A SIMULATION MODEL OF RIO GRANDE WILD TURKEY POPULATION DYNAMICS IN THE EDWARDS PLATEAU OF TEXAS

A Dissertation

by

THOMAS WAYNE SCHWERTNER

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

May 2005

Major Subject: Wildlife and Fisheries Sciences

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May 2005

Major Subject: Wildlife and Fisheries Sciences

ABSTRACT

A Simulation Model of Rio Grande Wild Turkey

Population Dynamics in the Edwards Plateau of Texas. (May 2005)

Thomas Wayne Schwertner, B.S., Texas A&M University;

M.S., Texas State University

Co-chairs of Advisory Committee: Dr. Nova J. Silvy
Dr. Markus J. Peterson

I investigated the effect of precipitation and predator abundance on Rio Grande wild turkey (*Meleagris gallopavo;* RGWT) in Texas. My results suggested that RGWT production was strongly correlated with cumulative winter precipitation over the range of the RGWT in Texas. However, I found no evidence that predator abundance influenced RGWT production, although spatial-asynchrony of predator populations at multiple spatial scales might have masked broad-scale effects. Using the results of these analyses, as well as empirical data derived from the literature and from field studies in the southern Edwards Plateau, I developed a stochastic, density-dependent, sex- and age-specific simulation model of wild turkey population dynamics. I used the model to evaluate the effect of alternative harvest management strategies on turkey populations. Sensitivity analysis of the model suggested that shape of the density-dependence relationship, clutch size, hatchability, juvenile sex ratio, poult survival, juvenile survival, and nonbreeding hen mortality most strongly influenced model outcome. Of these, density-dependence, sex ratio, and juvenile survival were least understood and merit further research. My evaluation of fall hen harvest suggested that current rates do not

pose a threat to turkey populations. Moreover, it appears that hen harvest can be extended to other portions of the RGWT range without reducing turkey abundance, assuming that population dynamics and harvest rates are similar to those in the current fall harvest zone. Finally, simulation of alternative hen harvest rates suggested that rates ≥5% of the fall hen population resulted in significant declines in the simulated population after 25 years, and rates ≥15% resulted in significant risk of extinction to the simulated population.

To Wendy.

ACKNOWLEDGMENTS

It is a cliché to say that a work of this magnitude requires the help of a great many people. But, clichés are clichés because they usually contain a grain of truth. It is no less so here.

I begin by acknowledging my committee for their patience with a stereotypical "non-traditional student." Few understand the demands placed on one's time by family, community obligations, work, and a residence 200 miles from campus. However, my committee did. I offer this not as an excuse for any shortcomings in this work, but as an honest assessment of the conditions under which I worked. There is no doubt that this project could have been of higher quality and completed in less time had it been my top priority. Fortunately, Drs. Peterson, Grant, and Smeins understood this, and did not abandon me out of exasperation, as they by every right could have. I especially thank Dr. Nova Silvy for his kindness, patience, and willingness to take me on as a student, despite knowing full well what he was getting into. I am truly grateful that anyone would be willing to take a chance on a mid-career, fully-employed student 6 years out of school. When I consider the regard with which Dr. Silvy is held in the academic and professional community, I am doubly honored.

Thanks to the many faculty and staff members who provided friendship, assistance, and encouragement during my tenure at Texas A&M. I am deeply indebted to Janice Crenshaw for helping me negotiate the ins and outs of grad school and helping me secure funding for my education. Thanks also to Shirley Konecny and Carol Gaas for

always being there. And, of course, I always will keep a special place in my heart for Val and Beth Silvy. Thanks for making me a small part of the "Silvy extended family."

Obviously, the Texas Parks and Wildlife Department played many critical roles in facilitating this research. I thank the many TPWD biologists and technicians who collected brood-count, carnivore, and harvest data over the years. I thank Mike Frisbie for providing access to TPWD brood-count data and Jon Purvis for providing similar access to harvest data. Thank you to Bobbye Ficke, Kevin Mote, Max Traweek, and Junie Sorola for assisting me in locating carnivore data. I thank Robert MacDonald for providing information regarding current and historical turkey seasons and bag limits. I am truly grateful to my various supervisors during this project, Donnie Frels, Max Traweek, Steve DeMaso, Jay Roberson, and Vernon Bevill, for allowing me time to complete this project. A special thanks to many of my TPWD coworkers who, in one way or another, helped create a working environment that encouraged me to better myself and further my education.

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It is not often that a graduating student acknowledges faculty at a previous university. But, I would like to thank John Baccus, Randy Simpson, Rick Manning, and

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Although everyone I have mentioned thus far played an important role in this work, I save my most heartfelt gratitude for the bedrock upon which I have built this work – my family. To my parents, Tommy and Debbie Schwertner, I thank you for your investment in me. You set a shining example of hard work, perseverance, and pride that made me what I am today. I can never hope to repay that. I just hope I make you proud.

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To my children – Trey, James, and Molly – thank you. Thank you for being you and providing the light of your smile during some otherwise dark days. You have my sincerest apologies for the time I could not give you when I was working on this project. It's been a long, hard road since Daddy first decided that "he thinks he's going to be a doctor."

Finally, Wendy. What can I say? You have put up with much more than any wife should be expected to bear. Words cannot express my love for you or what you have been to me. It is only by your faith in me that I was able to pull this off, and by all rights your name should be on the title page. You certainly paid more for this than I did. I love you.

