Identifying target reference points for harvesting assessment-limited wildlife populations: a case study

BRYAN S. STEVENS,1,2 JAMES R. BENCE,1 WILLIAM F. PORTER,1 AND MICHAEL L. JONES1

1Department of Fisheries and Wildlife, Michigan State University, East Lansing, Michigan 48824 USA

Abstract. Identifying appropriate strategies for sustainable harvest is a challenge for many terrestrial vertebrate species because of uncertain system dynamics, limited data to inform population models, and potentially conflicting objectives that seek to harvest and maintain populations at desirable levels. The absence of monitoring and assessment infrastructure needed to regularly estimate abundance accentuates this challenge for many species, and limits application of rigorous state-dependent frameworks for decision making that are commonly advocated in natural resource management. Reference points, which define management targets or triggers for changing management, are often used to guide decision-making, but suffer from ambiguity when developed without explicit consideration of uncertainty or trade-offs among competing objectives. We describe an approach for developing unambiguous target reference points for assessment-limited species using structured decision making, and demonstrate the approach to develop target harvest rates for management of fall Wild Turkey (Meleagris gallopavo) harvests in the face of uncertain population and harvest dynamics. We use simulation and decision analyses to identify harvest rates that are optimal for accomplishing explicit management objectives in the face of uncertainty, and harvest rates with robust performance over broad regions of the demographic and harvest model parameter space. We demonstrate that population and harvest parameters commonly uncertain to wildlife managers interact to determine appropriate target harvest rates for Wild Turkeys, and that formally acknowledging a range of plausible values for structurally uncertain parameters results in more conservative target reference points than suggested by previously published studies. The structured decision making framework described here provides a natural conceptual and quantitative framework for extending our approach to develop unambiguous harvest targets for other assessment-limited wildlife populations while formally acknowledging structural uncertainty in system dynamics.

Key words: decision analysis; decision support; harvest management; robust management; structural uncertainty; structured decision making; sustainable harvest; Wild Turkey.

INTRODUCTION

Identification of strategies for sustainable exploitation of natural populations is a problem of global significance for conservation 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, starting with interpretations derived from deterministic population models and a single, maximum harvest objective, progressing through more realistic interpretations that incorporated uncertainty about population dynamics, and more recently acknowledging additional objectives concerned with 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), so clarification of social objectives motivating management is needed to guide development of preferred strategies for achieving successful harvest management (Johnson et al. 1997, Quinn and Collie 2005, Nichols et al. 2007). Although some have explicitly demonstrated such clarification (e.g., Johnson et al. 1997), sustainable-harvest objectives for many populations unfortunately lack such clarity and thus remain difficult to scientifically assess (Quinn and Collie 2005).

Models of population dynamics are central to assessing performance of sustainable-harvest management, but structural uncertainty about system dynamics impedes identification of reliable harvest strategies (Hilborn and Ludwig 1993, Francis and Shotton 1997, Williams 1997). Scientists often acknowledge multiple hypothesized models of population and harvest dynamics, leading to uncertain predictions of harvest management outcomes (Williams 1997, Milner-Gulland et al. 2001, Runge and Johnson 2002). Derivation of strategies for sustainable harvesting should therefore consider a variety of plausible models to ensure management performs adequately in the
face of uncertainty, and decision-analytic methods are commonly advocated for such purposes (Hilborn and Ludwig 1993, Shea et al. 1998). Decision-analytic methods typically combine principles of structured decision making (SDM; e.g., Hammond et al. 1999) with models of system dynamics to identify management strategies that are likely to meet sustainable-harvest objectives in the presence of uncertainty (Nichols et al. 1995, Johnson et al. 1997, Martin et al. 2009).

Formal adaptive harvest management (AHM) for North American waterfowl is a widely cited example of SDM applied to harvest management (Johnson et al. 1997, Nichols et al. 2007). AHM employs dynamic decision analyses to identify optimal harvest strategies recurrently over time, and reduces uncertainty through targeted monitoring programs that provide rigorous estimates of important state variables (e.g., abundance) and the responses of those variables to management (Nichols et al. 1995, Williams and Johnson 1995, Johnson et al. 1997, 2015). Proponents of AHM emphasize use of dynamic optimization methods (e.g., Lubow 1996, Marescot et al. 2013) to identify optimal state-dependent policies at regular intervals over time as a function of population abundance and environmental conditions (Johnson et al. 1997, Martin et al. 2009, Nichols et al. 2014). Although theoretically optimal, implementation of these methods presupposes a formal monitoring and assessment program is in place to estimate abundance or provide reliable, unbiased indices of abundance at regular intervals so that optimal policies can be updated over time. However, many animal populations lack the basic monitoring infrastructure necessary to estimate abundance or population trends reliably for such purposes (Costello et al. 2012, Weinbaum et al. 2013). Moreover, state-dependent management decisions are often made using uncalibrated abundance indices of unknown quality (i.e., assumed, but not demonstrated to be proportional to abundance), which can result in reduced management performance when underlying assumptions are violated (Moore and Kendall 2004). Thus, we seek to demonstrate a framework for developing sustainable harvest strategies for assessment-limited populations that lack all of the pieces needed to rigorously estimate abundance and employ formal AHM.

