**RH: Wild turkey Life-stage Analysis**

**Review of range-wide vital rates quantifies Eastern Wild Turkey population trajectory**

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**Abstract**

Recent declines in eastern wild turkeys (*Meleagris gallopavo silvestris*) has prompted increased interest in management and research of this important game species. However, the causes of these declines are unclear, leaving uncertainty in how to manage eastern wild turkey. Foundational to effective management of any game species, including wild turkey, is understanding the biotic and abiotic factors that influence demographic parameters and the contribution of vital rates to population growth. Our objectives for this study were to: 1) conduct a literature review to collect all published vital rates for eastern wild turkey over the last 50 years, 2) perform a scoping review of the biotic and abiotic factors that have been found to influence vital rates and highlight areas that require additional research, and 3) use the published vital rates to populate a life-stage simulation analysis (LSA) and identify the vital rates that make the greatest contribution to population growth. Based on vital rates from the eastern wild turkey’s entire distribution, our LSA estimated a mean asymptotic population growth rate (λ) of 0.91 (95% CI = 0.71, 1.12). Vital rates associated with after second year (ASY) females were most influential in determining population growth. Survival of ASY hens had the greatest elasticity (0.53), while reproduction of ASY females had comparatively lower elasticity (0.21) but high process variance, causing it to explain a greater proportion of variance in λ. Our scoping review found that most research has focused on the effects of habitat characteristics at nest sites and the direct effects of harvest on adult survival, while topics such as disease, weather, predator-prey dynamics, social structure, and indirect effects of harvest on wild turkey vital rates generally have been understudied. We recommend that future research take a more mechanistic and experimental approach to understanding variation in wild turkey population vital rates and consider multiple competing mechanisms.

**Key Words:** eastern wild turkey, elasticity, *Meleagris gallopavo silvestris*, life-stage simulation analysis, survival, population growth

**Introduction**

Eastern wild turkeys (*Meleagris gallopavo silvestris*; hereafter, turkey) are a widespread and abundant gamebird species that inhabit a variety of landscapes in eastern North America (Kennamer et al. 1992). Overhunting and habitat loss in the early 1900s resulted in the extirpation of turkeys from much of its distribution (Kennamer et al. 1992), but extensive restoration and translocation efforts led to turkey populations not only recovering but also greatly expanding outside of their historical distribution in recent decades (Dickson et al. 1992). Following successful restoration, many states liberalized turkey hunting regulations (Isabelle et al. 2018), making this species economically important as well (Chapagain et al. 2020). However, turkey populations have begun to decline again throughout the United States (Eriksen et al. 2015, Casalena et al. 2015), with many states reporting reduced poult to hen ratios, suggesting changes in productivity (Byrne et al. 2015). The causes of these declines remain unclear in many locations and may be the result of several factors throughout the turkey’s distribution (Eriksen et al. 2015, Casalena et al. 2015). The widespread nature of these declines has prompted increased interest and investment in research to identify the causative factors and determine the best management strategies to stabilize turkey populations (Balkom et al. 2017, Casalena et al. 2018, Borum et al. 2020).

Understanding the contribution of different life history stages or vital rates to a population’s growth rate is a fundamental goal of population ecology, as this knowledge can be used to identify the life stages that can be targeted most effectively for management (Crowder et al. 1994, Mills and Lindberg 2002, Johnson et al. 2010). It is also necessary to consider the natural range of variability for vital rates, as small changes in some vital rates may cause substantial changes in population growth (i.e., high elasticity) while also exhibiting relatively little variation in wild populations, leaving few opportunities to alter these vital rates through management (Gaillard et al. 1998, Mills et al. 1999). Alternatively, vital rates that have relatively small influences on population growth (i.e., low elasticity) may have greater effects on population size if these vital rates also exhibit high levels of variability within and between populations (Coulson et al. 2005, Raithel et al. 2007, Chitwood et al. 2015). The use of life-stage simulation analysis (LSA; Wisdom et al. 2000) has been especially valuable for the identification of vital rates that have the greatest impact on population growth rate. This is because LSA allows for the modelling of population growth or persistence using complex age and life history structures while incorporating information about variability in vital rates into a single framework (Wisdom et al. 2000). Further, the results from these models can serve as the foundation for subsequent simulations to evaluate how management actions that change vital rates may affect population growth (Wisdom et al. 2000).

Rarely included in studies of wildlife populations are discussions of the biotic and abiotic factors that influence population demographics and how much actual control managers may have in altering specific vital rates. Many wildlife populations may undergo substantial year-to-year variation because of weather, disease, predation, or inter-specific/intra-specific competition (Sinclair et al. 1989, Krebs et al. 2005, Sibley and Hone 2002). For harvested wildlife populations, hunting season length, timing, and harvest rate can have significant impacts on subsequent population sizes as well (Burger et al. 1994, Ginberg et al. 1994, Cooch et al. 2014). However, the importance of different factors in determining vital rates often varies temporally, spatially, and with population size (i.e., density dependent factors), complicating the process of determining the mechanisms underlying population growth for many wildlife populations (Sinclair et al. 1989). For some species, the importance of different factors in regulating or limiting population growth has been the source of intense debate (Matinez-Padilla et al. 2014). However, lack of certainty about the factors most important to influencing a species growth rate can place a limit on a manager’s ability to address population declines (Runge et al. 2011) or lead to ineffective or counterproductive management practices and reduce public trust in management agencies (Riley et al. 2018).

Turkey have been the subject of considerable research over the last 30 years, resulting in a large body of literature. A synthesis of turkey vital rates and the factors that influence them across their distribution could provide a clearer understanding of potential causes for the recent large-scale decline in turkeys. Therefore, the objectives of this study were to: 1) conduct a review of published turkey literature over the last 50 years to obtain vital rates across the distribution of eastern wild turkey, 2) perform a scoping review of the biotic and abiotic factors that have been studied in relation to turkey vital rates and highlight areas that require additional research, and 3) use the published vital rates to populate a LSA population model and identify the life stages that provide the greatest contribution to wild turkey population growth rate and identify research needs for wild turkey demographic data. Our review specifically focused on population studies and the factors that regulate or limit turkey abundance, and as a result, our goal was not to formulate specific management recommendations but instead to review areas that have received more or less attention in the literature. Our intention is for this review to summarize and improve our understanding of turkey population dynamics and inform further discussions regarding wild turkey research and management.

