POTENTIAL DENSITY DEPENDENCE IN WILD TURKEY PRODUCTIVITY IN THE SOUTHEASTERN UNITED STATES

Michael E. Byrne\textsuperscript{1,2}  
Warnell School of Forestry and Natural Resources,  
University of Georgia,  
180 E Green St,  
Athens, GA 30602, USA  
Michael J. Chamberlain  
Warnell School of Forestry and Natural Resources,  
University of Georgia,  
180 E Green St,  
Athens, GA 30602, USA  
Bret A. Collier  
School of Renewable Natural Resources,  
Louisiana State University Agricultural Center,  
227 Highland Rd,  
Baton Rouge, LA 70803, USA

Abstract: Observations in recent years by state agency biologists in the southeastern United States that are members of the Southeast Wild Turkey Working Group (SEWTWG) have indicated region-wide declines in productivity indices of wild turkeys (*Meleagris gallopavo*; hereafter, turkey). Concerned that productivity declines were indicative of general large scale population declines, we initiated a study to assess productivity and population trends in the southeastern United States based on historical data collected by SEWTWG member states. Our goals were to summarize and analyze trends in demographic parameters temporally and spatially and generate hypotheses to account for observed declines in productivity. Thirteen states provided historical records (range: 17–54 years) of annual productivity, which we used to evaluate reproductive trends. We used a combination of spring harvest data (range: 8–52 years) and data from the U.S. Geological Survey’s Breeding Bird Survey (BBS; 1966–2011) to quantify trends in turkey population sizes. Because of wide discrepancies in data collection methodology and availability across states, we characterized productivity and population trends for individual states and made biological inferences based on similarities observed across the region. At the state level, our results suggested that productivity has declined concomitant with increasing or stabilizing population sizes. Declines in productivity indices appeared to be best characterized by historical increases in number of females observed without broods. However, brood size appeared to have remained relatively stable. A subsequent literature review suggested a historical trend of increasing annual female survival rates. This led us to hypothesize that productivity may be limited in a density dependent manner. Specifically, we posit that productivity is mediated through site dependent regulation: as population density increases, availability of good quality nesting habitat becomes a limiting factor and a greater percentage of the hen population is forced to attempt to nest in poor quality nesting habitat, thus reducing per capita reproductive success.

Key words: Breeding Bird Survey, brood counts, density dependence, harvest, *Meleagris gallopavo*, population ecology, productivity, reproduction, southeastern United States, survival, wild turkey.

\textsuperscript{1} Present address: Halmos College of Natural Resources and Oceanography, Nova Southeastern University, 8000 North Ocean Drive, Dania Beach, FL 33004, USA.  
\textsuperscript{2} E-mail: mbyrne@nova.edu

Associate Editor: Porter
Restoration of wild turkeys (Meleagris gallopavo; hereafter, turkey) is one of the greatest success stories in wildlife management and populations in many regions increased rapidly in the last decades of the 20th century (Kennamer et al. 1992, Eriksen et al. 2015). However, recent perceived declines in turkey abundance and reproductive output have caused concern (Eriksen et al. 2015). We initiated our study in response to these perceived, persistent declines in annual productivity indices of turkeys based on surveys conducted by biologists of state agencies that are members of the Southeast Wild Turkey Working Group (SEWTWG). There was concern among these state biologists that observed declines were an indicator that large scale, regional declines in turkey populations were presently occurring, or were likely to occur in the near future.

Influence of stochastic environmental variables, such as rainfall and temperature, on short term annual variations in reproduction of turkeys has been well documented in the literature (reviewed in Warnke and Rolley 2005). However, large scale, population level drivers of long-term reproductive trends remain largely unexplored. Density dependent mechanisms are potential drivers in long-term productivity trends, and need to be considered given rapid expansion of turkey populations following restoration efforts (Kennamer et al. 1992). A basic tenant of population biology is that if increasing populations reach sufficient densities, they will trigger negative feedback loops that limit population growth. As such, it is expected that a negative relationship should exist between population size and rate of population increase. Guthery and Shaw (2013) observed that evidence of density dependence in upland game birds has existed in the literature since the 1940s. Porter et al. (1990) and McGhee and Berkson (2007) both suggested density dependent population growth in turkey populations based on analyses of various harvest indices.

One way in which density dependence may manifest itself is through decreased recruitment. Density dependent effects on reproduction have been documented across a variety of avian taxa through both experimental (Dhondt et al. 1992, Both 1998, Pöysä and Pöysä 2002, Sillett et al. 2004, Brouwer et al. 2009) and observational studies (Larsson and Forslund 1994, Ferrer and Donazar 1996, Bennetts et al. 2000, Armstrong et al. 2005, Carrete et al. 2006). Negative relationships between population density and reproduction in gallinaceous birds were documented in the literature as early as the 1940s (Guthery and Shaw 2013). Specifically, Errington (1945) found such a relationship in both northern bobwhite (Colinus virginianus) and ring-necked pheasant (Phasianus colchicus) populations. Existence of a density dependent effect on turkey reproduction has been hypothesized by several authors, who have noted reduced productivity in populations considered stable, compared to recently introduced and expanding populations (Vangilder et al. 1987, Vander Haegen et al. 1988, Miller et al. 1998b, Bond et al. 2012).