Development of tools to assess performance of harvest management for populations lacking regular assessment is needed (Costello et al. 2012, Weinbaum et al. 2013). Reference points can be useful as indicators of performance in such cases, 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 to guide management by indicating performance of a single best policy that management attempts to achieve (e.g., a target harvest rate most likely to achieve objectives), or performance for a set of policies that are robust to uncertainty (e.g., a set of harvest rates with reliable performance in the face of uncertainty; Irwin and Conroy 2013). Reference levels of simple metrics are commonly used to indicate sustainable harvests for assessment-limited wildlife populations (Milner-Gulland and Akçakaya 2001, Weinbaum et al. 2013), although they are not commonly referred to as reference points (phrase comes from fisheries management; MacNeil 2013). Moreover, such metrics usually do not acknowledge uncertainty in system dynamics, nor are they developed in the context of explicit management objectives. This results in indices of sustainable harvest with ambiguous interpretation relative to conservation and harvest goals for many data-limited terrestrial populations (Milner-Gulland and Akçakaya 2001, Weinbaum et al. 2013).

Principles of SDM can be used to develop management reference points (Irwin and Conroy 2013), thereby clarifying the interpretation of these simplified metrics in terms of specific objectives and providing a framework to assess their performance under uncertainty. Our objective was to demonstrate an approach for identifying target harvest rate reference points that can be used as indicators of long-term performance for management of assessment-limited wildlife populations. We show how application of a SDM approach, including stochastic simulation and static optimization, can be used to identify optimal target harvest rates that accomplish management objectives in the absence of a formal framework for regular abundance estimation. We illustrate the approach in detail with a case-study involving management of Wild Turkey (Meleagris gallopavo) harvests. However, the approach is generalizable for other species that lack the infrastructure needed to employ monitoring-intensive management strategies such as AHM.

**General Approach**

We 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. 1). In the absence of formal assessment programs or calibrated indices needed to make optimal state-dependent decisions, we use SDM to identify static target harvest rates to serve as target reference points to guide management in data-limited environments. Such static harvest policies could be implemented without formal abundance estimation by manipulating regulatory frameworks or hunter effort (e.g., through constant-effort management; Ludwig 2001) so as to achieve, on average, the desired target harvest rate. The SDM approach requires careful deliberation about underlying objectives, possible actions, and likely outcomes of management decisions (Shea et al. 1998, Hammond et al. 1999, Clemen and Reilly 2001). Thus, we apply SDM principles to develop target harvest rates by structuring the selection of target reference points as a decision problem, developing system models to describe the dynamics of populations and their
harvests, and using decision analyses to identify target harvest rates most likely to meet objectives in the face of common uncertainties (Fig. 1).

We structure the selection of target reference points by identifying the decision to be made (decision framing), articulating the objectives of sustainable harvest management, and identifying alternative management actions (Hammond et al. 1999, Clemen and Reilly 2001; Fig. 1). In this context, we frame the decision as one of selecting target harvest rates that are likely to achieve sustainable-harvest objectives if implemented over the long term. Sustainable-harvest objectives therefore need to be carefully specified, but objectives will 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 other than absolute abundance. For instance, objectives could relate to minimizing the variation of harvests or population fluctuations over time (Walters 1975). We refer to specific metrics used to measure management success relative to objectives as performance measures, and combine performance measures into a utility function (see, for instance, Kendall 2001, Runge and Walshe 2014) that explicitly clarifies management trade-offs between potentially competing objectives (e.g., harvest vs. abundance). The utility function also permits straightforward summary of performance via a single mathematical function that can be optimized, thus providing a practical way to assess performance of management actions relative to multiple objectives in the presence of uncertainty. In this context, simple utility functions may permit optimization of target reference points with respect to one performance measure (e.g., harvest) while keeping others (e.g., abundance) at or above threshold levels (see Case Study with Wild Turkeys). After clarifying management objectives in the form of a utility function, we then finish decision structuring by identifying possible management actions that represent decision alternatives. For this problem, decision alternatives represent a set of possible target harvest rates that could serve as indicators of successful management if implemented as a harvest strategy over the long term.
We use stochastic models of population and harvest dynamics to predict how sustainable-harvest performance measures respond to alternative target harvest rates (Fig. 1) in the presence of uncertainties common to harvest management (structural uncertainty, partial controllability, environmental variation; Williams 1997). The mathematical structure and complexity of models will vary with the ecology and life-history characteristics for the species of interest, the information available to parameterize management models, and the performance measures needed to identify successful management (Runge and Johnson 2002, Irwin et al. 2011, Williams 2013). In practice, there is often considerable uncertainty surrounding the appropriate deterministic and stochastic model structures needed to represent dynamics of both populations and their harvests, as well as for the appropriate values of individual model parameters (Francis and Shotton 1997, Williams 1997, Reagan et al. 2002). Here we consider uncertainty about how to represent population and harvest dynamics mathematically as representing structural uncertainty. In contrast, we consider annual, random realizations from stochastic models of population and harvest dynamics as representing environmental variation and partial controllability, respectively. In assessment-limited situations careful collaboration between modelers and subject-matter experts will likely be required to develop models that adequately describe system dynamics. However, preliminary simulation and sensitivity analyses can be used to identify uncertainties that have large effects on performance of target harvest rates (Fig. 1). Simulation and sensitivity analyses can also be formally exploited to learn about the conditions under which different harvest rates are likely to achieve management objectives (see Case Study with Wild Turkeys).