**Methods**

*Literature Review*

In June 2021, we used SCOPUS and Google Scholar to conduct a web search of all ecological and wildlife journals to locate peer-reviewed articles that reported vital rates for turkeys (eastern subspecies only). We used combinations of primary search terms (i.e., wild turkey, eastern wild turkey, *Meleagris gallopavo silvestris, Meleagris gallopavo*) and secondary search terms (i.e., survival, adult survival, nest success, poult survival, recruitment, clutch size, vital rates, demographic rates) to develop a list of titles and abstracts for publications that reported information about turkey vital rates. We also searched the literature cited sections of published articles for additional publications. We excluded government reports and unpublished theses and dissertations from our final list because it was unclear to what extent most of these documents had undergone peer review, and much of this information was published in peer-reviewed outlets gathered by our search. Our search process also yielded papers focused on other turkey subspecies (e.g., Merriam’s [*M. gallopavo merriami*], Rio Grande [*M. gallopavo intermedia*], Gould’s [*M. gallopavo mexicana*]). Additionally, we conducted a complete review of the Proceedings of the National Wild Turkey Symposium (1959-2016), following the same procedure described below to extract vital rates and information about factors that influence wild turkey demography.

From the journal articles and conference proceedings retained for further review, a single reviewer (DWL) examined each paper and extracted any vital rates that were reported for males or females (vital rates defined in Appendix 1; Figure 1), as well as associated sample sizes and error estimates (e.g., standard errors, standard deviations, confidence intervals). When no error estimates or sample sizes were reported, we still recorded the vital rate, but those entries were only used for summary statistics and not in the subsequent distribution-wide analysis. In addition to vital rates, we assessed each paper to determine if it evaluated possible mechanisms for variation in vital rates. We considered a paper to have evaluated a mechanism if it reported some causative or correlative statistical analysis between a vital rate and an abiotic or biotic variable. Importantly, we did not consider hypotheses introduced by the authors in the introduction or discussion as a possible mechanism if the paper did not also include a quantitative evaluation of that mechanism (e.g., Wright et al. [1996] suggested low overwinter survival was the result of above average snowfall but did not provide an analysis to support the statement). As we did not review studies that did not report vital rates, we acknowledge that there are studies that were not included on topics such as behavior, habitat use, or disease occurrence. These studies are important, as they provide insight into wild turkey ecology and management, but because they do not provide a direct evaluation of how these factors influence vital rates, they provide only indirect information about the biotic and abiotic conditions that determine turkey population trajectories and could not be used in our analysis.

For studies that evaluated possible mechanisms for variation in vital rates, we categorized each of the possible mechanisms into five broad categories that described either intrinsic or extrinsic factors that may influence turkey populations. Within each of the five broad categories, we further classified studies into finer-scale sub-categories. These categories and sub-categories were selected because they represented different groups of variables that are believed to influence game species population dynamics and have been suggested to be important in influencing turkey populations in previous literature (Weinstein et al. 2007). For intrinsic factors, we included a category for individual or behavioral factors that included sub-categories for age, experience, or body condition, movement and space use, social structure, genetics, or life history/behavioral state. For extrinsic factors, we included categories for biotic interactions (e.g., predation, disease/parasitism, inter/intraspecific competition), habitat factors (e.g., fine scale habitat, landscape scale habitat, habitat management and forage availability/quality), weather conditions (e.g., breeding season weather and nonbreeding season weather), and anthropogenic factors (e.g., direct effects of harvest, indirect effects of harvest, and non-hunting related human related factors). We summarized the number of studies in each of these categories to provide an overview of existing published work and to highlight potential gaps in the literature.

*Data analysis*

Using the vital rates extracted from the literature, we conducted a life-stage simulation analysis (LSA; Wisdom et al. 2000) for eastern wild turkey. Turkey populations have expanded considerably beyond their historic distribution, but we restricted our LSA to vital rates collected within the eastern wild turkey’s historic distribution, as vital rates from newly colonized areas may not be representative of population dynamics within the historic distribution. We defined a female-only pre-birth pulse matrix model for two stages (SY = second-year adults [i.e., 1-year-olds], ASY = after-second-year adults [i.e., 2+ years old]):

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where *R* represents annual reproductive output and *S* represents annual survival rate. We defined *R* from the following components (see Eq 1): incubation initiation (*II*), apparent nest success (*NS*), clutch size (*C*), hatching rate (*H*), apparent poult survival to 28 days (*PS*), and youth survival from 29 days to 365 days (*S*Y) (Figure 1) (Taylor et al. 2012, McCaffery and Lukacs 2016). Vital rate definitions and how they were calculated can be found in Appendix 1. We limited our model to two adult stage classes because few studies reported actual ages of birds because of the difficulty of correctly aging adult turkeys in the field beyond broad classes (second year adult, after second year adult). Because most studies that reported nest success and brood survival used methods that likely resulted in biased survival estimates (Appendix 1), we choose to refer to these parameters as apparent nest survival and apparent poult survival to acknowledge the known biases in the estimates. Most studies reported nest initiation as the proportion of hens that began incubating a nest. However, these estimates likely do not accurately reflect nesting efforts, as hens that failed to begin incubation may have attempted a nest but lost it prior to the onset of incubation (McPherson et al. 2003). To highlight this potential bias in reported vital rates, we refer to nest initiation rates as incubation initiation (*II*).

