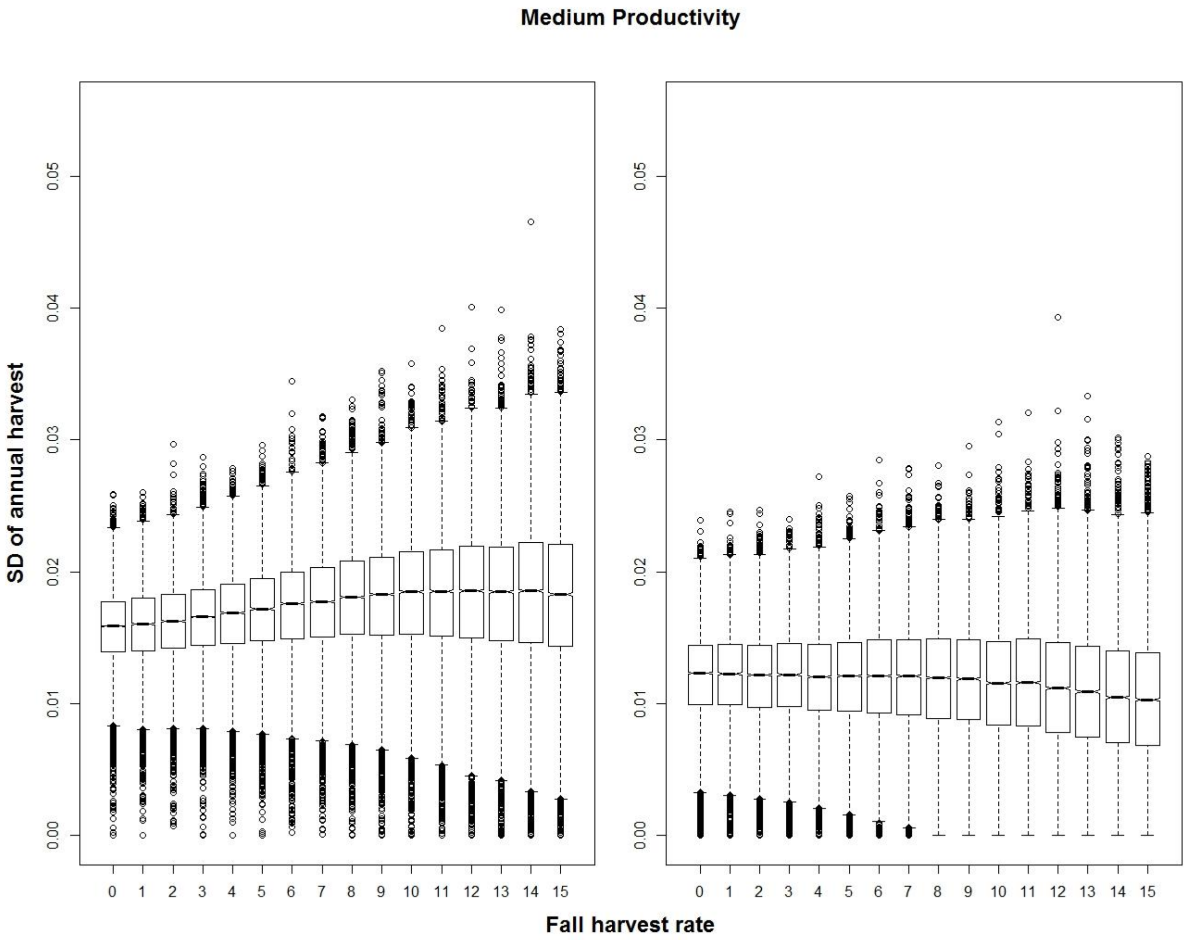
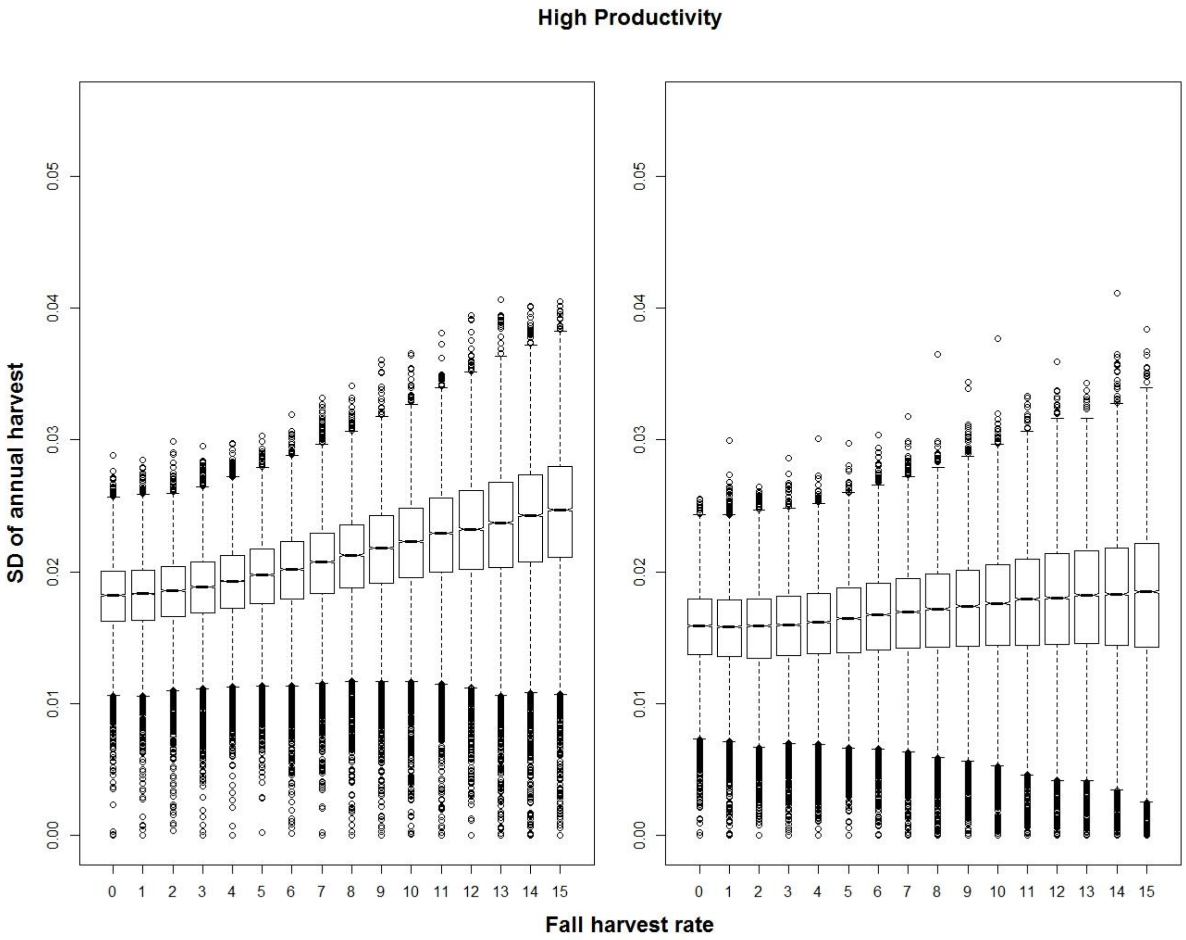


Figure 3.5 (cont'd)
c)



Removing structural uncertainty in the strength of density dependence by holding θ constant had little effect on central tendencies of management performance metrics (Figs. C3–C5), as demonstrated by minimal shifts to the medians of simulated distributions. However, assuming a constant known value for θ decreased variability in distributions of performance metrics as demonstrated by constriction of the interquartile ranges and spread of values (Figs. C3–C5).

Management Tradeoffs

Magnitude of management tradeoffs between achieving larger annual harvests and reducing risks of unintended population declines varied among simulation scenarios (Table 3.5). For scenarios with high productivity and low poaching, maintaining median proportion of years with large abundance > 0.5 was nearly always achievable at fall harvest rates ≤ 6% (Table 3.5). The exception was high gobbler harvest scenarios, where ≤3% fall harvest was required to maintain large abundances in more than half the simulations. For medium productivity scenarios with low poaching rates, maintaining the median proportion of years with large abundance > 0.5 occurred at fall harvest rates ≤ 5% and ≤ 2% for low and medium levels of spring gobbler harvest, respectively (Table 3.5). However, medium and high productivity scenarios also resulted in gains to annual harvest as fall harvest rate increased (Fig. 3.4), and thus reductions to population risk achieved by decreased fall harvest rates came at the expense of larger reductions to annual harvest. Specifically, reductions in median annual harvests of up to 20% from maximum values were required to maintain large abundances greater than half of the time under low poaching scenarios (Table 3.5). For low productivity scenarios the median proportion of years with large abundance was always < 0.5 for spring harvest rates considered, irrespective of other parameters (Table 3.5).

Table 3.5 Summary statistics illustrating tradeoffs between large wild turkey populations and large total annual harvest for all simulated demographic scenarios. Median proportion of years where population size prior to spring hunting was greater than half of environmental carrying capacity (N) is compared to the percent reduction in median annual harvest (Harvest reduction) from that achieved with the target fall harvest rate maximizing annual harvest (Table 3.3) for all productivity, hen poaching, spring gobbler harvest, and target fall harvest scenarios.

	Productivity[a]											
	Low				Medium				High			
	Poaching[b]											
	Low		High		Low		High		Low		High	
Fall harvest rate & gobbler harvest scenario[c]	N	Harvest reduction	N	Harvest reduction	N	Harvest reduction	N	Harvest reduction	N	Harvest reduction	N	Harvest reduction
Low gobbler harvest												
0	0.34	8.02	0.00	0.00	0.89	40.33	0.25	22.49	0.97	52.70	0.66	40.66
1	0.22	2.52	0.00	8.64	0.85	33.30	0.19	15.89	0.96	46.90	0.61	35.06
2	0.13	0.00	0.00	22.51	0.79	27.00	0.14	11.57	0.94	41.53	0.53	29.57
3	0.06	1.57	0.00	36.92	0.72	21.88	0.09	8.47	0.92	35.91	0.47	24.72
4	0.02	2.67	0.00	51.55	0.65	16.70	0.06	5.34	0.89	31.27	0.40	20.35
5	0.00	9.36	0.00	64.38	0.57	11.83	0.03	2.68	0.85	26.43	0.32	16.67
6	0.00	14.41	0.00	75.74	0.47	9.43	0.02	0.92	0.81	21.73	0.27	13.51
7	0.00	21.47	0.00	84.01	0.38	6.35	0.00	0.68	0.76	18.65	0.21	9.82
8	0.00	29.90	0.00	90.85	0.30	4.02	0.00	0.00	0.70	14.50	0.16	7.21
9	0.00	38.93	0.00	95.40	0.23	1.42	0.00	2.88	0.63	12.07	0.12	4.82
10	0.00	47.54	0.00	98.18	0.16	1.41	0.00	4.18	0.55	8.95	0.09	2.72
11	0.00	56.37	0.00	99.36	0.11	0.00	0.00	5.17	0.48	6.18	0.05	2.76
12	0.00	65.67	0.00	100.00	0.07	1.00	0.00	7.28	0.40	4.11	0.04	0.54

Table 3.5 (cont'd)

13	0.00	73.73	0.00	100.00	0.04	1.40	0.00	10.70	0.33	2.60	0.02	0.54
14	0.00	80.13	0.00	100.00	0.02	1.96	0.00	14.90	0.26	0.86	0.01	0.00
15	0.00	86.61	0.00	100.00	0.01	2.96	0.00	19.40	0.20	0.00	0.00	0.51
Medium gobbler harvest												
0	0.10	0.90	0.00	0.00	0.66	23.07	0.05	7.68	0.86	36.07	0.31	22.77
1	0.04	0.00	0.00	18.47	0.59	18.22	0.03	4.72	0.82	31.62	0.25	18.60
2	0.01	3.31	0.00	33.43	0.51	14.05	0.01	2.10	0.78	27.33	0.20	15.66
3	0.00	7.83	0.00	51.90	0.42	9.79	0.00	0.80	0.73	23.45	0.15	12.56
4	0.00	14.47	0.00	66.23	0.34	7.02	0.00	0.72	0.67	19.10	0.12	9.53
5	0.00	21.54	0.00	78.33	0.27	4.10	0.00	0.49	0.60	16.67	0.09	7.40
6	0.00	30.10	0.00	87.68	0.20	1.75	0.00	0.00	0.53	13.51	0.06	5.46
7	0.00	39.73	0.00	93.24	0.14	1.80	0.00	0.92	0.46	11.02	0.04	2.87
8	0.00	48.19	0.00	97.05	0.09	0.32	0.00	3.15	0.39	8.23	0.03	2.34
9	0.00	56.53	0.00	99.11	0.06	0.00	0.00	3.56	0.32	6.33	0.01	1.36
10	0.00	64.92	0.00	100.00	0.03	0.79	0.00	8.03	0.25	5.10	0.01	1.11
11	0.00	73.16	0.00	100.00	0.01	1.46	0.00	9.62	0.20	2.82	0.00	0.23
12	0.00	80.41	0.00	100.00	0.00	2.22	0.00	14.59	0.15	1.76	0.00	0.00
13	0.00	86.21	0.00	100.00	0.00	4.16	0.00	17.67	0.11	1.38	0.00	0.46
14	0.00	90.86	0.00	100.00	0.00	5.46	0.00	23.10	0.08	0.16	0.00	0.84
15	0.00	94.83	0.00	100.00	0.00	8.38	0.00	25.90	0.05	0.00	0.00	1.94
High gobbler harvest												
0	0.02	0.00	0.00	0.00	0.50	20.10	0.01	4.67	0.74	31.38	0.15	19.58

Table 3.5 (cont’d)

1	0.00	3.46	0.00	26.09	0.41	14.66	0.00	2.18	0.68	27.96	0.11	16.15
2	0.00	10.36	0.00	46.69	0.33	10.68	0.00	1.55	0.62	23.73	0.09	12.86
3	0.00	15.19	0.00	64.05	0.25	6.86	0.00	0.54	0.55	19.74	0.06	9.51
4	0.00	24.31	0.00	77.94	0.19	4.43	0.00	0.91	0.49	16.54	0.04	7.91
5	0.00	32.36	0.00	88.25	0.13	3.12	0.00	0.00	0.42	13.17	0.03	5.07
6	0.00	42.41	0.00	94.38	0.09	2.16	0.00	1.56	0.35	10.58	0.02	5.08
7	0.00	52.06	0.00	98.27	0.05	2.04	0.00	3.83	0.29	8.26	0.01	3.15
8	0.00	61.41	0.00	100.00	0.03	0.00	0.00	4.52	0.24	5.79	0.00	1.77
9	0.00	69.85	0.00	100.00	0.01	0.56	0.00	7.04	0.18	4.79	0.00	1.26
10	0.00	77.30	0.00	100.00	0.00	1.94	0.00	11.15	0.13	2.98	0.00	0.00
11	0.00	83.53	0.00	100.00	0.00	1.91	0.00	14.16	0.09	2.08	0.00	0.72
12	0.00	89.25	0.00	100.00	0.00	4.69	0.00	18.28	0.06	2.33	0.00	1.13
13	0.00	93.25	0.00	100.00	0.00	7.51	0.00	22.07	0.04	1.27	0.00	2.06
14	0.00	96.35	0.00	100.00	0.00	9.67	0.00	26.94	0.03	0.52	0.00	2.68
15	0.00	98.30	0.00	100.00	0.00	12.04	0.00	32.45	0.01	0.00	0.00	4.35

[a] Productivity was manipulated by changing the input number of per-capita number female recruits (*k*) to low (0.775), medium (1.440), and high (2.105) values (Table 3.1).

[b] Values of spring hen poaching rate were drawn from lognormal distributions with medians of 0.05 (low), or 0.15 (high; Table 3.1).

[c] Median spring harvest rates for gobbler hunting scenarios were 0.15 (Low), 0.30 (Medium), and 0.40 (High), respectively. Annual spring gobbler harvest rates for each scenario were drawn from lognormal distributions (Table 3.1).

Changes to hen poaching also affected the magnitude of management tradeoffs between maintenance of large annual harvests and large populations. When poaching rates were high, achieving a median proportion of years with large abundance > 0.5 was only accomplished at fall harvest rates ≤2% under the single scenario when spring gobbler harvest was low and productivity was high (Table 3.5). Such reduction in risk to populations was only accomplished with median annual harvest reductions of approximately 30% or more from their maximum values (Table 3.5). Maintaining large abundance more than half of the time was not achieved under any other combination of spring and fall harvest considered when poaching was high, irrespective of productivity parameters (Table 3.5).

DISCUSSION

Management Consequences of Uncertain Demographic Processes

Characterizing management risks and tradeoffs is a first step towards decision making that formally acknowledges and accounts for uncertainty (Walters 1986, Sethi 2010). My findings demonstrate that risks and tradeoffs accompanying management of fall turkey harvests depend on assumptions about population parameters, the values of which are uncertain in many areas. I demonstrate that implementing a proportional harvest strategy with a target of fall either-sex harvest consistent with existing recommendations (Vangilder and Kurzejeski 1995, Aplizar-Jara et al. 2001, McGhee et al. 2008) may only retain populations at desirably large levels under conditions of high productivity, low female losses, and low spring male harvest rates. In addition, the 9% fall harvest rates recently recommended rarely resulted in the highest possible total annual harvest over both spring and fall hunting seasons. Thus 9% fall harvest is not a generalizable management target for either maintaining large turkey populations or maximizing total annual harvest with high probability. Given widespread belief that fall harvests of up to

10% will result in maintenance of desirable populations over a variety of conditions (Healy and Powell 2000), these results have important implications for turkey harvest management in the post-restoration era. Specifically, I demonstrate that target fall harvest rates deduced from studies of individual turkey populations have not produced recommendations with a high probability of achieving modern population and harvest objectives across a plausible range of productivity, female loss, and spring male harvest scenarios.

My 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. In some areas fall harvest management seeks to ensure turkey populations remain protected under worst-case conditions (pg. 24, Healy and Powell 2000). I show that under worst-case recruitment scenarios, in particular, harvesting turkey populations at currently recommended levels may incur considerable risk that populations will not be maintained at desirable levels (see also Schwertner [2005]). However, I acknowledge the relative frequency of turkey populations whose dynamics are well represented by each of my scenarios is unknown. Moreover, fall harvesting risks are likely to be reduced in areas known to 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 production and recruitment of poults (Vangilder and Kurzejeski 1995, Roberts and Porter 1996, Rolley et al. 1998, McGhee et al. 2008).

Productivity at low abundance has strong implications for turkey management, yet even under high productivity conditions the magnitude of spring losses, which are often unknown locally, affect which target fall harvest rates will likely achieve population and harvest objectives with high probability. Others have demonstrated that female losses during spring reduce sustainable fall harvests when compared to models without such losses (Vangilder and Kurzejeski 1995). My work adds to the realization that high female losses earlier in the year can fundamentally alter the ability to meet management objectives through fall harvests. Moreover, anticipation of tradeoffs between the magnitude of fall harvest and size and growth of turkey populations is previously established in the literature (Vangilder and Kurzejeski 1995, Alpizar-Jara et al. 2001, McGhee et al. 2008). However, few have described how the nature and magnitude of such tradeoffs change as a function of systematic changes in turkey demography (Stevens et al. 2016). More generally, my results imply that appropriate fall harvest strategies for balancing harvest and population objectives are likely to be a function of processes occurring earlier in the year that determine recruitment and both legal and illegal harvest mortality.

Uncertain drivers of productivity changes have strong implications for modern turkey harvest management. Contemporary, broad-scale assessments suggested turkey production may be 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. As previously mentioned, one hypothesis suggests recruitment declines are associated with increased density (i.e., hypothesized density-dependent feedbacks on per-capita recruitment; Schwertner 2005, Bond et al. 2012, Byrne et al. 2016, Stevens et al. 2016), while an alternative hypothesis posits recruitment declines are a result of changes to habitat or other regional conditions (e.g., resulting in reduced female condition entering nesting season; Thogmartin and Johnson 1999). That is, changes to average recruitment at low density could occur as a result of systematic changes to environmental conditions (e.g., habitats, spring weather patterns, etc.) or community composition in different areas, or as a result of such changes in a single area over time. Recent analyses have been insufficient to determine support for these alternative hypotheses (see also McGhee and

Berkson [2007b]), however, and interpretation of temporal patterns of recruitment presented by these studies is complicated by a confounding of changes associated with density and those associated with environmental conditions or community composition.

Although causes of recent productivity declines are unknown, the sources of such declines have direct relevance to interpretation of my results in the context of modern management. Because the parameter *k* can be thought of as productivity prior to the onset of density-dependent feedbacks, the systematic changes I applied to will be more reflective of changes that might occur as a result of changes in habitat or other regional conditions that could reduce average recruitment at low abundances. Thus, if productivity declines are due solely or in part to degrading quality or quantity of nesting and brood-rearing habitats, then my results suggest fall harvests needed to achieve modern management objectives may be less than 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, I would expect reduction of densities through harvest to increase per-capita recruitment towards larger values (Stevens et al. 2016). The unknown causes of modern productivity declines thus contribute heavily to existing uncertainties in turkey demography 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 should be to be tailored to dynamics of regional populations; however, existing uncertainties create challenges for customizing management recommendations. Uncertainty about the value of demographic rates for a given population is a key source of structural uncertainty relevant to turkey management at local scales because rigorous estimates of demographic parameters are not available for many populations. Many studies have estimated demographic rates of turkey populations using field-intensive methods (e.g., Roberts et al. 1995, Rolley et al. 1998, Wright and Vangilder 2007), yet direct evidence and comparison of studies suggests there are systematic changes in population parameters through space and time (Vangilder et al. 2001, Norman et al. 2007, Byrne et al. 2016, Bowling et al. 2016). Moreover, little is known about potential causes of density dependence that may be operating within turkey populations (Warnke and Rolley 2007, Healy 2011, Porter et al. 2011). This creates uncertainty in the strength of density-induced feedbacks to population growth and the appropriate underlying forms of mathematical models used to represent turkey populations. McGhee and Berkson (2007a) estimated θ using index data from real turkey populations, assuming the value of θ was shared among spatially distinct populations. It remains unclear, however, how well their estimates of model parameters generalize across turkey populations in different habitats and regions.

Sensitivity of fall harvest performance to demographic parameter values suggests a need to explicitly address structural uncertainty when developing turkey harvest policies. There are 2 general approaches for dealing with the effects of structural uncertainty in management decision making. One approach is to focus on reduction of uncertainty through targeted research and monitoring efforts, and possibly through learning via formal adaptive management. The traditional approach to research would focus on eliminating uncertainty by directly estimating 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 habitats is certainly possible (e.g., Pack et al. 1999, Norman et al. 2001, Hubbard and Vangilder 2007, Diefenbach et al. 2012). Field-intensives studies are time consuming and costly to implement over broad management scales, however, and thus may not be possible for many populations. Uncertainty about local demography will therefore likely remain for many populations in an era of changing environmental conditions and limited agency budgets (Porter et al. 2011). If underlying management objectives can be clarified, however, formal value-of-information analyses (VoI; Canessa et al. 2015) could help management agencies determine which parameters should be estimated with high priority. Such analyses determine which uncertainties should be reduced to provide the largest gain in ability to make good decisions, where information gains are measured by improved ability to accomplish explicit management objectives (Canessa et al. 2015). Although I did not conduct formal VoI analyses here my results do imply information about productivity is likely to be important for balancing population and harvest objectives in fall harvest management.

Although vital rates could be estimated using traditional field research methods, additional tools would be needed to reduce structural uncertainty surrounding density-dependent processes operating within turkey populations. Estimating demographic parameters by itself does not necessarily reduce uncertainty surrounding the values of θ or interpretation of productivity declines in the face of multiple hypothesized causes. More formal adaptive harvest management approaches can be used to reduce structural uncertainty through time by intentionally making management decisions that facilitate learning about hypothesized system dynamics (Walters 1986). Importantly though, adaptive approaches that formally integrate learning into management processes require linkage of targeted monitoring data with tools to assess population responses to harvest (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 methods to assess populations at management scales is in progress (e.g., Gast et al. 2013, Clawsen et al.

2015), and such techniques are not yet widely used. Thus adaptive harvest management for turkeys may only become feasible as rigorous tools are more widely adopted to assess abundance and dynamics of turkey populations at appropriate scales.

A second approach to explicitly dealing with uncertainty incorporates structural uncertainty directly into the analysis of management options by using decision-analytic methods to identify policies that meet management objectives (Harwood 2000, Nichols et al. 2007, Gilboa 2011). This approach acknowledges decision makers will never know true values of population parameters, and uncertainty is embraced (but not necessarily reduced) instead of ignored in the evaluation of management options. Specifically, a traditional decision analysis would view unknown values of turkey demographic parameters as representing different plausible hypotheses about system dynamics (Peterman and Peters 1999), and assign probability distributions to these uncertain parameters to describe likely values using expert opinion or prior data. Harvest policies likely to meet objectives could then be identified visually from the marginal distributions of management performance metrics (Bence et al. 2008), or by using optimization tools after combining performance measures into an explicit utility function (Runge and Walshe 2014, Williams and Nichols 2014). In the context of turkey management this approach is intuitively appealing 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) can be viewed as iterative extensions of decision analysis that are used to integrate monitoring, assessment, and decision making, with the goal of identifying optimal decisions while reducing structural uncertainty and improving management decisions over time.

In this paper I focused on implications of structural uncertainty for management of fall harvests, yet development of regional management strategies will also be affected by additional uncertainties. For example, I modeled implementation uncertainty by allowing harvest rates to vary across simulation years, but I assumed equal harvest vulnerability between males and females during fall hunting seasons. There is discrepancy about differences in sex-specific fall harvest vulnerability among published turkey harvest models, where some recent studies assume equal vulnerability (Alpizar-Jara et al. 2001, McGhee et al. 2008, McGhee and Berkson 2011) but others assumed differential vulnerability (e.g., Vangilder 1992, Vangilder and Kurzejeski 1995). Differential harvest vulnerability thus represents an additional source of relevant uncertainty in the dynamics of turkey harvesting. On average I would expect risk to populations to be scaled higher (female vulnerability > male vulnerability) or lower (male vulnerability > female vulnerability) than those reported here if fall harvest vulnerabilities differ between the sexes (Stevens et al. 2016). However, the existence of additional uncertainty does not take away from my primary conclusion that fall harvest strategies are not robust to uncertainty. To the contrary, this suggests my assessment of robustness may be too conservative and that performance of fall harvest rates relative population and harvest objectives could be more heterogeneous through space and time than my analyses indicate.

A final but important challenge to scientific development of fall harvest strategies is elaboration of explicit population objectives for the post-restoration era of turkey management. Modeling studies conducted during restoration often assumed a primary population 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 harvests irrespective of resulting abundance, and thus turkeys are valued only if they are harvested. Yet abundance has likely plateaued in many areas (Warnke and Rolley 2007, Ericksen et al. 2016, Parent et al. 2016), and modern objectives appear more complex than simply to maximize harvest. My interactions with managers and stakeholders in the Midwestern U.S. suggest fundamental objectives often relate to hunter satisfaction, which is related to harvest and the ability of hunters to interact with large numbers of gobbling birds in spring (i.e., abundance; Cartwright and Smith 1990, Little et al. 2000, Swanson et al. 2007). Thus, for my purposes I defined a large population as half of what the environment could support; but population objectives likely vary through space, and should be refined locally. Regardless of specific objectives, however, my work suggests maintenance of larger, more desirable turkey populations may be challenging under some plausible scenarios when managing fall harvest as recommended by previous studies.

MANAGEMENT IMPLICATIONS

My results imply fall harvest recommendations deduced from modeling studies that only considered a small portion of the demographic parameter space may not meet modern turkey management objectives over a broader range of conditions. Lack of robustness implies that both risks to turkey populations that accompany fall harvest and management tradeoffs between harvest and abundance likely change through space and time with changes to demography, and thus harvest strategies needed to meet specific objectives could be tailored to characteristics of local populations. If reliable estimates of population parameters are available, use of my simulation results directly in development of regional management strategies is possible. This would require identifying scenarios that closely resemble the set of local demographic rates, and determining a level of risk that is acceptable to managers and stakeholders. If regional differences in objectives necessitate different thresholds for desirable abundance of turkeys than

I considered, the approach could be easily replicated easily with different objectives. However, decisions about desirable abundances, harvests, and risk tolerances are ultimately based on value judgements (Gilboa 2011, Runge and Walshe 2014), not science. Thus, additional discussion of risk preferences and population objectives with stakeholders may be warranted. In the absence of detailed demographic data, robust strategies for fall harvest could be identified with decision-analytic tools. Formal adaptive approaches aimed at reducing structural uncertainty in turkey management over time could also be adopted, but would require integration of monitoring and assessment programs currently lacking in many areas. Alternatively managers could focus on implementing conservative regulations to ensure population objectives are achieved at the expense of fall harvests. However, in the absence of detailed population data and in light of regional productivity declines, my results imply such an approach would require caution.

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CHAPTER 4: IDENTIFYING TARGET REFERENCE POINTS FOR HARVESTING ASSESSMENT-LIMITED WILDLIFE POPULATIONS: A CASE STUDY

INTRODUCTION

Identification of strategies for sustainable exploitation of natural populations is a problem of global significance for conservation biology and natural resource management (Ludwig et al. 1993, Hilborn et al. 1995, Weinbaum et al. 2013). The meaning of sustainable harvest has evolved over the last half century, however, starting with classical interpretations that used deterministic population models, progressing through probabilistic interpretations that incorporated uncertain population dynamics and stochastic environments, and resulting in modern interpretations that acknowledge explicit objectives that relate to conservation of harvested populations under uncertainty (Quinn and Collie 2005). For a given species there is a continuum of exploitation rates that will allow for biologically self-sustaining populations (Rosenberg et al. 1993, Quinn and Collie 2005), thus careful clarification of social objectives motivating management is required to define sustainability clearly. Unfortunately, sustainable-harvest objectives for many populations lack such clarity, and remain difficult to operationally assess (Quinn and Collie 2005). Careful articulation of objectives is therefore needed to allow for quantitative assessment of the ability to achieve socially driven sustainable-harvest goals through management activities (Johnson et al. 1997, Quinn and Collie 2005, Nichols et al. 2007).

Population models are also central to scientific assessment of the ability to achieve sustainable-harvest objectives, yet structural uncertainty in the dynamics of natural populations often impedes identification of reliable harvest strategies (Hilborn and Ludwig 1993, Francis and Shotton 1997, Williams 1997). Scientists and managers often have multiple models representing hypothesized population and harvest dynamics, which translates into uncertain predictions of the outcomes of harvest management decisions (Nichols et al. 1995, Williams 1997, Milner-Gulland et al. 2001, Runge and Johnson 2002). Derivation of strategies for sustainable harvest should therefore consider a variety of plausible models to ensure management performs adequately in the face of uncertainty, and a decision-analytic framework provides a set of useful tools for assessing reliability of management decisions (Hilborn and Ludwig 1993, Shae et al. 1998, Lahoz-Monfort et al. 2014). For example, a commonly advocated approach to decision making in the face of uncertainty combines principles of structured decision making (SDM; e.g., Hammond et al. 1999) with predictive models of system dynamics and optimization algorithms to identify optimal state-dependent decisions recurrently over time (Nichols et al. 1995, Johnson et al. 1997, Martin et al. 2009).