We use a process of simulation and optimization to conduct static decision analyses to determine how optimal target harvest rates change across specific values of model parameters for which there is strong uncertainty, to identify target harvests whose performance is robust but potentially suboptimal across values of these parameters, and to identify optimal target harvest rates in the face of ignorance about the values of structurally uncertain but important model parameters. We conduct decision analyses by determining how expected values of the utility function vary among alternative target harvest rates, where expected utilities are calculated using a combination of Monte Carlo simulation and static optimization (Williams and Nichols 2014:49). First, we use repeated stochastic population projections for each proposed harvest rate assuming discrete but known combinations of structurally uncertain model parameters. We calculate the utility for each simulation replicate and then the expected utility over all simulation replicates for each possible target harvest rate. We then repeat the entire process for different combinations of model parameter values to describe how optimal harvests change as a function of the unknown parameters, and to identify target reference points with robust performance over the parameter space. Last, we use decision analyses to identify optimal target harvest rates in the face of ignorance about the values of important parameters by replicating the simulation-optimization process using stochastic distributions, instead of discrete combinations of known values, to represent important but structurally uncertain parameters.

We identify optimal, and robust but potentially suboptimal, target harvest rates by comparing expected utilities among the set of possible harvest rate targets for each decision analysis. For analyses that simulated dynamics under discrete combinations of model parameters, the parameter combinations are intended to cover the plausible parameter space for the problem of interest, and optimal harvests are identified for each parameter combination by selecting the harvest rate with maximum expected utility. To understand robustness of potential reference points we also calculate relative utilities for each target harvest rate at each discrete combination of model parameters. We define relative utility as the expected utility for a given harvest rate divided by expected utility for the optimal harvest rate for the specific parameter values being considered (e.g., relative utility for the optimal harvest rate equals one). Comparison of relative utilities enables identification of target harvest rates that, while potentially suboptimal, perform close to optimally across a broad spectrum of the model parameter space. To identify optimal target harvest rates in the presence of ignorance about the values of important model parameters, the stochastic distributions used to describe plausible parameter values represent uncertainty nodes in the decision analyses (Peterman and Peters 1999), and thus expected utilities are calculated as expectations across distributions of values for these parameters. Last, we finish with post-hoc sensitivity analyses to ensure resulting inferences about appropriate target harvest rate reference points are robust to assumptions for which there are limited data to directly inform model development (Fig. 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 (Stevens et al. 2017b). Many Turkey population models were developed during a period of rapid population 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). 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., Clawson et al. 2015), monitoring data necessary to employ statistical 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 hunter effort and/or probability of harvest per unit effort) are either known or likely 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 decision**

The decision problem is to select target fall harvest rates that indicate 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 is not robust to structural uncertainty in Turkey demography that is common to modern management (Stevens et al. 2017b). While our primary focus is on developing reference points for management of either-sex fall harvests, male-only spring harvests also change in magnitude through space and time (Wright and Vangilder 2007, Diefenbach et al. 2012), and the degree of conservatism in spring harvest management varies by locality (Healy and Powell 2000). Moreover, for many data-limited populations, there is considerable uncertainty about how to mathematically describe the stochastic distributions used to represent partial controllability in management models, because the distributions of realized harvest rates resulting from management regulations have not been directly estimated. Thus, development of target reference points for management of fall harvests should consider multiple plausible scenarios of spring harvest to ensure robustness of results. Considering multiple spring harvest scenarios also facilitates development of reference points for management of fall harvests that are tailored to spring harvest experienced in the region of interest, if estimates of spring harvest mortality are available.

Evaluating performance of fall Turkey harvest requires careful articulation of objectives and the desired trade-offs between maintaining large harvests and large populations. Past studies often evaluated performance of proportional fall Turkey harvests for achieving simplified objectives relative to 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 or maintenance of current populations (i.e., $λ > 1$; 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 assume no limitation and thus populations could grow without an upper bound. More recently, population models were developed including density-dependent dynamics to reflect declining population growth over large scales (e.g., McGhee and Berkson 2007). Subsequent modeling exercises assumed the objective of Turkey management was to maximize harvest irrespective of abundances resulting from harvest maximization (McGhee et al. 2008). The objective of maximizing harvest implicitly assumes there is no desire to maintain large populations past the opportunities they provide for future harvest, and is inconsistent with social surveys of stakeholder groups that suggest hunters also value interacting with large numbers of Turkeys during the spring season (i.e., the perception of large populations; Cartwright and Smith 1990, Little et al. 2000, Swanson et al. 2007).