We allowed reproductive vital rates to vary between nesting attempts by the stage class of adult hens (second year adult, after second year adult). Turkeys generally only attempt a second nest if the first nest fails (1-*NS*1), so a single hen’s reproductive contribution for a year can come from either a first nest or a second nest (Dickson et al. 1992). Although additional nest attempts after failure of the second nest have been observed, these nesting events were rarely reported in studies, so we did not include them in our model. Therefore, we defined reproduction for each stage class (*a*) as:

(Eq 1)

The additive (bracketed) terms in the equation represent the number of poults from a first or second nesting attempt, respectively, that survive to 1 year of age. We assumed an equal sex ratio of eggs and therefore divided clutch size by 2 to estimate the number of female poults.

Because vital rate data were reported differently across studies, some standardization was necessary for use in our analysis. First, we transformed all vital rate estimates reported as percentages to probabilities by dividing the estimate and its standard error by 100. Second, we transformed mortality to survival by subtracting the mortality estimate from 1 (standard error remained unchanged under the binomial distribution). Third, we removed duplicate estimates to the best of our ability. For example, one study (Shields and Flake 2006) reported apparent poult survival from 0-14 days, 14-28 days, and 0-28 days (inclusive of the previous two estimates), so we only used the estimate for 0-28 days.

After standardizing the vital rates, we removed estimates that combined SY and ASY adults or did not report standard error or another measure of variation that allowed us to estimate standard error. For estimates that did not report a standard error but included another measure of variation, we calculated standard error in one of three ways. First, for estimates that reported a standard deviation and assumed a normal sampling distribution of the vital rate, we calculated standard error by dividing the standard deviation by the sample size. Second, for estimates that reported a confidence interval but no standard error, we assumed the sampling distribution was normally distributed and calculated SE from the CI as: (upper limit – lower limit)/3.92 for 95% CI, and (upper limit – lower limit)/3.29 for 90% CI. Third, for estimates of nesting rate, apparent nest success, or survival that had no reported SE or CI but reported sample size, we estimated standard error from the binomial distribution as:

, (Eq 2)

where *p* represents the point estimate of the vital rate and *n* represents the sample size. If we were not able to estimate standard error in any of these ways or the reported standard error was 0, we removed the estimate from our analysis.

To complete the LSA, we created process distributions for each vital rate defined in our matrix. Most vital rates reported in peer-reviewed studies include variability that is the result of biological process variance (true variance in a vital rate resulting from spatial or temporal variation in habitat, population dynamics, or life history) and variation resulting from sampling error (Raithel et al. 2007). To estimate the process distribution (i.e., mean and standard deviation) of each vital rate, we had to separate sampling error from process error. To do this, we modeled the observed estimates as random variables drawn from a normal distribution centered on the true parameter value, with a standard deviation equal to the standard error of the estimate. For example, we used observations of incubation initiation probability (*yII*) for age class *a* and nest attempt *n* to estimate mean incubation initiation probability *II* via the equation:

(Eq 3)

We did not have data on hatching rates for re-nesting attempts because few studies reported it separately for adult age classes, so we estimated the process distribution of hatching rate from first nests only. We defined youth survival from 29 – 365 days (*S*Y) from second-year adult annual survival standardized to this shorter time period, using

. (Eq 4)

We ran models for all parameters in JAGS 4.3.0 (Plummer 2003). We used uninformative Uniform (0, 1) priors for all vital rates except clutch size, which we gave a normal prior centered on the mean observed clutch size, with a standard deviation equal to the standard deviation of observed clutch sizes. We ran 3 chains for 30,000 iterations with the first 10,000 as burn-in, with no thinning. We inspected the MCMC plots visually for convergence and checked for R-hat values < 1.1 (Gelman and Rubin 1992). The mean and standard deviation of the posterior distribution describe the process distribution of each vital rate (Table 1).

After defining the process distributions for our vital rates, we performed the LSA in R 4.1.3 (R Core Team 2022). For each of 10,000 replicates, we drew a value for each vital rate from either a normal distribution (for clutch size) or a truncated normal defined between 0 and 1 (for all other vital rates). We used Equation 1 to calculate reproduction for each replicate and populated our matrix model accordingly. We assumed no correlation structure among vital rates because few estimates exist for these parameters in wild turkeys (Alpizar-Jara et al. 2001). We calculated the asymptotic growth rate, λ, from the dominant eigenvalue for each simulation replicate. We calculated elasticity for each replicate using the R package popbio and calculated mean elasticities across all replicates (Stubben and Milligan 2007). Finally, we performed linear regressions to compare our 10,000 values of λ to the 10,000 values of each vital rate. We used the resulting coefficient of determination (*R*2) values to determine the amount to which variation in each vital rate explained variation in λ (Wisdom et al. 2000).

**Results**

Our literature review resulted in an initial list of 89 peer-reviewed journal articles that reported vital rates for turkey. Twenty-one (24%) were focused on subspecies other than eastern wild turkey and were excluded from subsequent analyses. This left 68 papers (76%) for analysis inclusion, including 20 from the National Wild Turkey Symposia. Publication dates ranged from 1970 to 2021 (Figure 2). The most widely reported vital rate was apparent nest success (*n* = 36; 53%), followed by nesting rate (*n* = 31; 45%), annual survival (*n* = 28; 41%), and apparent poult survival (*n* = 20; 29%). Notably, no studies (0%) reported youth survival (i.e., survival from 28 days to the first breeding season). Of these 68 papers retained for analysis, 45% did not evaluate any underlying mechanisms (e.g., weather variability, predator removal, habitat management) for variation in vital rates and only presented vital rate estimates and raw sources of mortality.