A modern exemplar of sustainable harvest management via recurrent application of decision-analytic methods is formal adaptive harvest management. Adaptive harvest management employs dynamic decision analyses to identify optimal harvest strategies recurrently over time, and reduces uncertainty about population dynamics through learning (e.g., North American waterfowl management; Nichols et al. 1995, Johnson et al. 1997, Nichols et al. 2007, Johnson et al. 2015). This program integrates decision structuring and population modeling with targeted monitoring that provides data needed to estimate important state variables (e.g., abundance) and reduce structural uncertainty about system dynamics over time (Williams and Johnson 1995, Nichols and Williams 2006, Johnson et al. 2015). Proponents of adaptive harvest management often view decision making as a problem of optimal stochastic control, emphasizing use of dynamic optimization methods (Lubow 1996, Marescot et al. 2013) to identify optimal policies and decision thresholds as a function of abundance and environmental conditions at each point in time (Johnson et al. 1997, Martin et al. 2009, Nichols et al. 2014). Although theoretically optimal, this approach presupposes formal monitoring and assessment programs are in place to estimate abundance regularly, or at the very least provide reliable indices of abundance at regular intervals so that optimal policies can be updated adaptively over time. Indeed, adaptive harvest management for North American waterfowl (among the most widely cited examples of adaptive management) was developed around one of the premier broad-scale wildlife monitoring programs in the world (Nichols et al. 1995, Johnson et al. 1996). Despite existing demonstrations of adaptive harvest management (Nichols et al. 2007), however, many populations around the globe lack the basic monitoring infrastructure necessary to estimate abundance or population trends reliably for such purposes (Costello et al. 2012, Weinbaum et al. 2013).

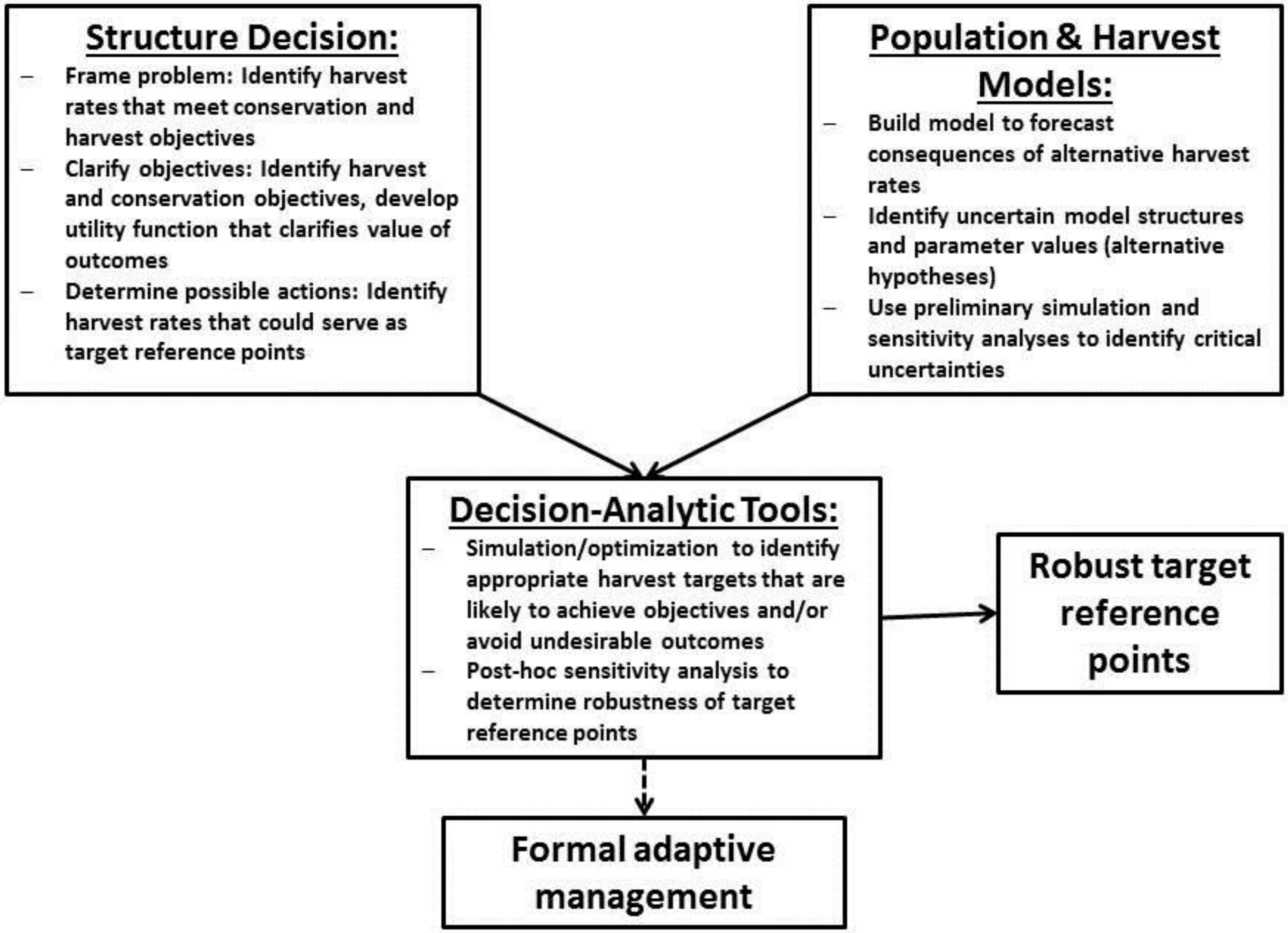
Harvest management for data-limited wildlife populations lacking formal population assessment programs often uses simplified metrics as indicators of sustainable harvest (reviewed by Weinbaum et al. 2013). Many sustainable-harvest metrics were not designed to explicitly account for uncertainty in system dynamics, nor were they developed with clear harvest-management objectives in mind. Quantitative assessment of the performance of such indicators is therefore difficult and often absent (Weinbaum et al. 2013). For example, annual harvest rates (i.e., fraction of population harvested) have sometimes been used to indicate sustainability of harvests by comparing spatial or temporal trends in harvest rates, or by comparison to specific reference values that are believed to indicate harvests that are sustainable (Caro et al. 1998, Hurtado-Gonzales and Bodmer 2004, Weinbaum et al. 2013). Like many of such indicators, however, harvest rates have generally proven to provide ambiguous information about management performance (Weinbaum et al. 2013). Moreover, quantitative assessment of the ability of reference harvest rates to accurately indicate management performance in the face of uncertainty is generally lacking. Thus many metrics used to indicate sustainable harvests for data-limited terrestrial populations have not been demonstrated to provide reliable information about the performance of harvest management at achieving conservation objectives (Milner-Gulland and Akçakaya 2001, Weinbaum et al. 2013).

Development of reliable tools to assess performance of harvest management for populations lacking regular assessment is needed (Costello et al. 2012, Weinbaum et al. 2013). In such cases reference points can be useful as indicators of management performance, whereby a reference point refers to a specific reference level of a simplified metric that indicates performance of management relative to some set of underlying objectives (Irwin and Conroy 2013). Target reference points, for instance, can be used as indicators of a single best policy that management attempts to achieve (e.g., a target harvest rate), or as representative of a set of policies with performance that is robust to uncertainty (e.g., a set of harvest rates with reliable performance under uncertainty; Irwin and Conroy 2013). Moreover, principles of SDM can be integrated into the process of developing reference points (Irwin and Conroy 2013), thereby clarifying the meaning of simplified metrics in terms of management objectives and providing a framework to assess performance for a set of potential reference points under uncertainty. Therefore, my objective was to demonstrate an approach for identifying target harvest rate reference points that can be used as indicators of long-term performance for sustainable harvest management of assessment-limited wildlife populations. I show how principles of SDM, along with decision-analytic tools and simulation modeling can be used to identify decision thresholds and target harvest rates that accomplish sustainable-harvest objectives in the absence of a formal framework for regular monitoring and assessment of population abundance. This approach is illustrated by a case-study involving management of wild turkey (*Meleagris gallopavo*) harvests, however, the ideas are generalizable to management of harvests for other species that lack the monitoring infrastructure needed to regularly identify and adapt optimal harvest policies.

GENERAL APPROACH

I describe a general approach, applied herein, that uses principles of SDM, models of population and harvest dynamics, and decision-analytic tools to identify harvest rates capable of achieving conservation and management objectives (Fig. 4.1). In the absence of rigorous population-assessment programs needed to make state-dependent harvest decisions, I use principles of SDM to identify static harvest rates that are likely to achieve clearly defined sustainable-harvest objectives, and thus serve as target reference points to guide management in data-limited environments. Application of SDM requires careful deliberation about underlying objectives, possible management actions, and likely outcomes of management decisions (Shae et al. 1998, Hammond et al. 1999, Clemen and Reilly 2001, Irwin et al. 2011). The first steps of structuring the decision are thus to frame the problem by identifying the decision to be made, clearly articulating objectives underlying the decision, and identifying alternative decision options (Hammond et al. 1999, Clemen and Reilly 2001). When developing target harvest rates to serve as reference points to guide harvest management, I frame the decision problem as one of identifying harvest rates that are likely to achieve sustainable-harvest objectives if implemented over the long term.

Figure 4.1 Conceptual model for developing robust target reference points to aide sustainable harvest management of assessment-limited wildlife populations using principles of structured decision making. Solid lines are used to indicate steps vital to the process, whereas the dashed line indicates the process could be used in the optional development of adaptive harvest management programs.



Sustainable-harvest objectives need to be clarified, but will likely be context specific and depend on the goals of decision makers and management stakeholders (Johnson and Case 2000, Irwin et al. 2011, Runge and Walshe 2014). Such objectives are likely to include maintenance of desirable sizes for both the abundance and harvest of a population (Johnson et al. 1997, Milner-Gulland et al. 2001), but could also relate to attributes of populations and harvest other than absolute abundance. For instance, objectives could relate to the variation of harvests or population fluctuations of the species of interest over time (Walters 1975). Metrics used to measure management success relative to objectives need to be clarified (hereafter called performance measures), but because specific objectives are a function of social values these will likely vary with the species and geographic region of interest.

I combine performance measures into a utility function (also sometimes called an objective function; Runge and Walshe 2014) that clarifies management tradeoffs explicitly, and permits straightforward summary of management performance via a single mathematical function that can be optimized. By using a utility function that included both harvest and abundance performance measures I was able to determine harvest strategies that maximize cumulative harvest while also maintaining populations at desirable levels. Although defining such a utility function is challenging, especially when stakeholders have varying values and objectives, this can be aided by careful collaboration between scientists, decision makers, and management stakeholder groups (Johnson and Case 2000, Lyons et al. 2008, Irwin et al. 2011). Lastly, I finish decision structuring by identifying possible actions, which in this case are viewed as a set of possible target harvest rates that could serve as indicators of performance if implemented as a harvest strategy over the long term.

Models of population and harvest dynamics provide a critical piece of decision-analytic applications that are necessary to predict responses of populations to harvest (Fig 4.1; Johnson et al. 1997, Irwin et al. 2011, Lahoz-Monfort et al. 2014). I use models to predict how performance measures respond to different possible management actions, which in this case are represented by alternative target harvest rates. I use stochastic models of population and harvest dynamics to characterize uncertainties common to harvest management (Williams 1997), thus resulting in probability distributions for performance measures of interest. The specific structure, functional form, and level of complexity of population models will vary with the ecology and life-history characteristics of the species of interest, as well as with management objectives and information available to parameterize such models (Runge and Johnson 2002, Irwin et al. 2011, Williams 2013). In practice there will often be considerable uncertainty surrounding the appropriate deterministic and stochastic model structures needed to reasonably represent dynamics, as well as for the appropriate values of individual model parameters (Francis and Shotton 1997, Williams 1997, Runge and Johnson 2002). Thus, a set of plausible models representing hypothesized system dynamics should be derived for each problem. In assessment-limited situations, careful collaboration between modelers and subject-matter experts will likely be required, as expert opinion may be necessary to develop and parameterize hypothesized models. Moreover, preliminary simulation and sensitivity analyses can be used to identify structural uncertainties that have large effects on management performance (Fig 4.1), and these uncertainties can be exploited to learn about the conditions under which different harvest rates are likely to achieve management objectives (see case study below).

Decision-analytic tools can be used to evaluate performance of the set of potential target harvest rates under uncertainty. I evaluate performance of alternative actions by determining how expected values of the utility function vary among alternative target harvest rates. To calculate expected utilities I use a combination of Monte Carlo simulation of and static optimization (i.e., pg. 49 of Williams and Nichols 2014). First, I use repeated stochastic population projections under each proposed harvest rate, while monitoring performance measures over time for each simulation replicate. I calculate the utility for each simulation replicate and then the expected utility over all simulation replicates for each harvest rate. Lastly, I identify optimal target harvest rates by comparing expected utility among potential target harvest rates, and selecting the harvest rate with maximum value.

I use the two-step process of simulation and optimization to understand how optimal target harvest rates change as a function of model parameters for which there is strong structural uncertainty, and to identify appropriate target harvests in the presence of such uncertainty. I first use the simulation-optimization process to understand the implications of structural uncertainty and locations of decision thresholds (sensu Nichols et al. 2014) by replicating the approach over discrete combinations of system-model parameters for which there is uncertainty, where combinations of parameters are intended to cover the plausible parameter space for the problem of interest. This facilitates determination of how optimal target harvest rates change across specific values of model parameters and identification of thresholds where optimal decisions change abruptly within the parameter space. To better understand robustness of performance for potential target harvest rates across the plausible parameter space, I also calculate relative utilities for each target harvest rate at each parameter combination. I define relative utility as expected utility for a harvest rate divided by expected utility for the optimal harvest rate for a specific set of parameters. This effectively allows researchers to identify target harvest rates with suboptimal, but nearly optimal performance across a broad spectrum of the model parameter space for which there is uncertainty. Lastly, to develop specific target harvest rates in the presence of structural uncertainty I use static decision analysis, whereby the simulation-optimization approach is repeated but with stochastic distributions representing uncertain system parameters (instead of combinations of discrete parameter values). Finally, I use post-hoc sensitivity analyses to ensure resulting inferences are robust to assumptions of population and harvest models for which there is limited data to directly inform model development (Fig. 4.1).

CASE STUDY WITH WILD TURKEYS

Wild turkeys (hereafter turkeys) are the second most popular game species in the United States (Harris 2010) and are managed by state natural resource agencies to provide recreational hunting opportunities. The most common regulatory framework consists of multiple discrete annual hunting seasons, with male-only harvests during spring breeding activities and either-sex harvests after young birds recruit into the population in the fall (Kurzejeski and Vangilder 1992, Healy and Powell 2000). Dynamics of turkey populations are sensitive to the magnitude of either-sex fall harvest (Vangilder 1992, Vangilder and Kurzejeski 1995), and thus a management challenge is to balance fall hunting opportunity with the desire to maintain large populations. Many models of turkey populations were developed during a period of rapid growth that characterized the restoration phase of management (Vangilder and Kurzejeski 1995, Alpizar-Jara et al. 2001), an era that ended successfully around the year 2000 (Lewis 2001, Tapley et al. 2007). Turkey populations in many areas now appear to be either stable or declining slowly (Ericksen et al. 2016, Parent et al. 2016). However, management in most states proceeds with highly uncertain information on the status of local populations. With some notable exceptions (e.g., Clawsen et al. 2015), the monitoring data necessary to employ rigorous abundance estimation techniques are not available at the broad spatial scales at which turkeys are managed.

Harvest-based metrics have been used for several decades to index populations (Healy and Powell 2000); however, the assumptions necessary for these indices to be reliable indicators of spatial-temporal population patterns (i.e., constant effort and/or probability of harvest per-unit-effort) are either known or suspected to be false (Harris 2010, Parent et al. 2016). When combined with recent concerns over perceived regional population declines (Ericksen et al. 2016), a clear need has emerged for developing target reference points that provide reliable indicators of performance of fall harvest management for assessment-limited turkey populations.

Structuring Harvest Management

The decision problem is to identify target fall harvest rates that facilitate achievement of both harvest and conservation objectives reliably. Previous work has recommended that either-sex turkey harvests of 5-10% of the fall population are capable of sustaining turkey populations (Healy and Powell 2000); yet recent work suggested this recommendation was not robust to structural uncertainty in turkey demography that is common to modern management (chapter 3). While the primary focus is on developing reference points for management of either-sex fall harvests, male-only spring harvests also vary in magnitude through space and time (Wright and Vangilder 2007, Diefenbach et al. 2012), and the degree of conservatism in spring harvest regulations varies by state (Healy and Powell 2000). Thus, development of reference points for management of fall harvests must consider multiple plausible scenarios of spring harvest to ensure robustness of results is understood. This also facilitates development of reference points for regional population management that are tailored to the magnitude of spring harvest mortality experienced locally.

Evaluating performance of fall turkey harvest requires careful articulation of management objectives and the tradeoffs between maintaining large harvests and large populations. Past studies often evaluated performance of proportional fall turkey harvests for achieving objectives with limited relevance in the modern context of management. During the restoration era of turkey management, modeling studies often assumed a harvest rate was sustainable if it allowed for continued growth of populations (Vangilder 1992, Vangilder and Kurzejeski 1995, Alpizar-Jara et al. 2001). These studies used density-independent population models to approximate growth of small turkey populations during restoration; however such models technically assume no limitation and thus populations could potentially grow without an upper bound. More recently, turkey population models were developed including density-dependent dynamics to reflect declining population growth over large scales (e.g., McGhee and Berkson 2007a). Subsequent modeling exercises assumed the primary objective of turkey management was to maximize harvests irrespective of resulting turkey abundance (McGhee et al. 2008). This objective implicitly assumes there is not a desire to maintain large populations past the opportunities they provide for harvest, and is inconsistent with social surveys of stakeholder groups that suggest hunters value interacting with large numbers of turkeys during the spring season (i.e., the perception of large populations on the landscape; Cartwright and Smith 1990, Little et al. 2000, Swanson et al. 2007) in addition to the actual harvest of a bird.

In Michigan specifically, my collaboration with a diverse management stakeholder group, including representatives from both hunting and wildlife viewing advocacy organizations, has provided insight into management objectives for this region. These interactions suggested turkey hunting groups are interested in maximizing opportunity to harvest during spring, male-only hunting seasons. Restoration efforts took decades to restore turkey populations after unlimited exploitation and habitat modification of the late 19th and early 20th centuries (Kennamer et al. 1992, Lewis 2001), and thus there is also a strong desire to ensure maintenance of large populations that were only recently restored. Because stakeholders favor the opportunity to pursue male turkeys during spring, the objective with respect to fall harvest is to maximize opportunity so long as fall harvest does not drive populations to socially undesirable levels in the short term, and thus negatively impact the quality of spring hunting. Using this information I developed a mathematical utility function that explicitly clarifies tradeoffs between maintenance of populations and harvests:

$$U\left(N, H_s, H_f\right) = \sum_{T} H_{s,t} + H_{f,t} \times u(N_{t+1})$$

$$u(N_{t+1}) = \begin{cases} 0 \; if N_{t+1} < {}^{K}/_{2} \\ 1 \; if N_{t+1} \geq {}^{K}/_{2} \end{cases}.$$

In this function, $H_{s,t}$ represents male-only spring harvest at time *t*, $H_{f,t}$ is either-sex fall harvest at time *t*, N_{t+1} is the total abundance of turkeys at the start of the spring hunting season in year *t+1*, and *K* represents the maximum number of turkeys the region is capable of supporting (so-called environmental carrying capacity). This composite utility function (U) combines three performance measures (abundance, spring harvest, and fall harvest) into a single expression that describes how outcomes of each management action are valued, and uses a utility threshold ($u(N_{t+1})$; Martin et al. 2009, Nichols et al. 2014) for abundance to define the lower bound on desirable population size relative to the carrying capacity of the habitat. This threshold effectively weights the value of fall harvest as all-or-nothing, depending on effects of that harvest on turkey abundance at the start of the subsequent spring. I identified target fall target harvest rates that maximized U over long time horizons (*T* = 100 years after model initialization). For this example the set of possible target fall harvest rates that served as potential target reference points was 0-15%, at increments of 1%, where a harvest of 15% of the fall population was the largest reported as sustainable in previous modeling studies (Alpizar-Jara et al. 2001).

However, because specific population objectives have not been articulated for most turkey populations (including populations in Michigan; Healy and Powell 2000) there is uncertainty about the appropriate location for the utility threshold and the valuation of fall harvests when spring abundance falls below the threshold (e.g., all-or-nothing vs. linear decrease). Thus I also determined sensitivity of results to changes in the utility function that reflect different risk preferences and valuation of fall harvests relative to spring abundance (see Simulation and Optimization Methods below).

Models of Population and Harvest Dynamics

I modeled population and harvest dynamics using a sex-specific theta-logistic model developed for wild turkeys (McGhee et al. 2008, chapter 3). Mechanisms of regulation for turkey populations are unknown (Healy 2011, Porter et al. 2011). It is therefore difficult to construct detailed, life-history based models that directly portray elements of a turkey life-cycle on an annual basis (sensu Vangilder and Kurzejeski 1995) that also include limitation of population growth at large abundances. The general theta-logistic model was therefore used to aggregate relevant biological processes into a composite growth function whose values were modified by density. This model was also fit previously to turkey population indices from 11 states by McGhee and Berkson (2007a) to estimate the strength and nonlinearity (θ) of declines to population growth that accompany increases in abundance, and used by McGhee et al. (2008) to identify maximum-sustainable harvests for a unique set of model input parameters. Model equations were slightly modified (chapter 2; Appendix A) to ensure female turkeys illegally killed during spring hunting seasons could not contribute to production of young, where annual dynamics are represented by

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

Here the abundance of turkeys at time *t+1* for sex *i* is a function of the abundance at time *t*, the proportional removal of birds from the population through spring harvest ($h_{i,s,t}$; either legal or illegal depending on the sex), the new population growth ($e^{r_{i,t}\left(1-\left(\frac{N_{i,t}}{K_i}\right)^{\theta}\right)+\varepsilon_{p,t}}$), and the birds removed via fall harvest ($H_{i,f,t}$). In this model, sex-specific instantaneous growth rate ($r_{i,t}$) is a function of additional parameters representing non-hunting survival and population productivity (i.e., the number of female recruits per female in the population after spring losses). Sex-specific environmental carrying capacities (K_i) were assumed equal, and the total carrying capacity used in the utility calculations was the sum of K_i for each sex (i.e., $K = K_m + K_f$). Uncertainty in the value of θ parameter was accounted for by drawing this parameter from a normal distribution whose parameters were determined by the point estimate and standard error of the estimate provided by previous work ($\theta \sim Normal(\mu = 0.36, \sigma_{\theta} = 0.09)$; McGhee and Berkson 2007a). Process variation in population growth associated with annual environmental conditions ($\varepsilon_{p,t}$) was drawn from a normal distribution using parameter values consistent with earlier studies ($\varepsilon_{p,t} \sim Normal\left(\mu = 0, \sigma_p = 0.15\right)$; McGhee et al. 2008, chapter 3). A full description of model components and parameters values is provided in Appendix D.

I modeled temporal variation in sex-specific harvests by assuming realized proportional harvests varied about a central tendency defined by their target values. Total harvest of sex *i* during season *j* at time *t* ($H_{i,j,t}$) was equal to the realized harvest rate ($h_{i,j,t}$) multiplied by the abundance at the start of the corresponding hunting season (Appendix D). Variation in realized fall harvests for the male segment of the population was modeled as coming from a lognormal distribution by multiplying target exploitation rates by an exponentiated log-scale random deviate ($h_{m,f,t} = target_{m,f,t}e^{\varepsilon_{f,t}}$), where variation in fall harvest was assumed consistent with previous work ($\varepsilon_{f,t} \sim Normal(\mu = 0, \sigma_f = 0.175)$; McGhee et al. 2008, chapter 3). Because realized fall harvest rates are often different between male and female turkeys (Vangilder and Kurzejeski 1995), I allowed for differential fall harvest vulnerability by scaling realized female harvest rates by a linear function of the male harvest rate ($h_{f,f,t} = vh_{m,f,t}$) using a relative harvest vulnerability coefficient (v). Realized values of spring harvest (both legal and illegal) were also drawn from lognormal distributions (Appendix D). Moreover, this analysis assumed harvest mortality was unrelated to natural mortality, and thus per-capita survival of remaining individuals during the non-hunting period was unaffected by harvest. This is a ubiquitous assumption in turkey harvest modeling (Vangilder 1992, Vangilder and Kurzejeski 1995, Alpizar-Jara et al. 2001, McGhee et al. 2008) with some empirical support from field studies (Little et al. 1990, Godwin et al. 1991, Pack et al. 1999).

Previous simulation analyses have demonstrated structural uncertainty in parameters governing population productivity and relative harvest vulnerability are important for predicting population responses to harvest with this model. Moreover, assumed values of productivity and relative vulnerability to fall harvest vary among previous turkey harvest models (chapter 3), and such values are heterogeneous through space and time for natural populations (Norman and Steffen 2003, Bowling et al. 2016). Changing assumed values of productivity over plausible ranges has direct impacts on the ability of turkey populations to sustain fall harvests (chapter 3), and preliminary simulation analyses also suggested harvest and abundance are sensitive to assumptions about relative harvest vulnerabilities among different segments of the population (chapter 2). Structural uncertainty in the value of these parameters for a specific assessment-limited turkey population is thus directly related to the ability of managers to tailor harvest regulation to the characteristics of local populations.

Simulation and Optimization Methods

I used a combination of stochastic simulation and static optimization to understand how optimal target harvest rates change as a function of important model parameters whose values are unknown in practice in many regions but known to be heterogeneous among turkey populations, and to develop target reference points in the presence of different levels of information about these parameters. To account for uncertain productivity at low abundance I systematically manipulated the parameter representing the number of female recruits per-female in the spring breeding population between upper and lower bounds identified by literature review (0.75-2.15 by increments of 0.05; see chapter 3). I also systematically manipulated harvest vulnerability (v) across a plausible range identified through literature review to account for uncertainty in differences of realized fall harvest rates between male and female turkeys (0.5-2.0 by increments of 0.1). Finally, I considered three scenarios of spring harvest by manipulating median values of male harvest during spring among low (15%), medium (30%), and high levels (40%) identified as plausible from literature review (chapter 3).

I conducted population projections to determine performance of target fall harvest rates over the range of input parameter values. I tested performance of all potential target harvest rates (0-15%), where for each harvest rate I conducted 1000 population projections (101 years each including initialization year) for each target harvest rate at each combination of productivity and relative harvest vulnerability (464 scenarios). These simulations were also replicated over all spring harvest scenarios (low, med, high), for a total of 1392 distinct scenarios representing all combinations of productivity, vulnerability, and spring harvest. A random value of θ was generated for each simulation replicate under each scenario, but θ values were assumed constant over time within a given population projection. Because exact population estimates are not available to initialize population projections, but populations are believed to be large in many areas of the Midwestern United States where I work, I initialized all population projections with sex-specific abundances equal to their environmental carrying capacities.

I determined optimal target harvests and robustness of harvest rate performance using static decision analyses, where utility function values were calculated from outputs of stochastic simulation analyses. For each simulation replicate I calculated values of the utility function at each time step using information on current harvest and subsequent abundance, and calculated the cumulative value by summing over the entire time horizon (T = 100). From the distribution of utility values (over simulation replicates) for each target fall harvest rate and parameter combination I identified optimal target harvest rates as those that maximized expected utility over its simulated distribution. This was equivalent to 1,392 classical decision analyses (one for each scenario; Peterman and Peters 1999), whereby probabilities characterizing uncertainty nodes (e.g., θ) were represented with continuous probability distributions (determined by literature review and expert opinion), and utility values were summarized for specified combinations of productivity and vulnerability parameters. Individual decision analyses thus assumed perfect knowledge of productivity and vulnerability parameters, reflecting conditions where reliable estimates of these parameters are available for local management. I evaluated robustness by determining which target harvests were approximately optimal over the largest range of conditions (i.e., largest area of parameter space considered). I defined approximately optimal harvest rates as those whose relative expected utility (i.e., relative to optimal expected utility for a specific set of parameters) was > 0.80, thus indicating performance close to, but not quite achieving optimality. For each target fall harvest rate I calculated the set of scenarios where the relative expected utility was > 0.80. To ensure robustness of these inferences I also repeated calculations by manipulating lower bounds for the relative expected utility (used to define approximately optimal performance) over a range of values (0.75-0.95, by 0.05), and determined approximately optimal harvest rates over the largest region of parameter space for each of these values.

I also performed a static decision analysis to develop target reference points in the absence of estimates for productivity and relative harvest vulnerability by assuming uniform distributions for these parameters over their plausible ranges (instead of discrete but constant values). For this analysis the values of productivity and vulnerability were drawn randomly across simulation replicates but held constant over each population projection (similar to θ above). As such, productivity and vulnerability parameters were treated as additional uncertainty nodes (Peterman and Peters 1999) and utility values were summarized over the distributions of these additional uncertainties. For this analysis I used 10000 stochastic population projections for each target fall harvest rate, and the entire analysis was replicated over each scenario of spring harvest (low, med, high) for a total of 3 distinct decision analyses. Thus I identified optimal target fall harvests in the absence of information about productivity and vulnerability by identifying the fall harvest rates that resulted in maximum expected utility over the distributions representing major uncertainties commonly faced in turkey management.

Lastly, I conducted sensitivity analyses to determine robustness of results to changes in population objectives and the stochastic distributions characterizing variation in realized fall harvests. Performance of harvest strategies can depend not only on the expected values of population and harvest processes, but also on the manner that realized values of stochastic quantities vary about their central tendencies through time (Deroba and Bence 2008). Unfortunately, the exact variation and structure of variability for sex-specific realized fall harvest rates resulting from a set of turkey harvest regulations are not well described. Thus, to ensure reference points I identified are robust to assumptions about variability in realized fall harvest rates (i.e., the nature of implementation uncertainty), I replicated analyses that used discrete parameter combinations described above with different distributions of realized fall harvest rates through time. I first lowered and increased the magnitude of fall harvest variation by eliminating variability ($\sigma_f = 0$) and then doubling ($\sigma_f = 0.35$) the variation relative to baseline levels ($\sigma_f = 0.175$). I also replicated analyses assuming realized fall harvest rates followed a first-order autoregressive process and were thus correlated through time (Appendix D). Lastly, to demonstrate sensitivity of harvest rate reference points to changes in population objectives, I replicated utility calculations with different locations for the utility threshold described above ($0.4K$, $0.6K$) and with a linear decrease in the value of fall harvest when spring abundance falls below the utility threshold of $0.5K$ (as opposed to the current all-or-nothing valuation of fall harvest). I programmed all simulation and optimization analyses using program R version 3.2.2.