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CHAPTER I

INTRODUCTION

Wild turkeys (*Meleagris gallopavo*) are one of the most important game animals in Texas. During the 2003–2004 hunting season, 127,327 hunters pursued wild turkeys in Texas, making it the second most popular game bird behind mourning dove (*Zenaida macroura*) and the third most popular game animal, behind white-tailed deer (*Odocoileus virginianus*) and mourning dove (Texas Parks and Wildlife Department 2003, Purvis 2004).

The importance of wild turkey as a game animal translates to significant economic impact. The U. S. Fish and Wildlife Service (U. S. Department of Interior – U. S. Fish and Wildlife Service and U. S. Department of Commerce – U. S. Census Bureau 2001) estimated the average Texas big game hunter, the category that includes turkey hunters, spent $858 on hunting-related activities in 2001. Assuming this value held constant through 2003, that extrapolates to a total economic impact of >$109 million dollars for trip and equipment expenditures alone. Although this figure is probably an overestimate due to hunters pursuing multiple big game species, turkey hunters undoubtedly contributed significantly to the >$776 million spent on trip and equipment related items by big game hunters in Texas in 2001.

For most of the twentieth century, the Edwards Plateau of Texas was considered a stronghold of wild turkeys, despite extirpation of the species from most of its range.

This dissertation follows the style of the Journal of Wildlife Management.

From a pre-settlement high of 1.8–2 million birds in Kansas, Oklahoma, and Texas, Rio Grande wild turkey (RGWT; *M. g. intermedia*) abundance was reduced to about 100,000 by the 1920s, found in remnant populations in the Edwards Plateau and South Texas Plains ecoregions of Texas (Gore 1969, Beasom and Wilson 1992). These populations provided the sources for a successful effort to translocate RGWTs into areas from which they had been extirpated, as well as locations outside their former range (Beasom and Wilson 1992). Rio Grande wild turkeys also expanded their range westward because of increased woody vegetation (Texas Game, Fish, and Oyster Commission 1945). By 1994, the RGWT population in Texas was estimated at 573,500 (Kennamer and Kennamer 1995).

Turkey abundance is prone to dramatic year-to-year fluctuations (Healy 1992b); however, Texas Parks and Wildlife Department (TPWD) biologists generally consider RGWT abundance over much of the Edwards Plateau to have remained stable over the long term. The southern Edwards Plateau was considered to support particularly robust RGWT populations (Texas Game, Fish, and Oyster Commission 1945). In recent years, however, TPWD biologists and landowners noticed an apparent decline in RGWT abundance in the southern Edwards Plateau, while no decline was observed in the rest of the ecoregion. This perception was substantiated with analysis of TPWD, RGWT production data (Markus Peterson, Texas A&M University, unpublished data). This decline in these counties where RGWT had been abundant historically has elicited considerable concern among biologists and landowners.

Even as biologists expressed alarm about a perceived population decline among RGWT in the southern Edwards Plateau, TPWD continued to increase exploitation of the population, particularly the female segment. Beginning in the early 1990's, various counties in north and central Texas were opened to fall hen turkey harvest. However, harvest and other factors influencing RGWT population dynamics in Texas were poorly understood. The purpose of this project was to investigate the influence of predation, weather, and harvest on RGWT populations at both broad and local scales.

Predators might limit turkey production through nest predation (Cook 1972, Reagan and Morgan 1980, Ransom et al. 1987), predation of poults (Speake et al. 1985, Vangilder et al. 1987), and predation of juvenile and adult birds (Kurzejeski et al. 1987, Ransom et al. 1987, Miller et al. 1995). Further, Chesness et al. (1968) and Beasom (1974) suggested that predator abundance might be linked to reduced production in ground nesting birds, at least at fine spatial scales. Common predators of RGWT that occur in the southern Edwards Plateau include bobcats (*Lynx rufus*), coyotes (*Canis latrans*), gray foxes (*Urocyon cinereoargenteus*), hognose skunks (*Conepatus mesoleucus*), raccoons (*Procyon lotor*), red foxes (*Vulpes vulpes*), striped skunks (*Mephitis mephitis*), and Virginia opossums (*Didelphis virginiana*).

Weather and climate affect short-term population fluctuations and the geographic distribution of wild turkeys, respectively. Several studies have reported correlations between precipitation and turkey production (Baker 1979, Beasom and Pattee 1980, Healy 1992b, Roberts and Porter 1998a). Of these, only Baker (1979) and Beasom and Pattee (1980) have studied the influences of precipitation on RGWT in Texas.

Most studies addressing the effect of harvest on turkey survival have been conducted on the eastern subspecies (*M. g. silvestris*), and have established that harvest can indeed affect eastern turkey populations (Vangilder 1992). Little et al. (1990) concluded that fall hunting mortality in Iowa was additive and, if excessive, could reduce survival of turkeys. Pack et al. (1998) found that fall hunting significantly reduced the annual survival rate of turkey hens in Virginia and West Virginia. I am unaware, however, of any research into the effects of harvest on RGWT populations.

Therefore, my study had 3 objectives. They were:

1. Investigate the effect of precipitation and predator abundance on turkey production at broad spatial scales.
2. Develop a simulation model of RGWT population dynamics that could be used to evaluate alternative management strategies and environmental effects on RGWT populations.
3. Use the simulation model to evaluate the effect of fall hen harvest on RGWT populations in the Edwards Plateau.