*Scoping Review--Nests*

The most studied factor relating to nest survival was the effects of vegetation, cover, or habitat (*n* = 17; 25%; Table 2). Studies occurred at both fine scale (i.e., vegetation composition or structure at the nest site) and landscape scale (i.e., composition of habitat over large areas or distance to landscape features), with nine studies (13%) and eight studies (12%) respectively (Table 2). Only three studies (4%) directly evaluated the effects of habitat management on nest sites, with all three studies being related to prescribed fire. One study (1%) examined the effects of predator removal. Nine studies (10%) evaluated intrinsic factors that may influence apparent nest success, with five (7%) of those studies evaluating the effects of the attending hen’s age or body condition and the remaining three (4%) studies evaluating the effects of the attending hen’s space use on apparent nest success (Table 2). Four studies (5%) reported effects of weather on apparent nest success, and no studies (0%) reported effects of biotic interactions (e.g., changes in predator communities or densities) for apparent nest success, despite predation being frequently reported as the main source of nest loss.

*Scoping Review--Adults*

The effects of hunting season timing and duration was among the most studied topics for adults (*n* = 6; 9%), with most of these studies focusing on males (Table 2). The next most studied topics were related to intrinsic factors, including individual age/body condition (*n* = 5; 7%), reproductive status (*n* = 4; 6%), and space use (*n* = 1; 1%) (Table 2). Three studies (4%) evaluated how habitat composition at landscape scale influenced survival, with only two studies (3%) evaluating the effects of management on survival (both related to supplemental feeding in the winter). Only one study (1%) directly evaluated the effects of weather on adult survival. Similar to nesting studies, no studies (0%) evaluated biotic interactions (e.g., changes in predator communities or disease), despite predation being frequently reported as the main source of adult mortality (Table 2).

*Scoping Review--Poults*

Only 6 studies (8%) reported variables that influenced poult survival, with all these studies using brood flush counts to estimate survival (Table 2), and no studies quantified poult survival from marked poults. Three (4%) of those studies evaluated the effects of breeding season weather on poult survival. Two studies (3%) evaluated both landscape-scale and fine-scale habitat factors on poult survival, and one study (1%) evaluated the effects of movement and space use on poult survival.

*Life-stage simulation analysis*

From the 89 peer-reviewed papers, we recorded 1144 vital rate estimates from all subspecies of wild turkey and documented 976 vital rates specific to eastern wild turkey (85% of all vital rates reported) from 68 papers. Of those 976 vital rate estimates, 637 (65%) were relevant for our analysis (Appendix 1). Further, 500 (51%) included a usable metric of variation and 174 (18%) provided female estimates appropriately separated by stage class (Table 1, Figure 2).

Our estimated mean λ across 10,000 replicates was 0.91 (95% CI = 0.71, 1.12; Figure 3), representing a mean estimate of 9% annual decline in turkey abundance. Of the 10,000 model iterations, 81% of lambda estimates were < 1. indicating a declining population trend (Figure 3). The mean elasticities across all replicates were 0.05 for second-year (SY) adult female reproduction, 0.21 for SY adult female survival, 0.21 for after-second-year (ASY) adult female reproduction, and 0.53 for ASY adult female survival, indicating that ASY adult female survival had the greatest proportional effect on population trajectory (Table 3).

Through our linear regression analysis, we determined that 12% of variation in λ was explained by ASY adult female survival and 74% was explained by ASY adult female reproduction (Table 3). Of the component vital rates making up ASY adult female reproduction, by far the most influential was apparent poult survival (explaining 51% of variation in λ); each of the other components of ASY adult female reproduction on its own accounted for 7% or less of variation in λ (Table 3). Variation in reproduction for second-year females explained only 8% of the variation in λ (Table 3).

**Discussion**

Understanding the influence of biotic and abiotic factors on wildlife population dynamics has been a foundational tenet of wildlife ecology since the earliest stages of wildlife management as a profession (Leopold 1933). Multiple authors have encouraged the need for wildlife science to place greater emphasis on the testing of hypotheses about the factors that regulate wildlife populations (Krebs 2002, Guthery 2007, Romesberg 1981, Sells et al. 2018) in addition to studies that describe the "state of nature" (Williams et al. 2020). These calls have become more urgent as biodiversity is declining globally, with even common species such as the wild turkey declining. Using an LSA incorporating information from the eastern wild turkey's entire historic distribution, we estimated a mean population trend of 9% decline per year. Our estimate for population growth may underestimate population trends, as much of the demographic data that we used was collected during a period before most areas noticed population declines (Figure 2). For example, trap-and-transfer restoration practices in the 1980s and 1990s might have masked low population trajectories in more established populations. The proposed causes for recent declines have included a range of factors, including reduced habitat quality and quantity, changes in predator abundance and predator communities, weather variability, increased disease prevalence, and changes in hunting pressure (Casalena et al. 2015). However, our review of the turkey literature suggests managers may be ill-equipped to understand and address current declines given the research that has been published. Specifically, approximately half of studies reviewed provided no analysis of mechanisms that may influence reported vital rates. For many factors that can influence turkeys, our knowledge is sparse (e.g., effects of weather during different life stages) or nearly non-existent (e.g., effects of changing predator communities). Additionally, information regarding certain demographic stages was unavailable, such as survival rates for the youth life stage, or based on data that is unreliable, such as brood flush counts (Dahlgren et al. 2010a, Orange et al. 2016, Kubečka et al. 2021). Overreliance on biased data collection methods may limit our understanding of turkey population dynamics and further hamper recovery efforts. Given the current decline of turkeys and the increased interest in turkey research, we believe the field is at a critical juncture requiring reflection on how we approach turkey research and whether our current approach is providing reliable and accurate management recommendations.