In Michigan, our collaboration with a diverse management stakeholder group, including representatives from both hunting and wildlife-viewing advocacy organizations, provided insight into Turkey management objectives. These interactions suggested hunters are interested in maximizing opportunity to harvest during spring, male-only hunting seasons. Because stakeholders favor the opportunity to pursue male Turkeys during spring, an objective of fall harvest is to maximize opportunity so long as fall harvest does not drive populations to socially undesirable levels in the short term, which would negatively impact the quality of spring hunting. Using this information, we developed a utility function that explicitly clarifies trade-offs between maintenance of populations and harvests

$$U(N, H_s, H_f) = \sum_t H_{sf} + H_{sf} \times u(N_{t+1})$$

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

In this function, $H_{sf}$ represents male-only spring harvest at time $t$, $H_{sf}$ 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 management are valued, and uses a utility threshold \((dT_{i+1}; \text{sensu Martin et al. 2009, Nichols et al. 2014})\) 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. Importantly, the value of \(K\) in this model (described in detail below) scales the absolute value of performance measures but does not affect the relative performance of different target harvest rates. Given that population size relative to \(K\) is used to define the utility threshold, and static decisions are being assumed, this ensures precise knowledge of carrying capacity is not needed to identify optimal target harvest rates. Optimizing this utility function seeks to maintain spring populations at or above half of \(K\), irrespective of its absolute value. If we were to set the utility threshold using a specific value of abundance (e.g., Johnson et al. 1997), however, we would then need knowledge of \(K\) because the absolute value of abundance would be used to weight fall harvest in the utility function, and absolute responses of \(N_{i+1}\) to harvest would be affected by the population position relative to \(K\). If an absolute abundance value was needed to define the utility threshold but no reliable estimates of \(K\) were available, one could also include the value of \(K\) as an additional uncertainty node in decision analyses (see treatment of \(\theta\) parameter in Decision analyses), and thus formally account for uncertain knowledge of carrying capacity when ranking target harvest rate reference points.

We considered target harvest rates that might serve as reference points for Turkey management as decision alternatives. Turkeys are somewhat unique among North American game animals in that they have multiple discrete, seasonal harvest periods each year (spring and fall). Target reference points could thus be developed for both spring and fall hunting seasons. Given that spring harvests are male only and either-sex fall harvests entail larger risks (Vangilder and Kurzejeski 1995, Stevens et al. 2017b), however, managers are often more concerned with the impacts of fall harvest on populations. Therefore, we focused on identifying target reference points for fall harvest management, and used a sensitivity analysis (see Decision analyses) to determine the robustness of appropriate fall harvest targets to the magnitude of spring harvest.

We compared target fall harvest rates by maximizing \(U\) over long time horizons \((T = 100 \text{ yr after model initialization})\). The set of possible target fall harvest rates 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 abundance 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 (with respect to spring abundance) and the valuation of fall harvests when spring abundance falls below the threshold (e.g., all-or-nothing vs. linear decrease). Thus we 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 Decision analyses).

Models of population and harvest dynamics

We modeled population and harvest dynamics using a sex-specific theta-logistic model developed for Wild Turkeys (McGhee et al. 2008, Stevens et al. 2017b). 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. As such, the general theta-logistic model was used to aggregate relevant biological processes into a composite growth function whose values were modified by density. This model was fit previously to Turkey population indices from 11 states by McGhee and Berksen (2007) to estimate the strength and form of the relationship between declines to population growth and abundance \((\theta)\), and used by McGhee et al. (2008) to identify maximum-sustainable harvests for a unique set of model input parameters. Model equations (Appendix S1) were used to represent population and harvest dynamics by

\[
N_{i+1} = N_i(1 - h_{i,i}z_i)\exp\left(1 - \left(\frac{N_i}{K}\right)\right) + \theta + 1 - H_{i,i},
\]

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 \((h_{i,i};\text{some incidental loss of females occurs during spring hunting})\), the new population growth \((\exp\left(1 - \left(\frac{N_i}{K}\right)\right)\)) \((\exp\left(1 - \left(\frac{N_i}{K}\right)\right))\), and the birds removed via fall harvest \((H_{i,i})\). In this model, sex-specific instantaneous growth rate \((r_{i,a})\) 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., \(K = K_m + K_f\)). Structural uncertainty in the value of \(\theta\) 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 \((\theta \sim \text{Normal}(\mu = 0.36, \sigma = 0.09))\); McGhee and Berksen 2007), and randomly drawn values were assumed constant for each individual population projection (see Decision analyses). Annual process variation in population growth
associated with environmental conditions ($\epsilon_f$) was drawn from a normal distribution using parameter values consistent with earlier studies ($\epsilon_f \sim \text{Normal} [\mu = 0, \sigma_f = 0.15]$; McGhee et al. 2008, Stevens et al. 2017b). A full description of the model and parameter values is provided in Appendix S1.

We modeled partial controllability as temporal variation of 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 S1). Variation in realized fall harvest for male Turkeys was modeled as coming from a lognormal distribution by multiplying target exploitation rates by an exponentiated log-scale random deviate ($h_{m,f,t} = \text{target}_{m,f} e^{\epsilon_f}$), where the magnitude of variation in fall harvests was assumed consistent with previous work ($\epsilon_f \sim \text{Normal} [\mu = 0, \sigma_f = 0.15]$; McGhee et al. 2008, Stevens et al. 2017b). Importantly, this approach to modeling partial controllability implicitly assumes that managers can manipulate the central tendency of realized fall harvest rates, for example by manipulating hunter effort through harvest regulations. Thus practical achievement of target harvest rates without knowledge of abundance would require some knowledge of the relationship between hunting regulations and realized harvest rates. As mentioned above with respect to spring harvest, the precise relationships between fall harvest regulations and realized harvest rates are poorly understood for many Turkey populations. Thus, in order to ensure target reference points ascertained in this study were achieved on average, management agencies would at least need some surveillance monitoring of realized harvest rates, for example using radio-marked or banded birds (e.g., Godwin et al. 1991, Diefenbach et al. 2012).