CHAPTER II

RIO GRANDE WILD TURKEY BROOD-COUNT DATA

Power analysis is a statistical technique whereby an investigator estimates the probability of committing a Type II statistical error, given the data examined. Whereas Type I error rate (α) is the probability of rejecting H_0 when H_1 is false, Type II error rate (β) is the probability of failing to reject H_0 when H_1 is true. Power of a statistical test ($1-\beta$), therefore, is the probability of rejecting H_0 when H_1 is true, and is a function of population standard deviation (σ), sample size (n), α, and the hypothesized (or actual) difference between population means or proportions ("effect size" or δ; Ott and Longnecker 2001).

Although statistical power is a fundamental statistical concept (Zar 1999), power analysis was rarely employed in the wildlife sciences prior to the mid-1990s (Steidl et al. 1997). Since that time, however, it has enjoyed increasing prominence. The Wildlife Society (1995) suggested several ways in which power analysis could be used in wildlife research, including calculation of required sample sizes prior to performing wildlife studies and the *a posteriori* interpretation of study results (so-called "retrospective power analysis"). Although Gerard et al. (1998) questioned the validity of retrospective analysis on theoretical grounds, Steidle et al. (1997) observed that retrospective power analysis had utility if calculated using effect sizes other than the observed effect size.

Several investigators have used power analyses to design wildlife population monitoring efforts (Gibbs and Melvin 1997, Crouch and Paton 2002). Others have used power analysis to evaluate existing wildlife surveys. Lougheed et al. (1999) used

retrospective power analysis to evaluate ongoing waterfowl surveys in Canada, finding the surveys had sufficient power to detect a 5% trend had one existed, although power, and hence survey duration required to detect a trend, varied among species. Rice (2003) evaluated the power of ring-necked pheasant (*Phasianus colchicus*) call and brood counts in Washington, and determined that both methods had sufficient power to detect only large (40%) year-to-year changes.

Recruitment may be the demographic parameter most important in determining wild turkey abundance trends (Roberts and Porter 1996). Hen:poult ratios, calculated from observations of turkeys during the brood-rearing season, are used as an index of recruitment by several states (Kurzejeski and Vangilder 1992). Observations of hens and poults are recorded by conservation personnel during the summer months either incidental to other duties (Schulz and McDowell 1957, Wunz and Shope 1980) or along predetermined routes (Shaw 1973, Menzel 1975, Bartush et al. 1985). Texas Parks and Wildlife Department (TPWD) has collected incidental RGWT brood observations across the range of the subspecies since 1976 (TPWD, unpublished data). Although usually referred to as a "survey," this technique is best classified as "convenience" or "haphazard" sampling (Anderson 2001, Morrison et al. 2001). This is the only method by which RGWT populations currently are monitored; however, I found no published assessment of the power of brood counts to detect changes in turkey production. Therefore, the objective of this study was to evaluate the power of TPWD brood counts for detecting changes in RGWT production across broad spatial scales. Specifically, I

calculated the power to detect differences among years and between 2 consecutive long-term-data sets.

METHODS

I evaluated RGWT production across the Edwards Plateau, Rolling Plains, Cross Timbers and Prairies, Post Oak Savannah, and South Texas Plains ecological regions. These regions encompassed the majority of RGWT range in Texas (Fig. 2.1).

Personnel from TPWD collected RGWT brood observations from 1 June through 15 August, 1976–2000. Observers recorded all RGWT hens and poults during the course of routine daily activities. Counts were not conducted along standardized routes; rather observers were encouraged to observe 10–25 hens per county during each 2-week period. Observations were recorded by county and latitude-longitude coordinates (Graham and George 2002).

Data Analysis

Brood-Count Data.– I grouped each year's data according to ecological region prior to analysis. Data from the Edwards Plateau and Cross Timbers and Prairies were available for 1976–2000, data from the Rolling Plains and Post Oak Savannah were available for 1977–2000, and data from the South Texas Plains were available for 1977–1978 and 1980–2000.

I calculated total number of hens and poults observed per year in each ecological region. I then calculated RGWT poult production (p) per region as