At the 2011 meeting, SEWTWG formalized research priorities and decided that, before initiating regional field studies, it would be informative and cost effective to examine demographic trends retrospectively, using existing datasets maintained by member states. Historical trend analyses would provide a long-term, large scale perspective on turkey population ecology in the region. In doing so, survey techniques could be examined critically and hypotheses could be developed from existing data to further refine research priorities moving forward. In the present study, we use long-term trend data for both productivity and population size collected on a large scale to assess plausibility of density dependent effects on reproduction in turkeys. Our specific goals were 2-fold: (1) summarize and analyze trends in demographic parameters temporally and spatially, and (2) generate hypotheses to account for observed declines in productivity. It is our hope that these hypotheses will stimulate discussion of turkey population dynamics and identify fruitful avenues of future research.

METHODS

Data Collection and Availability

We began data collection in April 2012 by contacting turkey coordinators of cooperating states within SEWTWG and asking them to provide all available data and historical records regarding productivity indices for turkeys. Inferences regarding productivity need to be made in the context of population density because, while productivity declines may result in population declines, under many density dependent scenarios, productivity declines may in fact be indicative of increasing population densities. As such, we also asked for historical data regarding harvest records, turkey restoration, and restocking information. We requested coordinators to provide as much associated metadata and background information as was available for each dataset. Data included 2 subspecies, eastern turkey (M. g. silvestris) and Florida or Osceola turkey (M. g. osceola).

Productivity

Thirteen states provided productivity index records (Table 1). Oklahoma data were from the southeastern portion of that state occupied by the eastern subspecies. Alabama initiated a statewide productivity monitoring program in 2010, and we did not use those data for making inferences on long-term productivity trends (Table 1). The primary metric used to index reproduction region-wide was poult per hen (PPH) ratio. This ratio was defined as ratio of total number of pouls to total number of females observed during the summer brood-rearing period. In most states, sightings of turkeys were recorded opportunistically during summer months by agency personnel, or a combination of agency personnel and citizen volunteers, as they went about their daily activities (e.g., Butler et al. 2015). Generally, observers were asked to record observations of females with and without broods. West Virginia was different in this regard, as observations of females without young often were not recorded. Thus, the reader should bear in mind that reported PPH ratios for West Virginia have a slightly different biological meaning than other states.

For most states, the observation period included June–August; Tennessee reported PPH ratios based only on observations recorded in August, the sample period for Kentucky and North Carolina was July–August, and West
Virginia used observations of broods during May–September. All states asked observers to record individual sightings as separate events. However, when states calculated PPH ratios, total numbers of poults and females from individual observations were combined to provide a single estimate. Guidelines for filtering spurious and unlikely observations prior to calculating PPH ratios, if they existed at all, were not standardized across states and in many cases were not standardized across time within a state. For example, a current biologist may have filtered observations considered spurious based on an improbably large ratio of females to poults, whereas his or her predecessors did not.

Of states that monitored productivity, Virginia was the only state in which PPH ratios were not calculated from summer observations. Rather, PPH ratios were derived from ratio of juveniles to adult females in fall harvest based on reports at mandatory hunter check stations. While Virginia did record summer brood observations, inferences regarding productivity were traditionally based on fall harvest data because (1) all cooperating states had a spring turkey season and (2) range-wide, spring seasons generally had fall turkey seasons during all or part of our study period. However, we concentrated our analyses on spring seasons generally

Abundance Indices

All states provided spring harvest records. Nine states had fall turkey seasons during all or part of our study period. However, we concentrated our analyses on spring harvest because (1) all cooperating states had a spring turkey season and (2) range-wide, spring seasons generally
see much greater hunter interest and participation than fall seasons, especially in recent decades (Eriksen et al. 2015). There was considerable inconsistency regarding data availability, how data were obtained, and length of historical records (Table 2). The 1 metric common to all states was an annual estimate of spring harvest, although methods of obtaining this estimate differed among states and methods often changed within states through time. Estimates of spring harvest were variously derived from information gathered at check stations, or through hunter surveys conducted via mail, phone, internet, or various combinations thereof. Calculations of harvest metrics were variously conducted in-house by agency personnel, or by outside entities such as universities or consulting firms. Data sufficient to provide estimates of hunter effort were available in 8 states (Alabama, Florida, Georgia, Kentucky, Louisiana, Mississippi, Missouri, and South Carolina) over a variable number of years. These data consisted of annual estimates of spring hunter effort derived from license sales or hunter surveys.