Gamebird survival and reproduction is often the result of complex interactions between factors such as habitat, predator-prey dynamics, weather, and harvest pressure, among other factors (Tanner et al. 2017, Shipley et al. 2020, Howell et al. 2021, Powell et al. 2022). We found that few studies considered many of these topics for turkeys, with most of the focus in the literature being on evaluating the effects of harvest on adult survival and habitat conditions on nest success. The focus on these topics is unsurprising given the importance of understanding the effects of hunting on populations in setting harvest regulations (Alpizar-Jara et al. 2001, McGhee et al. 2008) and because habitat conditions at the nest site are thought to influence factors related to nest success, including the ability of predators to detect the nest and protection of the nest from adverse weather (Conover et al. 2010, Hovick et al. 2014). However, this focus leaves considerable gaps in our knowledge of the factors influencing turkey population dynamics. For example, weather has been shown to influence various life stages in turkeys, including nesting (Roberts and Porter 1998b, Lavoie et al 2017), poult survival (Roberts and Porter 1998a), and over-winter survival (Lavoie et al. 2017), and weather is an important determinant of survival and reproduction in many other galliforms (Flanders-Wanner et al. 2004, Tanner et al. 2017, McConnell et al. 2018, Londe et al. 2021). However, with only limited studies for most life stages, it is unclear how the occurrence of specific weather or changing weather patterns influences the survival of turkeys during different life stages. Similarly, while turkey habitat selection has been extensively studied and turkeys have been shown to have diverse habitat needs throughout the year (Little et al. 2016, Pollentier et al. 2017, Parker et al. 2021), outside of the nesting season, there is little information on what habitat factors are most important for survival. Astonishingly, even for factors such as predation, that are frequently suggested as significant contributors to turkey mortality (Shields et al. 2006, Pollentier et al. 2014, Little et al. 2016, Byrne and Chamberlain 2018), there has been little effort to understand how changes in predator communities influence turkey populations. This is a significant gap in our understanding of turkey population dynamics given that predator community composition and abundance have changed significantly across the turkey's distribution during the period of turkey decline (Prugh et al. 2009, Casalena et al. 2015, Conner and Cherry 2017). Without understanding how different factors (e.g., predators, habitat quality, weather) influence vital rates or interact to shape population trends, it is difficult to assess the role of any given factor in limiting or regulating a population (Sinclair 1989). This uncertainty is a significant challenge for effective management of turkeys and increases the risk of making management decisions that are either ineffective or counterproductive.

Like previous population modeling efforts for turkeys (Roberts et al. 1996, Rolley et al. 1998, Pollentier et al. 2014), survival and reproduction of ASY females were the most influential vital rates for determining turkey population growth. Particularly, survival of ASY females had the greatest elasticity, suggesting minor changes in this parameter can significantly affect population growth; however, this parameter also had low variation. In contrast to survival of ASY females, reproduction by this stage class was less elastic, but was much more variable and explained a greater amount of variance in λ compared to their survival. The higher variance in ASY reproduction suggests managers may have greater ability to influence this life stage through management compared to ASY survival. However, the degree of actual control managers may have on turkey vital rates depends on the abiotic or biotic conditions that limit them. For example, managers may have only limited ability to improve survival or reproduction if weather is the dominant driver but may have greater control if other factors such as habitat quality, predators, or harvest are the primary drivers. Identifying the effects of different factors on a population's vital rates will be essential for determining the most appropriate management approaches going forward. For populations where limiting factors are largely unknown, the use of precautionary measures such as eliminating female harvest may be advisable given the importance of adult females to population growth. Finally, while changes in one or a few vital rates may cause local declines, improvements in multiple vital rates may be required to achieve stable growth for a recovering population (Allen et al. 2022). This implies that managers should attempt to address all potential limiting factors as they become more apparent with empirical data.

Our literature review of turkey vital rates revealed several basic research needs and data considerations that can improve our understanding of turkey demographics. These research needs largely echo challenges highlighted for other galliform species, emphasizing the pervasiveness of these problems in managing gamebirds (Sandercock et al. 2008, Taylor et al. 2016). First, most vital rates we extracted could not be included in our LSA because of inconsistencies in reporting sample sizes, error estimates, or stage-specific results (e.g., reproduction or survival of second year individuals versus after-second-year individuals). Additionally, many studies did not include these basic summary statistics associated with their estimates. Similar to the need to standardize population monitoring and reporting of harvest data for wild turkeys (Chamberlain et al. 2022), a similar effort is needed to standardize the reporting of vital rates in peer-reviewed works, as this could substantially improve the utility of study results to management and future research.

Second, while multiple studies have shown survival differs across the year (Nguyen et al. 2003, Norman et al. 2004, Humberg et al. 2009), we were unable to directly incorporate that information into our population models as most studies used different time frames to report seasonal survival. Including seasonal survival estimates may be beneficial for management as specific periods of low adult survival (e.g., winter in the northern portion of the turkey's distribution [Wright et al. 1996]) may represent demographic bottlenecks for turkeys (Pollentier et al. 2014). While developing a single standard for reporting seasonal survival may be difficult because the phenology of turkey behavior varies across the species' distribution (Whitaker et al. 2005), defining periods based on turkey behavior or biology rather than calendar dates may help standardize these results.

Third, by relying on incubation behavior, most estimates of nest survival or nest initiation did not account for nests lost prior to incubation or undetected by observers. As a result, nest success estimates are likely biased high in many cases if nests are frequently initiated but undetected prior to loss (Mayfield et al. 1961, Miller and Johnson 1978, Blomberg et al. 2015), and estimates of reproductive effort may be low if nests are frequently lost prior to detection (McPherson et al. 2003). It is unclear how these biases may affect the final output of the LSA, so caution should be used when interpreting the results for these parameters. Researchers need to clearly articulate whether they are reporting incubation initiation rates or actual nest initiation rates. Failure to account for the difference between nest initiation (i.e., nest site selection and egg laying) and incubation initiation can have implications for management. For example, in areas with low incubation initiation rates, it would be unclear if the low rates are the result of few hens attempting nests due to poor body condition (Porter et al. 1983) or if nest initiation rates are higher than reported but nests are experiencing high predation pressure or unfavorable weather conditions causing high rates of nest loss or abandonment. Each of these causes for low incubation initiation would require different management approaches, but managers would likely find it difficult to determine which management option is best suited for their situation until research can better determine actual nest initiation rates rather than incubation initiation rates. Use of analytical techniques that allow for more accurate estimation of nest initiation in a population (Byrne et al. 2014, Carpenter et al. 2022) or that adjust for undetected nests when estimating survival (Mayfield et al. 1961) should become standard practice when possible.