RESULTS

Optimal and approximately optimal fall harvests of turkeys were governed by the combination of spring harvesting, population productivity, and differential harvest vulnerability among the sexes. The marginal distribution of optimal harvest rates among simulation scenarios were right skewed and influenced by the magnitude of spring male-only harvests (Fig. 4.2). In general, larger spring harvests resulted in smaller optimal fall harvest rates and a greater frequency of no fall harvest being optimal (Figs. 4.2–4.3); approximately 6%, 25%, and 39% of all scenarios resulted in optimal fall harvests of zero under low, medium, and high spring harvest scenarios. More than half of optimal harvest rates across simulation scenarios were < 5% of the fall population (low spring harvest = 0.58, medium spring harvest = 0.86, large spring harvest =

0.96), whereas > 95% of optimal harvest rates for all scenarios were < 10% of the fall population (Fig. 4.2). Population productivity and relative sex-specific harvest vulnerabilities interacted to determine optimal fall harvest rates, and thresholds in optimal harvest rates demarcating management-relevant boundaries as a function of these parameters shifted as a result of changes to the magnitude of spring harvest (Fig. 4.3). Increased vulnerability of female turkeys overtook the beneficial offsets of increased population productivity to drive optimal harvest rates to < 5% of the fall population, and this effect became more dominant as the magnitude of spring harvest increased (Fig. 4.3). Optimal fall harvest rates of 5-9% were only realized for a small region of the parameter space representing high productivity and low female vulnerability to harvest, and this area was largest under low spring harvest levels (Fig. 4.3). Similarly, optimal harvest rates of ≥10% only occurred over a very narrow region of the parameter space, and disappeared entirely for medium-high spring harvest scenarios. Shifts to optimal fall harvest rates over scenarios representing combinations of productivity, vulnerability, and spring harvest were driven by responses of populations to fall harvest, where larger fall harvest rates drove populations below desirable levels (i.e., below the utility threshold of $K/2$; Fig. 4.4, Appendix E).

Figure 4.2 Marginal distributions of optimal fall harvest rates (expressed as percentages of the male population) across all structural uncertainty scenarios and three scenarios of spring male-only harvest (low = left, medium = middle, high = right).

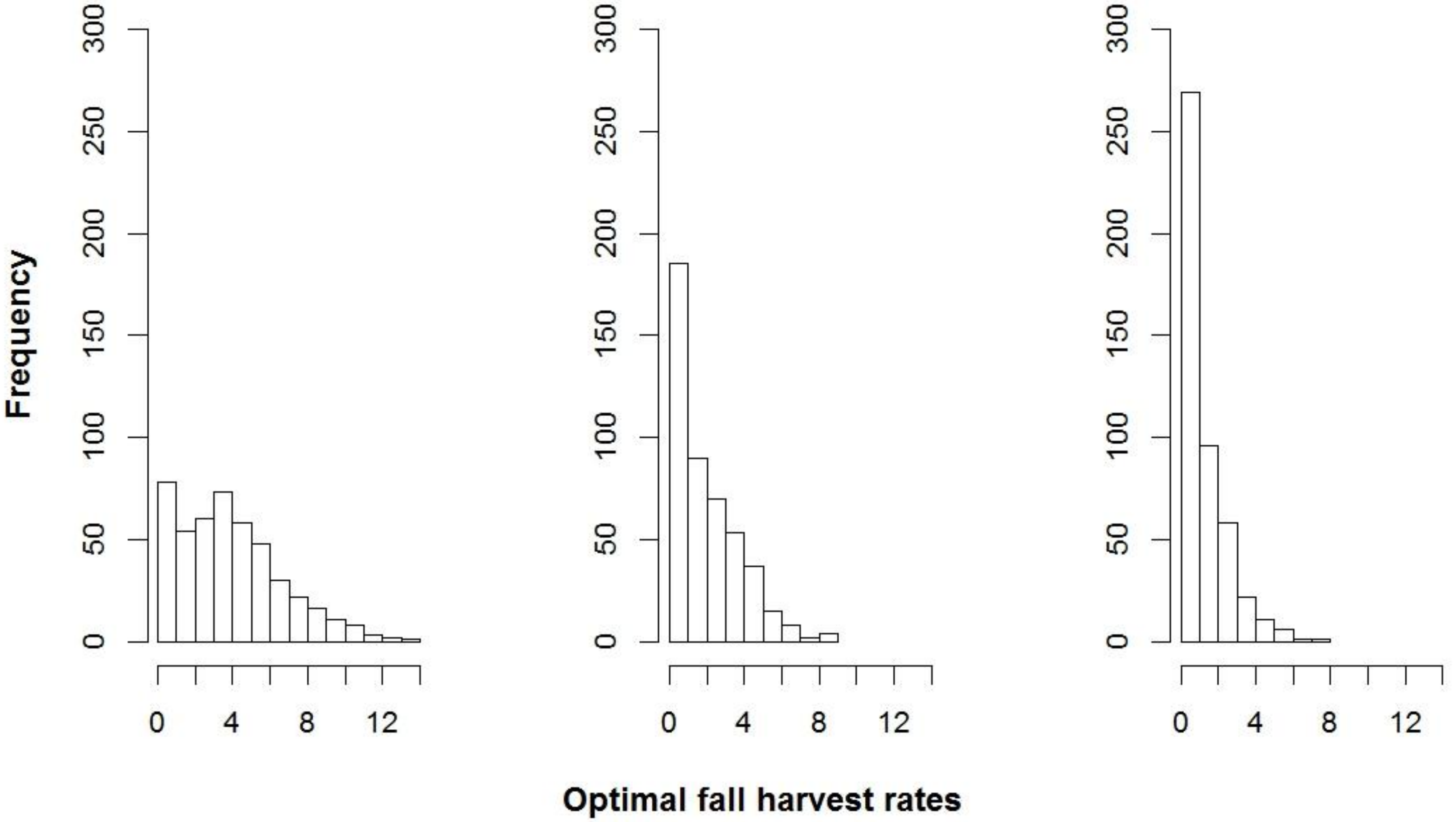


Figure 4.3 Optimal fall harvest rates (expressed as percentages of the male population at the start of fall hunting) as a function of population productivity (Productivity) and sex-specific fall harvest vulnerabilities (Relative vulnerability) parameters, and across three scenarios of spring male-only harvest (low = left, medium = middle, high = right). Colors indicate the ranges of optimal harvest rates, including no harvest (black), 1-4% (dark grey), 5-9% (light grey), and 10-15% (white).

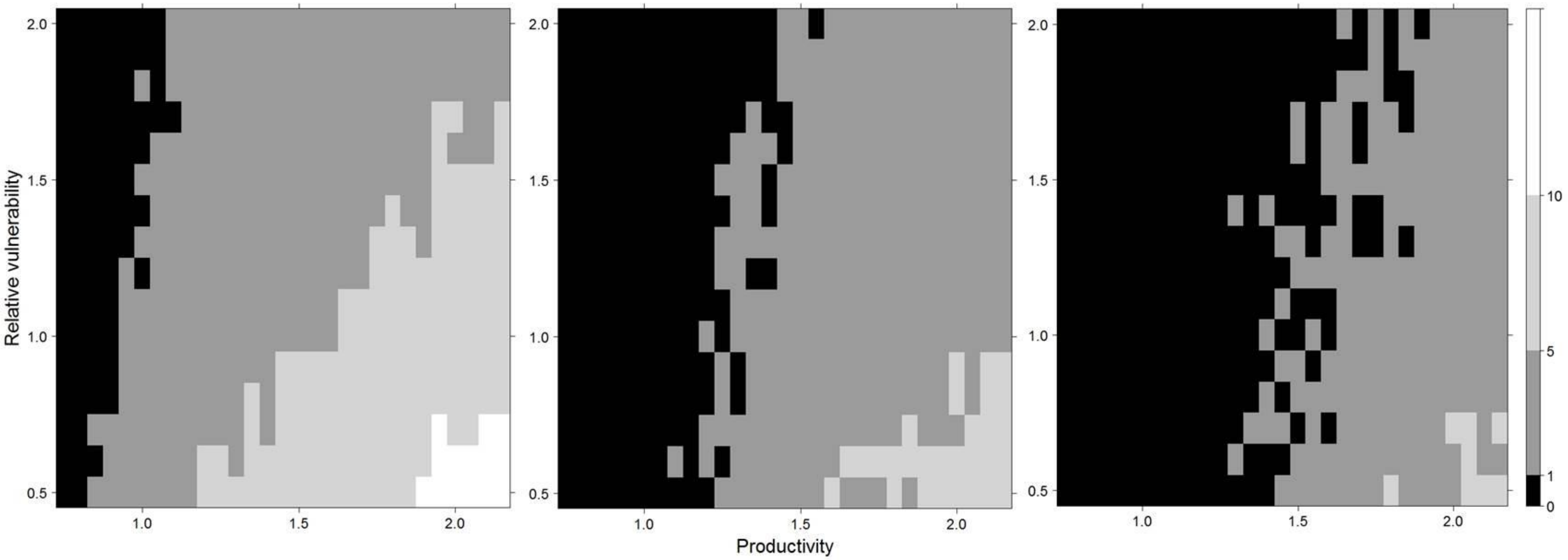


Figure 4.4 Median abundances over time for select scenarios representing parameter combinations for which there is strong structural uncertainty for low (a), medium (b), and high (c) levels of male-only spring harvest. Plots represent scenarios with no fall harvest (left), 5% fall harvest (middle), and 10% fall harvest (right). Solid lines are from distributions simulated with the lowest hen vulnerability ($v = 0.05$), and dashed are the highest hen vulnerability values ($v = 2$). Colors represent values of population productivity, with low (red = 0.75), medium (black = 1.45), and high (blue = 2.15) values.

Figure 4.4 (cont'd)
a)

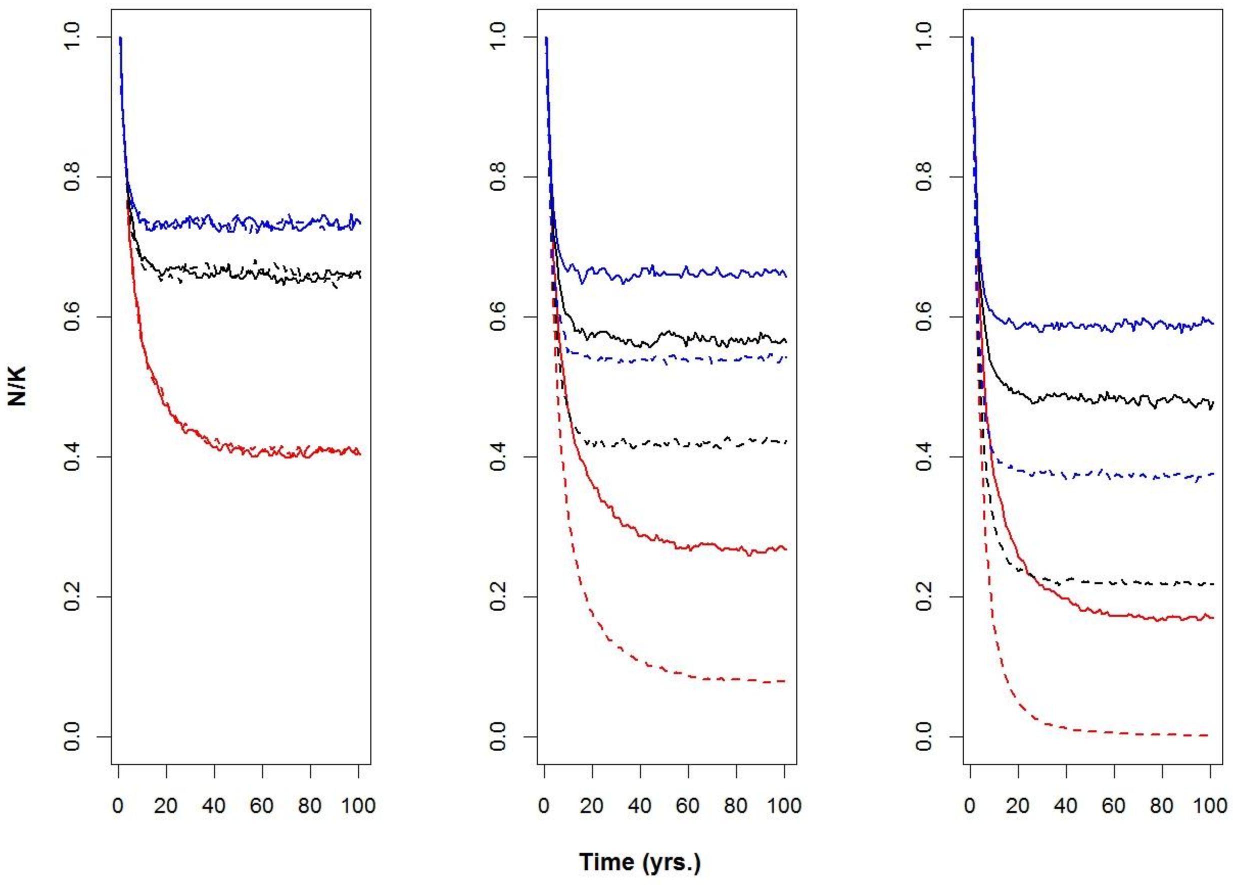


Figure 4.4 (cont’d)
b)

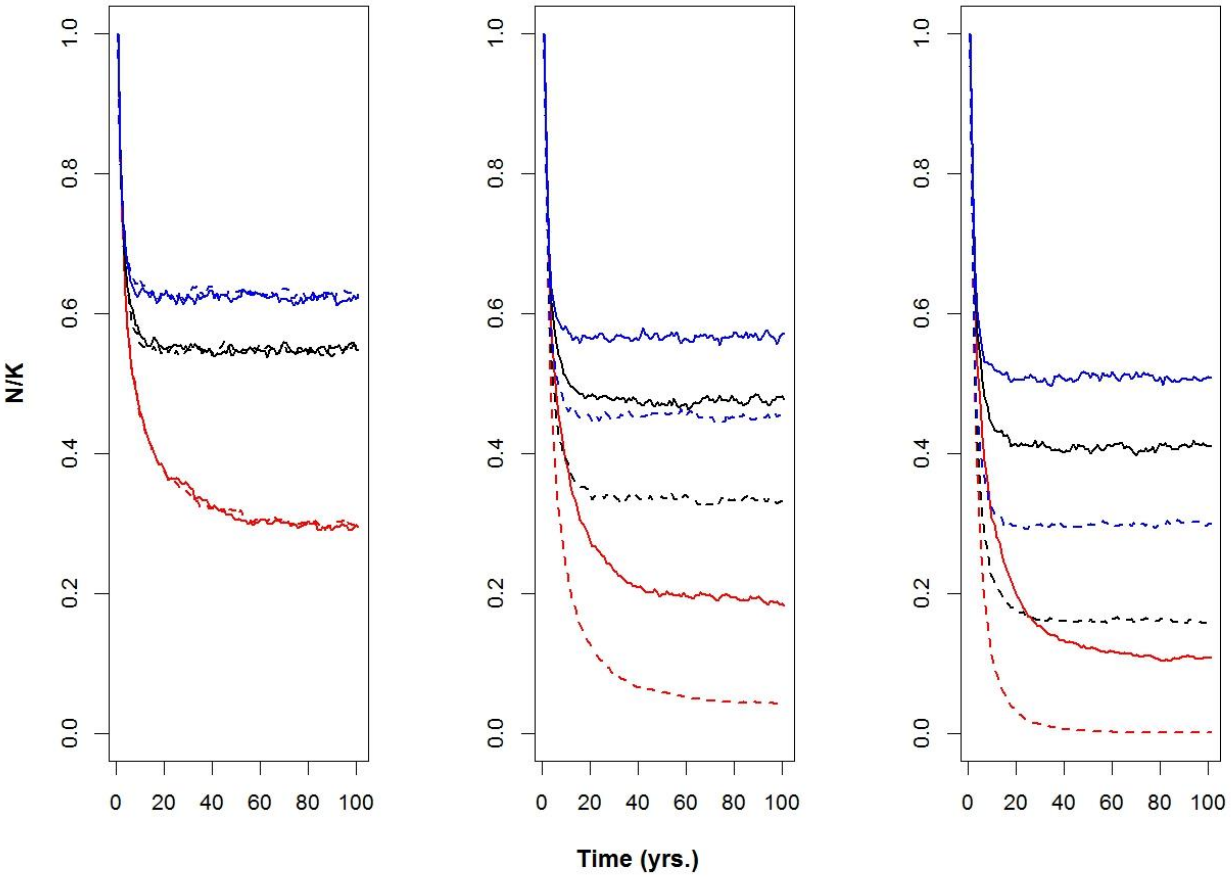
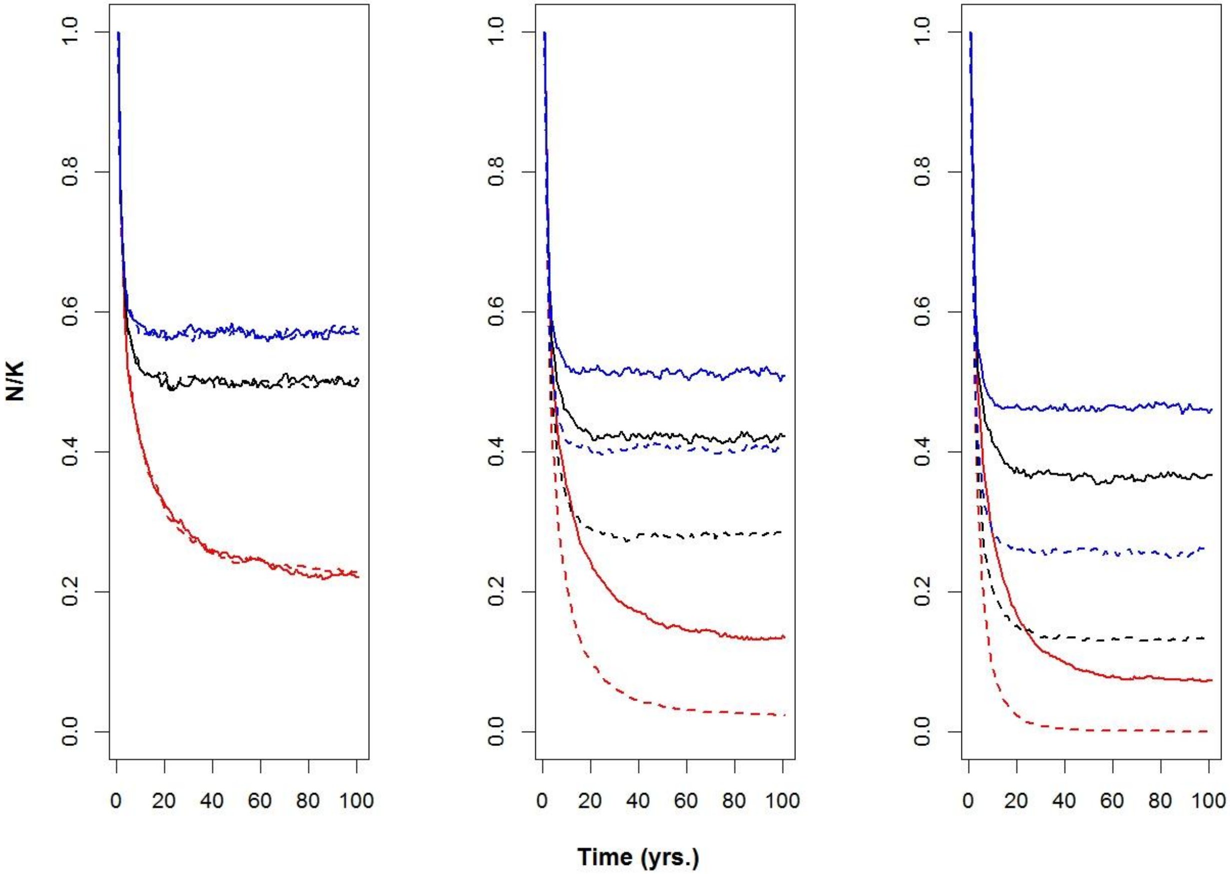


Figure 4.4 (cont'd)
c)



Optimal fall harvest rates in the presence of structural uncertainty, as well as robust fall harvest rates identified as approximately optimal over large regions of the parameter space, were all ≤ 4% of the male segment of the population at the start of fall hunting. Decision analyses conducted using vague stochastic distributions for productivity and vulnerability identified optimal fall harvest rates in the absence of estimates for these parameters as 4%, 2%, and 1% of fall populations for low, medium, and high levels of spring gobbler harvest, respectively. Robust fall harvest rates identified as approximately optimal (i.e., relative expected utility > threshold defining approximate optimality) over the largest region of parameter space were all ≤ 4% of the fall population, and within spring harvest scenarios these values were relatively insensitive to changes in the threshold used to define approximate optimality (Table 4.1). When spring harvests were low, approximately optimal fall harvest rates over broad ranges of productivity and vulnerability was 3–4% of the male segment of the population during fall; this range was reduced to 1–2% for scenarios with larger spring harvests (Table 4.1). The relative performance of 5% fall harvest rates (previously recommended lower bound of sustainable harvests; Healy and Powell 2000) was approximately optimal over most of the parameter space when spring harvest was low, but was approximately optimal under a much smaller range of conditions as spring harvest increased (Table 4.2). Importantly, the general patterns identified with my analyses were insensitive to magnitude and form of temporal variation in fall harvest rates (Appendix F). Thus my results appear to generally be robust to the magnitude and form of implementation uncertainty. Lastly, changing the location of the utility threshold resulted in small but subtle shifts in optimal fall harvest rates, and changing to a linear decrease in utility of fall harvests increased optimal fall harvest rates by 3 percentage points for each spring harvest scenario (Appendix F).

Table 4.1 Fall harvest rates (expressed as percentages of the male population) identified as approximately optimal over the largest regions of parameter space, for different magnitudes of spring harvest and different minimum values (Thresholds) of relative expected utility that were used to define approximate optimality.

	Threshold[b]				
Spring harvest[a]	0.75	0.80	0.85	0.90	0.95
Low	3	3	3	4	4
Medium	0	0	0	1	2
High	0	0	0	0	1

[a] Median spring harvests were 15% (low), 30% (Medium), and 40% (High) of the population of males alive at the start of spring hunting (Appendix D)

[b] Threshold is the value of relative expected utility used to define approximately optimal fall harvest rates, where a harvest rates was approximately optimal for a specific set of input parameters if expected utility for that harvest divided by expected utility for the optimal harvest rate (for the same set of parameters) was > threshold.

Table 4.2 Proportion of the parameter space where harvesting of 5% of the male population during fall was approximately optimal, over scenarios that represented uncertainty in wild turkey population and harvest dynamics.

	Threshold[b]				
Spring harvest[a]	0.75	0.80	0.85	0.90	0.95
Low	0.90	0.86	0.8	0.70	0.54
Medium	0.82	0.76	0.66	0.55	0.40
High	0.78	0.68	0.57	0.42	0.23

[a] Median spring harvests were 15% (low), 30% (Medium), and 40% (High) of the population of males alive at the start of spring hunting (Appendix D)

[b] Threshold is the value of relative expected utility used to define approximately optimal fall harvest rates, where a harvest rates was approximately optimal for a specific set of input parameters if expected utility for that harvest divided by expected utility for the optimal harvest rate (for the same set of parameters) was > threshold.

DISCUSSION

Target Reference Points for Management of Fall Wild Turkey Harvests

Structural uncertainty in parameters of population and harvest models has strong implications for the management of modern fall turkey harvests. Despite a rich history of field research and demographic studies, the current status and demography of many turkey populations is uncertain. Management agencies face this uncertainty in a time of declining budgets, and where the perceived need for continued research has waned due to past restoration successes (Healy 2011, Porter et al. 2011). However, my results imply the current paradigm of developing reference harvest rate targets for fall harvest management using models with unique sets of parameters estimated over relatively small spatial-temporal scales, or by reviewing results of multiple such studies (e.g., Healy and Powell 2000), has not produced indicators of performance that are robust to existing uncertainties about population and harvest dynamics. I demonstrate that all three processes for which I considered structural uncertainty govern the optimal harvest rates (productivity, vulnerability, spring harvest), and productivity and vulnerability interact to determine appropriate harvest rates. Thus, recommended harvest rates from earlier studies (5–10%; Healy and Powell 2000) may only be optimal for accomplishing modern management objectives over a narrow range of the plausible parameter space for turkeys. This is likely because previous studies evaluated management performance over very narrow slices of the plausible parameter space for turkey population and harvest dynamics (chapter 3), but also likely due in part to the subtle shifts in management objectives assumed by this study. In addition, spring harvests have also been liberalized in many areas (Healy and Powell 2000), and the subsequent implications for managing fall harvests were not fully described by earlier studies. My results demonstrate that increased magnitude of spring harvest drives optimal fall harvests to lower values when management seeks to maintain large turkey populations through time. Thus, previous management recommendations developed from studies of populations with different demographic and harvest parameters than currently exist cannot be assumed to accomplish turkey management objectives in the modern era.

My results demonstrate proportional harvest rates that were previously recommended may be too large to accomplish modern population objectives when structural uncertainty is formally acknowledged. After review of the turkey management literature, Healy and Powell (2000) recommended harvests of 5–10% to sustain turkey populations under worst-case conditions (i.e., low recruitment). Both my static decision analyses and my assessment of robust, approximately optimal harvest rates suggest that fall harvests < 5% may be more likely to achieve management objectives that were considered in this study, but that specific target reference points should change with the magnitude of spring harvest. These results illustrate two important points. First, when a broader and more plausible range of demographic parameters is considered, and uncertainty about their values formally acknowledged, the appropriate target harvest rates became more conservative than recommendations provided by modeling studies that used a unique set of input parameters. Second, the amount of information available to local turkey managers will determine the appropriate target harvest rates that are likely to perform adequately in the face of uncertainty. In the absence of reliable information about productivity, vulnerability, and the magnitude of spring harvests, my results imply 4% harvest should be viewed as the upper value of male harvest during fall that is likely to achieve management objectives consistent with those assumed in this study. Moreover, if spring harvest regulations are liberal, then a 1–2% harvest of males during fall hunting should be viewed as indicative of successful management. If reliable estimates of productivity and vulnerability are available to local managers, however, then target harvest rates that are tailored to local populations can be identified using my results. Thus, target harvest rates that are likely to meet a specific set of turkey management objectives may vary through space, and depend on the amount of uncertainty about demography and harvesting of local populations.

Specific recommendations of this study condition on a utility function that may not reflect management objectives in all areas. Turkey management objectives themselves likely vary through space and time with the values and perceptions of both local management agencies and local stakeholder groups. Indeed, discrepancies of my results with recommendations by earlier studies (Healy and Powell 2000, McGhee et al. 2008) may be partly related to subtle differences in the assumed objectives (e.g., maximizing annual harvest vs. maintaining large populations), in addition to differences in the range of model parameter space considered. For instance, my results implied that target harvest rates larger than the reference points I suggest may in fact be biologically sustainable under plausible conditions, but nonetheless may not sustain both populations and their harvests at desirably large levels. In addition, my sensitivity analyses demonstrated that if managers are less risk averse and more interested in large harvests, then fall harvest rates larger than 4% can likely be sustained at the expense of smaller populations. Importantly, my analyses can be easily replicated using different utility functions that portray objectives of local management if they differ than those considered in this study, and structured decision making provides a natural framework for such replication.

Developing Harvest Reference Points for Assessment-Limited Populations through Structured Decision Making

A primary goal of reference point development in harvest management is to ensure simplified metrics are indicative of management performance that achieves underlying sustainable-harvest objectives (Irwin and Conroy 2013). Reference points have been most formally used in fisheries management, but their use has been advocated as applicable to a wide range of problems in resource management (MacNeil 2013). Historically, fishery management reference points were developed as general exploitation rates to serve as targets or decision thresholds that were not tailored to individual populations or local objectives (Clark 1991, Mace 1994, Quinn and Collie 2005). Such use of reference points was subsequently criticized because performance of general, reference-point based decision rules was often erroneously assumed to be robust across dynamics of individual stocks, species, or ecosystems (Hilborn 2002, Hilborn et al. 2002). As demonstrated by the case study, parameters of population and harvest models can interact to determine optimal harvest strategies. Thus, evaluation of harvest policies using reference points should ideally be made on case-by case-basis, focusing on performance relative to local dynamics and objectives (Hilborn 2002, Hilborn et al. 2002, Deroba and Bence 2008). More generally, I demonstrate that development of reference points for assessment-limited terrestrial populations can provide targets to guide management in the face of limited data and uncertain system dynamics. This study and others (Hilborn 2002, Hilborn et al. 2002, Deroba and Bence 2008) suggest development of reference points to guide harvests of assessment-limited populations should consider performance of such management in the face of realistic uncertainties about system dynamics experienced locally.

Structured decision making and decision-analytic methods provide a natural conceptual and quantitative framework for developing harvest reference points in the face of uncertainty (Shae et al. 1998, Irwin et al. 2011). Reference points are not just scientific metrics indicating sustainability of harvests based on species biology. Rather, their interpretation and evaluation depends on what management is trying to accomplish, the existing sources of uncertainty, and the sensitivity of results to underlying assumptions about system models. These general attributes are also shared with evaluation of decision alternatives using decision-analytic methods (Shae et al. 1998, Peterman and Peters 1999, Clemen and Reilly 2001). Thus, a logical approach to developing useful reference points is to first clarify sustainable-harvest objectives and then evaluate a suite of potential reference points in the presence of realistic uncertainties. I demonstrated this process to identify target harvest rates to guide fall harvest management for wild turkeys, but the approach could also be used with alternatives other than harvest rate (e.g., total harvest or quota). Irrespective of the specific decision alternatives compared, structured decision making is a useful framework for structuring the harvest problem, building tradeoffs into the development and evaluation of reference points, and ensuring the resulting metrics are meaningful indicators of performance for sustainable harvest management.

Decision structuring provides a framework that facilitates deliberation about objectives, management options, and likely outcomes of each option, all of which are components of good decision making (Hammond et al. 1999, Clemen and Reilly 2001). Clarification of objectives permits quantitative evaluation of a set of potential reference points in the presence of uncertainty, ensuring their usefulness as performance indicators (Hilborn 2002, Irwin and Conroy 2013). The approach I demonstrate thus facilitates unambiguous interpretation of harvest rates with respect to successful long-term management that considers the societal desire to both harvest and maintain terrestrial wildlife populations. As such, clarification of objectives requires subjective identification of desirable outcomes, which reflect value judgements of managers and management stakeholders (Runge and Walshe 2014, Nichols et al. 2014). Such clarification of objectives is not a simple task, but can be aided by open dialogue with stakeholder groups and managers (Johnson and Case 2000, Irwin et al. 2011, Runge and Walshe 2014).

In my general approach and case study I clarified objectives by combining management performance measures into a single composite utility function that described how outcomes of different target harvest rates are valued. More generally, however, summarizing objectives into a single utility function can be challenging when there are multiple stakeholder groups with diverse sets of values (Johnson and Case 2000, Johnson et al. 2015), and may not be possible for contentious harvest management problems (Bence et al. 2008). If stakeholders and managers cannot agree on how to combine performance measures into a single utility function because they value management outcomes differently, then distributions of performance measures can be directly compared under different harvest strategies and the merits of each strategy debated until conflicts are resolved and consensus is reached (Bence et al. 2008, Irwin et al. 2011). This approach would make aspects of my analysis challenging (e.g., identification of decision thresholds) because a clearly defined optimal harvest rate would be absent. However, such an approach could still be useful for developing target harvest rates with robust performance under uncertainty.