$$p = \frac{n_p}{(n_p + n_h)}$$

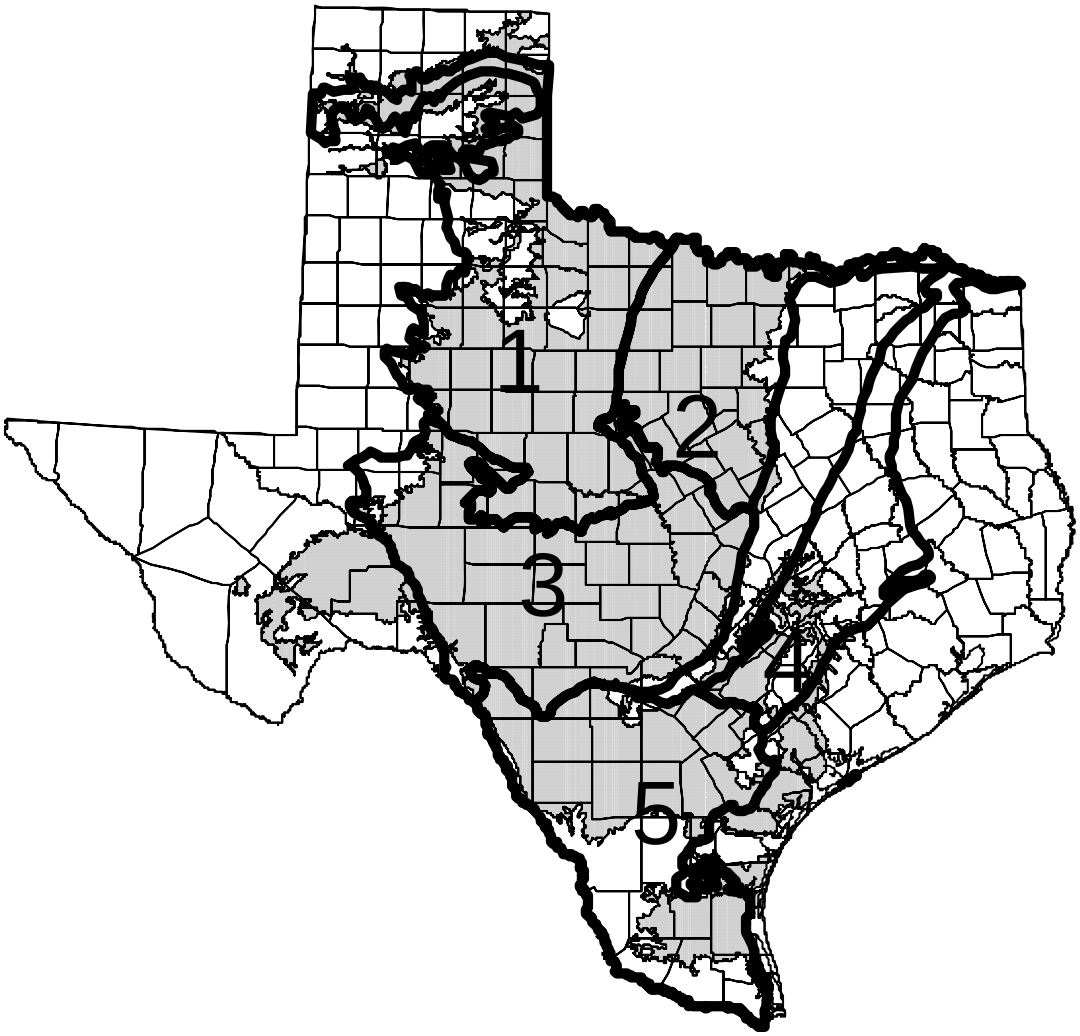


Fig. 2.1. Ecological regions (Gould 1975) of Texas containing significant populations of Rio Grande wild turkey. Names of ecological regions are 1 = Rolling Plains, 2 = Cross Timbers and Prairies, 3 = Edwards Plateau, 4 = Post Oak Savannah, and 5 = South Texas Plains. Gray area indicates approximate range of the Rio Grande wild turkey in Texas, adapted from Texas Parks and Wildlife Department (1997).

where, n_p = number of poults and n_h = number of hens. I also determined the total number of RGWT groups containing at least 1 poult or hen observed annually in each ecological region.

Power Analysis.– Steidle et al. (1997) advised that power analysis should be performed using biologically meaningful effect size. However, Gerard et al. (1998) noted that biologists often are reluctant to define what effect size is biologically meaningful, because it is a subjective decision, often with little data to support it. Published research addressing the sensitivity of turkey populations to changes in recruitment are sparse. Vangilder and Kurzejeski (1995) performed sensitivity analysis using a population model of eastern wild turkeys in northern Missouri to examine the effects of varying nest success and poult mortality, which are both important determinants of recruitment. They found that increasing annual nest success 10 and 20% increased the hypothetical population after 40 years by 937 and 12,696%, respectively; decreasing nest success 10 and 20% resulted in 13 and 88% declines in the population. Changes in poult mortality produced similar results. Increasing poult mortality 10 and 20% resulted in a population decrease of 68 and 98%, while decreasing poult mortality by 10 and 20% resulted in a population increase of 3,154 and 19,957%, respectively. These results suggested that changes in recruitment of 10–20% where biologically meaningful; however, differences in climatic and habitat conditions between northern Missouri and Texas may lesson the applicability of the results to turkeys in Texas. Therefore, I chose to perform my analysis using a wide range of effect sizes. I estimated power of the brood counts to detect a change in poult production between

consecutive years using the 1-proportion power calculation function in Minitab for Windows 12.2 (Minitab, Inc., State College, Pennsylvania). I calculated power to detect inter-annual difference in poult production (i.e., $p_1 – p_0 = \delta_p$), where δ_p = 0.05, 0.075, 0.10, 0.15, 0.20 and p_0 = 0.50, for a range of sample sizes (25–500) representative of actual sampling effort. I set p_0 = 0.50 because power is lowest and required n is highest for this value, thus corresponding estimates are most conservative (Ott and Longnecker 2001:474). I set α = 0.05 for all calculations.

I also estimated the power of the survey to detect long-term changes in poult proportion within each ecological region. I assumed that changes in production over time could be tested for by dividing the time series into 2 periods (labeled arbitrarily as periods #1 and #2) at the approximate mid-point of the time series and comparing the means of period #1 and #2 using a Student's *t*-test. Sample size equaled length of each period in years. Hence, power of the test was determined using the 2-sample *t*-test power analysis function in Minitab. Because the results of Levene's test indicated sample standard deviation did not differ within ecological region between the 2 periods (P = 0.492–0.910), pooled sample standard deviation (S_{pooled}) was calculated per region (Table 2.1) and used as an estimate of population standard deviation in power calculations. I calculated power to detect difference in mean poult production between the 2 consecutive long-term data sets (i.e., $\mu_1 – \mu_2 = \delta_\mu$), where δ_μ = 0.05–0.40 in 0.05 increments.

I also determined the minimum number of years that the count would have to be conducted to detect a mean difference in poult production (δ_μ) between the periods #1

Table 2.1. Pooled sample standard deviation and sample size (in years), by ecological region, used in power analysis of long-term recruitment trends.