We also identified a critical knowledge gap regarding demographic data for the poult and youth periods. Only six estimates from two studies provided sufficient data on poult survival (i.e., Shields and Flake 2006, Tyl et al. 2020), and no studies provided sufficient data for the youth period. As a result, our estimates of vital rate contributions to population growth should be viewed with caution, as these missing life stages are highly influential in other galliform species with similar life-history strategies (Bergerud et al. 1988, Sandercock et al. 2008, Taylor et al. 2016). In addition to the limited number of studies for these life-history stages, several methodological issues may bias the available data. Studies that reported poult survival relied on counts of poults observed with the attending hen at specified times during the brooding period (typically 14 days or 28 days; Vangilder et al. 1987, Porter et al. 1983, Thogmartin et al. 1999). Poult survival estimates based on these methods are biased if the detection probability of poults is consistently low or if imperfect detection is not corrected (Dahlgren et al. 2010a, Orange et al. 2016, Kubečka et al. 2021). Additionally, survival estimates based on poult counts may be biased by brood mixing or amalgamation, which is common in some galliforms (Dahlgren et al. 2010b, Orange et al. 2016), potentially including turkey (Vangilder et al. 1987). Therefore, greater effort to understand brooding ecology (including monitoring individual poult survival and space use) and the youth period between brooding and a hen's first reproductive season will provide critical insight into reproduction and recruitment in turkey populations.

Finally, we had to make several critical simplifying assumptions about turkey population dynamics for our LSA approach. We assumed limited (or no) correlation among vital rate parameters and that turkeys were predominately affected by density-independent factors. Many wildlife species exhibit correlations among vital rates either when the same environmental conditions influence multiple life stages (i.e., unfavorable weather reducing poult and adult survival) or when they experience trade-offs between life-history stages where behaviors or energy expenditure in one stage may influence the survival of another life stage (Sæther 1988). For example, adults of some species may have reduced survival following successful reproduction (Linden et al. 1989, Visser 2001, Blomberg et al. 2012), and failure to account for such trade-offs has the potential to bias population estimates (Van Tienderen 1995). Such trade-offs have potentially been observed in turkey (Yarnall et al. 2020). Alpizar-Jara et al. (2001) noted that assuming independence among demographic parameters might be tenuous for turkeys but that available data at the time were "far from adequate" to estimate correlations. Twenty years later, the situation has changed little, leading us and others to make the similar simplifying assumption (Lehman et al. 2021). Additionally, recent work has suggested that turkey populations may be controlled by density-dependent factors, with productivity potentially being negatively correlated with population size in eastern wild turkeys (Bond et al. 2012, Byrne et al. 2015). Due to the coarse resolution of the data that these conclusions are based on (i.e., poult: hen counts), it is unclear if or what life stages are affected by density dependence and the potential underlying mechanisms. While density dependence in turkeys is poorly understood at present, assumptions related to the strength of density dependence can affect estimates of population growth in turkeys (McGhee et al. 2008). Accounting for correlation structures and potential density dependence are necessary next steps for improving turkey population models and subsequent management strategies.

**Management Implications**

Based on our LSA, parameterized with the best available published data, management efforts that focus on increasing the survival and productivity of adult females will likely have the greatest effects on wild turkey population growth. Efforts to better quantify the causes of hen mortality and low productivity and understanding how the variation of biotic and abiotic factors influence these vital rates should be a priority for research. Despite the amount of turkey research that has been conducted, the limited quantitative data available evaluating the effects of biotic and abiotic factors on turkey demographic vital rates limits our ability to implement effective management practices, including predator control, vegetation manipulation, and hunting regulations. Therefore, future research that can provide a mechanistic understanding of the underlying causes of variation in vital rates and the effects of management actions on these vital rates is foundational for conserving this species. This may include using methods that improve our ability to determine/assign cause-specific mortality, experimental manipulation of predator communities, evaluating changes in vital rates based on management, and increased use of experimental approaches that allow for testing multiple hypotheses. Additionally, greater effort to quantify poult and youth survival using more standardized methods that better account for sources of bias will likely improve population models and our understanding of population ecology for turkeys. Finally, because of the significant role adult female survival has in determining population growth rates for eastern wild turkeys, the harvest of females should be reconsidered in areas where populations are below desired levels.

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Table 1. Range-wide process distributions and number of vital rate estimates (*n*) used for second year (SY) and after second year (ASY) adult eastern wild turkey in life-stage simulation analysis. Ninety-five percent of process variation is bounded by lower (2.5%) and upper (97.5%) percentiles. Process distributions based on data extracted from eastern wild turkey vital rates published between 1970-2021.