After objectives are sufficiently clear, decision-analytic tools enable quantitative assessment of performance for a suite of potential reference points in the presence of uncertainty. When using decision analysis to evaluate performance, predictions of performance metrics from individual models with unique parameter values effectively get translated into weighted average predictions across the model set (see also Johnson et al. 1997). In my example the weights were determined by continuous distributions placed on individual model parameters. Here I chose uniform distributions to reflect a management scenario with no recent or reliable data about the values of productivity and vulnerability parameters for a given population of wild turkeys. Because of the flat shape and symmetry of the assumed uniform distributions about their expectations, the resulting optimal fall harvest rates were effectively pulled toward those that are optimal near the center of the range of productivity and vulnerability parameters considered. This would not necessarily be the case if different stochastic distributions were assumed for model parameters. More generally, distributions used to represent uncertain parameters can be refined with local data (Haeseker et al. 2007) or generated using expert opinion (Runge et al. 2011), and paired with simulation and optimization to identify reference points for population management in the face of uncertainty.

Development of reference points by evaluation of static policies provides a framework to inform harvest management for populations lacking the monitoring and assessment infrastructure needed to apply current state-of-the art approaches to harvest management. My example showed that target harvest rates can be developed in the absence of information needed to determine optimal state-dependent decisions (e.g., Martin et al. 2009, Marescot et al. 2013) or employ robust state-dependent harvest control rules (e.g., Punt et al. 2006, Bence et al. 2008, Deroba and Bence 2008). I also demonstrated that thresholds in optimal static decisions can be identified as a function of structural parameters for which decision makers are uncertain, which is a step in the right direction for management of populations lacking the information needed to identify decision thresholds dynamically. Moreover, fixed harvest-rate policies can perform comparably to optimal policies identified using dynamic programming (Parma 1990, Walters and Parma 1996). For instance, Walters and Parma (1996) demonstrated that fixed exploitation-rate strategies achieved a relative performance ≥ 80% of the optimal policy, and this performance held over changing environmental conditions and a variety of iteroparous life-history strategies. Parma (1990) reported similar relative performance of static and dynamic harvest policies, and also reported reduced temporal variation of harvests for fixed-exploitation rate policies. Lastly, Milner-Gulland et al. (2001) reported that harvesting a small, fixed fraction of the population was among the most robust of a suite of harvest strategies considered for saiga antelope. Therefore I suggest there is considerable value to employing static decision analyses to provide guidance for harvest management in the absence of rigorous population assessment frameworks.

Replication of my general approach for developing harvest rate reference points requires development of explicit models for dynamics of populations and harvests, which may be challenging for some assessment-limited populations. However, some form of modeling is inevitable when quantitatively assessing performance of management and conservation actions, as models are a fundamental component of decision making (Nichols and Williams 2006, Lyons et al. 2008, Irwin et al. 2011). Even if mathematical system models are not developed explicitly, decision makers use implicit mental models of dynamics to generate expected outcomes of management actions (i.e., expected ability of decision alternatives to achieve sustainable-harvest objectives). Such mental modeling lacks clear assumptions about, and transparent links between, the decisions that are made and the expected outcomes of those decisions. As my case study demonstrates, use of SDM to develop harvest targets for data-limited populations will likely require more general, production-type population models (Hilborn and Walters 1992) that are adapted to specific life-history characteristics believed to be similar to the species of interest (Williams 2013; this study). Important considerations that will affect harvest reference points developed in this manner include the form and strength of density dependence operating through survival and recruitment processes (Walters 1975, Mace 1994, Runge and Johnson 2002), as well as the assumed risk preferences of decision makers and stakeholders (and hence the specific utility function used; Parma 1990).

The decision-analytic approach provides a framework to identify harvest rates that are indicators of management performance, but implementing such harvest policies in assessment-limited environments may also prove challenging. Target reference points can serve either as specific targets that management is attempting to achieve, or as indicators of harvest that are inconsistent with management objectives and thus should be avoided (Irwin and Conroy 2013).

If harvest rates serve as specific targets that managers are trying to actively achieve, then management control would need to be able to change the expected harvest rates experienced by the population being managed. In the past such implementation has often involved direct estimation of abundance, where total-allowable catch is set by multiplying harvest rates by the abundance estimate (Hilborn 2002, Hilborn et al. 2002). This is obviously not possible if abundance is not estimated, and thus managers would need to employ constant effort strategies (Ludwig 2001) but be cognizant that catchability, and thus the fraction of the population harvested, can systematically shift over time (Maunder et al. 2006). In assessment-limited environments it is perhaps more likely that reference points would be used to indicate harvest rates that should be avoided (e.g., > 5% fall harvest in my example). In this case, harvest rates could be estimated regularly or periodically via surveillance monitoring to ensure harvest is not exceeding levels consistent with objectives (e.g., using telemetry or tagging data), which would be easier than developing large-scale monitoring programs for the purposes of estimating abundance. I consider this to be a step forward from the current status quo where harvesting of many wildlife populations is monitored using ambiguous metrics whose performance has not been rigorously demonstrated (Weinbaum et al. 2013). However, a limitation still remains whereby knowledge that harvest rates have exceeded targets does not indicate specifically how management tactics should change to reduce harvest to a level that will accomplish management objectives (Nichols and Williams 2006).

Lastly, the approach described can also be viewed as a formalized set of tools for the set-up phase of adaptive management programs aimed at reducing structural uncertainty over time (Lahoz-Monfort et al. 2014, Williams and Brown 2015). The value of adaptive approaches is described extensively elsewhere (Walters 1986, Lancia et al. 1996, Nichols et al. 2007, Williams and Brown 2015), but such approaches require targeted monitoring for decision making and learning about population responses to harvest (Williams and Johnson 1995, Nichols and Williams 2006). The set-up phase of adaptive management requires all of the decision structuring elements I describe, as well as the development and evaluation of preliminary models to represent hypothesized system dynamics (Lahoz-Monfort et al. 2014). The process of decision structuring and preliminary model development can also aide development of monitoring programs by informing which data to collect and system states to monitor (Lyons et al. 2008). Ideally then, use of static target reference points as developed here would not be needed indefinitely, but could provide useful information to guide management during the development of monitoring and assessment programs that link estimation of system states to specific decision processes. Such developments would go a long way towards ameliorating the existing need for a stronger, evidence-based approach to management of many species (Sutherland et al. 2004, Cook et al. 2010).

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CHAPTER 5: CONCLUSIONS, MANAGEMENT IMPLICATIONS, AND FUTURE DIRECTIONS

In chapter 1 I posed 3 questions about turkey harvest management that this research sought to answer: 1) How reliable are recently recommended strategies for maximizing turkey harvests to existing structural uncertainties in the form of both population and harvest models? 2) Are existing fall harvest recommendations robust to structural uncertainty? 3) Can I develop reliable harvest recommendations that are indicative of satisfactory management performance relative to modern objectives in the face of structural uncertainty? Here I briefly review the answers to these questions and the subsequent implications for management of turkey harvests in the post-restoration era. I also discuss this work in light of state-dependent decision frameworks presented in chapter 1, and the implications for development of adaptive harvest management programs that reduce structural uncertainty over time through learning.

Chapter 2 sought to determine if recently recommended strategies for maximizing turkey harvests are robust to uncertain aspects of population and their harvest dynamics. Analyses of chapter 2 demonstrate that combined spring-fall proportional harvests needed to achieve maximum turkey harvests are highly sensitive to aspects of turkey demography and harvest that are poorly understood. For example, harvest rates that would achieve maximum annual harvest (combined spring and fall) or maximum either-sex fall harvest are not robust across plausible models. Thus, proportional harvesting is an unreliable approach to maximizing annual or fall harvest of turkeys, as the target proportional harvests depend on processes that are not fully understood, such as the mechanisms underlying density dependence. In contrast, proportional harvests that maximize male-only harvest during spring (all males or adults only) do not appear to be sensitive to uncertainty surrounding the most appropriate form of density dependence. However, if managers seek to maximize spring harvest while also maintaining a desired number of adult males in the population, then information about differential harvest vulnerability between adults and juveniles during spring hunting seasons is needed. This information is available in some regions (e.g., Diefenbach et al. 2012), but is lacking in many others. Thus designing regulations to achieve maximum harvests of adult male turkeys during spring also appears unrealistic at present. Moreover, maximization of spring harvests would likely require a policy shift to management that stops harvesting turkeys in the fall, which appears inconsistent with management objectives related to maintaining hunter opportunity. Thus, chapter 2 also demonstrates the importance of clarifying fundamental objectives of management, as policy approaches needed to achieve different objectives will likely vary with objectives themselves.

Chapter 3 sought to determine if existing recommendations for management of fall harvests are robust to the value of demographic parameters related to recruitment and harvest mortality that are often uncertain for regional management. My results demonstrate that existing recommendations are not robust to changes in parameter values that are often uncertain in contemporary management, and thus currently accepted guidelines may not achieve modern objectives over a broad range of conditions. Turkey managers should thus expect the magnitude of risks to populations and the tradeoffs between harvest and abundance to change through space and time with systematic changes to demography. The causes of modern recruitment declines, in particular, will likely have a strong bearing on risks posed by fall harvests, and directly affect the magnitude of fall harvest a population can withstand. Importantly, 9% fall harvests recommended for maximizing annual harvest (McGhee et al. 2008) appeared risky for all scenarios but those representing the most productive turkey populations, and 5-10% fall harvests recommended as sustainable under worst case conditions (Healy and Powell 2000) did not have robust performance under conditions of consistently poor productivity or high hen poaching. More generally this work makes evident the need to either tailor fall harvest strategies to characteristics of local populations, or identify harvest strategies with adequate performance in the face of uncertainty for populations lacking detailed demographic data.

Chapter 4 sought to develop recommendations for managing fall harvests that are indicative of satisfactory performance in the face of existing uncertainties. Results of chapter 4 demonstrate that fall harvests recommended by earlier studies may only be optimal for accomplishing modern management objectives over a narrow range of the plausible parameter space for turkeys. Specifically, target fall harvests < 5% are more likely to achieve management objectives across a broad range of demographic and harvest parameter values than harvests ≥ 5%. However, the specific target should change with the magnitude of spring harvest, and may also change with different population objectives. If information about neither productivity, relative harvest vulnerability (between males and females), or the magnitude of spring harvests (fraction of male population harvested) are available to managers, then 4% fall harvest of males should be viewed as the upper value that is likely to achieve modern management objectives. If spring harvest regulations are liberal but information on productivity and relative harvest vulnerability are unavailable, then 1-2% harvest of males during fall hunting should be viewed as indicative of successful management for the objectives considered in this study. Inclusion of a broader range of values for demographic and harvest parameters, and uncertainty about the specific values of these parameters locally (i.e., reflective of conditions faced for management of data-limited populations) thus resulted in the need for more conservative harvesting than has been suggested by earlier studies. Moreover, this work demonstrated that appropriate harvest targets should depend on the amount and precision of information available to decision makers at a local level. However, my specific recommendations are conditional on my assumption that management objectives were to maximize cumulative spring harvest while maintaining turkey populations at large, socially desirable levels (defined as > half of number of turkeys the habitat can support), and to provide additional opportunities for fall harvest so long as it does not drive populations to undesirable levels in the short term (and thus negatively impact the quality of spring hunting). If specific population and harvest objectives of local management differ from these, the decision-analytic framework I described in chapter 4 can easily be replicated with a different objective function. As such, the methods of chapter 4 could be used to generate recommended target fall harvest rates in the presence of uncertainty for other realistic sets of objectives used in modern turkey management.

This dissertation can be viewed as one step moving turkey harvest management closer to a rigorous decision-analytic approach that is consistent with current state-of-the art frameworks for harvest management under uncertainty. My analyses culminated in a static decision analysis (chapter 4) that was used to develop target fall harvests to be used in the absence of detailed demographic data and annual population estimates. The results of such analyses can be used to guide harvest management during the process of developing state-dependent decision frameworks that are tailored to local conditions and available data (e.g., during the set-up, or deliberative phase of adaptive management; Lahoz-Monfort et al. 2014, Williams and Brown 2015). When tailored to local data, population dynamics, and management processes (e.g., regulation cycle lengths), performance of state-dependent harvest strategies can be quantitatively tested to ensure they are likely to meet management objectives for a variety of plausible conditions (Butterworth and Punt 1999, Punt 2006, Deroba and Bence 2008). Alternatively, optimal regulatory packages could also be identified iteratively over time as a function of changing abundance using dynamic decision analyses (Nichols et al. 1995, Johnson et al. 1997, Nichols et al. 2007). Moreover, both approaches could be implemented in an adaptive framework that updates dynamic forecasting models over time as more is learned about dynamics of turkey populations and their harvests (Fig. 1.2).

Despite the appeal of developing scientifically tested state-dependent harvest strategies, a quick review of published harvest models (Table 1.1) suggests there are disconnects between the science of turkey harvest management and the actual practices of management. Most management agencies already update turkey hunting regulations at regular intervals, yet the emphasis of nearly all modeling studies was on evaluation of static policies that do not update target harvests regularly as new information is gained. Evaluation of static policies has provided general recommendations for sustainable harvests that appear to have been used more like management reference points that indicate an upper bound to acceptable fall harvest mortality (see chapter 4 and Irwin and Conroy [2013] for more discussion of reference points). However, I demonstrated that commonly accepted reference points are not robust to existing uncertainties (chapters 3 & 4), and I am not aware of any quantitatively-tested decision rules that specify how regulations should be manipulated if harvests exceed existing reference points. Indeed, it is generally unclear how to manipulate specific regulations to harvest a desired fraction of a turkey population (Kurzejeski and Vangilder 1992, Healy and Powell 2000). In the one published occasion that I am aware of where state-dependent harvest strategies were tested via simulation (McGhee and Berkson 2011), important sources of uncertainty were not included (e.g., structural and observation uncertainty), and thus robustness of performance was not adequately demonstrated in a manner that would suggest general applicability of the tested harvest strategies. More common, however, has been to describe decision rules for managing turkeys but never actually test their performance under uncertainty (e.g., Healy and Powell 2000, Kimmel 2001, and Bellamy and Pollard 2007). It is possible that the impetus for a tighter linkage between management practices and scientific models is now being realized more acutely because of slowed population growth, increased hunter demand, and declining recruitment. Regardless, application of dynamic harvest policies will require reduction of existing disconnects between management models and the actual practices of harvest regulation.

Development of scientifically tested, state-dependent harvest policies also faces the challenge of realistically portraying uncertainties in turkey management models. Evaluation of harvest policies requires careful representation of uncertainties, many of which have not been emphasized in turkey harvest models. Only a few studies have included implementation uncertainty that describes realized variation in harvests resulting from a set of management regulations, and inclusion of observation uncertainty is basically nonexistent. Ideally the stochastic distributions used to describe uncertainties should be estimated using data from real populations in the region of interest so that models can accurately portray outcomes of local management. For example, tailoring the distributions of harvest rates to local management would require estimating realized harvest rates that result from a set of hunting regulations (e.g., using marked animals; Diefenbach et al. 2012), as well as the variation of these harvests through time (and possibly space). Yet when the links between monitoring data, predicted outcomes of management decisions (e.g., responses of populations), and decision making are not made explicit, it becomes challenging to design models that realistically portray performance of management. If one is trying to design a robust harvest policy using simulation, for example, it is unclear how to represent common uncertainties when there are no formal population assessments and no decision rules that specify how monitoring data are used to adjust harvest regulations with new information. In this case it becomes difficult to adequately represent both observation and implementation uncertainty, because the relationship between monitoring data and the population state of interest (i.e., abundance) is unknown, and it is not clear how regulations should be adjusted to achieve specific changes in expected harvest rates. Similarly, if abundance is not actually estimated it becomes difficult to employ dynamic approaches that seek to update optimal harvest regulations over time as population size changes. More careful linkage of existing monitoring data, population assessment, and decision-making processes are therefore needed if managers hope to develop rigorous state-dependent strategies for turkey management.

Assuming the aforementioned challenges can be addressed effectively, adaptive harvest management provides an ideal pathway for reducing uncertainty and refining harvest policies over time through learning. It has been previously suggested that adaptive management is a common practice more generally in turkey management (Porter et al. 2011). However, this does not appear to be the typical case for management of turkey harvests. A primary emphasis of adaptive management is on reducing structural uncertainty over time through monitoring the responses of populations to management actions (Walters 1986, Nichols et al. 2007, Allen et al. 2011, Irwin and Conroy 2013), yet the existence of structural uncertainty has rarely even been acknowledged formally in turkey harvest models. Claims of application of adaptive management that lack the original intent of reducing key uncertainties via learning appear to be common in natural resource management (Allen et al. 2011). An obvious exception in turkey management, however, was modeling that demonstrated implications of different hypothesized responses of populations to fall harvest (i.e., additive and compensatory harvest mortality; Suchy et al. 1983), which were subsequently evaluated using both observational studies and large-scale management experiments (Little et al. 1990, Pack et al. 1999).

In the context of modern management, my results imply that learning more about harvest processes and causes of recruitment declines would directly benefit management. Differential vulnerability to harvest among different segments of the population will have a direct bearing on the ability of management to optimize spring harvests subject to age-related objectives (chapter 2), as well as the magnitude of fall hunting pressure a turkey population can withstand while also meeting population-maintenance objectives (chapter 4). Such differential vulnerabilities to harvest can be an explicit result of management regulations (e.g., jake-only harvest during spring; Butler et al. 2016), or could be a result of factors outside of management control (e.g., behavior of hunters). Differential vulnerability to harvest may even change through space and time with environmental conditions (e.g., hard mast availability; Norman and Steffen 2003), and thus more information about segment-specific harvest rates resulting from a set of regulations, and the degree to which these vary through space and time is warranted. Fortunately, estimating harvest rates that arise from a set of regulations is straightforward using radiotelemetry and tagging studies conducted at appropriate spatial scales (Diefenbach et al. 2012).

Although estimating differential vulnerability to harvest is straightforward, learning about drivers of recruitment will likely prove much more challenging. There are multiple plausible causal mechanisms underlying modern recruitment declines. A common hypothesis is that increased turkey density has resulted in decreased per-capita recruitment of poults into fall populations (Bond et al. 2012, Byrne et al. 2016, chapter 2), and there are multiple reasonable mechanisms that could result in such a pattern (discussed more in Byrne et al. [2016] and Appendices A–B). However, another potential cause of recruitment declines is large scale changes to conditions of turkey habitats. This could include, as one example, broad-scale changes to age-structure and composition of forests resulting in reduced quantity and/or quality of nesting and brood rearing habitats (e.g., through reduced lateral ground cover, fewer forest openings, etc.), and possibly reduced condition of hens entering the nesting season (e.g., as a result of fewer mast-producing trees; McShea et al. 2007). Changes to the structure of vertebrate communities over time (e.g., increased mesopredator abundance and/or diversity) may have also contributed to reductions in average recruitment for some turkey populations. Of course these hypotheses are not exhaustive or even mutually exclusive; different mechanisms could be operating in different regions, or drivers could be interacting to affect turkey recruitment over a variety of spatial-temporal scales.

Learning about the role of density in turkey recruitment could be facilitated by adaptively managing harvests, but large-scale manipulative experiments will likely be needed. To understand the relationships between turkey density and recruitment at scales relevant to management, recruitment must be measured accurately across a range of densities while also controlling for possible confounding drivers of recruitment (e.g., habitat and predator community changes). Thus, active adaptive management whereby spatially-replicated experiments reduce turkey densities over large scales for the purposes of learning about recruitment dynamics would be the most efficient manner to evaluate support for the density-dependent recruitment hypothesis. Long-term management benefits of learning about population dynamics would come at the cost of short-term reductions to abundance and hunting opportunity in the areas under study, and the relative values of long-term learning and short-term opportunity would need to be evaluated by agencies responsible for management. However, the history of turkey restoration suggests managers are highly successful at restoring locally depleted populations. Thus postexperimentation restoration efforts could be implemented, and potentially even exploited to accelerate learning by studying temporal recruitment trends at spatially replicated study areas as densities are restored.

Passive adaptive management, whereby knowledge accumulates over time in the absence of explicit experimentation (Walters and Holling 1990) would likely result in much slower learning about relationships between turkey density and recruitment. This slower rate of learning would result because necessary observations over a range of turkey densities would rely on natural population fluctuations. As such, the range of densities observed could in principle never approach the range of densities needed to adequately understand recruitment dynamics. Thus, this approach may fail to realize the long-term benefits of learning that characterize adaptive management, but would also not face the short-term management costs of reduced densities and hunting opportunities, and therefore may be more palatable to management stakeholders.

Regardless of the desire of agencies to implement adaptive harvest management, turkey management is unlikely to reliably learn about the role of densities in population dynamics, and therefore the true risks of fall harvest, without the ability to estimate turkey abundance more accurately. Accurate estimation of abundance is a necessary component of reliably characterizing population responses to reduced density, and measurement error in abundance estimates makes statistical estimation of density dependence particularly challenging (Walters and Ludwig 1981, Shenk et al. 1998, Lebreton et al. 2009). Modern statistical tools needed for assessing density dependence are technically complex, and require simultaneous estimation of both process and measurement error (e.g., using state-space methods; Dennis et al. 2006, Lebreton and Gimenez 2013). Although challenging, such inferences can be strengthened greatly through spatial replication (Dennis et al. 2010), which is also beneficial if explicit experimentation is to be used to learn about the role of density in turkey recruitment. Thus, learning about density-dependent recruitment and developing state-dependent strategies for rigorously managing turkey harvests should not be viewed as mutually exclusive endeavors, as both require similar advancements in the ability to assess turkey populations at management scales. Indeed, development and implementation of adaptive harvest management programs for wild turkeys will require a more explicit linkage of the data used to monitor turkey populations, the statistical assessment of such populations, and the decision-making processes that relate population status to regulation of turkey harvests.

APPENDICES

APPENDIX A: DESCRIPTIONS AND MATHEMATICAL DETAILS OF ALL PRODUCTION MODELS DEVELOPED TO SIMULATE DENSITY-DEPENDENT DYNAMICS 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. I used the following general equation to simulate dynamics under the theta-Ricker model:

$$N_{female,t+1} = N_{female,t}(1-p) \times growth_{f,t} - H_{f,fall,t}$$
$$N_{male,t+1} = N_{male,t} \times growth_{m,t} - H_{m,spring,t} - H_{m,fall,t}$$

where:

$$H_{f,fall,t} = N_{female,t}(1-p) \times growth_{f,t} \times h_{f,fall}$$
$$H_{m,spring,t} = N_{male,t} \times h_{m,spring}$$
$$H_{m,fall,t} = \left[N_{male,t} \times growth_{m,t} - H_{m,spring,t}\right] \times h_{m,fall}.$$
$$p = \text{hen poaching rate}$$
$$h_{i,j} = \text{harvest rate for sex } i \text{ in season } j$$
$$H_{i,j,t} = \text{total harvest for sex } i \text{ in season } j \text{ at time } t.$$

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 (2007a), and was used to simulate harvest dynamics by McGhee et al. (2008) and McGhee and Berkson (2011). The sex-specific growth term in the dynamic model equations (i.e., $growth_{i,t}$) was presented by McGhee et al. (2008) as

$$Growth_{f,t} = e^{r_{f,t}\left(1-\left(\frac{N_{f,t}}{K_f}\right)^{\theta}\right)}$$

$$Growth_{m,t} = e^{r_{m,t}\left(1-\left(\frac{N_{m,t}}{K_m}\right)^{\theta}\right)}$$

where:

$$\theta = \text{nonlinear density dependent feedback parameter} = 0.37$$
$$K_i = \text{environmental carrying capacity for sex } i = 10{,}000$$
$$r_{i,t} = \text{intrinsic rate of increase for sex i at time } t.$$

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 I replaced $\frac{N_{f,t}}{K_f}$ in the female growth equation with $\frac{(1-p)N_{f,t}}{K_f}$, 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 ($r_{i,t}$). 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

$$r_{i,t} = ln\left(\frac{B_t}{2(N_{m,t}+N_{f,t})} + s_i\right),$$

where:

$$s_m = \text{male natural survival rate} = 0.74$$
$$s_f = \text{female natural survival rate} = 0.64$$
$$B_t = \frac{2aN_{m,t}N_{f,t}}{N_{m,t} + \frac{N_{f,t}}{q}} = \text{number of births at time } t$$
$$a = \text{number of female recruits per fertilized hen } = 2.105$$
$$q = \text{parameter accounts for skewed sex ratio effects on fetilization} = 10.$$

The equation for number of births (B_t) 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. 2.2). In the formula for sex-specific per capita rate of increase ($r_{i,t}$), number of births (B_t) 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, I modified the above equations to use sex-specific per capita birth rates:

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

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

$$B_t = \frac{2aN_{m,t}(1-p)N_{f,t}}{N_{m,t} + \frac{(1-p)N_{f,t}}{q}}.$$

All other model equations and parameters values remained unchanged.

Density Dependent Recruitment Models

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

$$N_{female,t+1} = \left[N_{female,t}(1-p) + 0.5R_t - H_{f,fall,t}\right] \times s_f$$
$$N_{male,t+1} = \left[N_{male,t} + 0.5R_t - H_{m,spring,t} - H_{m,fall,t}\right] \times s_m$$

where:

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

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:

$$R_t \ = \ \frac{a(1-p)N_{f,t}}{1 \ + \ b(1-p)N_{f,t}} \ = \ \text{total number of recruits at time } t$$
$$a \ = \ \text{density independent per-capita recruitment at low } N_{f,t}$$
$$b \ = \ s\text{trength of density dependent reductions in recruitment}$$
$$\frac{a}{b} \ = \ \text{maximum number of total recruits produced for population.}$$

I assumed the density independent number of recruits (a) was 3 turkeys per female, whereas I calibrated the density dependence parameter to produce an un-harvested 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:

$$R_t \ = \begin{cases} a(1-p)N_{f,t} & if \ (1-p)N_{f,t} < N_f^* \\ aN_f^* & if \ (1-p)N_{f,t} \geq N_f^* \end{cases}$$
$$a \ = \ \text{density independent recruits per female}$$
$$N_f^* \ = \ \text{threshold female abundance for density dependent production.}$$

I again calibrated the parameter affecting density dependence to produce an un-harvested 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-DENENDENT DYNAMICS OF WILD TURKEYS

General Form of Stage-Structured Models

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

$$N_{juv,f,t+1} \;=\; \left[0.5R_t \;-\; H_{juv,f,fall,t}\right] \times s_{juv,f}$$
$$N_{juv,m,t+1} \;=\; \left[0.5R_t \;-\; H_{juv,m,fall,t}\right] \times s_{juv,m}$$
$$N_{ad,f,t+1} \;=\; \left[(1-p)N_{ad,f,t} \;+\; (1-p)N_{juv,f,t} \;-\; H_{ad,f,fall,t}\right] \times s_{ad,f}$$
$$N_{ad,m,t+1} \;=\; \left[N_{ad,m,t} \;-\; H_{ad,m,spring,t} \;+\; N_{juv,m,t} \;-\; H_{juv,m,spring,t} \;-\; H_{ad,m,fall,t}\right] \times s_{ad,m}$$

where:

$$R_t \;=\; \text{total number of recruits into the fall population at time t}$$
$$s_{l,i} \;=\; \text{natural survival rate } f\text{or stage } l \text{ and sex } i$$
$$H_{l,i,j,t} \;=\; \text{total harvest of stage } l \text{ and sex } i \text{ in season } j \text{ at time } t$$
$$h_{l,i,j} \;=\; \text{proportional harvest rate for stage l and sex } i \text{ in season } j$$
$$H_{juv,i,fall,t} \;=\; 0.5R_t h_{juv,i,fall}$$
$$H_{ad,f,fall,t} \;=\; \left((1-p)N_{ad,f,t} \;+\; (1-p)N_{juv,f,t}\right)h_{ad,f,fall}$$
$$H_{ad,m,spring,t} \;=\; N_{ad,m,t}h_{ad,m,spring}$$
$$H_{juv,m,spring,t} \;=\; N_{juv,m,t}h_{juv,m,spring}$$
$$H_{ad,m,fall,t} \;=\; \left[N_{ad,m,t} \;+\; N_{juv,m,t} \;-\; H_{ad,m,spring,t} \;-\; H_{juv,m,spring,t}\right]h_{ad,m,fall}.$$

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., un-harvested equilibrium abundance) of 20,000 turkeys for consistency, and all models were initiated with 10,000 birds 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.

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

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

$$b = \text{ density dependent feedback parameter} = 0.0001579$$

$$\frac{a}{b} = \text{ maximum number of total recruits produced for population}$$

$$N_{f,t} = (1-p)N_{ad,f,t} + (1-p)N_{juv,f,t} = \text{total number of hens at time } t.$$

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 (Table 2.2). Thus, my 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:

$$f_l = \text{ nesting rate for stage } l$$

$$Nest_t = f_{juv}(1-p)N_{juv,f,t} + f_{ad}(1-p)N_{ad,f,t} = \text{ total number of nests at time } t$$

$$R_t = \frac{aNest_t}{1 + bNest_t}$$

$$a = \text{density independent number of recruits per initiated nest} = 3$$

$$b = \text{density dependent feedback parameter} = 0.0001204$$

$$\frac{a}{b} = \text{maximum number of total recruits produced for population.}$$

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 were thresholds of hen density above which density-dependent predation of nests or broods commenced:

$$R_t = \begin{cases} aN_{f,t} & if\ N_{f,t} < N_f^* \\ aN_f^* & if\ N_{f,t} \geq N_f^* \end{cases}$$

$$N_{f,t} = (1-p)N_{ad,f,t} + (1-p)N_{juv,f,t}$$

$$a = \text{density independent number of recruits per female} = 3$$

$$N_f^* = \text{threshold female abundance for density-dependent recruitment} = 3307.76.$$

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:

$$f_l = \text{nesting rate of stage } l$$

$$Nest_t \;=\; f_{juv}(1-p)N_{juv,f,t} \;+\; f_{ad}(1-p)N_{ad,f,t} \;=\; \text{total number of nests at time } t$$
$$Nest^* \;=\; \text{threshold nest abundance for density dependent recruitment} \;=\; 3307.76$$
$$R_t \;=\; \begin{cases} aNest_t & if\ Nest_t < Nest^* \\ aNest^* & if\ Nest_t \geq Nest^* \end{cases}$$
$$a \;=\; \text{density independent number of recruits produced per initiated nest} \;=\; 3.$$

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 gobbler segment of the population for the corresponding season following Vangilder and Kurzejeski (1995):

$$h_{juv,m,spring} \;=\; 0.5h_{ad,m,spring}$$
$$h_{juv,m,fall} \;=\; 2.33h_{ad,m,fall}$$
$$h_{juv,f,fall} \;=\; 2h_{ad,m,fall}$$
$$h_{ad,f,fall} \;=\; 1.33h_{ad,m,fall}.$$

APPENDIX C: SUPPLEMENTARY RESULTS FOR CHAPTER 3

Figure C.1 Examples of simulated distributions of spring harvest rates used to represent implementation uncertainty in wild turkey harvest models. Plots show empirical frequency distributions for 10,000 replications of realized harvest rates for the low (median = 0.15), medium (median = 0.3), and high (median = 0.4) spring gobbler harvest scenarios. Although very unlikely at assumed parameter values, any simulated harvest rate > 1 was set to equal 1. Additional mathematical details about stochastic distributions can be found in Table 3.1.