Ecological region	S_{pooled}	n_1	n_2
South Texas Plains	0.2238	11	12
Low Rolling Plains	0.1848	12	12
Edwards Plateau	0.2192	13	12
Cross Timbers and Prairies	0.1287	13	12
Post Oak Savannah	0.1796	12	12

and #2 for each region, where δ_μ = 0.05–0.40 in 0.05 increments, p_0 = 0.50, and 1–β = 0.80. For these analyses, I assumed that brood counts accurately estimated the mean poult proportion for each ecoregion.

RESULTS

Power analysis indicated 50 turkey brood observations per year were required for ≥80% chance of detecting δ_p = 0.200. For the same probability of detection, required group size increased to 100 for δ_p = 0.150, 200 for δ_p = 0.100, 350 for δ_p = 0.075, and >500 for δ_p = 0.050 (Fig. 2.2).

Power analysis indicated the current data set had power ≥0.80 to detect ≥0.30 difference in poult production between the two consecutive time series in all regions.

Only the Cross Timbers and Prairies data had similar power to detect a difference of 0.20. No region's data had power ≥0.80 to detect a difference of ≤0.15 (Fig. 2.3).

Time-series data sets of 16–30 years had power ≥0.80 to detect long-term mean differences in poult production of 0.20 in the Rolling Plains, Cross Timbers and Prairies, and Post Oak Savannah regions. Counts of ≥40 years would be required for similar results in the Edwards Plateau and South Texas Plains (Table 2.2).

DISCUSSION

Vangilder and Kurzejeski (1995) suggested that a 10–20% change in turkey recruitment was biologically meaningful. This corresponds to δ_p = 0.050–0.10 when p_0 = 0.50. My results suggest that a sample size of n = 200–>500 turkey-group observations were needed to detect this level of inter-annual difference in poult production when power ≥0.80. Sample size averaged 65–306 for the 5 regions. Number of observations likely differed among regions due to sampling effort and turkey density.

My results indicated that existing production data had very low power (<0.50) to detect a long-term change of <20%. Further, time series of 54–160 years would be required to detect this effect size in all ecological regions. This low power resulted from the high degree of inter-annual variation in poult production.

A further complication is that collection of incidental brood count data was "haphazard" or "convenience" sampling, not a true survey. Samples were not random; therefore, samples may not have been representative of the population. This may have biased estimates of turkey production.

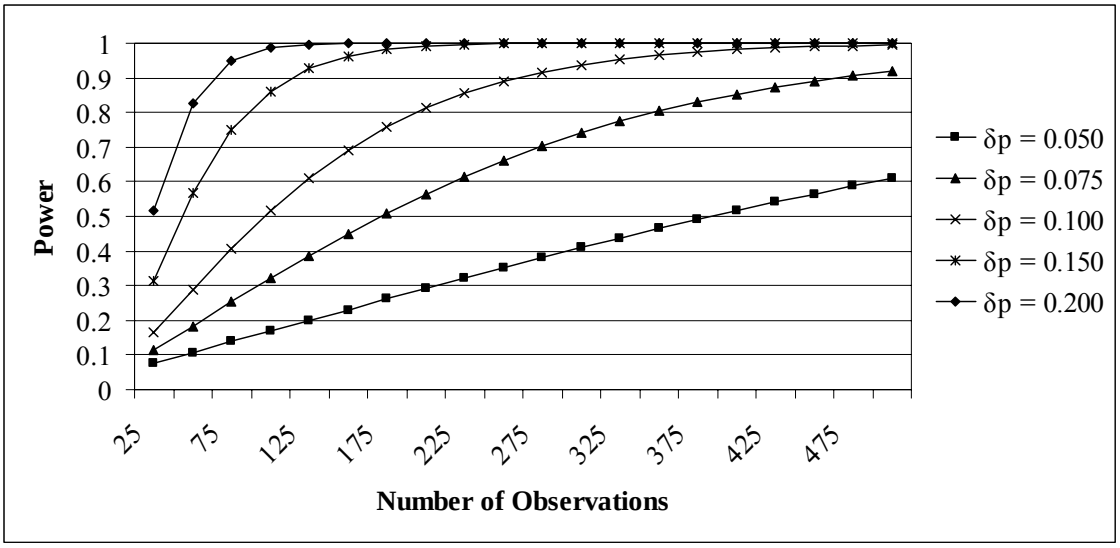


Figure 2.2. Power of TPWD brood surveys to detect inter-annual change of δ_p away from hypothetical proportion of 0.50 poults in the hen:poult population.