Harvest estimates are often used as proxies of population density, although few studies have tested veracity of this relationship (Lint et al. 1995). Inferring a direct relationship between harvest and population size is difficult, as harvest is a function of availability of turkeys to hunters, and rate at which hunters are able to harvest turkeys. Likewise, there is obvious age and location specific selection in turkey harvest events. Harvest may be a sufficient index if hunter effort remains constant over time (Lint et al. 1995); otherwise, trends in overall harvest may be representative of hunter population dynamics and behavior more so than changes in turkey populations. To test for a relationship between hunter numbers and spring harvest, we performed a simple linear regression for the 8 states above that provided estimated hunter numbers. A great correlation between harvest estimates and hunter numbers would indicate that raw harvest estimates are unsuitable as indices of turkey populations. Theoretically, accounting for hunter effort should provide a more accurate link between harvest data and turkey population density. If turkey populations are experiencing noticeable long-term changes in density, there should be corresponding changes in hunter success per unit effort. To account for effort, we examined trends in spring hunter success (defined as percentage of hunters to harvest ≥1 turkey), or harvest proportion (defined as turkeys harvested per number of turkey hunters) for states that reported such information directly, or in which we were able to calculate these metrics ourselves from data provided. In Florida, we chose to model trends in hunter success rather than harvest proportion because this metric was based directly on responses to hunter surveys, and thus did not introduce bias associated with estimating hunter numbers. We also modeled hunter success for Mississippi, as these values were reported annually during 1980–2009 (Hunt 2010). We note that more information is required to derive a truly accurate measure of catch per effort. For example, ratio of harvested turkeys to number of hunters may remain the same, but days required to harvest a turkey may change. However, this level of information was not commonly available.

State agencies work independently to collect and summarize turkey population metrics and resulting inconsistencies make comparisons among states problematic (also see Eriksen et al. 2015). This, along with issues inherent in using harvest data as an index of population, prompted us to use data from the U.S. Geological Survey’s Breeding Bird Survey (BBS; https://www.pub.usgs.gov/BBS/) as an independent and methodologically consistent index to overall population trends for each state. The BBS is an annual road-based survey designed to track large scale changes in avian abundance over time. Over 4,000 survey routes exist in the United States and Canada; each route is 39.43 km in length, is surveyed by a qualified observer once each year, and is often surveyed by the same observer consecutively for a series of years. Each route contains 50 evenly spaced sample points from which an observer conducts a 3-minute point-count, recording all bird species seen and heard. Annual surveys in the southeastern United States are normally conducted in early–mid June, with the exception of Florida, where surveys may occur in May. BBS data are summarized for individual states and larger physiogeographic regions of the continent. For any geographic region, a hierarchical model, which accounts for varying regional survey quality and observer effects (Link and Sauer 2002, Sauer and Link 2011), is used to estimate an annual population index (measured as observations per route).

For our purposes, the standard protocol over space and time was an obvious advantage of BBS indices. The BBS has been ongoing since 1966, providing a long-term data set that encompasses restoration of turkeys in the southeastern United States to present day. Additionally, the BBS index incorporates observations of all turkeys regardless of age or sex and, as such, provides a general index of total turkey population density as opposed to most state-derived estimates, which are based on data pertaining to specific sexes (e.g., spring harvest data). Timing of BBS
surveys coincides with end of nesting season and beginning of the brood survey period over much of the region. Theoretically, this should allow all members of the population, except late nesting females, to be available for detection in surveys.

We queried annual BBS abundance indices and associated 95% credibility intervals for each individual state during 1966–2011 through the interactive online BBS results and analysis portal (http://www.mbr-pwrc.usgs.gov/bbs/bbs.html). We did not include BBS data for Oklahoma and Texas because the eastern subspecies only occurred in a relatively small portion of each state, containing few BBS routes. Additionally, BBS analyses are performed at the state and species level, making it difficult to separate eastern turkeys from Rio Grande turkeys (M. g. intermedia) present in large portions of these states.

### Restoration Efforts

Turkey populations in many parts of the southeastern United States are largely the result of intensive, large scale restoration efforts. Restoration was largely accomplished through live release of turkeys captured from extant populations into areas containing suitable habitat in which turkeys were absent or existed at very small densities (Kennamer et al. 1992). Given large scale introductions and dispersals of turkeys into new areas from restoration efforts, we investigated if release efforts conferred a noticeable change in productivity trends. Historical restoration information was available from 6 states that also provided productivity data (Georgia, Louisiana, Mississippi, Missouri, North Carolina, and Tennessee). This information primarily consisted of counts of turkeys released, sometimes detailed to specific release sites, and in other cases summarized by county or parish. Given the large scale nature of this study, and inconsistencies in reporting, we tabulated number of turkeys released statewide in a given year. We determined when restoration was 50%, 75%, and 95% complete in each state based on total cumulative releases and qualitatively compared historical releases to trends in PPH indices.