Realized fall harvest rates can be different between males and females (Vangilder and Kurzejeski 1995), so we allowed for differential fall harvest vulnerability by scaling female harvest rates by a linear function of the male harvest rate ($h_{f,f,s} = v_{m,f,s}$) using a relative harvest vulnerability coefficient ($v$). Realized values of spring harvest rates were also drawn from lognormal distributions (Appendix S1). Moreover, we assumed a priori that harvest mortality was unrelated and additive 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 models (Vangilder 1992, Vangilder and Kurzejeski 1995, Alpizar-Jara et al. 2001, McGhee et al. 2008) with some empirical support (Little et al. 1990, Godwin et al. 1991, Pack et al. 1999).

Previous analyses demonstrated that structural uncertainty in parameters governing population productivity and relative harvest vulnerability are important for predicting population responses to harvest with this model (Stevens et al. 2016, 2017b). Moreover, values of productivity and vulnerability appear to be 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 (Stevens et al. 2017b), and harvest and abundance resulting from a target harvest rate are sensitive to differences in relative harvest vulnerability among different segments of the population (Stevens et al. 2016). Structural uncertainty in the underlying values of these parameters for a specific population is thus directly related to the ability of managers to tailor harvest management to characteristics of local populations.

### Decision analyses

We used stochastic simulation and static optimization to understand how optimal target harvest rates change as a function of structurally uncertain model parameters whose values are often unknown to managers of data-limited Turkey populations, and to understand robustness of target reference points across a broad range of plausible conditions. To account for uncertain productivity, we 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 Stevens et al. 2017b). We also systematically manipulated harvest vulnerability ($v$) across a plausible range identified through literature review to account for uncertain differences in the central tendencies of realized fall harvest rates between male and female Turkeys (0.5–2.0 by increments of 0.1; see Stevens et al. 2016). Finally, to understand robustness of our conclusions to the magnitude of spring harvest, we replicated our analyses over three levels of spring harvest identified as plausible from literature review (Stevens et al. 2017b). Specifically, median male harvest during spring was manipulated among low (15%), medium (30%), and high levels (40%).

We conducted population projections to determine performance of target fall harvest rates over the range of model parameter values. For each potential target harvest rate (0–15%) we conducted 1,000 population projections (101 years each including initialization year) at each combination of productivity and harvest vulnerability (464 scenarios), and replicated the simulations over all median spring harvest levels for a total of 1,392 distinct scenarios. To account for structural uncertainty in the strength of density dependence we generated a random value of $\theta$ for each individual simulation replicate, but $\theta$ 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 we work,
we initialized all population projections with sex-specific abundances equal to their environmental carrying capacities.

We determined optimal target harvests and robustness of harvest rate performance using static decision analyses, where utility function values were calculated from outputs of stochastic simulations. For each simulation replicate we calculated values of the utility function at each time, and calculated the cumulative utility by summing over the entire time horizon (T = 100). From the distribution of utility values (over simulation replicates) for each target harvest rate we identified optimal target harvest rates for each parameter combination as those that maximized expected utility. 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, ϵp,t, ϵr,t, ϵf,t; Appendix S1) were represented with continuous probability distributions determined by literature review, and optimal target harvest rates were identified for specified combinations of productivity and vulnerability parameters. These 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.

We identified target harvest rates with robust performance by determining which target harvests were approximately optimal over the largest range of conditions (i.e., largest area of parameter space). We defined approximately optimal harvest rates as those whose relative expected utility (i.e., relative to optimal expected utility for a given set of parameters) was >0.80, thus indicating performance close to, but not quite achieving optimality. For each target fall harvest rate we calculated the proportion of the parameter space (i.e., the proportion of the 1,392 scenarios) where the relative expected utility for the harvest rate under consideration was >0.80. To evaluate sensitivity of these inferences we also repeated calculations over a range of lower bounds used to define approximately optimal performance for the relative expected utility calculations (0.75–0.95, by 0.05).

We also performed decision analyses to develop target reference points in the face of ignorance about the values of productivity and relative harvest vulnerability by assuming stochastic distributions for these parameters over their plausible ranges (instead of discrete but constant values described above). For this analysis the values of productivity and vulnerability were drawn randomly from uniform distributions for each simulation replicate 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) for this analysis, and utility values were summarized over the distributions of these additional uncertainties. For this analysis we used 10,000 stochastic population projections for each target fall harvest rate, and the entire analysis was replicated over each scenario of median spring harvest for a total of three decision analyses. Thus we identified optimal target fall harvests in the absence of estimates for productivity and vulnerability by identifying fall harvest rates that resulted in maximum expected utility over the distributions representing major uncertainties common to Turkey management.