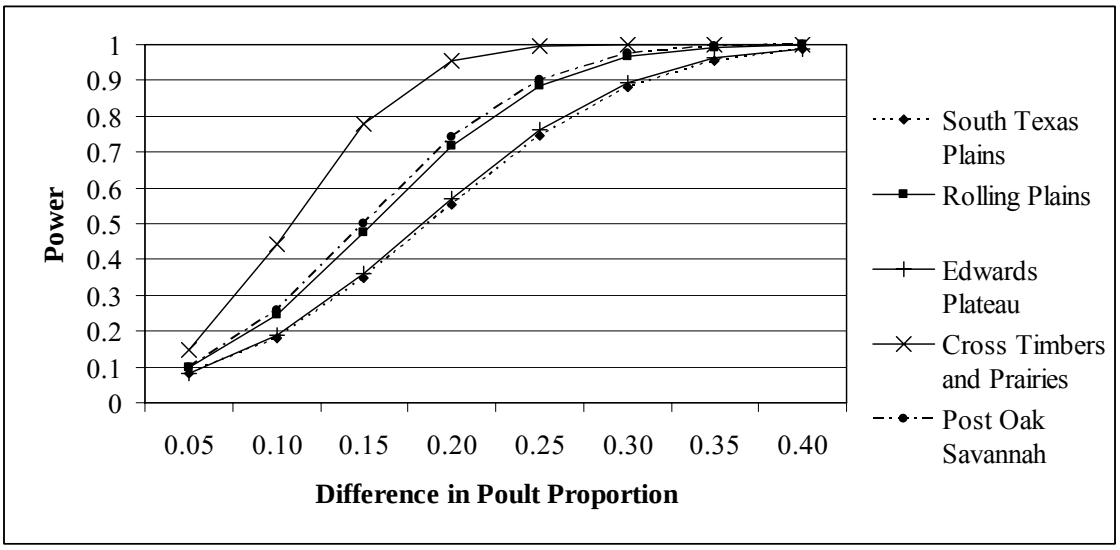


Figure 2.3. Power of current TPWD brood-count data sets to detect a given difference in mean poult production between 2 consecutive long-term-data sets.

Table 2.2. Minimum length (in years) of time series required to detect a long-term change (δ_μ) of 0.05–0.40 in poult proportion with power ≥0.80, for 5 ecological regions of Texas.

δ_p	South Texas Plains	Low Rolling Plains	Edwards Plateau	Cross Timbers and Prairies	Post Oak Savannah
0.05	632	432	606	210	408
0.10	160	110	154	54	104
0.15	72	50	70	26	48
0.20	42	30	40	16	28
0.25	28	20	28	12	20
0.30	20	16	20	10	14
0.35	16	12	16	8	12
0.40	14	10	12	6	10

My evaluation of TPWD brood-count data was based on the assumption that a 10–20% change in recruitment is biologically meaningful to RGWT population dynamics in Texas, as it was for eastern wild turkey in Missouri (Vangilder and Kurzejeski 1995).

There is some evidence to suggest that Texas populations may behave differently than those in Missouri. Annual turkey survival on 4 study sites in the Edwards Plateau was 0.566–0.737 (Beau Willesey, unpublished data), versus 0.445–0.693 used in Vangilder and Kurzejeski's model. Higher annual survival rates may lesson the sensitivity of turkey populations to changes in recruitment.

Rio Grande wild turkey brood counts, as currently conducted by the TPWD, have little value for detecting biologically-significant inter-annual or long-term changes in turkey recruitment. Further, haphazard sampling may bias recruitment estimates. Nevertheless, brood counts have been shown to be correlated with precipitation in Texas (Chapter III). This correlation with an independent variable suggests that brood-count data do in fact reflect real biological processes despite an apparent lack of statistical power.

Wild turkey management and the setting of harvest regulations require reliable information regarding turkey population dynamics, including recruitment. Power analysis is a powerful tool for designing and evaluating population monitoring efforts. Without a clear understanding of statistical power, managers may falsely conclude that populations are stable when, in fact, changes are occurring. I encourage the use of power analysis in population monitoring efforts to strengthen the rigor and reliability of knowledge upon which management decisions are based. At a more fundamental level, I encourage research into RGWT population dynamics, in order to more adequately define the role of recruitment in regulating populations and determine the biologically meaningful effect size that surveys should be designed to detect.

CHAPTER III

INFLUENCE OF PRECIPITATION ON RIO GRANDE WILD TURKEY PRODUCTION IN TEXAS

Precipitation is 1 of the most important factors influencing the distribution and abundance of terrestrial organisms (Krebs 1994). It is known to affect avian populations directly by killing individuals (Welty and Baptist 1988), destroying nests, and regulating the timing of breeding (Marshall 1959), and indirectly through its effects on vegetation and other environmental factors (Welty and Baptista 1988). Precipitation affects the abundance or production of several species of gallinaceous birds, including black grouse (*Tetrao tetrix*; Baines 1991), capercaillie (*T. urogallus*; Moss 1986), grey partridge (*Perdix perdix*; Panek 1992), northern bobwhites (*Colinus virginianus*; Bridges et al. 2001, Lusk et al. 2002), and scaled quail (*Callipepla squamata*; Campbell et al. 1973, Bridges et al. 2001).

The influence of precipitation also extends to wild turkeys. Precipitation can directly affect turkey production by flooding nests or drowning poults (DeArment 1969, Kennamer et al. 1975, Zwank et al. 1988, Healy 1992), and causing hypothermia-induced mortality among poults (Markley 1967, Healy and Nenno 1985, Roberts and Porter 1998a). It also might indirectly influence turkey production by facilitating predation (Palmer et al. 1993, Roberts et al. 1995, Roberts and Porter 1998b) or altering intermediate environmental variables believed to be correlated with turkey production. These include the structure of vegetative cover (Beasom 1973, Cable 1975), as well as the abundance of forbs (Beasom 1973) and arthropods (Johnson and Worobec 1988,

Belovsky and Slade 1995, Frampton et al. 2000), which are important food items for turkey poults (Hurst 1992).

Most research regarding the influence of precipitation on wild turkey populations has been conducted in the eastern and northern United States, where the climate is relatively wet and/or cool. In New York, Roberts and Porter (1998a,b) found that nest survival of eastern wild turkeys (*M. g. sylvestris*) was negatively correlated with precipitation during incubation, and poult survival was negatively correlated with precipitation during the second week following hatching. Precipitation also was negatively correlated with eastern wild turkey production in West Virginia (Healy and Nenno 1985), and wild turkey recruitment declined in Mississippi following droughts (Palmer et al. 1993).

