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Correlation of Eastern Wild Turkey Poult:hen Ratios with Population Indices to Detect Reproductive Density Dependence

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ABSTRACT

Knowledge of how density affects population growth is important for the harvest management of wild turkey. Unfortunately, available time-series are often too short for statistical detection of density dependence. The correlation between wild turkey recruitment and population size was assessed using data from 7 state wildlife agencies, circumventing the problem of short time-series by using multiple datasets. Correlation coefficients were calculated between surveyed poult:hen ratios and harvest-based population indices for 31 geographic or harvest management regions. Estimated correlation coefficients were tested for homogeneity to determine if an average correlation could be calculated. Correlation coefficients for the 29 regions ranged from -0.82 to 0.70. A Q-test for homogeneity indicated that correlation coefficients were similar enough to warrant averaging [Q=25.45, df = 28, P = 0.603]. The weighted average correlation coefficient (± standard error) was $\bar{r}$ = -0.30 ± 0.45. Population size accounted for little of the variation associated with production ($r^2 = 0.09$). Graphical analysis indicated that a negative correlation between poult:hen ratios and population size tended to occur when the range of population sizes was large. Density dependence appears to have little effect on production. Density-independent models should have better success modeling wild turkey production, while density-dependent effects may have stronger influence on survival or immigration at low population sizes.

Key words: correlation, density dependence, harvest, *Meleagris gallopavo silvestris*, meta-analysis, wild turkey

INTRODUCTION

Evidence that density dependence, the functional relationship between population growth rate and population density, acts on eastern wild turkey (*Meleagris gallopavo silvestris*) populations has increased over the past 30 years (Glidden and Austin, 1975; Healy and Powell, 2001; Turchin, 2003: 398; McGhee, 2006). High growth rates have been reported for reintroduced populations (Little and Varland, 1981; Healy and

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Powell, 2001), while some researchers have attributed low recruitment rates in established populations to the effect of reaching carrying capacity (Glidden and Austin, 1975; Vander Haegan et al., 1988; Miller et al., 1998). Examinations of harvest indices in New York have indicated that wild turkey population growth decreases curvilinearly for population densities of 0-20% of carrying capacity (Porter et al., 1990). McGhee and Berkson's (2007) analysis of harvest time-series from 11 states also indicated a curvilinear decrease in growth rate as populations increased. While observational evidence suggests density-dependent effects on wild turkey population growth, to be useful in harvest management, the mechanisms (i.e., productivity or survival) by which they operate need to be determined.

Population growth in a given region is determined by the rates of births, deaths, immigration and emigration in the population (Pulliam 1988), and density must act on one or a combination of these factors to change the population growth rate under a density-dependent system. It has been assumed that both density-dependent and density-independent factors operate in conjunction to determine annual population growth in harvested species (Bayliss, 1989; McCullough, 1990; Aanes et al., 2002; Guthery, 2002). Detecting density-dependent mechanisms in an environmentally stochastic system typically requires labor and cost-intensive experiments, especially if multiple vital rates must be examined (Armstrong et al., 2005; Hixon and Jones, 2005). However, if researchers can use existing data to explore which vital rates are likely candidates for detecting density-dependent effects, much time and expense may be saved. For example, poult:hen ratios are often collected by state wildlife agencies as indices to recruitment or population size (Healy and Powell, 2000), and may provide an opportunity to examine the linear association between population density and poult production. Poult:hen ratios represent the combined effects of numerous, difficult to estimate reproductive parameters, such as nest rate, nest success, hen success, clutch size and hatching rate (Vangilder 1992). Since poult:hen ratios represent a large portion of the reproductive parameters in a wild turkey population, and are easier for state agencies to obtain, they make a good candidate variable to test the hypothesis that production is density-dependent. If density dependence acts only weakly on production, further research should explore other vital rates more closely. Conversely, if density dependence appears to strongly affect production, further research should focus on specific reproductive mechanisms (e.g., nest rate, hen success, poult survival).

Unfortunately, available time-series are often too short for statistical detection of density dependence (Wolda and Dennis, 1993), and the power of statistical tests are reduced by demographic, environmental and measurement error (McCullough, 1990). These sources of error are expected to be high for indices, increasing the uncertainty in, and possibly biasing parameter estimates (Walters, 1985; Anderson, 2001). Under these limitations, one would not expect any single time-series to produce reliable results. However, if multiple indices are examined for a common parameter, the consequent increase in spatial data may allow consistent patterns to emerge. In essence, statistical power is improved by increasing the number of populations examined, instead of the length of the time-series for a single population, to determine the common parameter among populations (Myers, 2000).