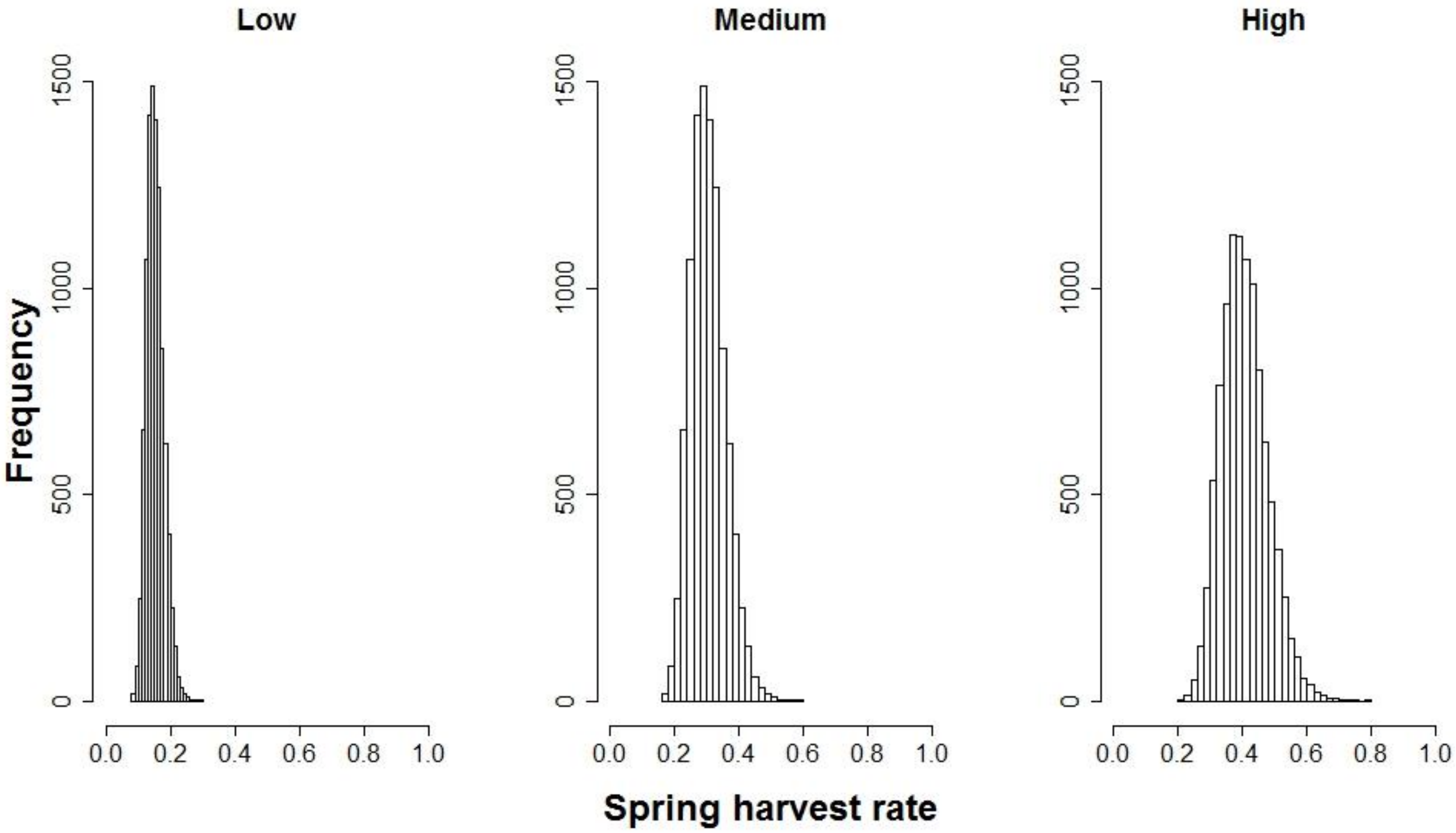


Figure C.2 Examples of simulated distributions of hen poaching rates used to represent implementation uncertainty in wild turkey harvest models. Plots show empirical distributions for 10,000 replications of realized harvest rates for low (median = 0.05) and high (median = 0.15) poaching scenarios. Although very unlikely at assumed parameter values, any simulated harvest rate > 1 was set equal to 1. Low poaching scenarios were intended to produce hen poaching rates similar to those simulated by previous harvest modeling studies (e.g., McGhee et al. 2008). High poaching rate scenarios were intended to approximate the distribution of the highest hen poaching rates recorded for a study area that I discovered in the turkey literature (i.e., Area 1-2 from Table 2 of Norman et al. [2007]). Additional mathematical details can be found in Table 3.1.

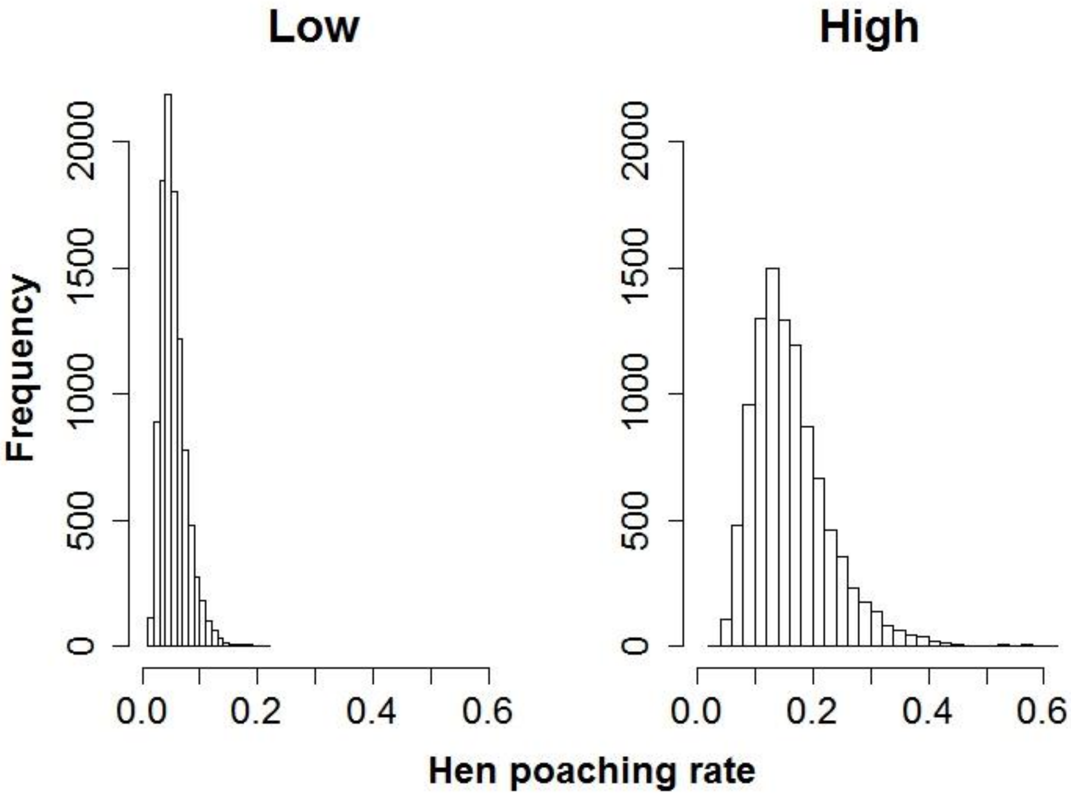
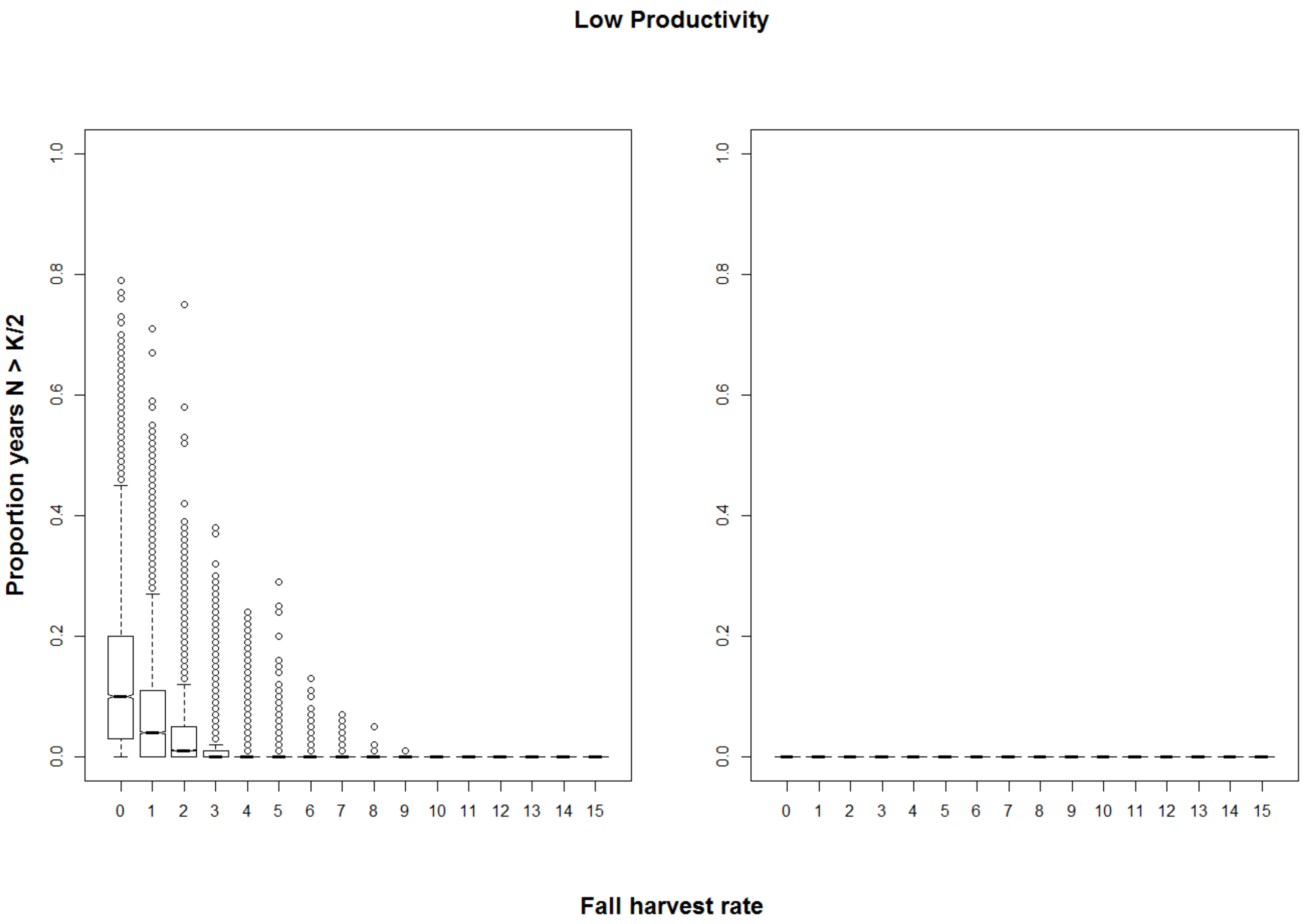


Figure C.3 Evaluation of population risks for target fall harvest rates of 0–15% across changing demographic scenarios for simulated wild turkey populations assuming no structural uncertainty in density-dependent population dynamics ($\theta = 0.36$). Scenarios represent combinations of low (a; k = 0.775), 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 hen poaching during the spring hunting season, at medium spring gobbler 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, boxplot notches represent an approximate 95% confidence intervals for medians ($\pm 1.58 * \frac{IQR}{\sqrt{n}}$; Chambers et al. 1983), and boxplot whiskers delineate IQR boundaries values $\pm$1.5×IQR. Individual points represent simulated metrics whose absolute values were greater than 1.5×IQR. Parameter definitions can be found in Table 3.1.

Figure C.3 (cont'd)
a)



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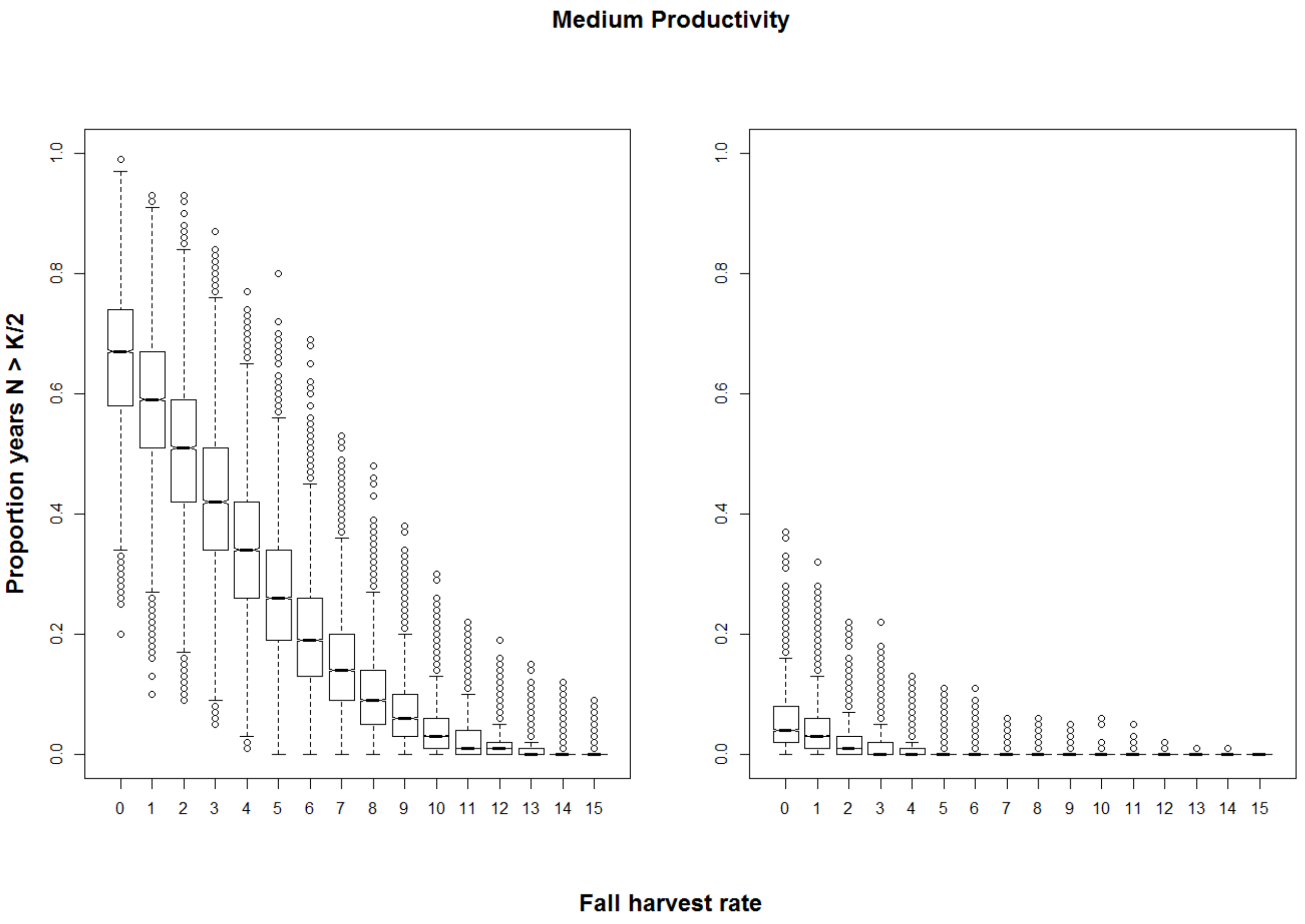

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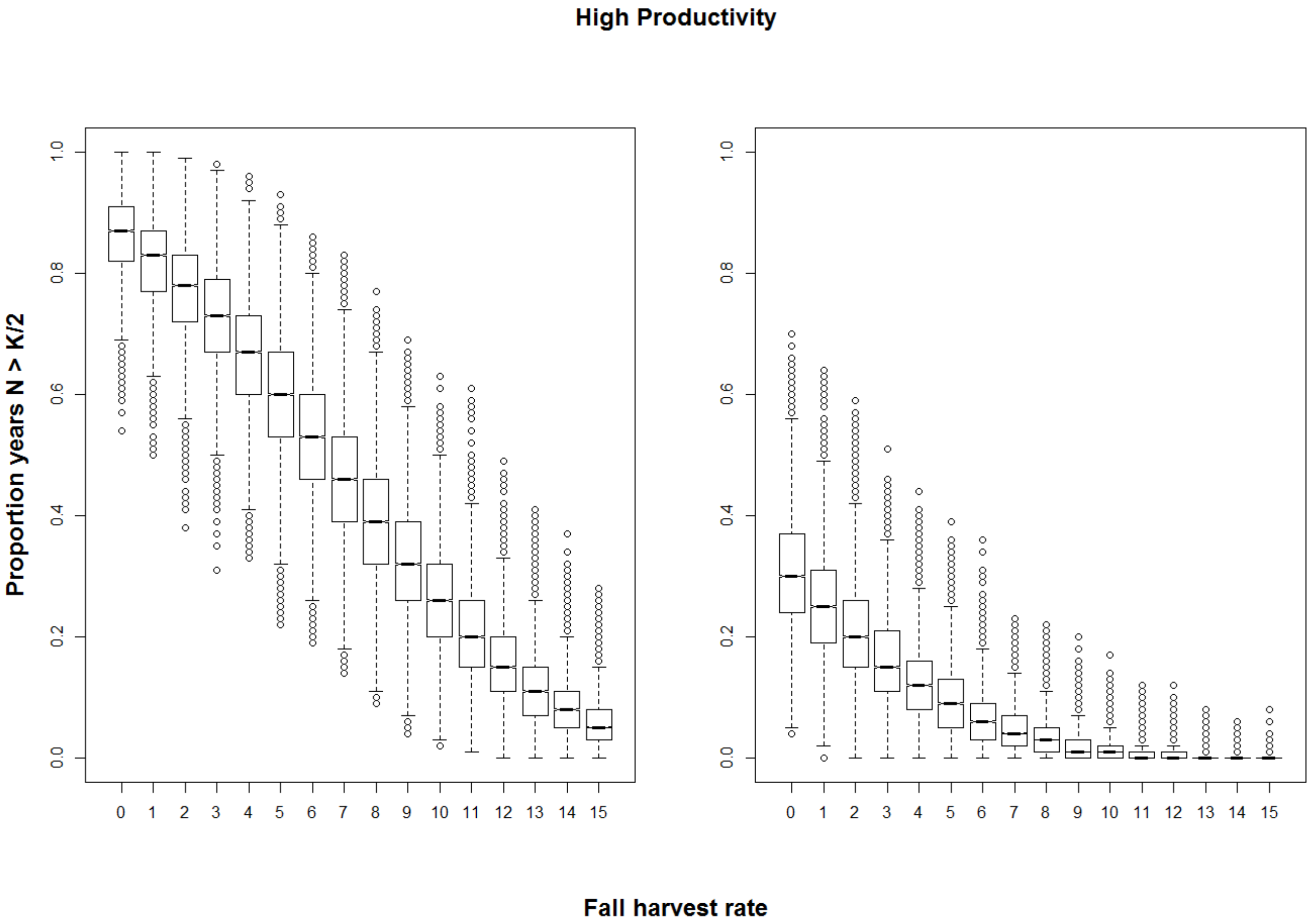
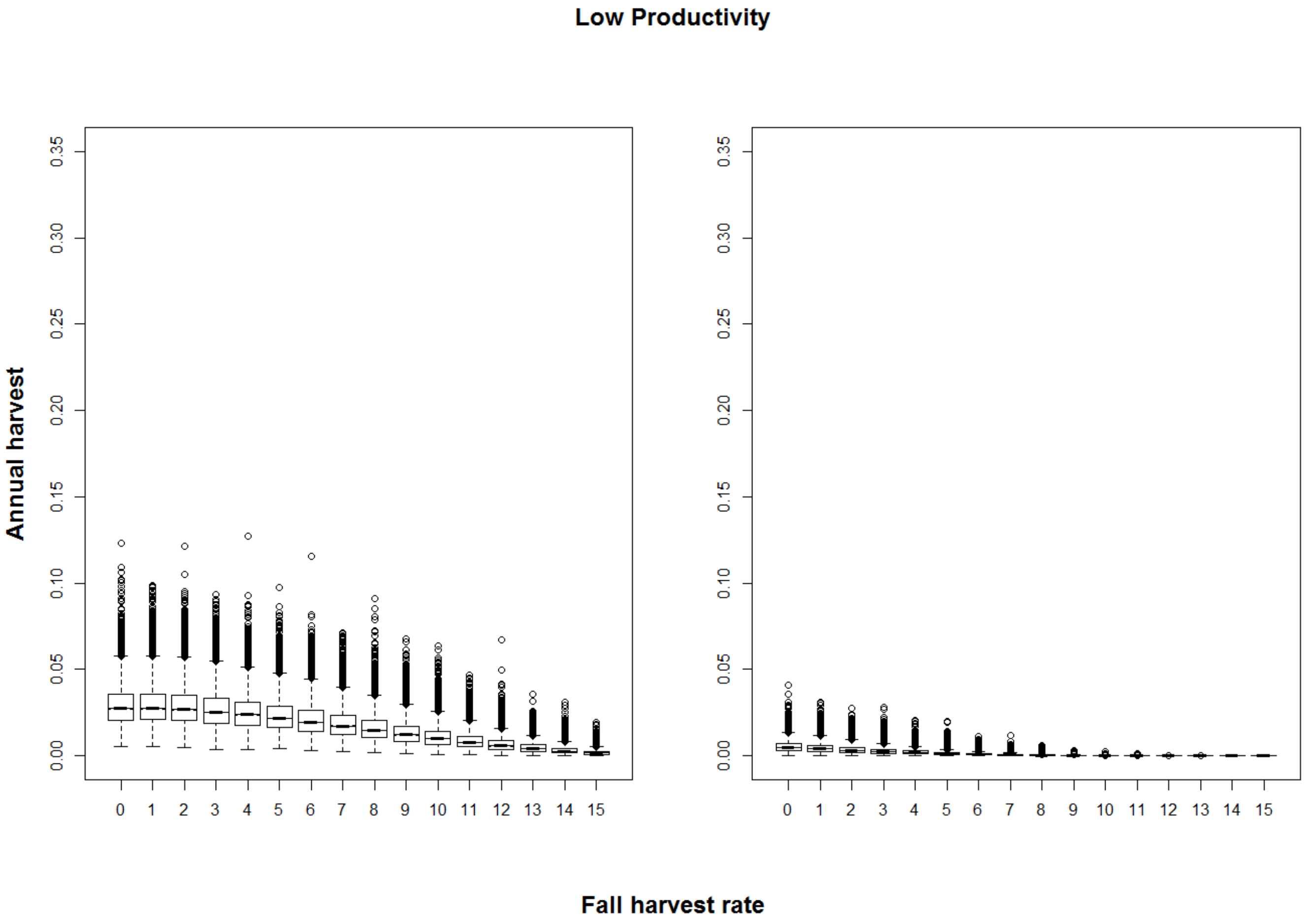


Figure C.4 Distributions of total annual harvest (sum of spring and fall hunting seasons) from simulations of wild turkey populations for target fall harvest rates of 0–15% for a range of demographic scenarios assuming no structural uncertainty in density-dependent population dynamics ($\theta = 0.36$). 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 hen poaching during the spring hunting season, at medium spring gobbler harvest rates (median = 0.30). Boxplots represent the simulated distribution of annual harvest on the last year of stochastic population projection ($H_{Total,200}$; Table 1). Solid horizontal lines represent median annual harvests, boxes delineate the interquartile ranges, boxplot notches represent an approximate 95% confidence intervals for medians ($\pm 1.58 * \frac{IQR}{\sqrt{n}}$; Chambers et al. 1983), and boxplot whiskers delineate IQR boundaries values $\pm$1.5×IQR. Individual points represent simulated metrics whose absolute values were greater than 1.5×IQR. Parameter definitions can be found in Table 3.1.

Figure C.4 (cont'd)
a)



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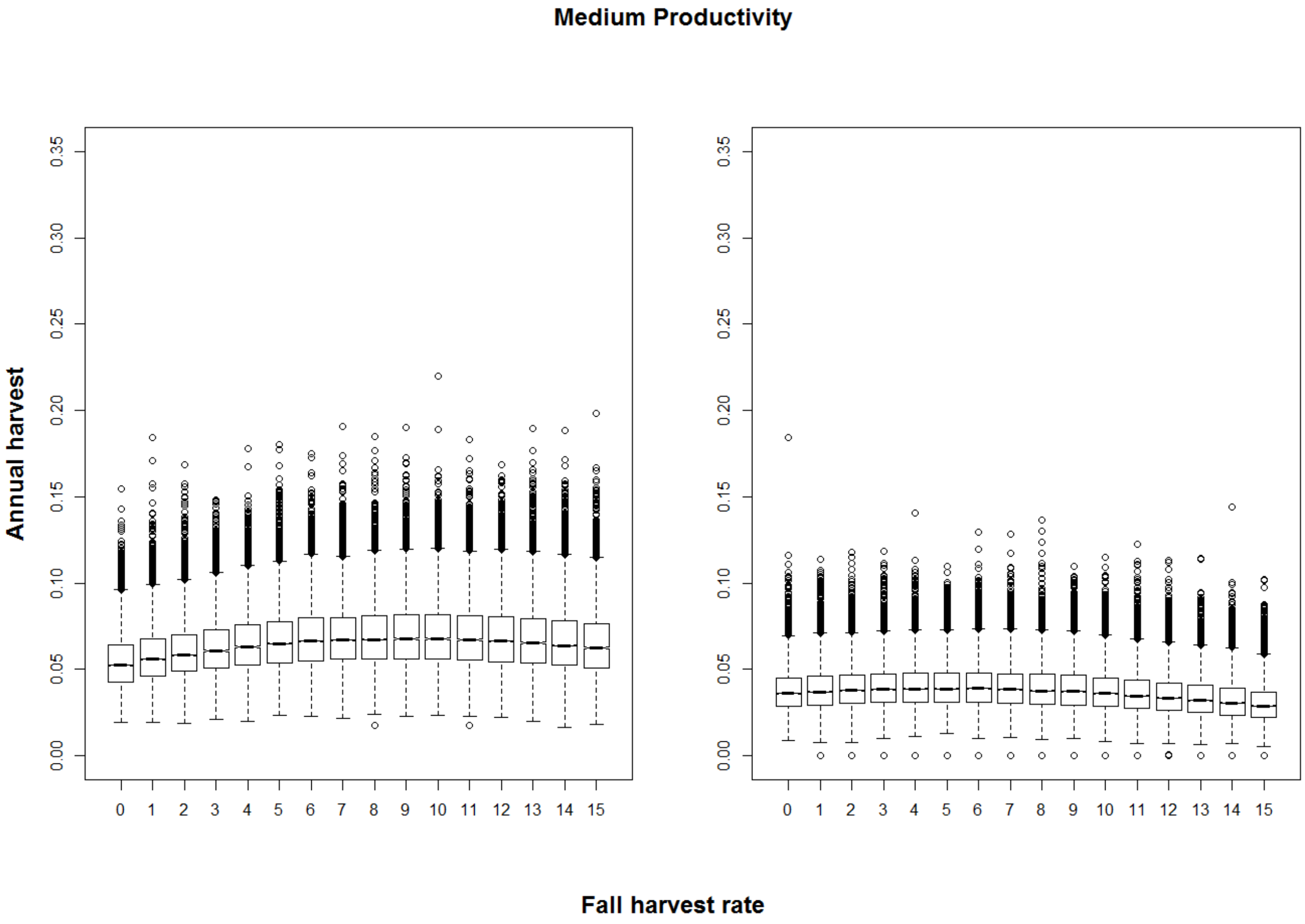

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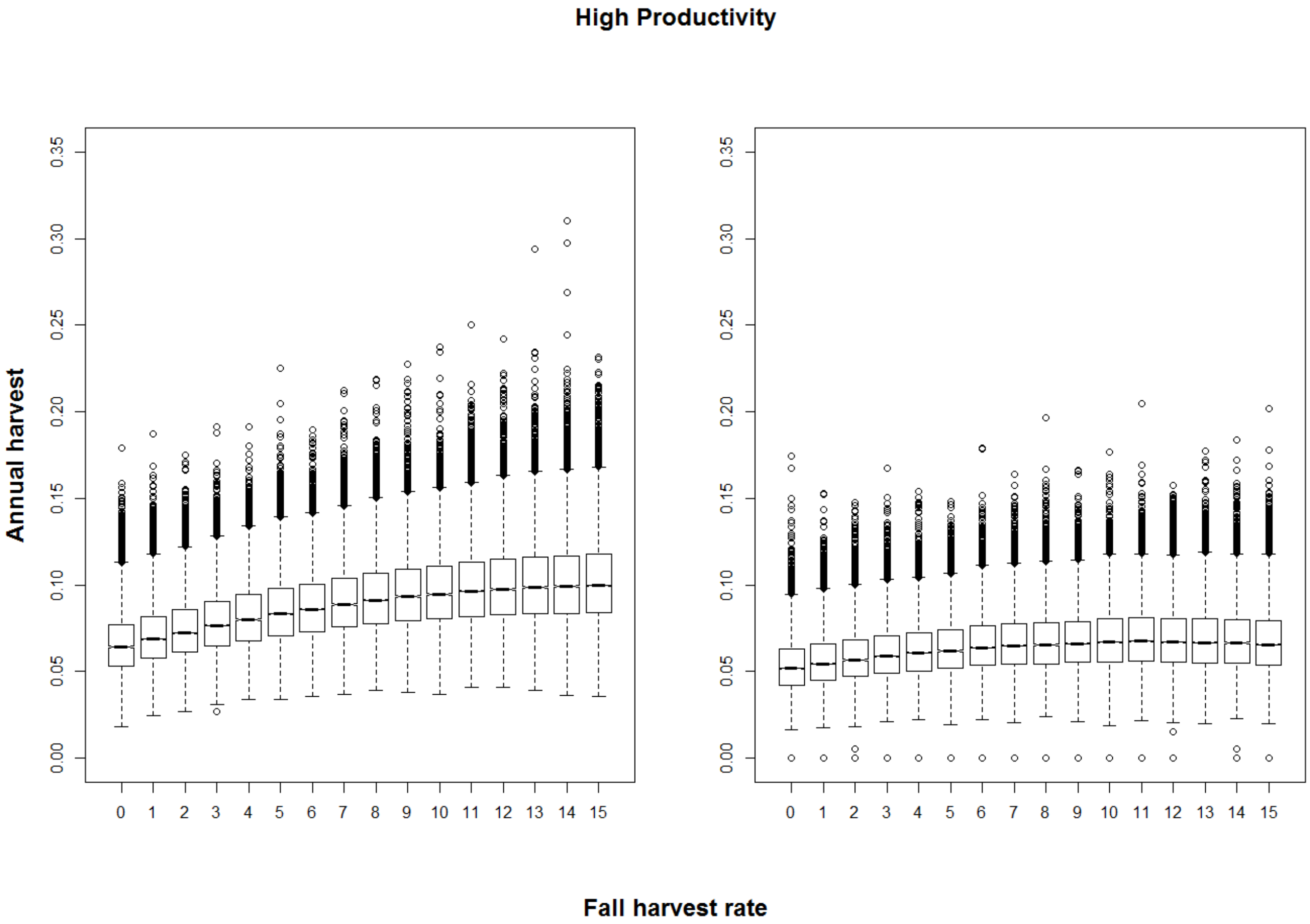
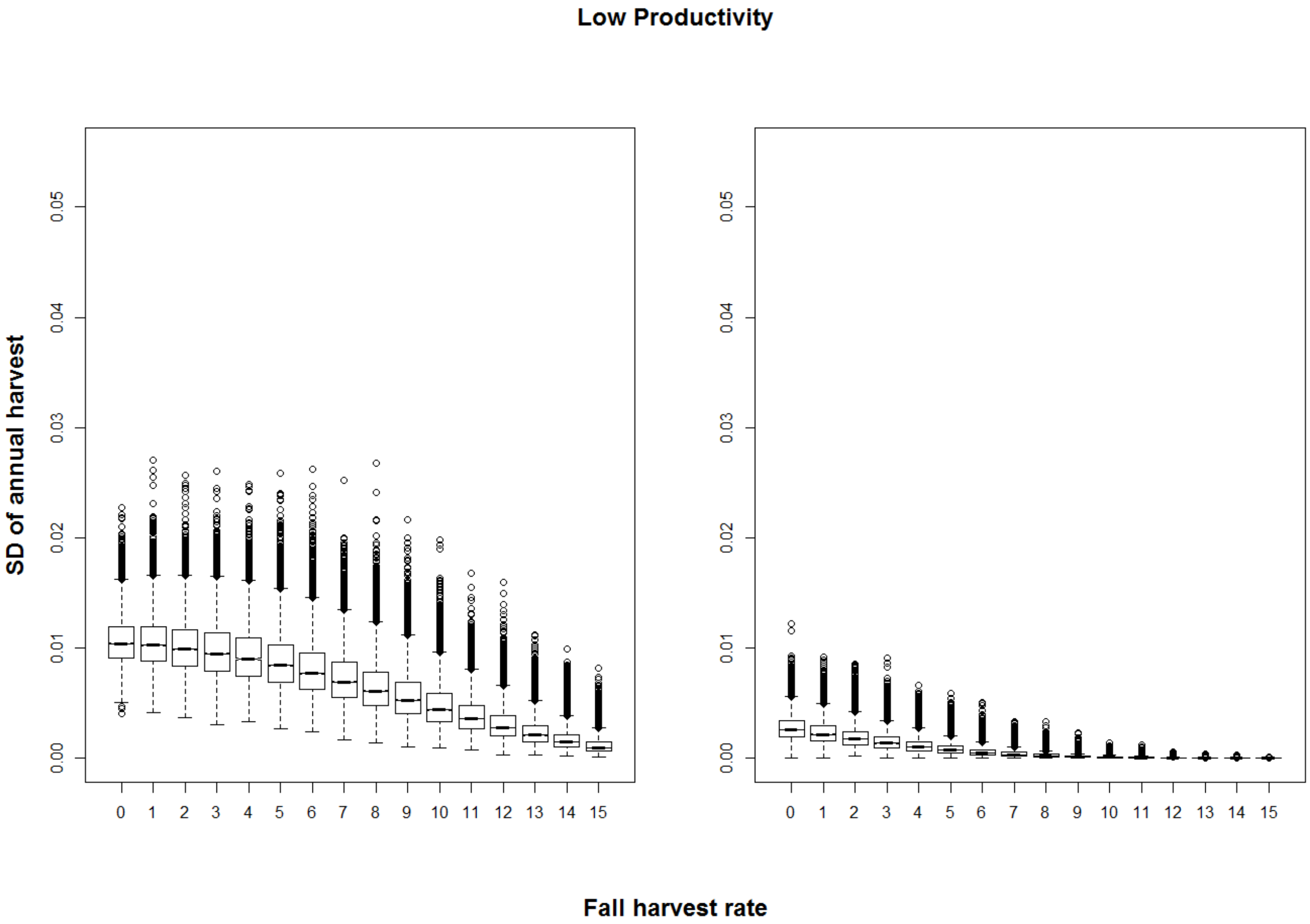


Figure C.5 Distributions of standard deviation of total annual harvest across spring and fall hunting seasons for target fall harvest rates of 0–15% across changing demographic scenarios for simulated wild turkey populations assuming no structural uncertainty in density-dependent population dynamics ($\theta = 0.36$). 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 hen poaching during the spring hunting season, at medium spring gobbler harvest rates (median = 0.30). Boxplots represent the distributions of standard deviation of annual harvest from years 100-200 of simulated stochastic population projections (σ_{H_T}; Table 1). Solid horizontal lines represent median standard deviations, boxes delineate the interquartile ranges, boxplot notches represent an approximate 95% confidence intervals for medians ($\pm 1.58 * \frac{IQR}{\sqrt{n}}$; Chambers et al. 1983), and boxplot whiskers delineate IQR boundaries values $\pm 1.5 \times \text{IQR}$. Individual points represent simulated values greater than IQR boundaries $\pm 1.5 \times \text{IQR}$. Parameter definitions can be found in Table 3.1.