Studies addressing how precipitation affects Rio Grande wild turkeys are uncommon. DeArment (1969:31) maintained that RGWT hen:poult ratios on 3 study areas in the Texas panhandle "closely paralleled" rainfall during 1954–1958. On 2 study areas in south Texas, Beasom and Pattee (1980) found a strong correlation between previous year's rainfall and poult production. However, both studies investigated localized effects of precipitation over relatively short (≤10 years) periods. To my knowledge, no one has examined the relationship between weather and Rio Grande wild turkey production at broad spatial scales over long time-periods (>20 years).

I tested 2 precipitation-related hypotheses: (1) precipitation strongly influences Rio Grande wild turkey production in Texas, and (2) Rio Grande wild turkey production in Texas responds indirectly to cumulative effects of precipitation (e.g., effects on vegetation structure or food availability), rather than directly to episodic events such as

flooding, exposure, or enhanced predation. If my first hypothesis is supported by data, then Rio Grande wild turkey production and precipitation should be strongly correlated. If this correlation is strongest with cumulative precipitation over several months, rather than individual monthly precipitation, it would lend support to my second hypothesis. Also, positive correlations would suggest that precipitation influences turkey production by affecting factors that respond positively to soil moisture, such as vegetation structure or food availability; negative correlations would suggest precipitation directly increases mortality by increasing risk to drowning, nest inundation, and hypothermia. Finally, I performed exploratory analyses to determine (1) whether a moisture index that incorporated a number of weather variables would be a better predictor of turkey production than raw precipitation alone, in order to suggest to managers a suitable weather-based index to Rio Grande wild turkey production in Texas; and (2) if there was a relationship between seasonality of rainfall and Rio Grande wild turkey poult production, to generate hypotheses for future investigation.

STUDY AREAS

I evaluated the effects of precipitation on Rio Grande wild turkey production in the Edwards Plateau, Rolling Plains, Cross Timbers and Prairies, Post Oak Savannah, and South Texas Plains ecological regions of Texas (Gould 1975; Fig 3.1A). These regions encompassed the majority of Rio Grande wild turkey range in Texas (Fig. 3.1A). Mean annual precipitation was 584–864 mm, and generally decreased from east to west. Although Rio Grande wild turkeys were present in the High Plains, Trans-Pecos, and