Meta-analysis quantitatively combines information across multiple studies to test a particular hypothesis (Hedges and Olkin, 1985). Independent datasets are the units

of comparison for which summary statistics are calculated and from which inferences are drawn. Meta-analysis techniques have been used successfully with harvest and production indices for sockeye salmon, *Oncorhynchus nerka* (Myers et al., 1997), northern bobwhite quail, *Colinus virginianus* (Williams et al., 2003), ring-necked pheasant, *Phasianus colchicus* (Williams et al., 2003) and eastern cottontail rabbits, *Sylvilagus floridanus* (Williams et al., 2003), and multiple species of marine demersal fish (Myers and Cadigan, 1993). It was assumed that wild turkey harvest indices served as an adequate index to population change for a given management region, requiring the further assumption that harvest of gobblers was proportional to gobbler population size, and that the population sex ratio was constant. Lint et al. (1995) found that this assumption held for wild turkey populations on the Tallahala Wildlife Management Area in Mississippi.

The purpose of this study was to investigate, using meta-analysis, whether wild turkey density affects reproduction. It was hypothesized that a negative linear association existed between population density and poult production. If so, a standard population index, annual spring harvest, should correlate with observed poult:hen ratios (production index) for multiple populations.

METHODS

Harvest and brood data were acquired from seven state wildlife agencies (MD:1996-2001, MS:1995-2002, NC:1988-2001, NJ:1988-2002, NY:1996-2001, RI:1993-2001, VA:1990-1999). Harvest data took five forms: the number of spring gobblers harvested per year (NC, NJ, MD), spring gobblers harvested per km^2 of forest (VA), spring gobblers harvested per hunter effort (NY, RI), hunter sample surveys (NY, MS, VA), and gobblers heard per 100 hours (survey of hunters in VA). These harvest-based indices were used to track population change over time, assuming a proportional relationship between the indices and true population change for the participating management regions. Datasets were checked for consistent spring harvest regulations and hunter effort, since changes in these would shift or alter the proportional relationship between harvest indices and true density or abundance, potentially invalidating the analysis. Spring season length and bag limits for MD, NC, NY, NJ and VA remained relatively unchanged over the period examined, although issued permits increased in NJ over the time period examined. Participation in spring hunting increased in RI over the period examined, and, in 1998, MS implemented a requirement for harvested gobblers to possess beards ≥ 6 inches. It was assumed that hunter/effort indices incorporated regulation changes such that effort accounted for hunter behavior (MS, NJ, RI).

Brood data took the form of poult:hen ratios for all hens observed, with the exception of RI, where only brood hens were observed. Kurzejeski and Vangilder (1992) state that poult:hen ratios provide a reliable index to annual reproduction. State agencies collect brood survey data during summer over differing months using conservation officers, district biologists, or citizen volunteers. In most cases, brood surveys are conducted during the routine fieldwork by staff, making standardization across samples difficult. This, in addition to the variable effort by volunteers makes direct comparison of poult:hen ratios between states or management regions impossible (Healy and Powell, 2000). This problem is addressed by comparing correlation coefficients, a standardized measure of the relationship between poult:hen ratios and harvest-based population indices, rather than comparing the raw data (Hedges and Olkin, 1985).

The data were divided into geographic or management regions, producing a total of 29 management units, each comprised of a time-series of poult:hen ratios and some combination of harvest-based population indices. Regions were based on pre-existing management areas or groups of counties conforming roughly to Level III ecoregions as designated by the Environmental Protection Agency (Omernik, 1987). It was assumed that wild turkey habitat remained unchanged over the periods examined for each region (max time-series length = 14 yrs), and that regions were large enough for immigration and emigration to be equal. In some states, management regions changed in area over time. Since this might bias the analysis these regions were not used.

For comparison across populations, estimates of effect size should be dimensionless (Myers, 1997). In this case, the effect size is the slope of the relationship between poult:hen ratios and population density as measured by harvest indices. The correlation coefficient is a dimensionless parameter measuring the degree of association between two variables, and equates to a standardized regression slope (Zar, 1999). This makes it useful for comparing the association of these two variables across populations (Myers, 1997). Since the indices contain unknown amounts of measurement error, it is better to require as few assumptions about the statistical nature of the data as possible. By using the correlation coefficient, a linear relationship is assumed between the compared variables, with observations of both drawn independently of each other (Zar, 1999). For all the states examined, poult:hen ratios and harvest data were collected independently.