Figure C.5 (cont'd)
a)



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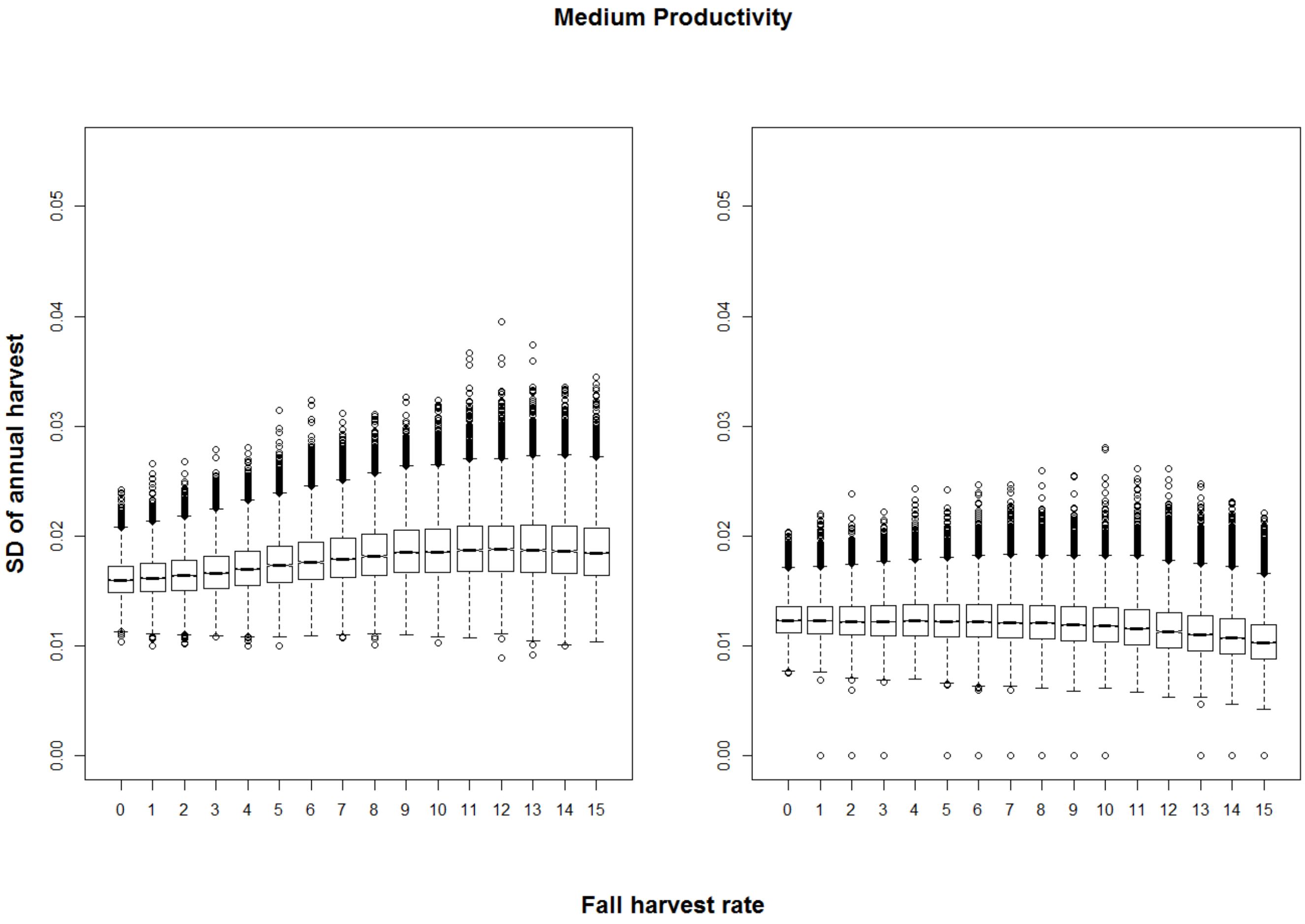

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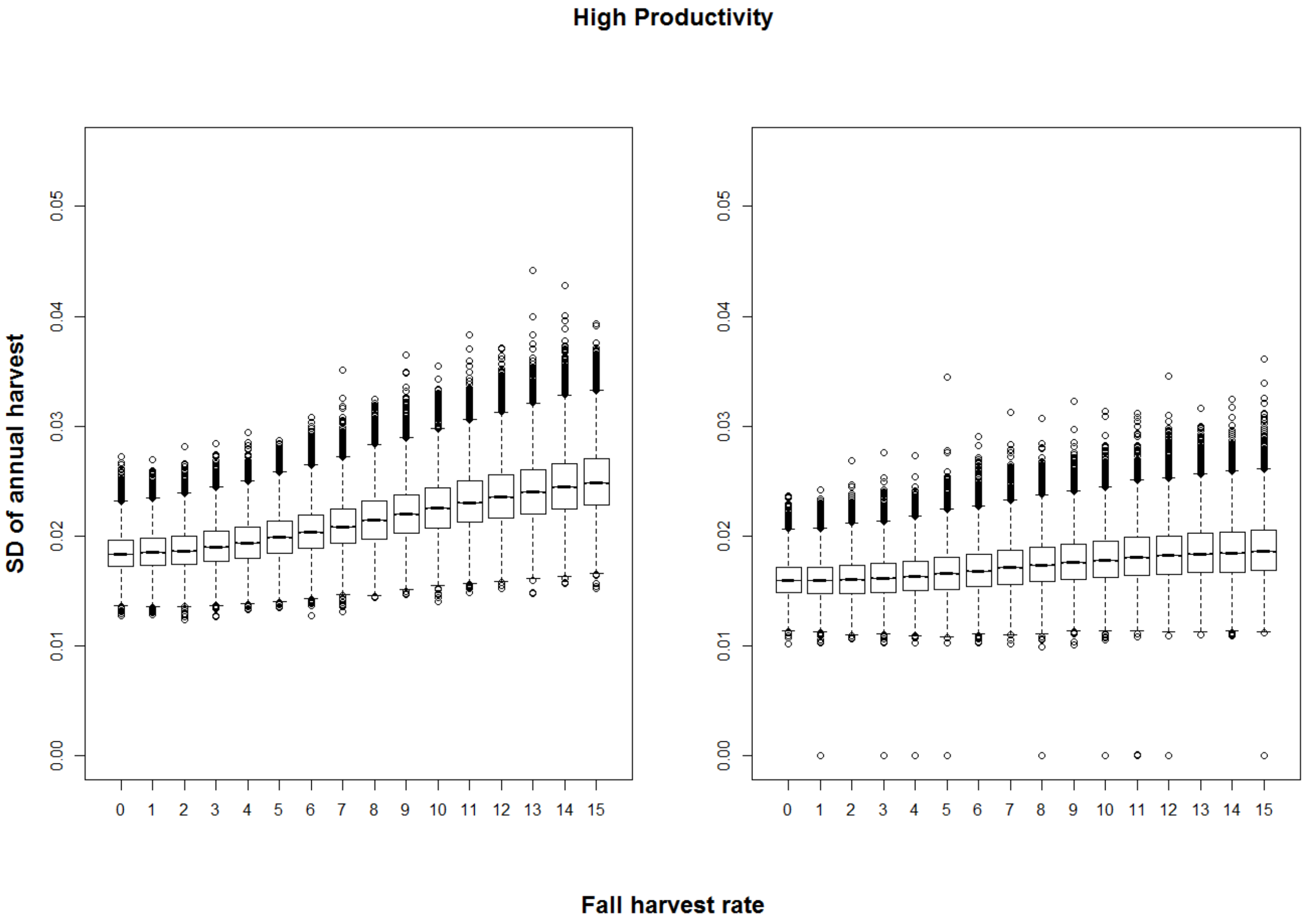


APPENDIX D: POPULATION AND HARVEST MODELS USED TO SIMULATE WILD TURKEY POPULATION RESPONSES TO FALL HARVEST IN CHAPTER 4

I used a theta-logistic population model developed previously for wild turkeys (McGhee et al. 2008, Appendix A) to simulate responses of turkey populations to spring and fall harvests. Sex-specific dynamics were simulated, where sexes were linked through reproduction:

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

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

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

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

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

Definitions of terms are as follows: $N_{i,t}$ is the number of turkeys for sex *i* alive at the start of spring hunting in year *t*; $r_{i,t}$ is the instantaneous growth rate for sex *i* at time *t*, expressed as a log-scale sum of the per-capita birth and death rates; B_t is total number of births (both sexes), expressed as a harmonic-mean function (see Caswell and Weeks 1986, McGhee et al. 2008, chapter 3) of the number of male and female turkeys, the number of female recruits per fertilized female turkey (*k*; so-called population productivity), and the number of females bred per male (*q*; called harem size by Caswell and Weeks 1986); s_i represents per-capita survival for sex *i*; K_i is the environmental carrying capacity for sex *i*; θ controls the degree of nonlinearity in density dependence (θ = 1 is analogous to a logistic population model); $\varepsilon_{p,t}$ are the realized process errors in population growth at time *t* (associated with variation in environmental conditions); $h_{i,j,t}$ represents realized harvest rates for sex *i* in hunting season *j* at time *t*; and $H_{i,j,t}$ represents realized total harvest of sex *i* during season *j* at time *t*. I assume the number of male and females recruits is equal, and the harmonic mean birth function accounts for the effect of skewed sex-ratio (induced by sex-specific harvest rates) on production of young. I also assumes that males breed hens prior to removal during spring, and that females poached during spring cannot contribute to production of young in the year they are killed (i.e., per-capita female birth rate removes poached females from the denominator: $\frac{0.5B_t}{(1-h_{f,s,t})N_{f,t}}$).

In this model total realized spring and fall harvests ($H_{i,j,t}$) can be calculated from the product of the harvest rate and the sex-specific population size at the start of the respective hunting season

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

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

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

where realized harvest rates ($h_{i,j,t}$) at time *t* were generated from lognormal distributions by multiplying the target proportions (spring: low = 0.15, medium = 0.30, high = 0.40; fall: 0-0.15 by 0.01) by exponentiated normal random deviates (Table D1). For fall hunting, realized harvest rates of females were scaled by the relative harvest vulnerability coefficient (v), which increased or decreased the value of female harvest relative to males. Values for all parameters used were selected consistently with previous turkey harvest models, and are described below (Table D1).

To evaluate sensitivity of results to assumptions about the temporal distribution of realized harvest rates through time (i.e., the model of implementation uncertainty), I replicated simulations for all parameter combinations (464 scenarios, each with 16 target proportional fall harvests) assuming different models of harvest variation. In addition to changing the magnitude of variation for the baseline lognormal distribution (described in text; no variation: σ_f = 0; double of baseline variation: σ_f = 0.35), I considered performance of target fall harvest rates for each parameter combination when realized fall harvest rates followed a first-order auto-regressive process (AR1) with the same stationary variance as the baseline lognormal model. The magnitude of temporal variation in realized harvest rates for this model was thus equal to that of the baseline lognormal model; however, the individual realizations were temporally autocorrelated. I generated AR1 realizations of fall harvest rates for the male segment of the turkey population using the following model (female harvests were scaled linearly as previously described):

$$target \times e^{\varepsilon_{f,t}}$$

$$\varepsilon_{f,t} = \rho\varepsilon_{f,t-1} + \delta_t$$

$$\delta_t \sim Normal(0, \sigma^2)$$

$$var(\varepsilon_{f,t}) = \frac{\sigma^2}{1-\rho^2}.$$

I set $\rho = 0.5$ and solved for the value of σ when $var(\varepsilon_{f,t}) = 0.175$ (same as baseline lognormal model), which produced a value of $\sigma = 0.1515544$. To initialize the simulations I generated a realized fall harvest rate from the baseline lognormal model, and then generated AR1 realizations for every year thereafter following the above model.

Table D.1 Parameters and their values or stochastic distributions used to simulate population and harvest dynamics for wild turkeys.

Symbol	Value/Distribution
s_i[a]	0.74 (male), 0.64 (female)
K_i	10,000
θ[b]	$N(0.36, \sigma_\theta)$
σ_θ	0.09
$\varepsilon_{p,t}$[a]	$N(0, \sigma_p)$
σ_p	0.15
k[c]	0.75-2.15
q[a]	10
$h_{m,s,t}$[a,d]	$0.15e^{\varepsilon_{s,t}}$, $0.30e^{\varepsilon_{s,t}}$, $0.40e^{\varepsilon_{s,t}}$
$h_{f,s,t}$[a]	$0.05e^{\varepsilon_{s,t}}$
$\varepsilon_{s,t}$[a]	$N(0, \sigma_s)$
σ_s	0.175 (males), 0.400 (females)
$h_{m,f,t}$	$target \times e^{\varepsilon_{f,t}}$
$h_{f,f,t}$	$v \times target \times e^{\varepsilon_{f,t}}$
v[e]	0.5-2.0
$\varepsilon_{f,t}$	$N(0, \sigma_f)$
σ_f[a]	0.175

[a] Parameter values selected consistently with previous turkey harvest modeling studies (McGhee et al. 2008, Chapter 2, Chapter 3).

[b] Values of θ Drawn randomly across replicate simulations but were assumed to be constant over time within a simulation replicate. The distribution used to simulate θ is consistent with findings of McGhee and Berkson (2007a).

[c] Range of per-capita productivity values selected to approximate the range of productivity values (i.e., poults-per-hen recruited into fall population) described or assumed by turkey field studies and harvest models (chapter 3).

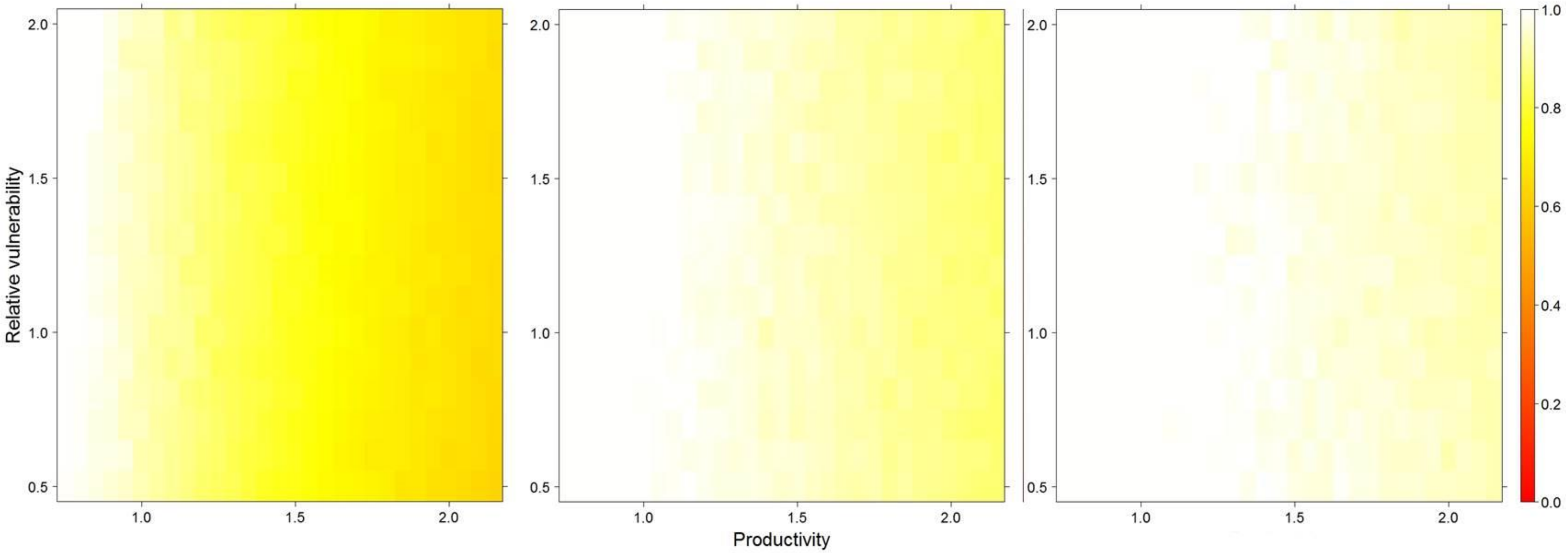
[d] Realized harvest rates were simulated from lognormal distributions annually within simulations, but capped at a maximum value of 100%. If a simulated harvest rate was greater than 100% (very rare at parameter values assumed), the value was adjusted inside the simulation script to be set equal to 100%.

[e] Range of sex-specific relative harvest vulnerability selected to approximate the range of values assumed in Chapter 2.

APPENDIX E: RELATIVE PERFORMANCE OF FALL HARVEST RATES AND RESPONSES OF WILD TURKEY POPULATIONS ACROSS SCENARIOS REPRESENTING STRUCTURAL UNCERTAINTY IN POPULATION AND HARVEST DYNAMICS

Figure E.1 Relative utility of fall harvest rates (a = no fall harvest to k = 10%, by 1%) as a function of population productivity (Productivity) and sex-specific fall harvest vulnerabilities (Relative vulnerability) across 3 scenarios of spring harvest (low = left, medium = middle, high = right). Relative utility for each fall harvest under each set of productivity and vulnerability parameters was defined as the expected utility for that harvest divided by the expected utility for the optimal fall harvest rate for the corresponding parameter-combination scenario.

a)



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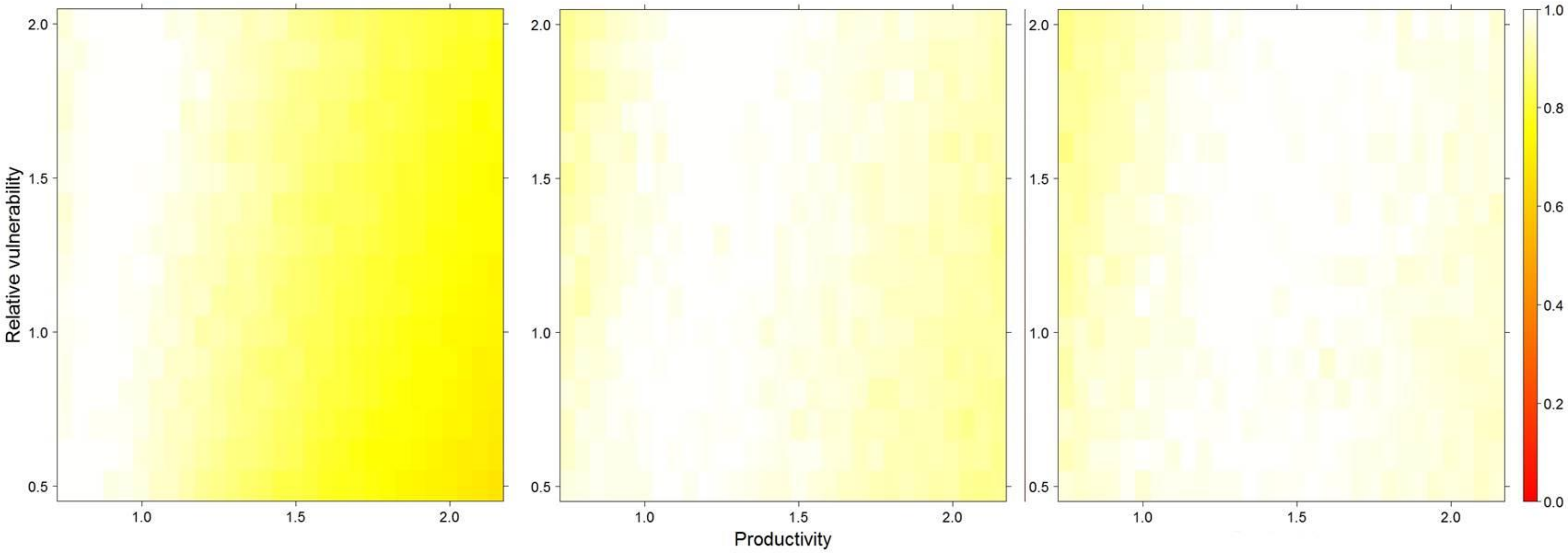
b)



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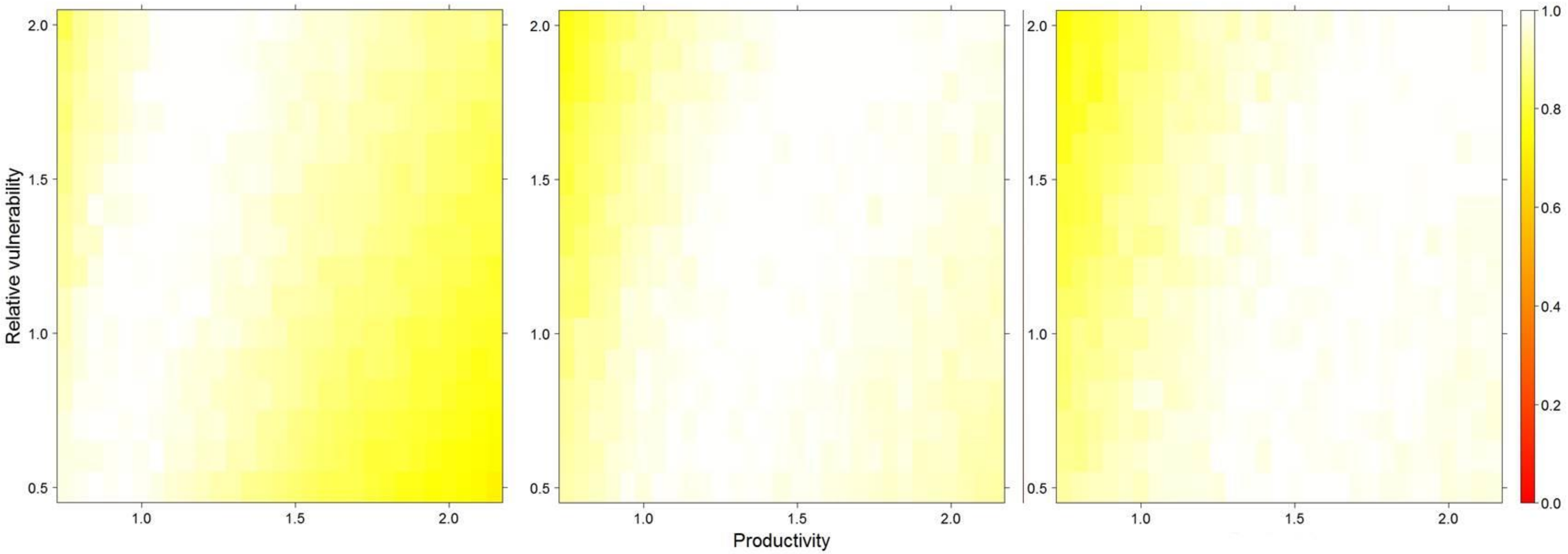

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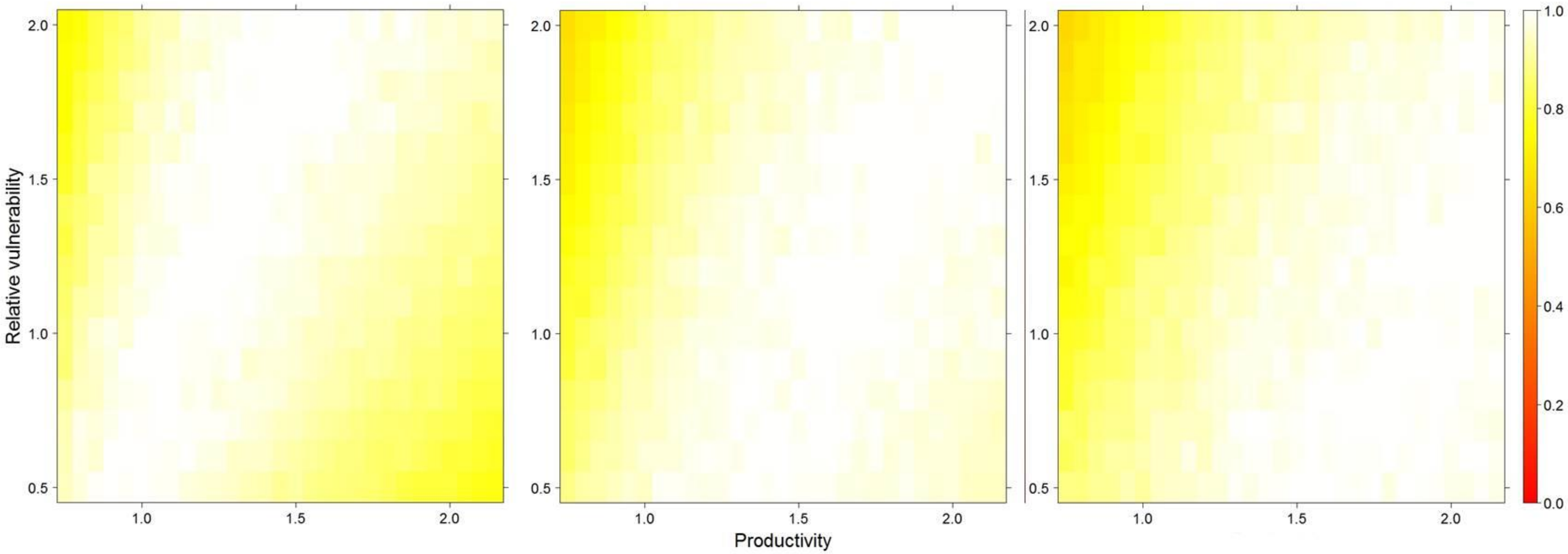

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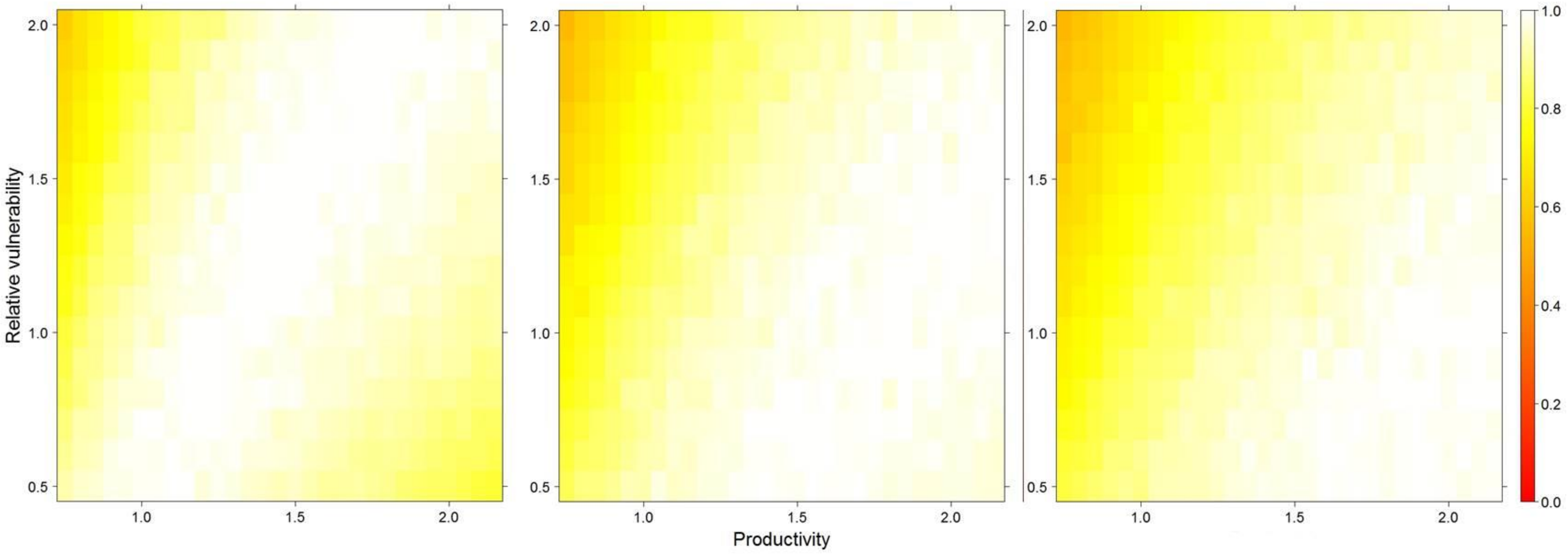