### Female Survival

To provide further context for interpreting observed productivity trends, we reviewed the literature for female survival estimates. We limited our review to studies which used robust statistical methods such as Kaplan–Meier (Pollock et al. 1989) or Heisey–Fuller (Heisey and Fuller 1985) to derive annual survival estimates from radiotelemetry data. Additionally, we queried researchers currently engaged in studies of female survival to obtain preliminary results (Table 3). To bolster sample sizes, we considered studies that spanned the entire geographic range of the eastern subspecies. To investigate how survival may have changed over time, we binned studies into one of 3 time periods, (1980–1989, 1990–1999, and ≥2000) and recorded mean annual survival estimate for each study. For multiyear studies that spanned across time bins and reported annual survival estimates for individual years, we classified years into their respective time period and calculated a mean annual survival rate. For example, Miller et al. (1998a) reported annual survival rates during 1984–1994. In this case, we calculated a mean survival rate for 1984–1989 and 1990–1994, respectively. If a study spanned 2 time periods but did not report individual survival rates for each year, we placed it in the time period in which most of the study occurred. For example, Moore et al. (2010) reported only a single survival rate estimate from a study during 1998–2000. Because most of the study occurred prior to 2000, we grouped this study into the 1990s. Additionally, in cases in which successive studies of specific study sites built on and incorporated data reported in earlier studies, we only used survival estimates reported in the most recent study. For example, Byrne (2011) incorporated data reported in Wilson et al. (2005) and, as such, we only used results from Byrne (2011).

### Analyses

Because considerable differences in data availability and quality among states precluded pooling data across states, we used a comparative analysis approach. We accomplished this by first analyzing available data from...
each state independently, then making biological inferences based on broad-scale similarities in trends observed across states. Statistical imprecision in productivity and harvest datasets is caused by inherent biases resulting from unquantified levels of measurement error in data collection methodologies and inconsistent survey protocols. Additionally, stochastic annual variation in conditions that influence nesting success can lead to annual variation in long-term productivity averages (Vangilder et al. 1987, Healy 1992). Similarly, factors such as weather conditions and timing of hunting seasons relative to timing of a given year’s nesting cycle may introduce annual variation in harvest numbers. These combined factors cause variation that may obfuscate underlying trends representing larger, population-level processes in which we were interested.

To account for expected nonlinearity in our data due to stochasticity, we used generalized additive models (GAM; Wood 2006), which provide a flexible, regression-based method for fitting a curve to noisy, non-linear data. General additive models are similar in nature to generalized linear models, but in a GAM, the linear predictor incorporates a set of smooth functions of any number of predictor variables (in our case, time). Variables are smoothed via a spline function, which is essentially a series of multiple polynomial regressions connected at various points (knots) to create a continuous smooth line through data. Applying GAMs allowed us to smooth time series data to elucidate underlying trends. Specifically, we fit GAMs to time series data of PPH ratios, proportion of females observed without broods, spring harvest numbers, and spring harvest proportions. We adjusted number of knots used to produce spline curves for each model to improve model fit. We evaluated goodness-of-fit for each model based on visual inspection of residual normality via standard diagnostic residual plots, Q-Q plots, and residual histograms. We report model predicted estimate and 95% confidence interval for each year. We fit GAMs in the statistical program R (R Core Team 2013) using the mgcv package (Wood 2013).

To illustrate relationships between trends in abundance and productivity, we plotted GAM predicted productivity (PPH) values as a function of relative population size (BBS indices) for each state in which productivity data were available. To account for differing scales among states, we first scaled PPH ratios and BBS indices from 0 to 1 for each respective state, with 0 being least value of each metric and 1 being largest value of each metric.

RESULTS

Productivity

Twelve states provided historical productivity data ranging from 17 to 54 years (mean = 31 years, Table 1). Productivity generally declined across all states where data were available (Fig. 1), but the nature and severity of declines was variable. For example, Tennessee experienced a particularly steep decline, whereas productivity in Mississippi remained relatively stable over the record keeping period (Fig. 1). Percentage of females observed without poultis generally increased through time in the 8 states from which data were available (Fig. 2). Again, strength of this trend varied among states but, in 5 states, ranges in model-predicted estimates approached or exceeded 20% (Mississippi = 18.7%, Louisiana = 19%, Missouri = 25.8%, Oklahoma = 26.8%, Tennessee = 28.8%). Difference between largest and smallest annual mean brood size was <2 poultis for all states except Oklahoma and West Virginia (Fig. 3). Mean observed brood size (±95% CI) ranged 4.5 (±0.6) to 6.4 (±0.8) in Louisiana, 5.1 (±0.2) to 6.7 (±0.3) in Missouri, 4.5 (±0.3) to 6.1 (±0.4) in Mississippi, 4.4 (±0.3) to 5.4 (±0.4) in North Carolina, and 5.1 (±0.4) to 6.2 (±0.4) in Tennessee. Mean observed brood size ranged 4.6 (±0.9) to 7.3 (±0.7) and 5.2 (±0.6) to 9.0 (±1.2) for Oklahoma and West Virginia, respectively.

Abundance

All 15 states provided historical data on estimated spring harvest ranging 8–52 years (mean = 28 years, Table 2). Trends in spring harvest were greatly variable across states, and it was difficult to generalize a region-wide trend (Fig. 4). A number of states, including Kentucky, North Carolina, and Tennessee, exhibited consistently increasing trends in spring harvest through time, whereas states such as Arkansas, Missouri, South Carolina, and West Virginia exhibited a trend of stabilizing or decreasing harvest following a peak in the late 1990s or early 2000s. The most precipitous and persistent decline was observed in Mississippi (Fig. 4).