Density-dependent effects are more likely to be detected when a wide range of population densities are included in a dataset. To examine the effect that the range of population sizes available exerted on correlations, a ratio of the maximum index value to the minimum index value was calculated for each regional time-series (I_{max}/I_{min}). Regional datasets containing a wide range of population index values (and presumably, population densities) had high values of I_{max}/I_{min}, while those containing a narrower range of values had lower values of I_{max}/I_{min}. A population with an I_{max}/I_{min} near 1 would be nearly constant over the time-series with little change in population density.

Correlation coefficients were calculated between poult:hen ratios and population indices by region. When states used more than one index, an average correlation was calculated for each region. Estimated correlation coefficients across regions were tested for homogeneity via a Q-test to determine the appropriateness of calculating an average correlation (Hedges and Olkin, 1985). This test compares each z-transformed correlation coefficient to the weighted average coefficient. Weights were calculated based on the amount of information contributed (I_{max}/I_{min}). The weighted z-score was then converted back to a correlation. The standard error of the weighted mean correlation assuming the correlation between indices and poult:hen ratio is fixed across populations is $1/(N\text{-}3k)$ where N is the total number of data points across k studies. However, it's more likely that the true correlation varies between populations because habitats are likely to differ, changing the relationship between density and production. In this case the estimated standard error of the true correlation ($\hat{\sigma}(P)$) may be calculated according to a random effects model, which assumes that the correlation for any one population is drawn from a distribution (Hedges and Olkin, 1985).

$$\hat{\sigma}(P)=\sqrt{s^2(\hat{p})-\frac{1}{k}\sum_{i=1}^{k}\left(\hat{p}_i^2-r_i^2\right)} \tag{1}$$

where $\hat{p}_i$ is an unbiased estimate of the correlation for the ith population when sample sizes are small, $s^2(\hat{p})$ is the sample variance of the population correlation, and r_i is the sample correlation coefficient for the ith population (Hedges and Olkin, 1985).

RESULTS

Correlation coefficients ranged widely for the 29 regions examined (-0.82–0.70: Table 1). The number of years contributed by each region ranged from 6–14 ($\bar{x}$ = 8.0, sd = 2.8). The Q-test for homogeneity indicated that correlation coefficients were similar enough to warrant averaging [Q = 25.45, df = 28, P = 0.603]. The weighted average correlation across regions was $\bar{r}$ (± SE) = -0.30 ± 0.45. Population indices accounted for little of the variation associated with production (r^2 = 0.09). For those populations with >1 index, (NY, VA), we assessed the effect on $\bar{r}$ of using only a single index instead of averaging the correlation of both indices. The mean correlation changed little when only single indices were used (range: -0.29– -0.30). Among single regions, only the NJ Coastal Plain demonstrated a significant negative correlation between poult:hen ratio and harvest index ($Z_{0.05(1)}$ = -2.84, P = 0.002), however, other regions approached significance (NC Coast: $Z_{0.05(1)}$ = -1.49, P = 0.068; NC Piedmont: $Z_{0.05(1)}$ = -1.31, P = 0.100; NJ Piedmont: $Z_{0.05(1)}$ = -1.51, P = 0.066). A graph of regional correlation coefficients against population range (I_{max}/I_{min}) shows that those regions with a wider range in population fluctuations tended to have negative correlations between poult:hen ratios and harvest index magnitude (Fig. 1). Those populations with less variation in population fluctuations (low I_{max}/I_{min}) showed no relationship between poult:hen ratios and harvest index magnitude. We calculated a post-hoc correlation for those 8 regions having the greatest range of densities (I_{max}/I_{min} > 4, a natural break in the data: NC, NJ, RI). The correlation for the reduced dataset was stronger, but still statistically insignificant, $\bar{r}$ (± SE) = -0.39 ± 0.40.

DISCUSSION

This analysis indicates a biologically insignificant negative relationship between reproduction and population size, explaining only 9% of the variation in poult:hen ratios. This implies that density-dependent factors have little effect on annual production, such that density-independent factors, such as rainfall and temperature during the nesting and brood seasons, may primarily determine annual production (Beasom and Pattee, 1980; Healy and Nenno, 1985). Those states contributing the most information (> 4 I_{max}/I_{min}: NC, NJ, RI) were geographically widespread, indicating that these results were generally applicable to the central eastern U.S.