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| **Vital Rate** | **Age of Hen1** | **Nest Attempt** | **Mean** | **Standard Deviation** | **2.5%** | **97.5%** | ***n*** |
| **Clutch Size** | SY | 1 | 10.72 | 0.28 | 10.16 | 11.27 | 6 |
| **Clutch Size** | ASY | 1 | 10.91 | 0.27 | 10.37 | 11.44 | 6 |
| **Clutch Size** | SY | 2 | 10.14 | 0.54 | 9.08 | 11.2 | 1 |
| **Clutch Size2** | ASY | 2 | 10.68 | 1.18 | 8.36 | 12.99 | 0 |
| **Hatching Rate** | SY | 1 | 0.83 | 0.1 | 0.62 | 0.99 | 4 |
| **Hatching Rate** | ASY | 1 | 0.83 | 0.09 | 0.64 | 0.98 | 4 |
| **Nest Initiation** | SY | 1 | 0.73 | 0.06 | 0.61 | 0.86 | 17 |
| **Nest Initiation** | ASY | 1 | 0.87 | 0.05 | 0.77 | 0.96 | 18 |
| **Nest Initiation** | SY | 2 | 0.26 | 0.08 | 0.11 | 0.41 | 14 |
| **Nest Initiation** | ASY | 2 | 0.25 | 0.06 | 0.12 | 0.38 | 14 |
| **Nest Success** | SY | 1 | 0.29 | 0.07 | 0.14 | 0.43 | 15 |
| **Nest Success** | ASY | 1 | 0.38 | 0.06 | 0.27 | 0.49 | 24 |
| **Nest Success** | SY | 2 | 0.44 | 0.21 | 0.06 | 0.87 | 4 |
| **Nest Success** | ASY | 2 | 0.23 | 0.11 | 0.04 | 0.45 | 5 |
| **Poult Survival** | SY |  | 0.24 | 0.13 | 0.02 | 0.51 | 3 |
| **Poult Survival** | ASY |  | 0.33 | 0.12 | 0.09 | 0.57 | 3 |
| **Reproduction3** | SY |  | 0.18 | 0.11 | 0.02 | 0.43 | NA |
| **Reproduction3** | ASY |  | 0.34 | 0.15 | 0.09 | 0.66 | NA |
| **Annual Survival** | SY |  | 0.6 | 0.05 | 0.5 | 0.7 | 18 |
| **Annual Survival** | ASY |  | 0.64 | 0.05 | 0.54 | 0.74 | 18 |
| **Youth Survival (28-365 days)4** | | | 0.63 | 0.05 | 0.53 | 0.72 | 18 |
| 1SY = Second year adult; ASY = After second year adult  2Sample size of 0 indicates estimate equivalent to prior  3Reproduction estimated from Equation 1; value derived, so no sample size  4No studies reported youth survival; estimated based on second year adult survival following Roberts et al. (1996) | | | | | | | |

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| --- | --- | --- | --- | --- |
| Table 2. Summary of the number of studies evaluating how biotic and abiotic factors influence life stage vital rates for eastern wild turkeys from 1970-2021. We only included studies that contained either causal or correlative statistical analysis between a vital rate and an abiotic or biotic variable. Blank cells indicate no studies were identified for that topic and life stage. | | | | |
| **Categories and subcategories** | **Nesting** | **Poult survival** | **Youth Survival** | **Adult Survival** |
| **Individual/ behavioral factors** |  |  |  |  |
| Age/ experience/body condition | 5 31, 37, 26, 28, 39 | 1 38 |  | 5 20, 9, 33, 10, 40 |
| Genetics |  |  |  |  |
| Movement and space use | 4 1,2,3,19 | 1 6 |  | 1 12 |
| Reproductive status/ seasonal variation |  |  |  | 4 20, 4, 18, 8 |
| **Biotic Interactions** |  |  |  |  |
| Predation | 1 29 |  |  |  |
| Competition (inter or intraspecific) |  |  |  |  |
| Disease/parasitism |  |  |  |  |
| **Habitat** |  |  |  |  |
| Fine scale habitat | 9 3, 17,14, 42, 11, 38, 41, 19, 36 | 2 22, 41 |  |  |
| Landscape scale habitat | 8 17,14, 42,11, 38, 41, 8, 36 | 2 22,41 |  | 3 12, 24, 32 |
| Forage availability |  |  |  |  |
| **Weather** |  |  |  |  |
| Breeding season weather | 4 35, 38, 20,16 | 3 34, 19,38 |  |  |
| Nonbreeding season weather | 1 16 |  |  | 1 16 |
| **Anthropogenic Factors** |  |  |  |  |
| Hunting season timing and duration |  |  |  | 6 7, 25, 6, 27, 9, 23 |
| Habitat management | 3 30, 14, 42 |  |  | 2 13, 24 |
| 1 Bakner et al. 2019, 2Badyaev and Faust 1996, 3 Badyaev et al. 1996, 4Byrne and Chamberlain 2018, 5Chamberlain et al. 2012, 6Chamberlain et al. 2020, 7Conner et al. 2006, 8Crawford et al. 2021, 9Diefenbach et al. 2012, 10Eriksen et al. 2010, 11Fuller et al. 2013, 12Hubbard et al. 1999, 13Kane et al. 2007, 14Kilburg et al. 2014, 15Kurzejeski et al. 1987, 16Lavoie et al. 2017, 17Little et al. 2014, 18Little et al. 2016, 19Lohr et al. 2020, 20Lowrey et al. 2000, 21Miller et al. 1998, 22Metzler and Speake 1985, 23Moore et al. 1993, 24Niedzielski and Bowman 2015, 25Norman et al. 2001, 26Norman et al. 2004, 27Pack et al. 1999, 28Paisley et al. 1998, 29Petty et al. 2005, 30Pittman and Krementz 2016, 31Porter et al. 1983, 32Pollentier et al. 2014, 33Reynolds and Swanson 2010, 34Roberts and Porter 1998a, 35Roberts and Porter 1998b, 36Seiss et al. 1990, 37Thogmartin and Johnson 1999, 38Tyl et al. 2020, 39Vangilder and Kurzejeski 1995, 40Wright et al. 1996, 41Wood et al. 2019, 42Yeldell et al. 2017. | | | | |

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| Table 3. The amount of variation in asymptotic growth rate, λ, explained by each vital rate for second-year (SY) and after-second-year (ASY) adult eastern wild turkeys, as determined by coefficient of determination (*R2*). Vital rate estimates were derived from studies published between 1970 and 2021. | | |
| Vital Rate | SY | ASY |
| Incubation initiation (first nest) | 0.00 | 0.01 |
| Apparent nest success (first nest) | 0.01 | 0.05 |
| Clutch size (first nest) | 0.00 | 0.00 |
| Hatching rate | 0.00 | 0.05 |
| Apparent poult survival | 0.04 | 0.51 |
| Incubation initiation (renest) | 0.00 | 0.01 |
| Apparent nest success (renest) | 0.00 | 0.01 |
| Clutch size (renest) | 0.00 | 0.00 |
| Reproduction1 | 0.08 | 0.74 |
| Annual Survival | 0.11 | 0.16 |
| 1Reproduction estimated from Equation 1 | | |

Figure 1. Conceptual model of eastern wild turkey life history stages used to parameterize the life-stage simulation analysis. Life stages indicated by circles with bold arrows showing the transitions to subsequent life stages. Vital rates associated with each life stage transition indicated by italicized parameters and equations. Vital rates associated with reproduction include incubation initiation (*II*), nest success (*NS*), clutch size (*C*), hatching rate (*H*), poult survival (*S*P), and youth survival (*S*Y). Vital rates associated with the adult stages include second year adult survival (*S*SY) and after second year adult survival (*S*ASY).