We found that correlations between hunter numbers and spring harvest were great in all states, and that hunter numbers were a significant predictor of total harvest (Table 4; Fig. 5). Thus, harvest estimates were likely strongly biased by hunter participation. We also noted an additional potential confounding relationship between harvest and hunter numbers in that hunter participation may itself be influenced to some degree by turkey population densities (i.e., a functional response in which, when turkey populations are perceived to be great, a greater number of hunters may participate in spring hunting). When accounting for harvest effort, harvest trends were generally less variable over time than raw harvest estimates (Fig. 6). For instance, hunter success in Mississippi has consistently hovered around 50% despite persistent declines in numbers of turkeys harvested. In Missouri, an increase in estimated harvest of 60,650 turkeys between 1960 and 2004 corresponded with an increased harvest proportion of only 0.32 turkeys harvested per hunter.

Trends in data from BBS suggested population increases over time, but magnitude of increase varied considerably across states (Fig. 7). Tennessee, for example, exhibited a particularly sharp population increase beginning in 2000, with estimated observations/route increasing from 0.4 to 4.9 between years 2000 and 2010. Conversely, trends were least pronounced in Louisiana and Mississippi, with total net increases of model estimated observations per route of 0.21 and 0.36 for each state, respectively. When plotting annual productivity indices as a function of BBS-derived population indices, a clear negative relationship between population size and productivity was apparent in all states from which both data sets were available (Fig. 8).
Figure 1. Historical trends in turkey productivity, as measured by poult per hen ratios, of 12 states in the southeastern United States based on available records during 1960–2012. Lines represent generalized additive model estimates (solid line) and 95% confidence intervals (dashed lines).
Figure 2. Historical trends in proportion of turkey females observed without broods during summer brood counts in 8 states in the southeastern United States based on available records during 1978–2012. Lines represent generalized additive model estimates (solid line) and 95% confidence intervals (dashed lines).
Figure 3. Mean turkey brood size (± 95% C.I.) based on summer brood survey observations of single females with ≤16 poults for 7 states in the southeastern United States with data availability during 1967–2012.
Figure 4. Historical trends in spring harvest of male turkeys in the southeastern United States based on available records during 1961–2012. Lines represent generalized additive model estimates (solid line) and 95% confidence intervals (dashed lines). No estimate provided for Georgia because data were not sufficient to fit a model.
Figure 4. Continued: Historical trends in spring harvest of male turkeys in the southeastern United States based on available records during 1961–2012. Lines represent generalized additive model estimates (solid line) and 95% confidence intervals (dashed lines).
Curve shape varied somewhat among states but, in general, years with greatest PPH ratios corresponded to years when BBS indices were least.

**Productivity and Restoration**

When comparing restoration efforts to productivity trends, we noted that declines in productivity began prior to restoration efforts reaching 50% completion in states that had historical productivity data extending back beyond that point (Fig. 9). Restoration efforts in Georgia, Missouri, North Carolina, and Tennessee were characterized by time periods in which restocking activity was especially intense. For instance, in North Carolina, there was a clear peak in releases in the 1990s. However, in all of the above states, steep downward trends in productivity began prior to these intensive restoration efforts and continued for duration of restocking years. Restocking efforts in Louisiana and Mississippi did not exhibit clear spikes in activity observed in other states. Louisiana is the only state in which productivity declines began after restoration was 95% complete. Overall, no clear pattern existed to allow us to draw inference regarding a direct link between intensity of restoration efforts and productivity, as it appeared that prevailing productivity trends began prior to intense restoration efforts. We add the caveat that it was difficult to ascertain spatial overlap between counties in which restoration efforts were concentrated and those in which brood surveys were being actively conducted, especially during early restoration periods. Thus, potential exists that some small scale correlations may have been obfuscated by brood surveys not simultaneously occurring in areas experiencing intense restoration efforts.

**Female Survival**

We found that range-wide female survival rates have generally increased over time, from an average annual survival rate of 0.51 (range: 0.44–0.61) for studies in the 1980s to 0.68 (range 0.56–0.78) for studies in the 2000s (Fig. 10).

**DISCUSSION**

Our findings suggest that there has been a general long-term decline in turkey productivity (to varying degrees) across the southeastern United States, based on trends in PPH ratios observed across states. We offer that direct comparisons among states regarding actual PPH ratios are tenuous, as there are many confounding, latent variables to consider. As such, it is difficult to parse out whether differences in scale represent actual differences in true productivity among states, or are artifacts of differing data collection or survey protocols. For example, West Virginia had consistently larger PPH ratios than other states, but West Virginia’s sampling protocol also varied considerably from other states, as females without pouls were not recorded. However, the important observation is a consistent, generally declining trend region-wide, and not absolute PPH estimates.

Based on data available, it appeared that decreasing PPH ratios were at least in part due to an increasing proportion of females observed without broods. Conversely, there was little evidence to suggest meaningful declines in brood sizes for 7 states in which such data were available, based on small variation in mean brood sizes (<2 poult) in 5 states, and great degree overlapping confidence interval among years. The most persistent negative historical trend appeared in West Virginia, although sample sizes early in the historical record were generally small, which was reflected by wide confidence intervals. Thus, apparent decline in mean brood size from very great values in the early part of the West Virginia record was likely influenced to some degree by sampling effort.