TABLE 1. Average correlations between wild turkey poult:hen ratios and harvest indices from 7 U.S. states, ranging from 1988 to 2002. A weighted average correlation was calculated based on the number of years of data available (n). The magnitude of variation in indexed abundance was calculated by dividing the largest index value by the smallest index value (I_{max}/I_{min}) as a measure of the variation in population densities available in a time-series. Large values of I_{max}/I_{min} represent a greater variety of population densities.

State	Region	r	SE	n	weight	I_{max}/I_{min} [a]
MD	Appalachian Plateau	0.17	0.41	9	0.01	1.91
	Blue Ridge	-0.18	0.50	7	0.01	1.62
	Coastal Plain	-0.82	0.41	9	0.04	6.28
	Piedmont	0.19	0.41	9	0.02	2.77
	Ridge and Valley	-0.47	0.41	9	0.01	1.54
MS	Region 1	0.70	0.58	6	0.01	2.04
	Region 2	-0.43	0.58	6	0.01	2.17
	Region 3	0.12	0.58	6	0.01	1.78
	Region 4	0.29	0.58	6	0.01	1.56
	Region 5	-0.36	0.58	6	0.01	1.61
	Region 6	0.63	0.58	6	0.02	2.64
NC	Coastal	-0.42	0.30	14	0.06	8.43
	Piedmont	-0.38	0.30	14	0.06	8.58
	Mountains	-0.33	0.30	14	0.05	7.70
NJ	Coastal Plain	-0.46	0.33	12	0.09	13.37
	NE Highlands	-0.31	0.38	10	0.03	4.40
	Piedmont	-0.27	0.32	13	0.09	13.35
	Pine Barrens	-0.18	0.33	12	0.30	43.87
NY	Region 3	-0.35	0.58	6	0.01	1.83
	Region 4	0.32	0.58	6	0.01	1.38
	Region 5	0.27	0.58	6	0.01	1.92
	Region 6	-0.22	0.58	6	0.01	1.52
	Region 7	0.29	0.58	6	0.01	1.96
	Region 8	0.00	0.58	6	0.01	1.33
	Region 9	0.09	0.58	6	0.01	1.86
RI	RI	0.31	0.41	9	0.03	4.96
VA	Northern	-0.18	0.41	10	0.01	1.77
	SW Mountains	-0.13	0.45	9	0.01	1.76
	Tidewater	-0.18	0.41	10	0.01	1.68

[a] I_{max}/I_{min} for states with multiple indices (NY, VA) are presented as averages

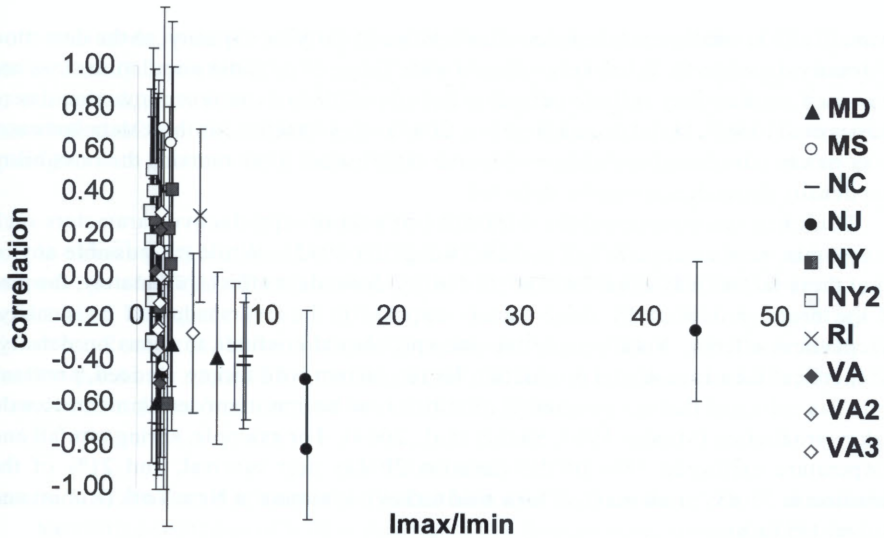

FIGURE 1. Correlations (± SE) between wild turkey spring harvest indices and poult:hen ratios for 29 regions in 7 U.S. states, ranging from 1988 to 2002. The x-axis represents the I_{max}/I_{min} value for each region, a measure of the population fluctuation within the time-series. Large I_{max}/I_{min} values have more information about density changes than low I_{max}/I_{min} values. Multiple correlations are listed for states having >1 harvest index. Correlations show high uncertainty and variation between regions, but regions with large I_{max}/I_{min} values tend to show a negative correlation between population abundance (harvest indices) and poult:hen ratios. NY refers to reported spring gobblers harvested/effort; NY2 refers to surveyed spring gobblers harvested/effort; VA refers to gobblers heard/100 hours; VA2 refers to surveyed spring gobblers harvested/effort; VA3 refers to spring gobblers harvested/forest km^2.