Finally, we conducted sensitivity analyses to ensure inferences about appropriate target reference points were not sensitive to assumptions for which there were limited data to directly inform model development. Performance of harvest strategies can depend not only on the expected values of population and harvest models, 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 structure of temporal variability for fall harvest rates that result from a set of Turkey hunting regulations are not well described; thus the model of partial controllability described above was not directly estimated using data. To ensure reference points we identified are robust to assumptions about the nature of partial control, we replicated analyses described above that used discrete parameter combinations with different distributions of realized fall harvest rates through time. We lowered and increased the magnitude of fall harvest variation by eliminating variability (σt = 0) and then doubling (σt = 0.35) the variation relative to baseline levels (σt = 0.175), and also assumed realized fall harvest rates followed a first-order autoregressive process and were thus correlated through time (Appendix S1).

Because utility calculations include transient stochastic dynamics, inferences about appropriate target reference points could also be sensitive to assumption that initial abundance was equal to K. Thus we replicated simulations and utility calculations that assumed stochastic distributions for productivity and vulnerability, but with initial abundances equal to K/2 and K/4. Lastly, to demonstrate effects of changes to risk tolerances and specific population objectives, we replicated utility calculations with different locations for the utility threshold described above (0.4K, 0.6K), and assuming a linear decrease in the value of fall harvest when spring abundance falls below the utility threshold of 0.5K, where u(Nt+1) = Nt+1/0.5K if Nt+1 < K/2, and u(Nt+1) = 1 otherwise (as opposed to the all-or-nothing valuation of full harvest). For comparative purposes we also replicated utility calculations with no utility threshold, thus assuming the objective was to maximize cumulative spring and fall harvest over time. We programmed all analyses using R version 3.2.2 (Data S1, Metadata S1), and simulation outputs and are provided by Stevens et al. (2017a).

Results

Optimal and approximately optimal fall harvest rates were governed by the combination of spring harvest, population productivity, and differential harvest
vulnerability among the sexes. The marginal distribution of optimal harvest rates among simulation scenarios was right skewed and influenced by the magnitude of spring male-only harvests (Fig. 2). In general, larger spring harvests resulted in smaller optimal fall harvest rates and a greater frequency of no fall harvest being optimal (Figs. 2–3). More than one-half of optimal harvest rates across discrete combinations of productivity and vulnerability 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. 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. 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. 3). Moreover, 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, Appendix S2).

Robust fall harvest rates identified as approximately optimal over large regions of the parameter space, as well as optimal fall harvest rates in the presence of ignorance about the values of productivity and vulnerability were all ≤4% of the male segment of the population at the start of fall hunting. Robust fall harvest rates identified as approximately optimal (i.e., relative expected utility >0.8) over the largest region of parameter space ranged from 0% to 3% of the fall population (low spring harvest, 3%; medium spring harvest, 0%; high spring harvest, 0%), and within spring harvest scenarios, these values were relatively insensitive to changes in

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**Fig. 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 (a, low; b, medium; c, high).

**Fig. 3.** Optimal fall harvest rates (expressed as percentages of the male population at the start of fall) as a function of population productivity (productivity) and sex-specific fall harvest vulnerabilities (relative vulnerability), and across three scenarios of spring male-only harvest (low = left, medium = middle, high = right). Colors indicate ranges of optimal harvest rates, including no harvest (black), 1–4% (dark gray), 5–9% (light gray), and 10–15% (white).
the threshold used to define approximate optimality (Appendix S2). 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 male-only harvest, respectively. Importantly, the general patterns identified with our analyses were robust to magnitude and form of temporal variation in fall harvest rates (Appendix S3). Similarly, changes to optimal harvest rates as a function of initial population size at the start of simulations were trivial (Appendix S3). However, changes to the utility function were more consequential. Although changing locations of utility thresholds resulted in shifts in optimal harvest rates of only 1–2%, changing to a less risk-averse utility function with a linear decrease in utility of fall harvests, or to a utility function seeking to maximize annual harvest irrespective of spring abundance, increased the optimal fall harvest rates by 2–7 percentage points across scenario (Appendix S3).

**DISCUSSION**

**Target reference points for management of fall Wild Turkey harvests**

Uncertainty in parameters of population and harvest models has strong implications for the management of modern fall Turkey harvests. Uncertain parameters
representing productivity, vulnerability, and spring harvest govern the optimal target fall harvest rate, where productivity and vulnerability interact to determine appropriate targets. We demonstrate that fall harvest rates lower than those currently recommended (5–10%; Healy and Powell 2000) would outperform recommended rates for accomplishing modern objectives over most of the plausible parameter space for Turkey populations. These differences are due to a combination of differences in the treatment of uncertain parameters and the underlying management objectives assumed by this and earlier studies. For instance, previous simulation studies typically evaluated Turkey management performance over very narrow (and generally optimistic) slices of the plausible parameter space by assuming a unique set of model parameters (Stevens 2016). In addition, spring harvests have been liberalized in many areas and may be larger now than in earlier periods when accepted management guidelines were published (e.g., Healy and Powell 2000). We demonstrate that higher spring harvests combined with management objectives valuing sustained large Turkey populations drives optimal fall harvests to lower values. Our results point to more conservative fall harvests in the face of incomplete information about population and harvest dynamics, and suggest that target reference points should be set taking into account the magnitude of spring harvest when such information is available.