Congruent with declining productivity indices, we observed increasing population trends based on BBS data. Breeding Bird Survey routes are surveyed once annually, and not all routes in a given state necessarily traverse ideal or suitable turkey habitat. Additionally, survey methods are not specifically designed to detect turkeys. Despite these shortcomings, BBS was consistent in methodology and spatial coverage over time, and suggested that turkey populations increased over time.

Raw harvest data are only informative given assumptions of constant hunter effort and availability of turkeys. However, hunter numbers change through time, and we demonstrated that raw harvest numbers were greatly correlated with hunter numbers. The implication is that caution should be used in extrapolating information regarding population trends from harvest data. When considering indices that accounted for hunter effort, we found no evidence to suggest population declines in the 8 states in which such data was available. At the time of our study, populations appeared to be in a state of either relative stability or slow growth.

At the same time, annual survival rates of female turkeys reported in the literature have generally increased. We recognize that this is a relatively crude estimation of survival trends, and that variation in predator communities and climatic conditions across the species’ range may have influenced local survivorship differently. However, we believe that the general trend towards increased survival over time and across regions is worth noting, especially as other demographic trends (i.e., reproductive and harvest
Figure 5. Relationships between annual estimates of spring hunter numbers and total male harvests for 8 states in the southeastern United States based on available records during 1960–2012. Lines indicate linear regression fits.
Figure 6. Historical trends in hunter success or harvest proportion of male turkeys during spring hunting seasons in the southeastern United States based on available records during 1960–2012. Lines represent generalized additive model estimates (solid line) and 95% confidence intervals (dashed lines).
data) in other regions are similar to that observed in the southeastern United States (Eriksen et al. 2015). Thus, our results indicate that turkeys in the southeastern United States have followed a historical pattern of large scale decreases in per capita productivity, increasing and stabilizing population abundance, and increases in female survival rates. Almost universally, years with least productivity indices were associated with greatest indices of population abundance (Fig. 8). While the notion of little productivity and simultaneous stability in turkey populations may initially seem counterintuitive, this relationship has been discussed in previous literature. Most notably, Vangilder et al. (1987) used modeling approaches to conclude that, even when female success rates (defined as portion of females alive each spring to successfully hatch a brood) were as small as 30–40%, large population densities could be maintained if annual female survival rates averaged approximately 0.44.

Negative correlation between population and productivity indices leads us to hypothesize that large scale, historic declines in productivity we observed are evidence that reproduction is mediated in a density dependent manner. Despite observational evidence, there is no experimental evidence of a density dependent relationship between population density and reproduction in turkeys and, as a result, traditional models of turkey population dynamics have assumed no such relationships (Roberts and Porter 1995, Vangilder and Kurzejeski 1995, Rolley et al. 1998, Alpizar-Jara et al. 2001). Here, we present a theoretical mechanism in which density dependent reproduction may operate on turkey populations. While our proposed mechanism is in some respects speculative, it is based on our observed trends in reproduction, population densities, female survival, and our knowledge of turkey ecology in general. It is our hope that presenting our thoughts will stimulate discussion and novel thought on nature of turkey population dynamics and will help guide future turkey research.

Turkeys exhibit life history traits commonly associated with r-selected species, such as early age of maturity, short life span, great reproductive potential, and an association with dynamic and early successional environments (Stearns 1977). Species with these life history traits are hypothesized to exhibit their greatest population growth rates at small population densities relative to environmental carrying capacity (\( K \); Fowler 1981). This hypothesis is supported for turkeys by Porter et al. (1990) and McGhee and Berkson (2007), who both found population growth to be greatest at small densities. A correlate of this is that greatest levels of per capita recruitment would be expected to be associated with these periods of great growth occurring at small densities, and historical trends in the southeastern United States largely conform to this pattern.

A number of general mechanisms to explain how density dependent reproduction arises in populations have been hypothesized. The concept of site dependent population regulation (also termed the habitat heterogeneity hypothesis) suggests that as population density increases, a progressively larger proportion of the population is forced into using poor quality breeding habitat, resulting in declines in per capita reproductive success (Rodenhouse et al. 1997, McPeek et al. 2001). Under this paradigm, while per capita reproductive output declines, variation among individuals is great as individuals that are able to access good quality breeding habitat reproduce more successfully than individuals in marginal habitat conditions. Our observed trends of reduced PPH ratios concomitant with variable proportions of females observed without young suggests a per capita decrease in recruitment along with increasingly variable nesting success among individuals. As such, we hypothesize that density dependent reproduction in turkeys is most likely to be a form of site-dependent population regulation.