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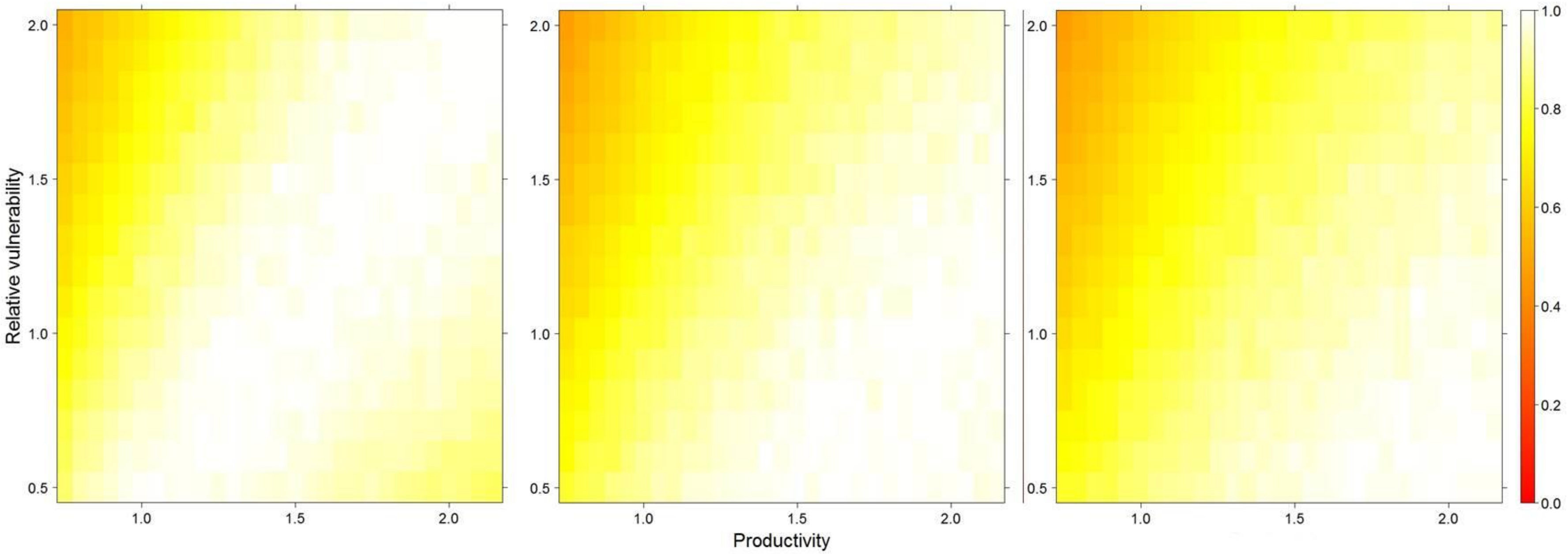

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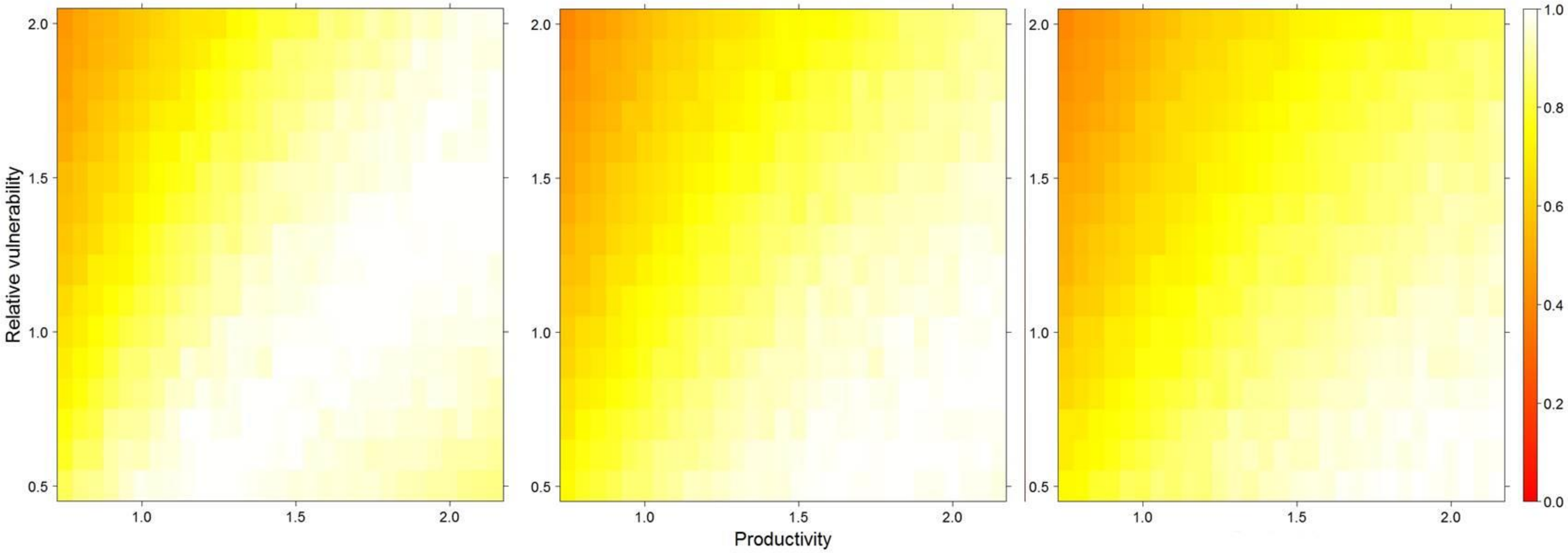

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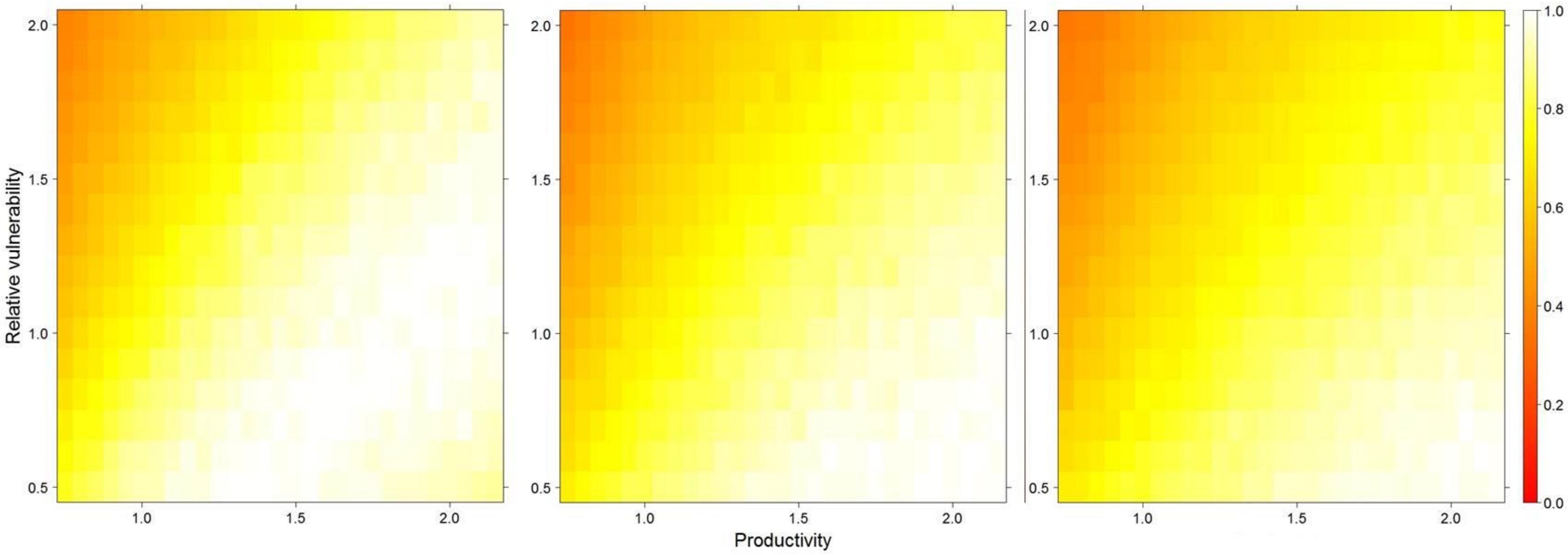

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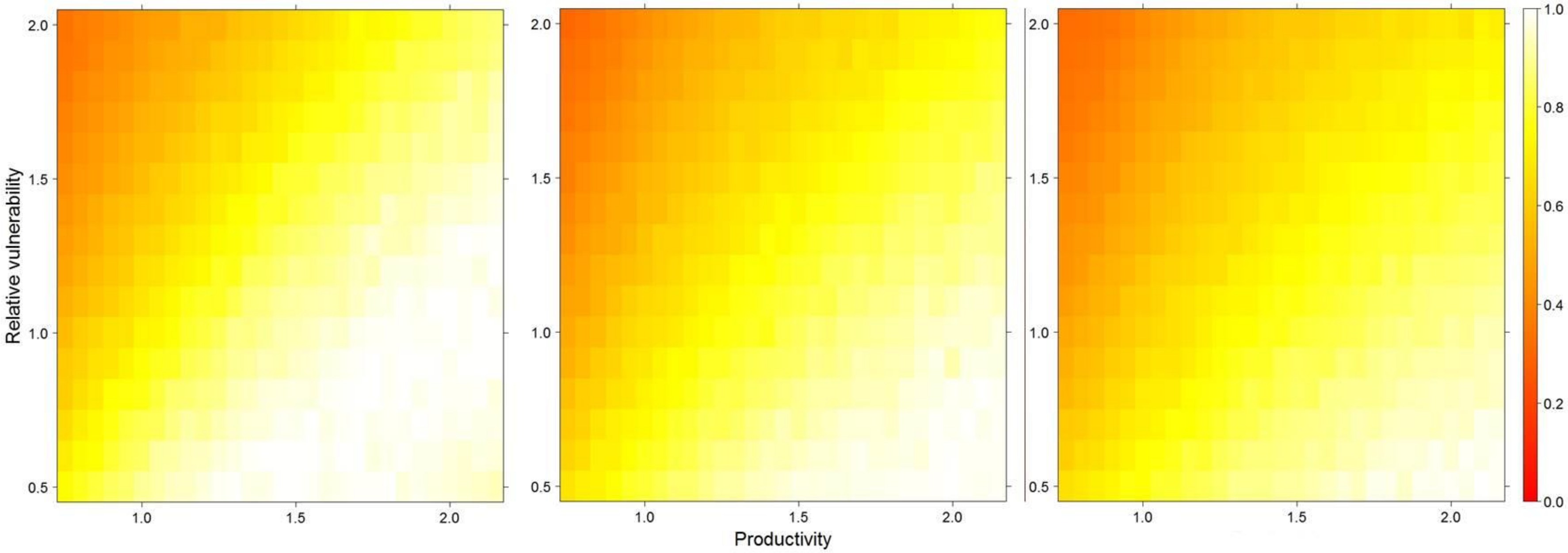
i)



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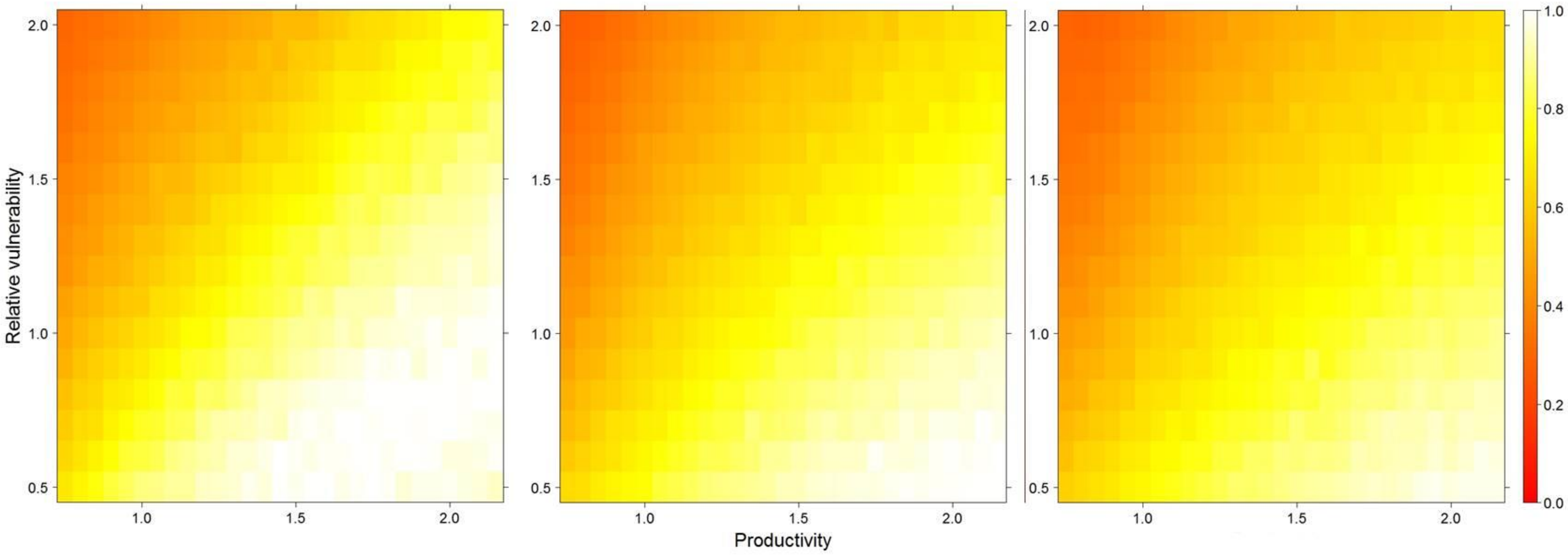


Figure E.1 (cont'd)
k)

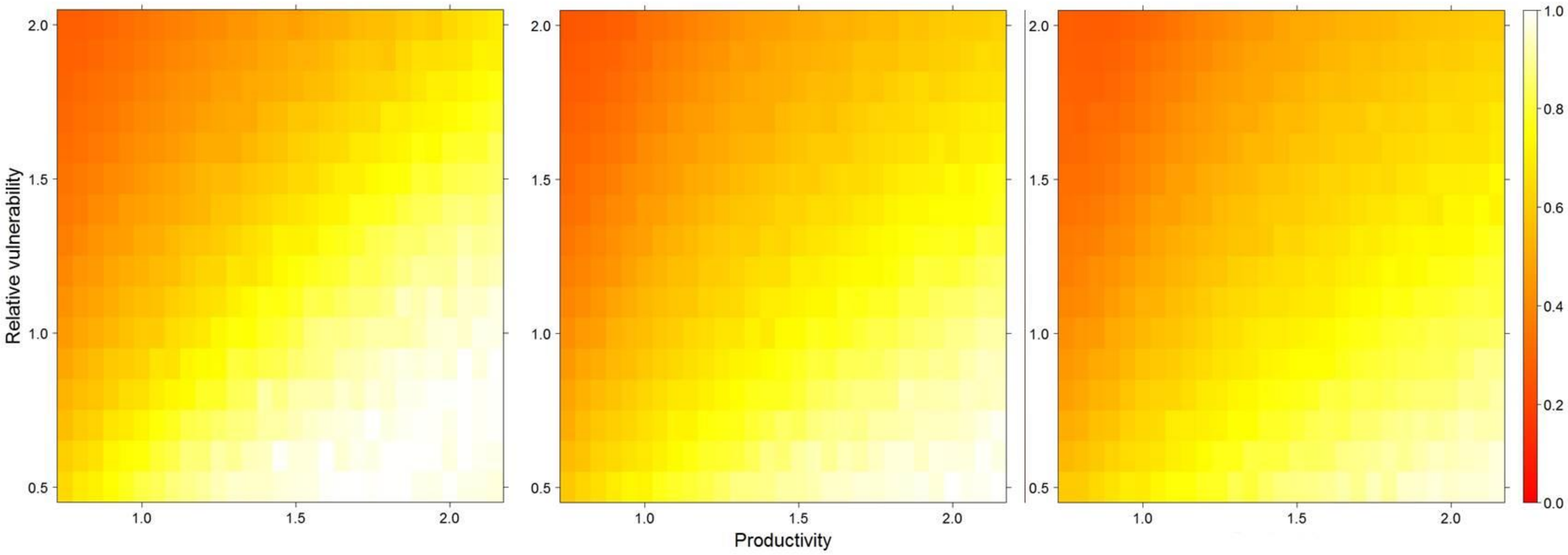
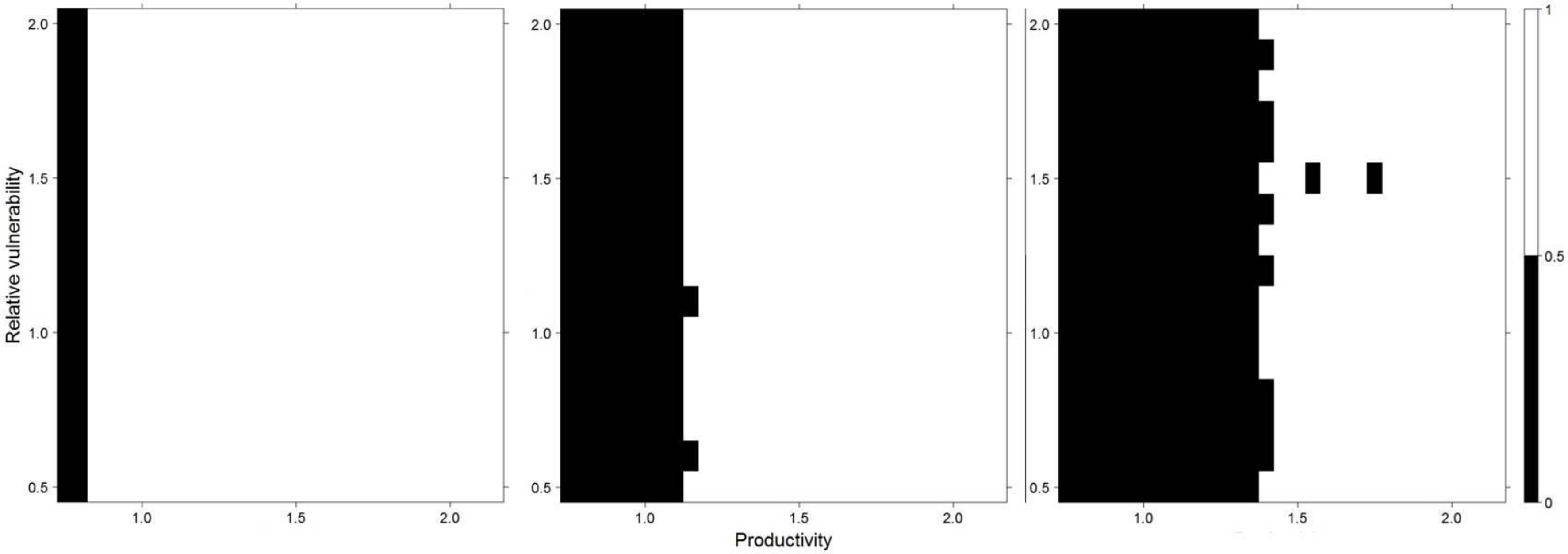


Figure E.2 Median (over simulation runs) proportion of years (within a simulation run) where spring population size was > utility threshold (*K*/2) for fall harvest rates (a = no fall harvest to k = 10%, by 1%) as a function of population productivity (Productivity) and sex-specific fall harvest vulnerabilities (Relative vulnerability) across 3 scenarios of spring harvest (low = left, medium = middle, high = right). White areas represent regions of parameter space where abundance was > threshold for > half of time during simulations at each fall harvest rate.

a)



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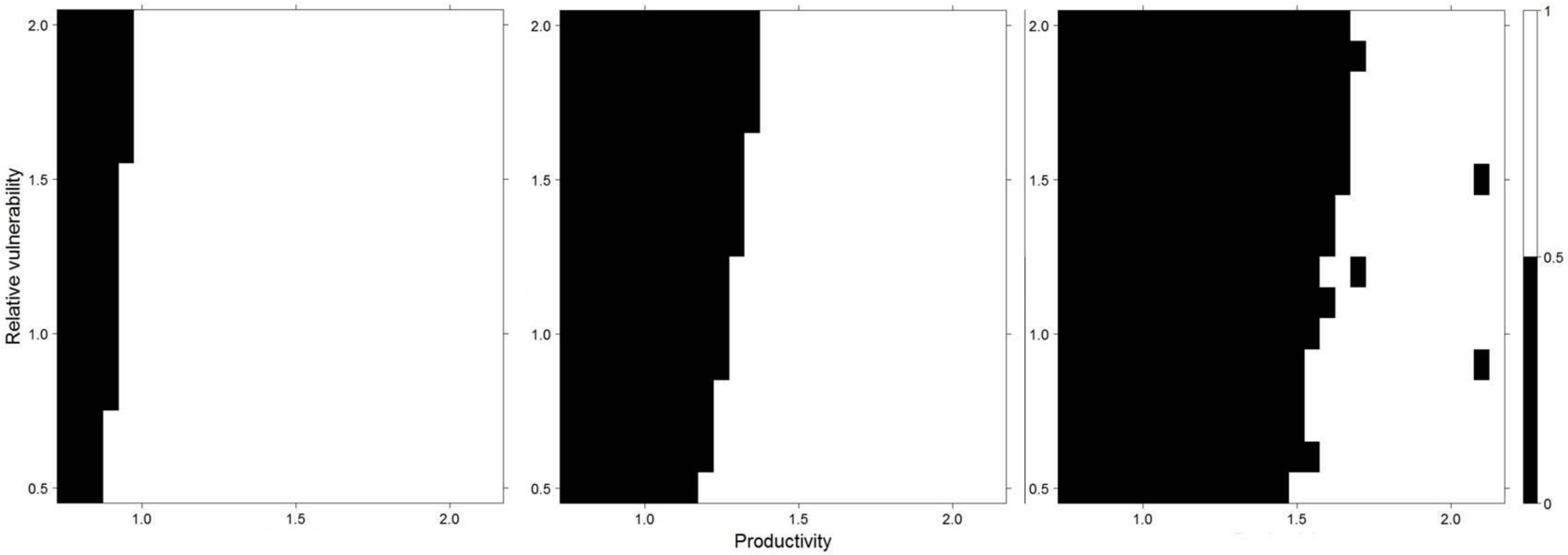
b)



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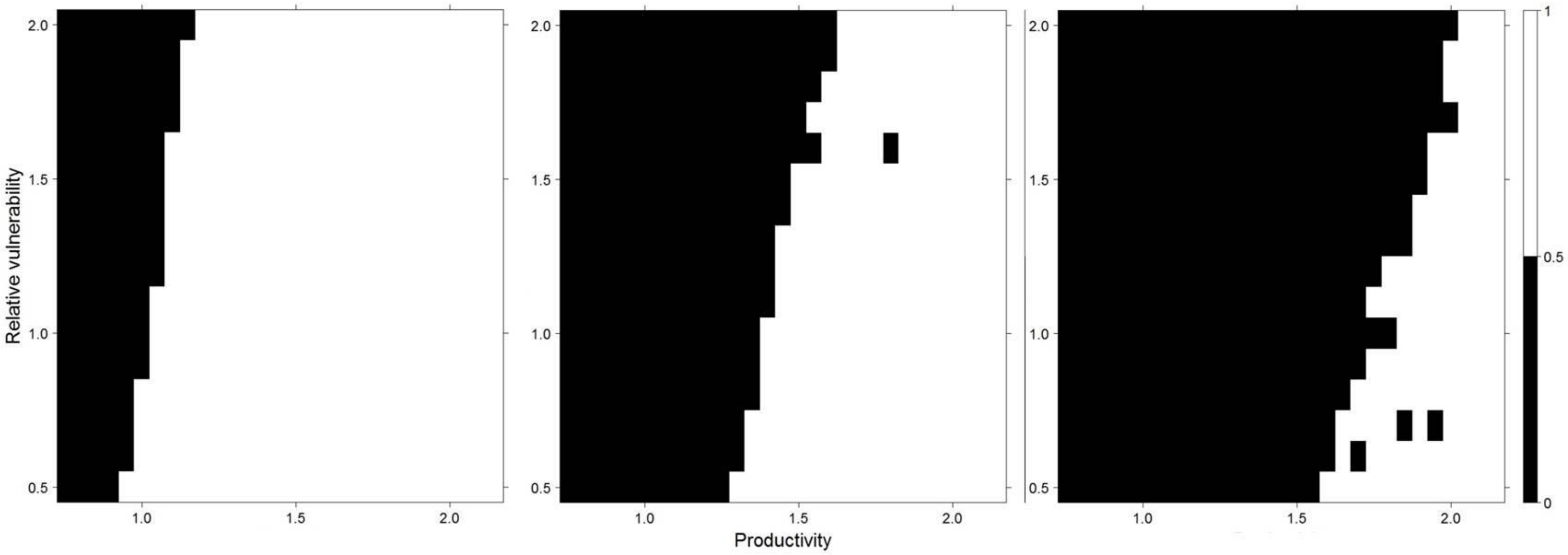
c)



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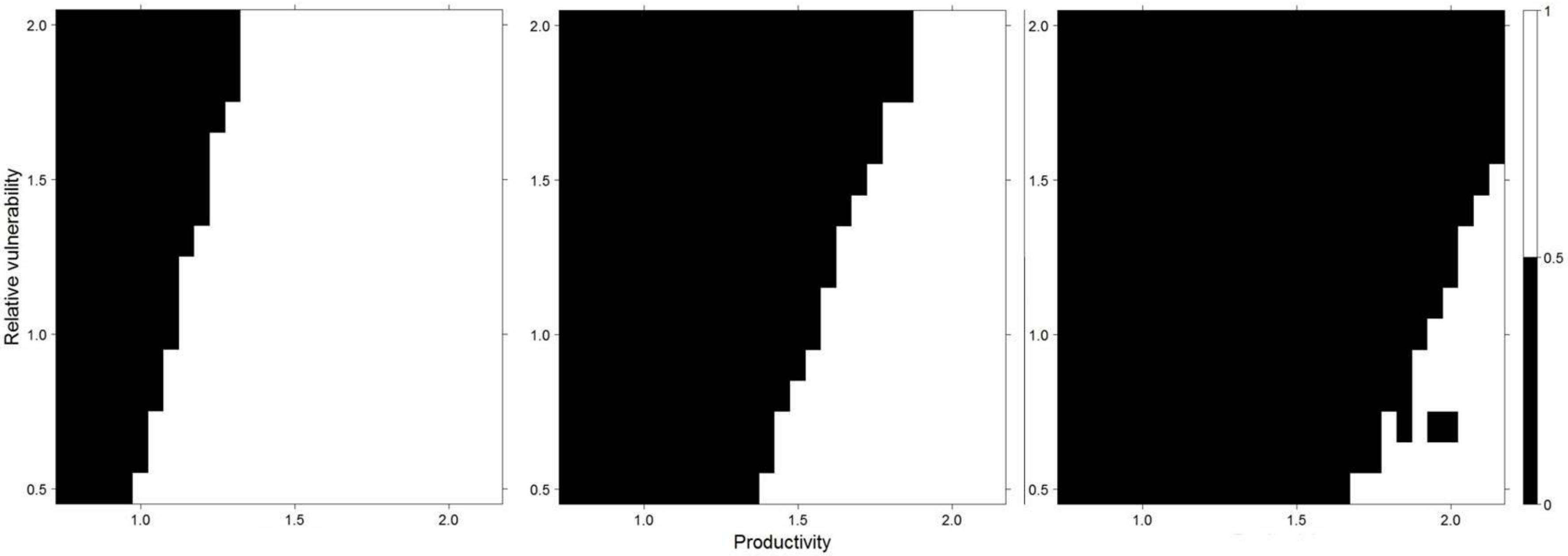
d)



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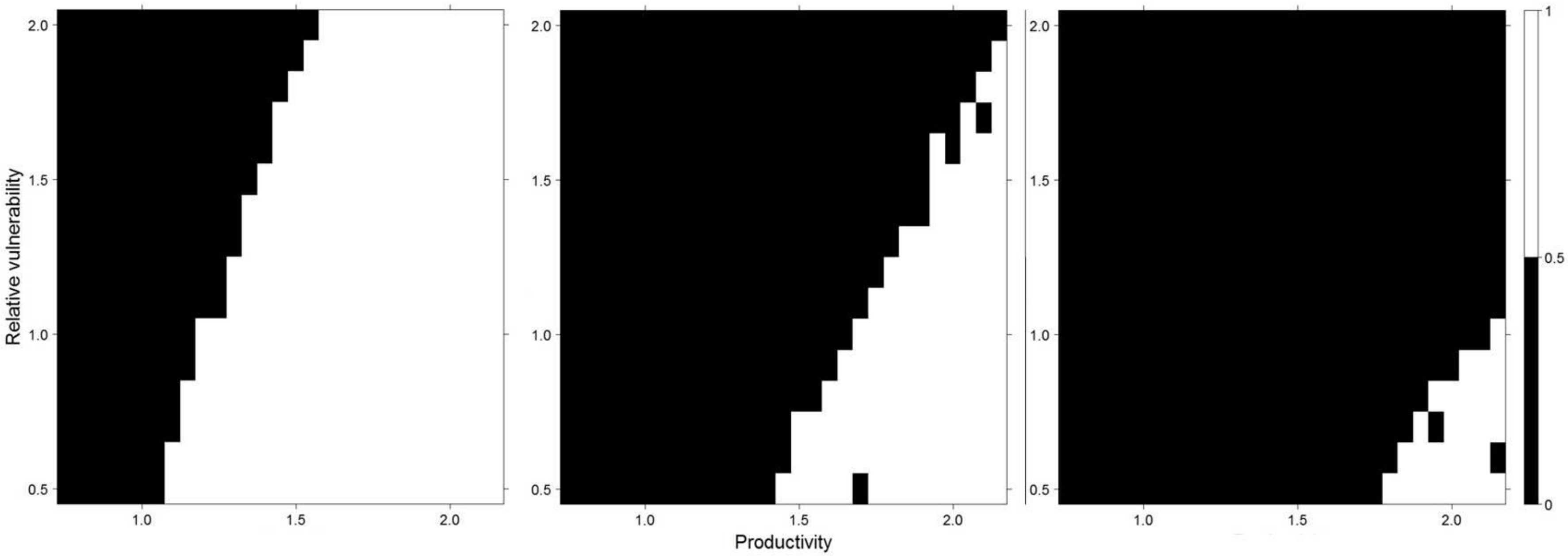
e)