The optimal performance of reduced harvest rates relative to previous recommendations is important but also anticipated. Given that multiple hunting seasons occur annually, it is intuitive that larger spring harvests should leave less room for large fall harvests. Inclusion of additional parameter uncertainty in simulation models also commonly results in more conservative harvest recommendations than those deduced with a unique set of input parameters (Deroba and Bence 2008). In our case, the effect of additional structural uncertainty was exacerbated by the high sensitivity of optimal fall harvest rates to the values of model parameters (optimal target harvest rates ranged from 0% to >10%, Fig. 3), which also occurs when annual harvest maximization is the management objective (Stevens et al. 2017b). Thus, when our results are considered in light of earlier modeling studies that often used optimistic parameter combinations (i.e., high productivity, equal fall harvest vulnerability, and low spring harvest; Alpizar-Jara et al. 2001, McGhee et al. 2008) relative to the broader range of values we considered for structurally uncertain parameters, more conservative harvest recommendations are not a surprise.

Although our results suggest more conservative fall harvest recommendations than those provided by earlier studies, the amount of information available to local Turkey managers will determine the appropriate target reference points that are indicative of management success. In the absence of reliable information about productivity, vulnerability, and the magnitude of spring harvests, our 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 here. Moreover, if spring harvest regulations are liberal (e.g., harvest rates ≥30%), then a 1–2% harvest of males during fall hunting should be viewed as indicative of management that is likely to accomplish population and harvest objectives. If reliable estimates of productivity and vulnerability are available to local managers, however, then target harvest rates tailored to local populations can be identified using our results (i.e., Fig. 3).

We demonstrate that target reference points will be determined by management objectives, tolerance for risk of population declines, and the valuation of harvest and abundance, in addition to differences in structurally uncertain model parameters. This result is intuitive because optimal harvest strategies will be sensitive to assumed management objectives and choice of utility functions used to represent the value of management outcomes relative to those objectives (Walters 1975, Deriso 1985, Parma 1990). Our sensitivity analyses comparing multiple utility functions supported previous recommendations that larger fall harvest rates are likely warranted if managers primarily want large harvests and are not concerned with maintaining populations above a maintenance level (McGhee et al. 2008, Stevens et al. 2017b). Our results also imply that target harvest rates larger than the reference points we suggest may be biologically sustainable under some conditions (e.g., high productivity and low female harvest vulnerability). In addition, our sensitivity analyses demonstrate that if managers do seek to maintain populations above minimum maintenance levels but are less risk averse with respect to short-term population declines at the start of spring hunting (e.g., linear decrease in utility as abundance drops below utility threshold), then fall harvest rates >4% can likely be sustained at the expense of having smaller spring populations, at least when spring harvests are at low or medium levels. Importantly, our analyses can be easily adapted to use other utility functions that portray specific regional objectives if they differ than those considered here. Moreover, structured decision making provides a natural framework to identify target reference points under alternative Turkey management objectives.

**Identifying reference points for assessment-limited populations**

A primary goal of reference point development is to ensure reference metrics are indicative of management performance that achieves the underlying objectives (Irwin and Conroy 2013). Reference points have been most formally used for harvest management in fisheries, but their use has been advocated as applicable to a wide range of problems in resource management (MacNeil 2013). Fishery management reference points were originally developed to serve as general targets or decision thresholds in the absence of local information about
population dynamics or management objectives (Clark 1991, Mace 1994, Quinn and Collie 2005), but their development evolved to be tailored to specific problems because performance was often not robust to changes in species- and stock-specific dynamics and the management objectives assumed (Hilborn 2002, Hilborn et al. 2002). We demonstrate that unknown model parameters can interact to determine reference points that are indicative of successful management, and reiterate the need to evaluate potential reference points for a given problem using species-specific information about population and harvest dynamics. Although one can view using a reference point chosen to provide robust performance across a range of uncertain conditions (e.g., when specific parameter estimates are not available) as a somewhat generic approach, robustness is a desirable property in such situations and robust reference points can be tailored to the information available for a given problem. As our case study demonstrates, the development of target reference points for assessment-limited terrestrial populations can provide robust target harvest rates in the face of limited data and uncertain dynamics, and structured decision making is a natural framework for reference point development.

Development of reference points by evaluation of static policies provides a useful approach to inform harvest management for populations lacking the monitoring and assessment infrastructure needed to apply dynamic, state-dependent strategies to harvest management. We showed that SDM can be used to identify appropriate target harvest rates 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 2006, Deroba and Bence 2008, Hilborn 2012). However, we acknowledge that static policies likely come at the expense of reduced utility (e.g., more conservative harvest) relative to policies that provide feedback between annual harvest and abundance (Deroba and Bence 2008), and that the relative performance of static policies in general remains unclear. Under some conditions optimal static policies can perform comparably to state-dependent policies identified using dynamic programming (e.g., for cyclic environmental conditions or temporally correlated vital rates; Parma 1990, Walters and Parma 1996). Moreover, harvesting a small, fixed fraction of the population appears to be a static harvest strategy that is generally robust to uncertainty (Walters and Parma 1996, Milner-Gulland et al. 2001, this study). Thus we suggest there is value to employing static decision analyses to provide guidance for management of assessment-limited populations when the information needed to employ monitoring-intensive dynamic harvest policies is unavailable. However, additional research comparing performance for optimal static and dynamic harvest strategies in the face of realistic management uncertainties would provide valuable context and shed light on management performance gains that are possible with investments in assessment programs.