To understand how site-dependent population regulation may influence reproductive output of turkeys, consider that turkeys inhabit heterogeneous landscapes. A natural consequence of this is that quality of nesting habitat in any given system is heterogeneous as well, ranging from good quality to unsuitable. Thus, only a certain portion of any landscape will contain suitable nesting habitat (e.g., habitat conditions that are conducive to successful nesting attempts). Given that predation is often identified as primary cause of nest loss (Vangilder et al. 1987, Vander Haegen et al. 1988, Miller et al. 1998a, Paisley et al. 1998, Byrne and Chamberlain 2013), it is reasonable to assume that good quality areas are often those associated with small nest predation risk. At small population densities, a large proportion of a breeding population would be able to access what good quality nesting habitat is available. As a result, per capita recruitment would be expected to be great, as per capita nesting success is also expected to be great. As the population continues to grow, proportion of females forced to nest in suboptimal habitat conditions grows as well. At great population densities, a small proportion of total female population would be able to nest in these good quality areas, with the remainder forced to attempt to nest in poorer quality areas. As a result, per capita recruitment would be reduced, as nest loss becomes significant for proportion of the population nesting in suboptimal habitat conditions. This would be expected to be reflected in annual summer brood counts. After allowing for some degree of annual variation resulting from density independent environmental factors (temperature, precipitation, etc.), absolute numbers of females successfully producing poults may be relatively consistent across years. However, despite increasing population density, absolute number of successful females remains relatively static, and proportion of the population that experience failed nesting attempts rises. The expected result is what we observed in historical trends, reduced PPH ratios concomitant with an increasing percentage of the female population observed without broods.

Female survival rates may be linked to decreases in per capita reproductive success. Female survival rates have been observed to exhibit seasonal variation, with least survival rates often associated with reproductive seasons (Vander Haegen et al. 1988, Palmer et al. 1993, Wright et al. 1996). Female survival outside of reproductive seasons, assuming harvest (legal or illegal) is not a major cause of mortality, can be quite great (e.g., Pack et al. 1999). This makes intuitive sense, as incubation and brood-rearing activities leave females especially vulnerable to predation. Conversely, females that experience early nest loss, or alternatively do not attempt to nest at all, may be spared the risk associated with reproductive activities. Collier et al.
(2009) documented negative influence of reproductive effort on survival for Rio Grande turkeys. Thus, as proportion of reproductively unsuccessful females increases, overall population level survival rate may increase as well.

A number of hypotheses based on assumptions we used could be explicitly tested via properly designed studies. Results of such studies would serve to better elucidate mechanisms linking turkey reproduction and density. These hypotheses include:

1. For any given population, female reproductive success, defined as proportion of females alive at beginning of a reproductive season to successfully hatch young (Vangilder 1992), is negatively correlated with population density.

2. For a given landscape, females that do not attempt to reproduce or those that experience early nest failure (i.e., do not incubate a nest or tend a brood) have greater annual survival rates than females that are reproductively active, after controlling for factors such as legal and illegal harvest.

3. Following from hypothesis 2, for a given landscape, mean annual survival rate of females is positively correlated with population density.

4. If quality nesting areas are settled first as site-dependent regulation would suggest, then for a given landscape, with all else being equal, there should exist a negative correlation between nest initiation date and nest success when population densities are great. This is to say that early nesting females will first settle and

Figure 8. Relationship between annual indices of population density (measured through Breeding Bird Survey data) and productivity (measured through poult per hen ratios) for 11 states in the southeastern United States during 1966–2011. Values for both indices are scaled from 0 (least values) to 1 (greatest value) for each state.
Figure 9. Productivity trends as determined through poult per hen ratios (solid lines) and annual restoration efforts as measured through numbers of turkeys released within a given state (grey bars) for 6 states in the southeastern United States during 1950–2012. Vertical dashed lines represent 50%, 75%, and 95% cumulative releases respectively.
occupy limited available quality habitat and, as a result, late nesting females will be forced into marginal habitat conditions. Strength of this relationship should be weak when population densities are small.

Clearly, our inferences are based on data summarized over coarse spatial scales. In reality, a state’s turkey population likely consists of a number of relatively distinct subpopulations with varying levels of connectivity (Fleming and Porter 2007). By making inferences at the state level, we are necessarily making inferences based on data sets that represent aggregations of these various subpopulations. At any given point in time, it is reasonable to expect that variation exists between these populations, in that some populations may be growing, whereas others are stable or decreasing (e.g., Butler et al. 2015). Furthermore, these populations are likely influenced to different degrees by localized changes in factors such as habitat conditions and availability, predator populations, and harvest regimes. When we aggregated across these populations, we necessarily missed some of this localized variation. For these reasons, we did not attempt to draw correlative inferences regarding state level habitat changes and productivity trends, as attempting to draw inferences between habitat conditions and demographic trends on such scales would not have been especially informative. It is our hope to instigate future research aimed at testing these hypotheses, further refining these ideas, and exploring alternative hypotheses as appropriate. However, we stress that such work should focus on elucidating population processes at scales relevant to turkey population ecology.