Figure 2. Number of eastern wild turkey vital rate estimates used in the life-stage simulation analysis by the year they were published (1970-2021). We used only vital rates that were estimated for second-year or after-second-year adult female eastern wild turkeys and included a measure of variation that could be converted into standard error. If the estimate was an average over a range of years, we plotted the estimate in the final year. If no year was associated with the estimate, we used the publication year. We show all estimates of clutch size, hatching rate, apparent nest success, apparent poult survival, and incubation initiation, regardless of nesting attempt.

Figure 3. Estimated asymptotic growth rate (λ) for eastern wild turkey, 1970-2021. Dashed line represents mean value from 10,000 iterations, and dotted lines represent 95% confidence intervals. Values <1 indicate declining population size, while values >1 indicate increasing population size. Shaded area (81%) indicates values representing a declining population (λ < 1), unshaded area shows area indicating an increasing population (λ > 1).

Figure 4. Population growth rate (λ) regressed on reproduction (*R*) and survival (*S*) for second year adults (SY) and after second year adults (ASY) for 10,000 simulated population model replicates generated from our life-stage stage simulation analysis. Coefficent of determination (*R2*) values are presented for each vital rate indicating the amount of variation in λ explained by each vital rate.

Appendix 1. Definitions of vital rates used in life-stage simulation analysis.

We populated our life-stage simulation analysis (LSA) with turkey vital rates derived from the literature. Here, we provide additional information on how each vital rate was defined and estimated by these studies.

* Annual Survival—Survival for second year adults (*S*SY) and after second year adults (*S*ASY) was estimated as the proportion of individuals in that age class in year *t* that survived to the next year (*t*+1). In most studies survival is estimated from individuals marked with VHF or GPS radio tags that allow individuals to be monitored throughout the annual cycle. Survival was estimated as the percent of individuals that survived over a given period or by extrapolating daily survival estimates over the period of interest.
* Incubation initiation— We used the term incubation initiation (*II*) to refer to the vital rate called nest initiation (*NI*) in published literature to emphasize the fact that observations of this vital rate occur when hens begin to incubate nests, not when they begin to build nests or lay eggs. Typical estimates of nest initiation likely underestimate the actual proportion of females that attempted a nest, as many nests that are lost prior to incubation are not detected. However, it should be noted that estimates of nest success, clutch size, hatching rate, and poult survival are also conditional on incubation (not nest initiation), so this did not bias our estimates of reproduction or LSA results. Incubation initiation rate for first nests (*II*1) was defined as the proportion of females who were alive at the beginning of the nesting period that attempted at least one nest. Because turkeys only attempt to renest if the first nest fails, incubation initiation rate for second nests (*II*2) was conditional on failure of the first nest. *II*2 was defined as the proportion of females with a failed first nest who then attempted a second nest. While an individual female may attempt as many as three to four nests, these are rare, and we did not include third or fourth nesting attempts in our model. We report incubation initiation separately for second year adults (*II*1,SY and *II*2,SY) and after second year adults (*II*1,ASY and *II*2,ASY).
* Nest success—Nest success for first and second nests (*NS*1and *NS*2) was estimated as the proportion of nests that survived from detection to the end of the incubation period (approximately 25-28 days)and produced ≥1 poult. Nest success estimates from most studies typically overestimate actual nest success because they do not account for nests lost prior to detection. As a result, reproductive estimates may be biased high in some cases. We reported nest success separately for second year adults (*NS*SY) and after second year adults (*NS*ASY).
* Clutch size—Clutch size for first nests (*C*1) and renests (*C*2) was recorded as the average number of eggs laid per nest. We assumed an average of 1:1 sex ratio in each clutch and multiplied clutch sizes by 0.5 to create an estimate of the approximate number of female eggs per clutch. We reported clutch size separately for second year adults (*C*SY) and after second year adults (*C*ASY).
* Hatching rate—Hatching rate for first nests (*H*1) and renests (*H*2) is defined as the proportion of eggs in a nest that hatched. We reported clutch size separately for second year adults (*H*SY) and after second year adults (*H*ASY). Hatching rate is typically estimated as the number of hatched eggs in a successful nest (produced ≥1 poult) divided by the number of eggs in the nest at the start of the incubation period.
* Poult survival—We defined poult survival (*PS*) as the proportion of poults surviving from hatch to 28 days. We selected 28 days as our cutoff for poult survival because most studies only report survival until 4-5 weeks following hatch and because while poults may still be associated with females at this age, they are also largely independent of the female, making their own decisions about foraging and roosting. We only used poult survival estimates that were reported separately for second year adults (*PS*SY) and after second year adults (*PS*ASY). Most studies relied on simple flush counts of poults at approximately 28 days and estimated survival as the proportion of chicks observed during a flush count relative to the number of eggs that hatched in a given female’s nest. These methods are likely biased in that they do not account for brood amalgamation or adoption of lost poults by unmarked females. These methods also assume complete detection of poults during the flush count which is an assumption that is largely unverified in turkeys but has been shown to be untrue in other galliforms.
* Youth Survival— No studies reported survival estimates for the period between poult fledging and an individual’s first breeding season, which roughly corresponds to the ages 28 days to 365 days. We estimated this youth survival (*S*Y) following a procedure similar to Roberts et al. (1996). To do this we assumed daily survival of individuals during this period would be equal to daily survival rates of second-year adults. We calculated youth daily survival as *S*SY(1/365), then we calculated survival over the period of 28 – 365 days by raising daily survival to the power of (365-28).

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