In our case study, we clarified specific population and harvest objectives by combining performance measures into a single composite utility function that described how outcomes of different target harvest rates are valued, which may be challenging for some data-limited populations. Summarizing objectives into a single utility function can be challenging when there are multiple stakeholder groups with diverse interests and values (Johnson and Case 2000, Johnson et al. 2015), and may not be possible for contentious harvest management problems (Bence et al. 2008) or situations where there are no estimates of past abundance to provide the context necessary for clarifying specific population objectives. If stakeholders and managers cannot agree on how to combine performance measures into a single utility function, then other approaches that directly compare simulated distributions of performance measures under different harvest strategies can be employed, and the merits of each strategy debated to resolve conflicts and reach consensus (Bence et al. 2008, Irwin et al. 2011). However, assessing robustness of reference points across changing conditions is more challenging in such a situation because there is no clearly defined optimal harvest. Identifying robust reference points without an explicit utility function would thus require much more effort and engagement between scientists, managers, and stakeholder groups to ensure that the degree of robustness is satisfactory for the problem at hand (Irwin et al. 2011).

Models are a fundamental component of decision making in conservation and resource management (Nichols and Williams 2006, Lyons et al. 2008, Irwin et al. 2011), and assessment-limited populations pose unique challenges for development of explicit models needed to identify target reference points through SDM. While decision makers often use implicit mental models to anticipate expected outcomes of management, mathematical models have the advantage of making linkages between management decisions and their expected outcomes transparent. In the absence of information needed to develop detailed models tailored to the ecology of individual populations, more general, production-type, population models (Hilborn and Walters 1992) that are adapted to specific life-history characteristics will likely be needed (Williams 2013, this study). Toward this end, important considerations for model development will clearly include the form and strength of density dependence operating through survival and recruitment processes (Walters 1975, Mace 1994, Runge and Johnson 2002, Ratikainen et al. 2008).

Although we demonstrated reference point development for a relatively short-lived species with the potential for large recruitment cohorts, the process of reference point development presented here is amenable to a variety of life-history strategies. For example, a theme of fishery management has been to link reference points to attributes of life-history characteristics (e.g., stock-recruitment dynamics and natural mortality; Clark 1991, Zhou et al. 2012). However, we would
expect reference points developed for more $K$-selected species to favor more conservative harvesting, and thus the previously described costs of reduced harvest potential relative to dynamic harvest policies could be large and depend on life history. Moreover, given that assessment-limited populations by definition have incomplete information on abundance, reference point development should include evaluation of robustness to starting population sizes used to simulate harvest dynamics, irrespective of life-history of the focal species.

An SDM approach provides a framework to identify harvest rates that are indicators of management performance, but on-the-ground implementation of such policies in assessment-limited environments may still prove challenging. Target reference points can serve either as specific targets that management is attempting to achieve, or as indicators of harvests 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 manipulate expected harvest rates experienced by the population being managed through regulatory processes. In fisheries contexts, implementation has often involved direct estimation of abundance, where total-allowable catch is set by multiplying target 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 alternatives. One such alternative is a constant effort strategy (Ludwig 2001), perhaps with occasional updates to effort that take into account changes in catchability, thus recognizing that the fraction of the population harvested per unit of effort can systematically shift over time (Maunder et al. 2006, Wilberg et al. 2010).

In assessment-limited environments it is perhaps more likely that reference points would be used not as specific harvest rates that management seeks to achieve, but as indicators of harvest rates that should be avoided. In this case, realized harvest rates could be estimated periodically via surveillance monitoring (e.g., using telemetry or tagging data) to ensure harvest is not exceeding reference levels, with regulations (e.g., seasons, bag limits, quotas, etc.) adjusted if they were. In this situation, a limitation remains whereby knowledge that harvest rates have exceeded reference levels does not indicate precisely how regulations should change to reduce harvest to target levels (Nichols and Williams 2006). Despite potential implementation challenges, however, we consider this to be a step forward from the current status quo where appropriate harvest of many populations is inferred using ambiguous metrics whose performance as indicators of management success has not been adequately demonstrated (Weinbaum et al. 2013).

Use of target reference points as developed here would help address the need for a stronger, evidence-based approach to management for many terrestrial species (Sutherland et al. 2004, Cook et al. 2010), and could form the basis for defensible long-term management or provide useful guidance during the development of AHM programs. Indeed, the approach described can be viewed as a formalized set of tools for the set-up phase of an adaptive management program (also referred to as deliberative phase; Lahoz-Monfort et al. 2014, Williams and Brown 2015). The general benefits of adaptive approaches are 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). If regulatory authorities were considering development of AHM programs, value-of-information analyses (Runge et al. 2011, Canessa et al. 2015) could supplement the process described here to formally elucidate the costs, benefits, and trade-offs involved when investing limited resources toward monitoring and assessment programs instead of other management actions (e.g., more efficient regulation enforcement; Hansen and Jones 2008). Regardless of the desire to develop formal AHM programs, development of target reference points as demonstrated here would provide a stronger scientific foundation to harvest management for many assessment-limited wildlife populations.

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LITERATURE CITED


SUPPORTING INFORMATION

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.1577/full

DATA AVAILABILITY

Data available from Figshare: https://doi.org/10.6084/m9.figshare.4980740.v1