Our work highlights an important issue regarding use and interpretation of methods used to survey turkey demographic parameters. The lack of a universally accepted and accurate tool to measure turkey population size is a problem that was first identified several decades ago (Mosby 1967) and is still an issue today. While commonly used, current harvest metrics are likely poor indices of population size or density. Hunter numbers change through time, and the great correlation observed between hunter numbers and raw harvest estimates invalidates use of raw harvest as a meaningful index to population size. Additionally, not all turkeys are available

to hunters, and hunters may exhibit selectivity in turkeys they harvest (adult males are preferable to juveniles for instance; Isabelle and Reitz 2015). Accounting for hunter effort and reporting harvest as a measure of catch per effort should provide a more accurate index. However, often the information necessary to accurately quantify effort is missing. Finally, male-only spring harvest metrics only serve as a good index of total population assuming there are no long term changes in sex ratios. Recent advances in statistical techniques to reconstruct populations from harvest data are promising (Gast et al. 2013), but these techniques are still developing and have yet to be adopted by management agencies. Unfortunately, given lack of required information and violation of multiple important assumptions, we feel that attempting to draw inferences regarding population changes based on currently available harvest data is tenuous at best.

BBS routes are surveyed once annually, and not all routes in a given state necessarily traverse ideal or suitable turkey habitat. Additionally the survey methods are not specifically designed to detect turkeys. Despite these short comings, given consistency in methodology and spatial coverage over time, the fact that turkeys are encountered with sufficient frequency so that relative abundance estimates increased strongly suggests actual population increases over time. Thus, the BBS appears useful for detecting long-term population changes, but lack of turkey-specific survey protocols likely limits its effectiveness at detecting short-term population changes and its usefulness as a short-term monitoring tool.

Summer brood surveys represented the most common method of indexing productivity, but methodologies varied widely, hindering direct comparisons across states and regions, and little work has been done assessing ability of such surveys to accurately index productivity. The few studies that have been conducted in this regard, on Rio Grande turkeys, indicated poor correlations between survey results and reproductive parameters of radiotagged populations (Butler et al. 2005) and lack of statistical power necessary to detect biologically meaningful changes (Schwertner et al. 2003). Future work should assess ability of brood surveys to accurately index productivity and measure detection probabilities in a variety of landscapes.

**MANAGEMENT IMPLICATIONS**

We offer that the time has come for studies specifically designed to elucidate mechanism relationships between population density and demographic processes in turkeys. An understanding of processes that regulate turkey populations, and how these processes may vary with respect to population density, would allow for further refinement of population models. This would allow generating more precise predictive models and promote more informed decisions regarding harvest management. Additionally, while it may not be feasible to measure population density directly at large scales, an understanding of mechanistic connections between density and demographic parameters would potentially allow sufficient inferences to be drawn by tracking relationships among reproduction, survival, and harvest. Accounting for density dependence is an important aspect of creating sound policy
to meet specific management goals (Stevens et al. 2015). However, given how little is presently known about processes linking turkey population density and demographic parameters, we hesitate to provide specific management recommendation until further research is conducted.

ACKNOWLEDGMENTS

We thank the cooperating states of the SEWTWG (Alabama, Arkansas, Florida, Georgia, Kentucky, Louisiana, Mississippi, Missouri, North Carolina, Oklahoma, South Carolina, Tennessee, Texas, Virginia, and West Virginia) that provided access to their respective historical data, and agency personnel who provided information regarding data collection and helpful thoughts and comments that improved this manuscript: S. Barnett, B. Bond, A. Butler, S. Dobey, D. Godwin, J. Hardin, J. Honey, C. Hunter, J. Isabelle, K. Krantz, K. Lowery, G. Norman, C. Ruth, D. Sawyer, R. Shields, J. Stafford, E. Stanford, D. Steffen, C. Taylor, and J. Waymire. We thank our cooperating state agencies and state chapters of the National Wild Turkey Federation (NWTF) that provided funding for this project, and we thank the NWTF for logistical support in handling distribution of funding. Additional support was provided by the University of Georgia Warnell School of Forestry and Natural Resources.

LITERATURE CITED


Larsson, K., and P. Forslund. 1994. Population dynamics of the barnacle goose Branta leucopsis in the Baltic area: density-
Productivity and Survival


Michael E. Byrne is currently a postdoc at the Nova Southeastern Oceanographic Institute. He received his Ph.D. from Louisiana State University and his M.S from the University of Rhode Island. Mike is a vertebrate ecologist with research interests in behavioral and population ecology, with a particular focus on animal movement ecology, habitat use, and elucidating the links between individual behaviors and population level processes. He conducts research on a wide variety of species in both marine and terrestrial ecosystems, and has been involved in wild turkey research since 2007.

Michael J. Chamberlain is a Professor of Wildlife at the Warnell School of Forestry and Natural Resources at the University of Georgia. Mike received his B.S. degree from Virginia Tech, and his M.S. and Ph.D. degrees from Mississippi State University. Mike’s research interests are broad, but he focuses much effort into evaluating relationships between wildlife and their habitats. He has conducted research on wild turkeys for the past 20 years. Mike is a dedicated hunter and dad, and enjoys spending time outdoors regardless of the pursuit.

Bret A. Collier is an Assistant Professor in the School of Renewable Natural Resources at Louisiana State University. Bret’s research focus is wildlife population dynamics and development of statistical methods for wildlife biologists, although he has been known to delve into a variety of wildlife-related topics. He has been actively conducting research on wild turkey demography and spatial ecology for the past 12 years. Bret and his wife, Reagan, have a daughter, Kennedy, and he is both a hunter and landowner.