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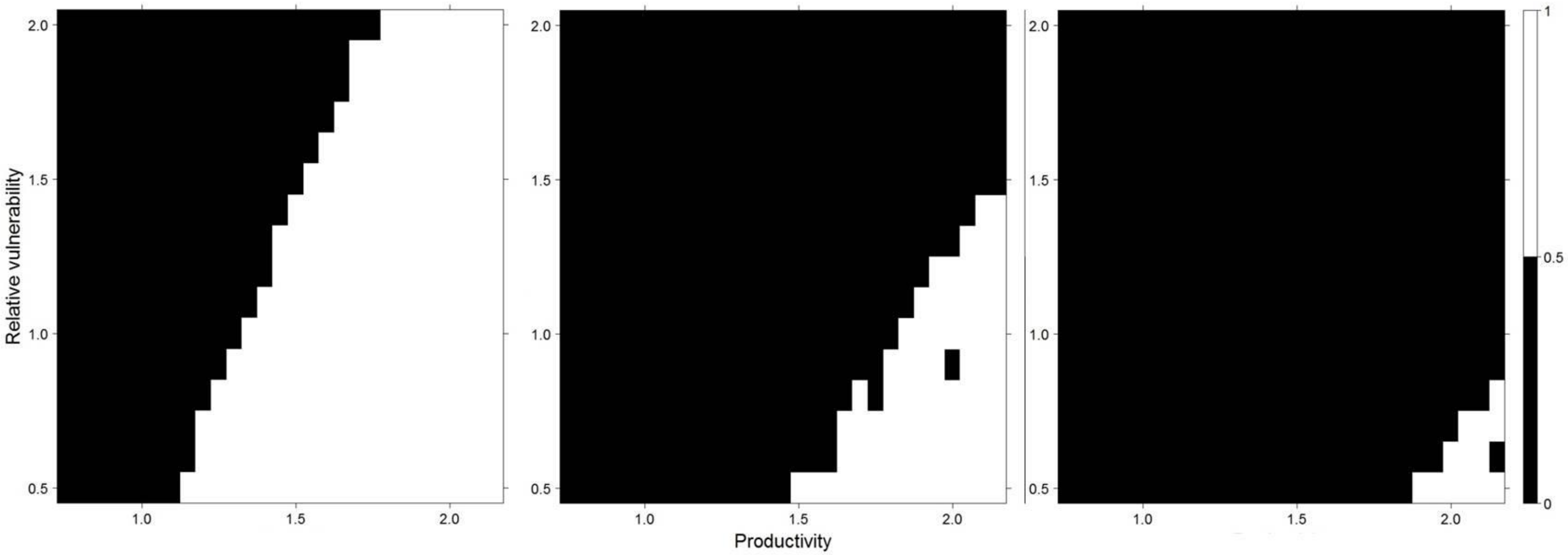
f)



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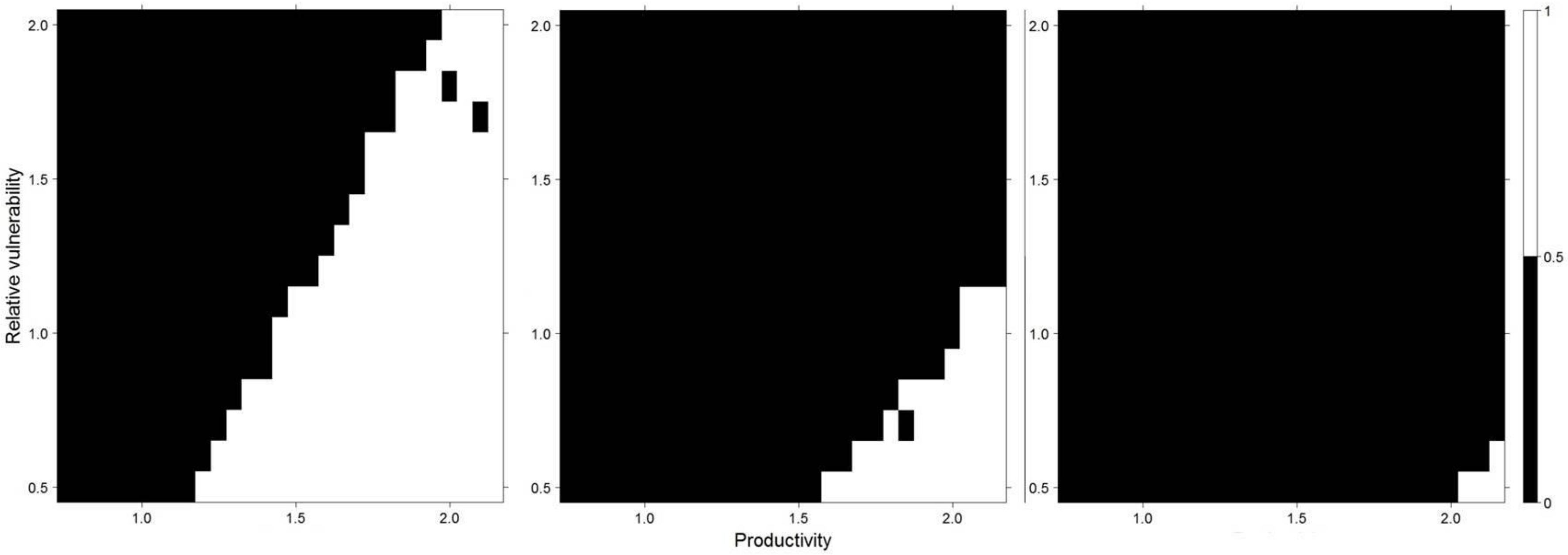
g)



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h)

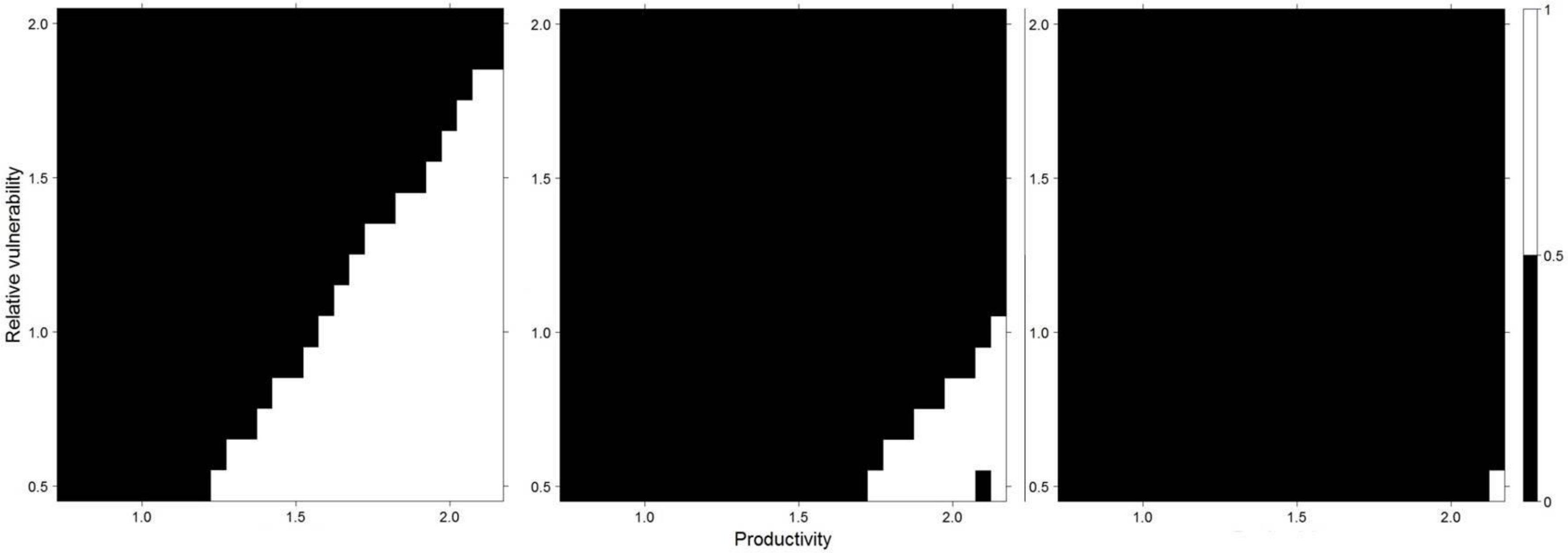
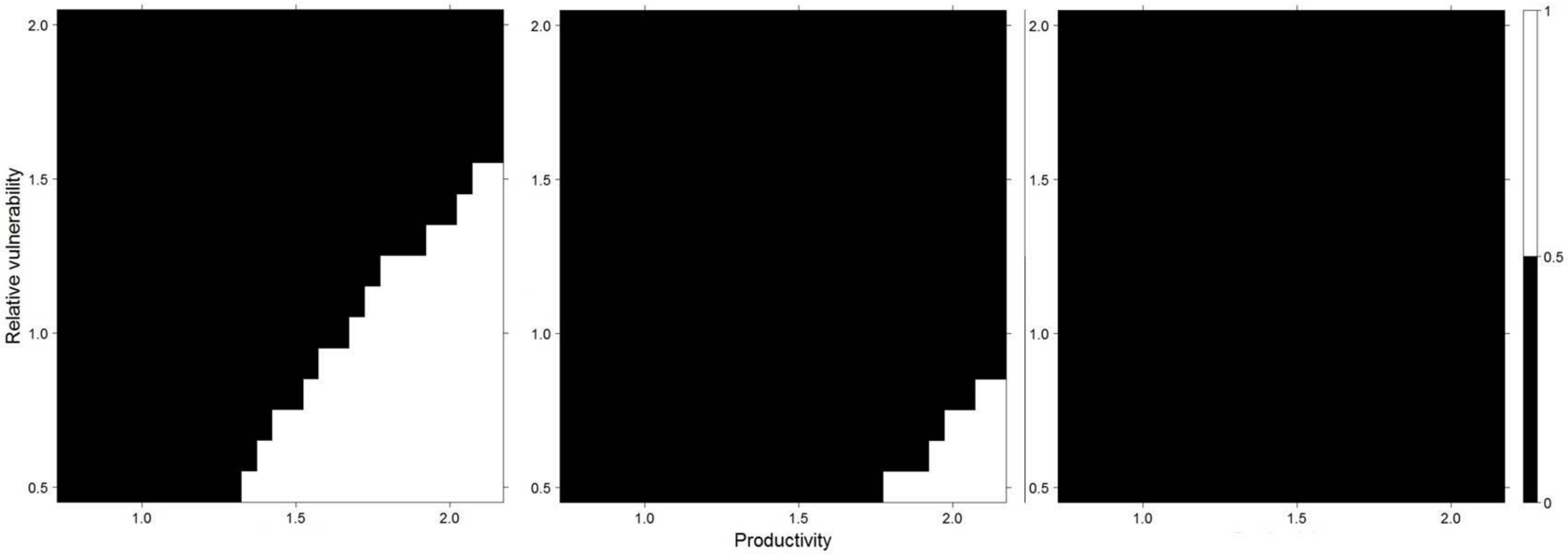


Figure E.2 (cont'd)
i)



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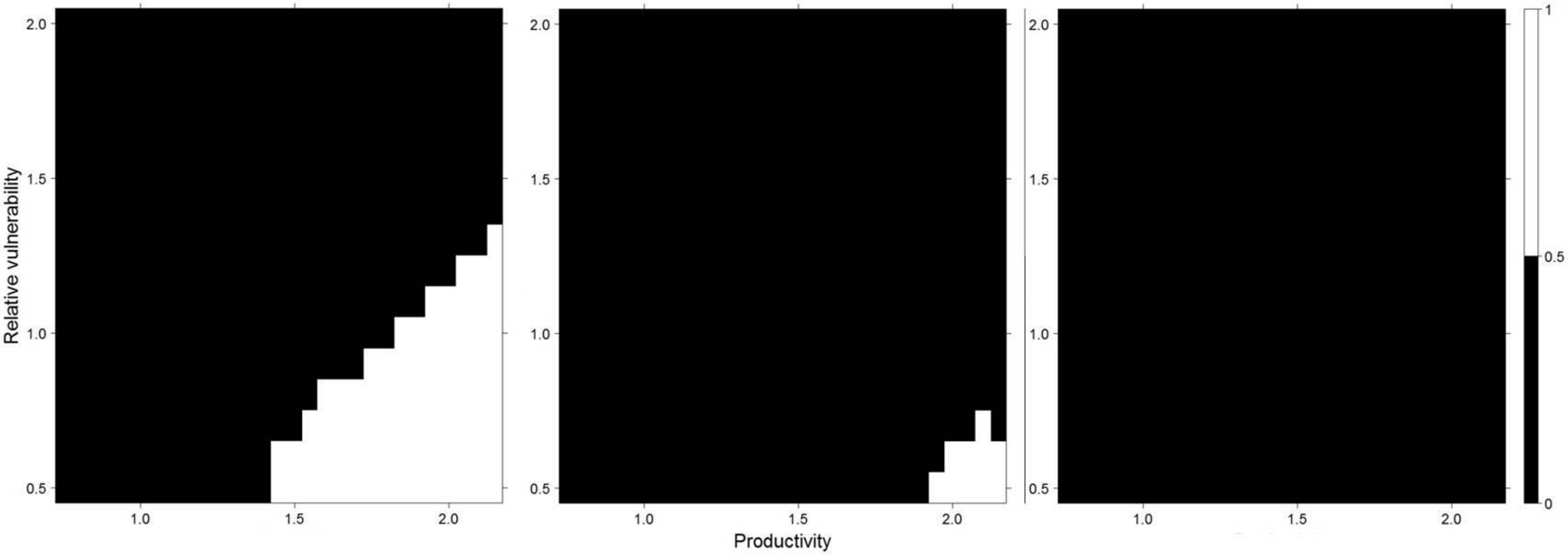
j)



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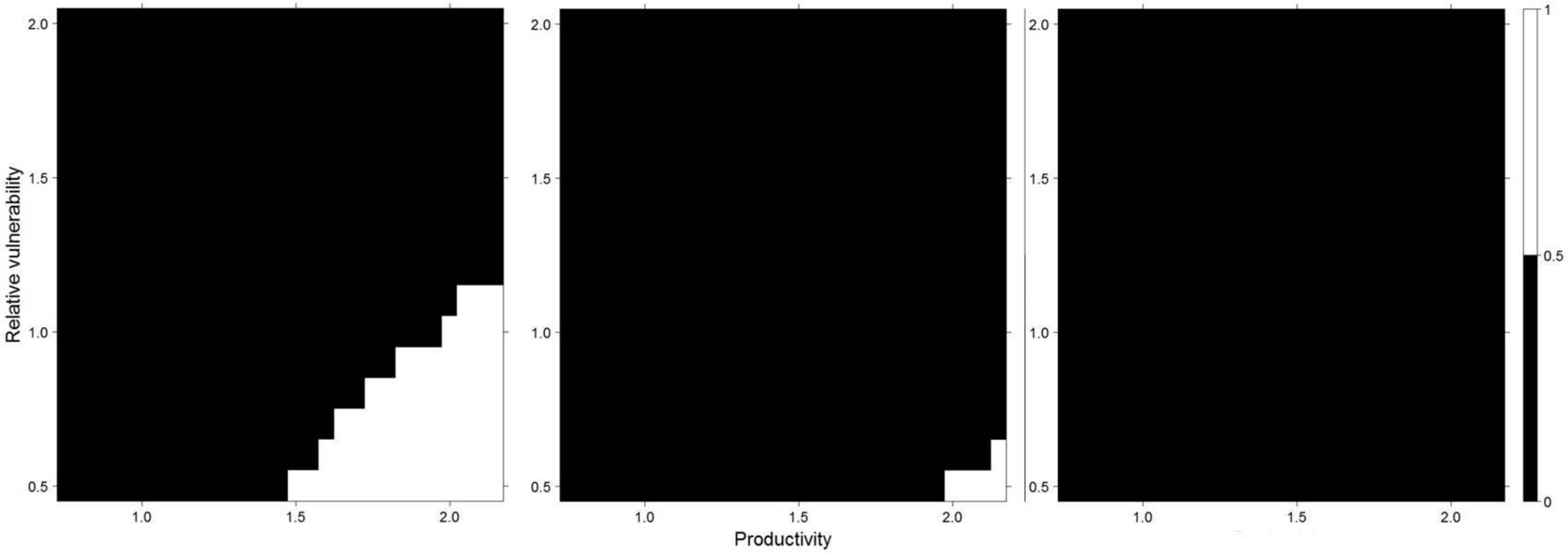
k)



APPENDIX F: RESULTS FROM SUPPLEMENTAL SENSITIVITY ANALYSES FOR CHAPTER 4

Figure F.1 Optimal fall harvest rates (expressed as percentages of the male population) as a function of population productivity (Productivity) and sex-specific fall harvest vulnerabilities (Relative vulnerability) across three scenarios of implementation uncertainty (no variation: left; double the baseline variation: middle; first-order auto-regressive variation: right). Spring male-only harvest was at low levels (median = 15%). Colors indicate the ranges of optimal fall harvest rates, including no harvest (black), 1-4% (dark grey), 5-9% (light grey), and 10-15% (white).

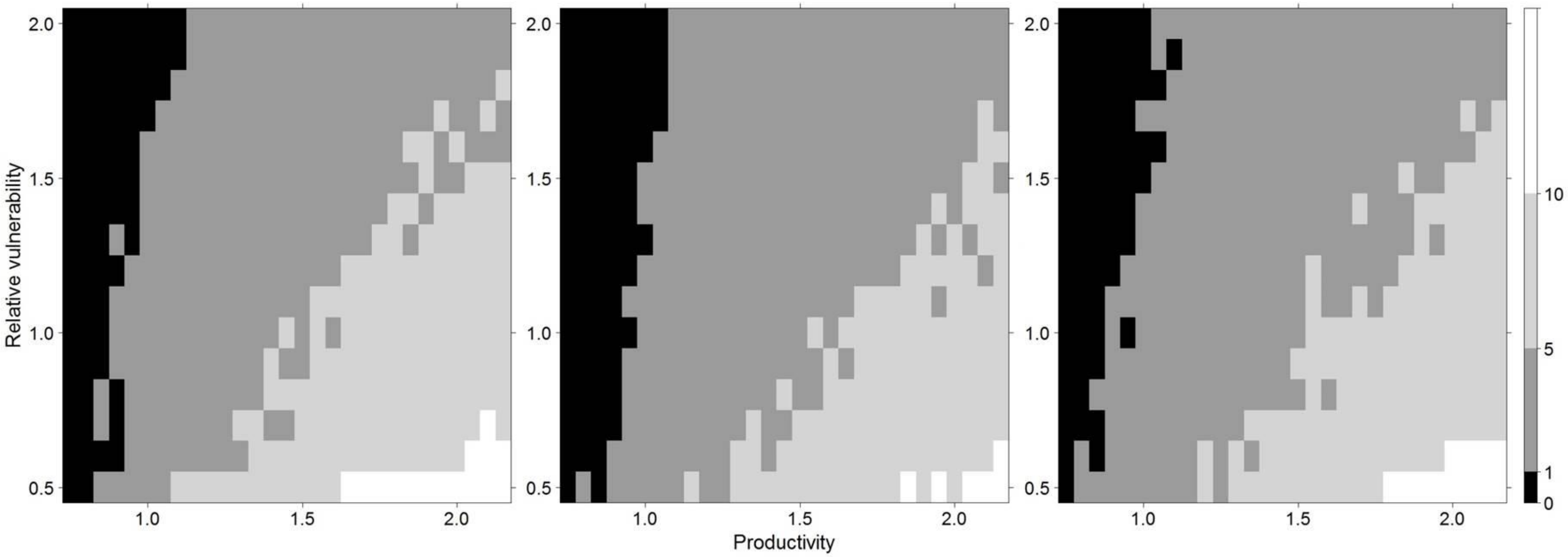


Figure F.2 Optimal fall harvest rates (expressed as percentages of the male population) as a function of population productivity (Productivity) and sex-specific fall harvest vulnerabilities (Relative vulnerability) across three scenarios of implementation uncertainty (no variation: left; double the baseline variation: middle; first-order auto-regressive variation: right). Spring male-only harvest was at medium levels (median = 30%). Colors indicate the ranges of optimal fall harvest rates, including no harvest (black), 1-4% (dark grey), 5-9% (light grey), and 10-15% (white).

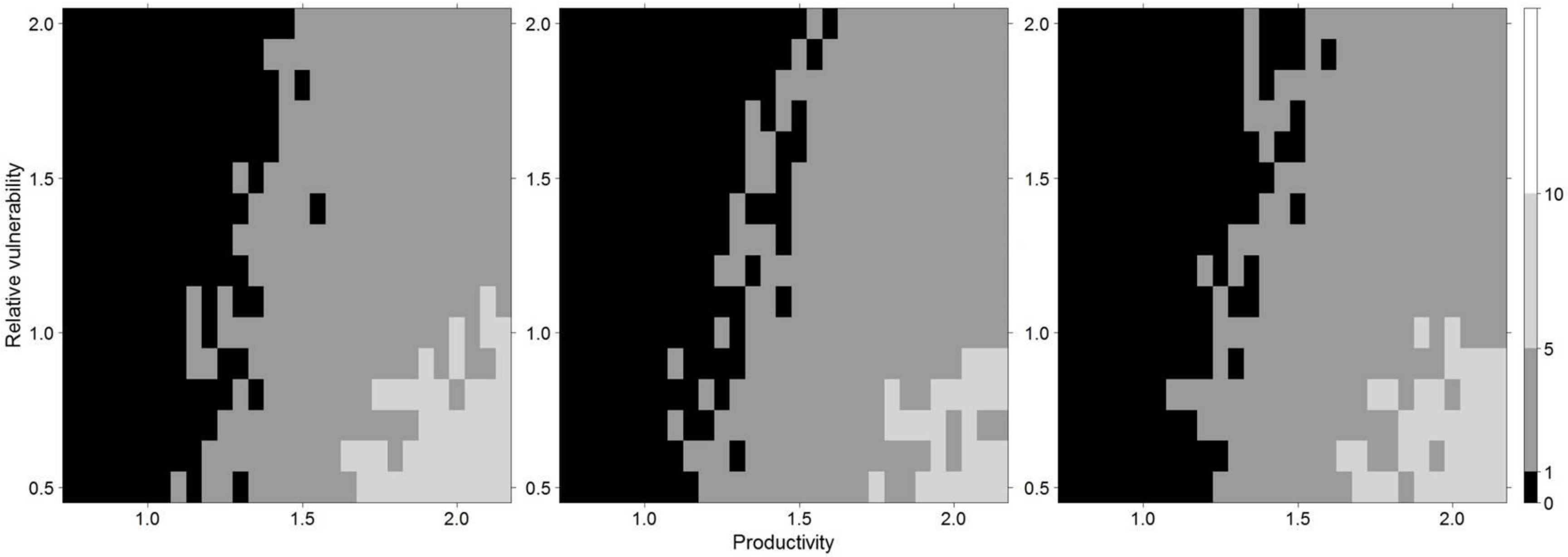


Figure F.3 Optimal fall harvest rates (expressed as percentages of the male population) as a function of population productivity (Productivity) and sex-specific fall harvest vulnerabilities (Relative vulnerability) across three scenarios of implementation uncertainty (no variation: left; double the baseline variation: middle; first-order auto-regressive variation: right). Spring male-only harvest was at high levels (median = 40%). Colors indicate the ranges of optimal fall harvest rates, including no harvest (black), 1-4% (dark grey), 5-9% (light grey), and 10-15% (white).

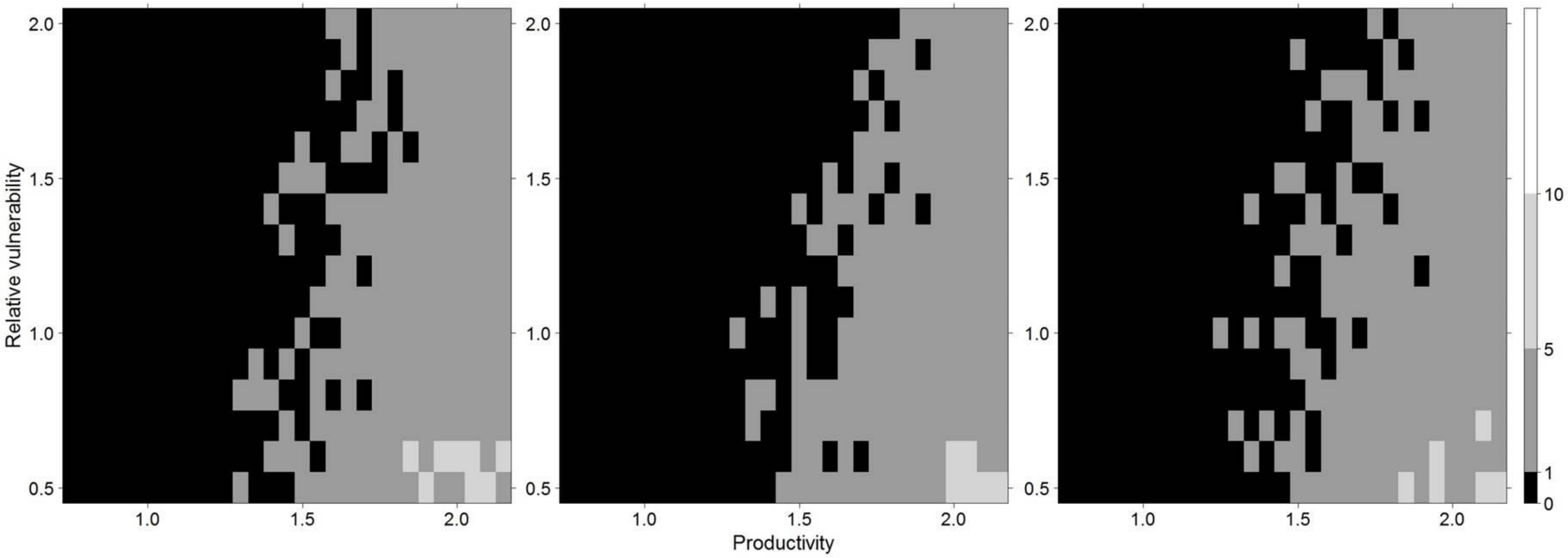


Figure F.4 Median abundances over time for simulations with uncertain values of productivity and vulnerability parameters, for low (blue), medium (black), and high (red) spring gobbler harvest scenarios. Median abundances are plotted over time for fall harvests of 7% (low spring harvest), 5% (medium spring harvest), and 4% (high spring harvest), which represent the optimal fall harvest rates in the presence of uncertain productivity and vulnerability when a utility function is used that represents linear changes to the value of fall harvest below the threshold of 0.5K (see Table F.1). The dotted line indicates the utility threshold of 0.5K, and this figure therefore demonstrates that reduced densities can likely be maintained if managers are less risk averse (as opposed to the original utility function) and more interested in maximizing annual harvests.

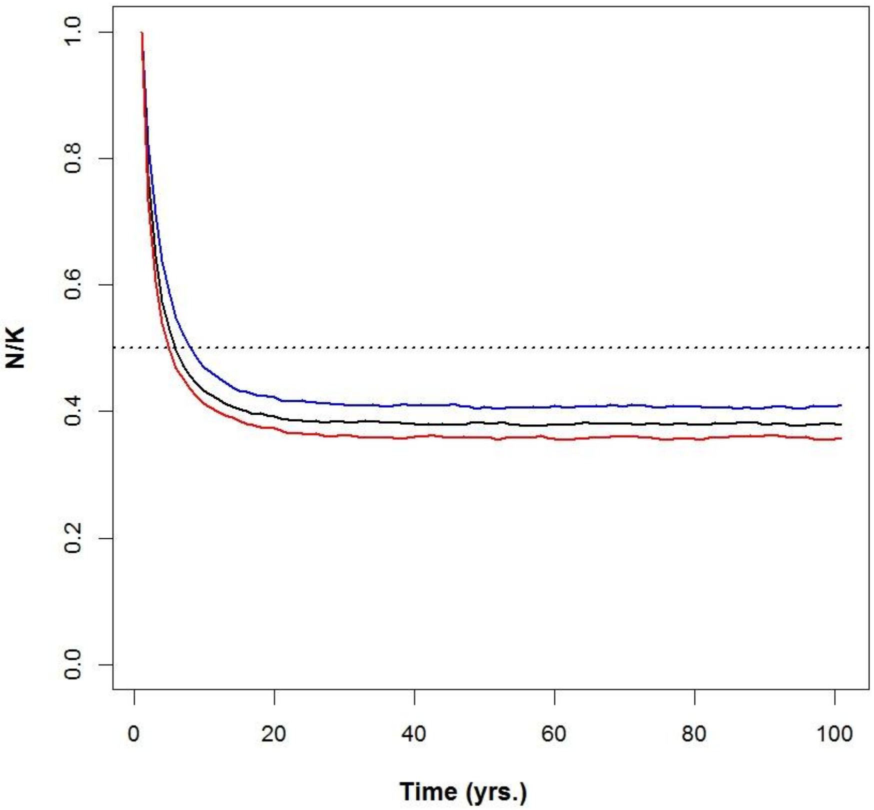


Table F.1 Optimal fall harvest rates (expressed as percentages of the male population) identified from decision analyses assuming uncertainty about the value of productivity and fall harvest vulnerability parameters, for different magnitudes of spring harvest and different composite utility functions. The utility function of original analyses (chapter 4) used a utility threshold of half of the environmental carrying capacity (K) to weight the value of fall harvest, where fall harvest was valued equal to spring harvest if abundance of turkeys the following spring was greater than 0.5K, and not valued at all otherwise. Here the threshold of used to determine value of fall harvest in the utility function was manipulated across multiple values (Threshold), and sensitivity of optimal fall harvest rates was determined. A utility function that decreases the value of fall harvest linearly if spring abundance falls below the threshold of 0.5 was also considered. Changes to optimal fall harvest rates as a function to changes in the assumed utility function demonstrate the effects of changes to fundamental population objectives, risk preferences, and the relative value of spring and fall harvests as a function of abundance at the start of spring hunting.

	Threshold[b]			
Spring harvest[a]	0.4	0.5	0.6	Linear[c]
Low	6	4	3	7
Medium	3	2	0	5
High	2	1	0	4

[a] Median spring harvests were 15% (low), 30% (medium), and 40% (high) of the population of males alive at the start of spring hunting (Appendix D)

[b] Utility threshold changes the value of abundance (originally 0.5K) used to determine the weight spring and fall harvest in the original composite utility function: $U(N, H_s, H_f) = \sum_T H_{s,t} + H_{f,t} \times u(N_{t+1})$, where

$$u(N_{t+1}) = \begin{cases} 0 \; if N_{t+1} < 0.5K \\ 1 \; if N_{t+1} \geq 0.5K \end{cases}.$$

[c] Composite utility function with linear change in the value of fall harvest as abundance falls below 0.5K: $U(N, H_s, H_f) = \sum_T H_{s,t} + H_{f,t} \times u(N_{t+1})$, where

$$u(N_{t+1}) = \begin{cases} {N_{t+1}}/{0.5K} & if N_{t+1} < 0.5K \\ 1 & if N_{t+1} \geq 0.5K \end{cases}.$$

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