Although few studies have attempted to test for density dependence in wild turkey time-series, other bird species have shown much stronger relationships between population density and production. Indices of northeastern U.S. mallard, *Anas platyrhynchos*, population change have been shown to explain 20-36% of the variation in recruitment indices (Sheaffer, 1998). For an experimentally manipulated central European population of collared flycatchers, *Ficedula albicollis*, density explained 59% of the variation in breeding success (Torok and Toth, 1988). Similar associations with population abundance have been shown with partridge chick mortality, *Perdix perdix* (Blank et al., 1967); song sparrow fledgling success, *Melospiza melodia* (Arcese and Smith, 1988); and great tit juvenile winter mortality, *Parus major* (McCleery and Perrins, 1985).

Post-hoc analysis of the most informative datasets showed a slightly stronger correlation, implying that current data may be inadequate to test this hypothesis, even in a meta-analysis framework. However, for the region with the widest fluctuations in population abundance (NJ pine barrens), and therefore, potentially the most informative, harvest indices explained little of the variation in poult:hen ratios (r^2 = 6%). Other studies have indicated that growth rates for wild turkey populations decreased most dramatically at small population densities relative to carrying capacity, so the detection of density dependence is unlikely unless a wide range of possible population sizes are examined, so that they include periods when populations experience low abundance (Porter et al., 1990; McGhee and Berkson, 2007). Nevertheless, as these data increase, or as newly introduced populations become established, there remains the possibility that density dependence may be detected.

Poult:hen ratios represent the integration of a set of reproductive parameters such as nest rate, nest success, & hen success (Vangilder 1992). While it's possible any or all of these factors may experience some density-dependent effects, ultimately, the size of the brood produced by these factors appears to be overshadowed by density-independent effects. Future modeling attempts should continue to focus on density-independent factors to model production for the eastern wild turkey. Indeed, previous work has indicated that environmental conditions can be important determinants to wild turkey production (Mosby, 1967; Sæther et al., 2004). For example, spring rainfall and temperature explained 58% of the variation 20-day nest survival, and 21% of the variation in 25-day poult survival for a wild turkey population in New York (Robert and Porter, 1998a,b).

A caveat to our results is that the indices used in this analysis are subject to unknown amounts of measurement error, which may have confounded detection of a relationship. Regional correlations varied widely, presumably because the short time-series, lack of population change, inherent environmental variation and measurement error reduced the reliability of any single correlation (Anderson, 2001). Limited data or data with large amounts of measurement error will introduce uncertainty or bias about inferences or parameter estimates (Walters and Ludwig, 1981). Well-designed long-term studies specifically focused on the relationship between reproduction and population density may yield stronger results. However, harvest and brood survey data currently represent the only information available approaching the necessary length and variety of population densities to address the question. Based on this current data, it appears that density is biologically unimportant to poult production.

Poult:hen indices are subject to multiple biases that can potentially affect inferences (Healy and Powell, 2000). These include observation bias by cooperating volunteers and field staff, and the formation of multiple broods as summer progresses (Leopold 1944). As the probability of observing a poult varies by habitat and age, poults may be undercounted, resulting in a consistent negative bias independent of population abundance. As counts are usually taken from roadsides, differences between roadside and non-roadside broods will also consistently affect poult:hen ratios. While consistent biases independent of population abundance would not affect the inferences made here, poult:hen ratios would artificially decrease if sampling times shifted to later summer with the formation of multiple broods. Such a change seems not to have occurred in the data sets examined, as they are either conducted over the entire summer or consistently during specific months.

While the results of this paper imply primarily density-independent production, other vital rates may be more strongly influenced by density-dependent effects. It is likely that both act on population growth at varying degrees at different abundances. Indications of density-dependent effects on presumably r-selected species have increased, producing useful management implications (Higgins et al., 1997; Aanes et al., 2002). Research in harvest management for the wild turkey should attempt to include both density-dependent and independent influences in harvest models. The effects of strong density dependence at low population abundances may act to offset over harvests or poor production years. In addition, such research would provide a more complete knowledge of the population dynamics at various densities, necessarily providing managers with greater ability for sustainable management of an important game species.

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