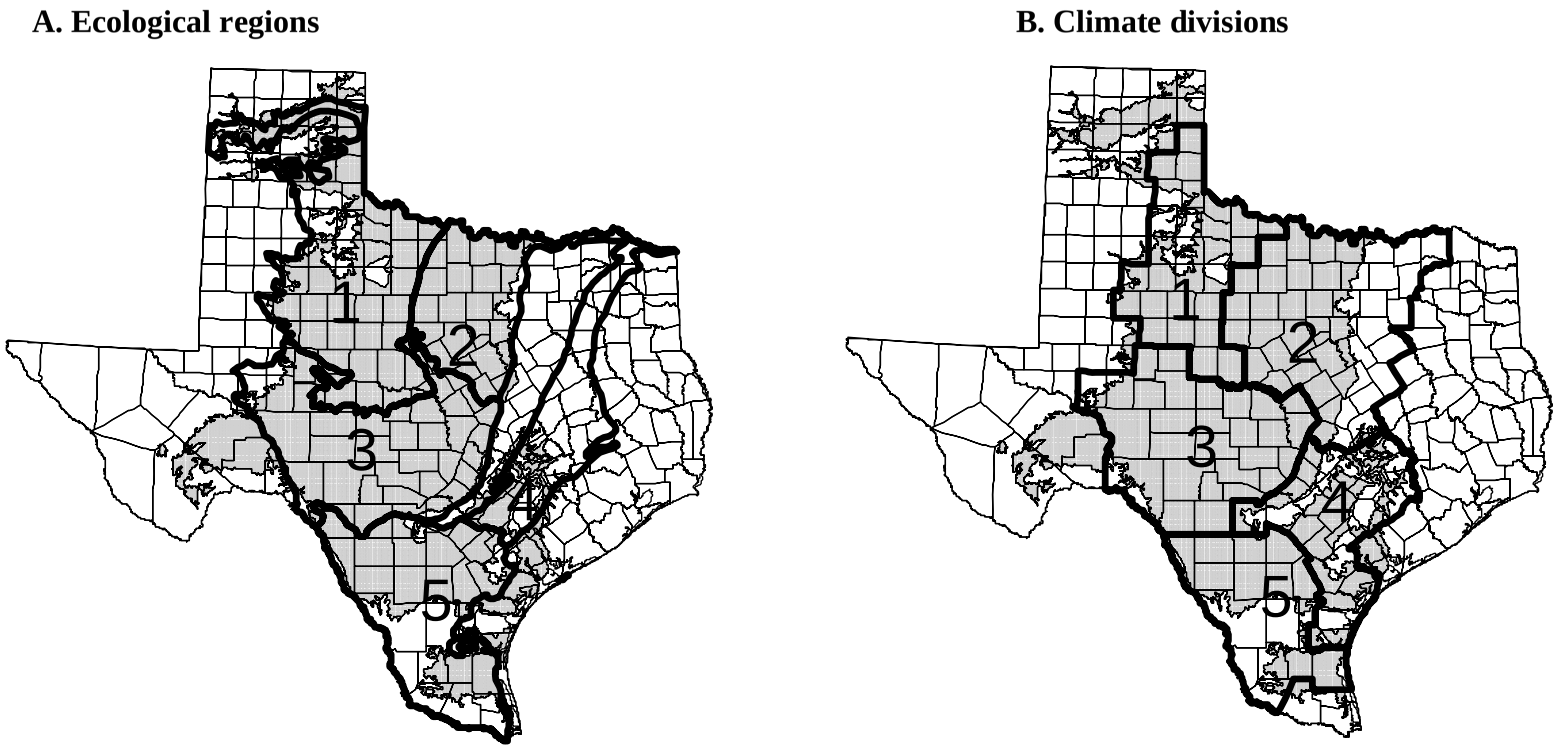


Fig. 3.1. (**A**) Ecological regions (Gould 1975) and (**B**) climate divisions (National Climate Data Center) of Texas containing significant populations of Rio Grande wild turkey. Names of ecological regions (and climate divisions, where different) are 1 = Rolling Plains (Low Rolling Plains), 2 = Cross Timbers and Prairies (North Central), 3 = Edwards Plateau, 4 = Post Oak Savannah (South Central), and 5 = South Texas Plains (Southern). Gray area indicates approximate range of the Rio Grande wild turkey in Texas, adapted from Texas Parks and Wildlife Department (1997).

Gulf Prairies and Marshes ecological regions (Gould 1975), their limited abundance and range in these regions resulted in little historical data being available, and thus precluded analysis.

METHODS

Production Data

Texas Parks and Wildlife Department biologists conducted annual RGWT brood counts during 1976–2000 across the subspecies' range in Texas (Chapter II). I grouped each year's data according to ecological region prior to analysis. Data from the Edwards Plateau and Cross Timbers and Prairies were available for 1976–2000, data from the Rolling Plains and Post Oak Savannah were available for 1977–2000, and data from the South Texas Plains were available for 1977–1978 and 1980–2000. I calculated the total number of hens and poults observed per year during the surveys in each ecological region. I then calculated an index of Rio Grande wild turkey poult production as $n_p / (n_p + n_h)$, where n_p = the number of poults, and n_h = the number of hens observed per year (Table 3.1).

Climate Data

I selected *a priori* 4 precipitation indices, based on either PMDI or raw precipitation, for analysis: June PMDI, September–June PMDI, June raw precipitation, and September–June raw precipitation. I used precipitation indices for June or periods ending in June because this coincided with peak Rio Grande wild turkey hatching across Texas (Beasom 1973, Ransom et al. 1987, Hohensee and Wallace 2001). Therefore, precipitation-induced alterations in Rio Grande wild turkey production should

Table 3.1. Raw RGWT poult production by ecological region (Gould 1975), 1976–2000.

	Region				
Year	EP	RP	CT&P	POS	STP
1976	0.33		0.66		
1977	0.78	0.62	0.77	0.73	0.57
1978	0.51	0.47	0.72	0.16	0.29
1979	0.79	0.80	0.83	0.64	
1980	0.39	0.64	0.74	0.46	0.11
1981	0.84	0.80	0.81	0.71	0.57
1982	0.44	0.67	0.71	0.58	0.40
1983	0.60	0.58	0.66	0.46	0.51
1984	0.21	0.29	0.58	0.23	0.24
1985	0.78	0.74	0.71	0.61	0.68
1986	0.66	0.64	0.67	0.57	0.30
1987	0.77	0.73	0.74	0.57	0.66
1988	0.27	0.18	0.40	0.41	0.12
1989	0.47	0.63	0.61	0.26	0.16
1990	0.66	0.55	0.55	0.72	0.73
1991	0.63	0.77	0.65	0.53	0.62
1992	0.70	0.75	0.59	0.72	0.80
1993	0.39	0.55	0.64	0.52	0.53
1994	0.41	0.40	0.39	0.33	0.56
1995	0.71	0.68	0.53	0.26	0.24
1996	0.17	0.44	0.39	0.23	0.05
1997	0.78	0.84	0.70	0.64	0.67
1998	0.31	0.38	0.49	0.53	0.29
1999	0.60	0.70	0.50	0.41	0.50
2000	0.11	0.24	0.46	0.25	0.22

have been most pronounced during this period. Also, because precipitation across most RGWT range in Texas exhibits a bimodal pattern, with peaks in early autumn and late spring (Carr 1967), and rainfall prior to the growing season plays an important role in plant growth (Cable 1975), I chose precipitation and drought indices for the previous September–June to assess cumulative weather effects.

The PMDI is a meteorological drought index that uses deviations from long-term average precipitation and temperature, and the duration of the current dry or wet period, to estimate the severity of a dry or wet period (Heddinghaus and Sabol 1991). Usual PMDI values range between – 4.0 and 4.0, although more extreme values occasionally occur. Negative values indicate dry periods, positive values indicate wet periods, and values near 0 indicate near normal conditions. Bridges et al. (2001) determined that 12-month cumulative and monthly PMDI were more correlated with quail abundance than were a number of other precipitation indices, including raw precipitation. I chose June PMDI to represent cumulative weather effects for the months during and immediately preceding the RGWT nesting season. September–June PMDI (calculated by summing the PMDI values of each September–June period) represented cumulative weather effects beginning with the onset of the autumn wet-season prior to breeding.

Unfortunately, PMDI data are readily available only at the spatial scale of the climate division (Fig. 3.1B). Calculation of this index for geographic areas that do not closely approximate the size or geographic extent of these divisions requires weather data and specialized knowledge that may not readily be available to wildlife managers. For this reason, I examined total raw precipitation as well. I chose total June

precipitation as an index of monthly precipitation at the peak of hatching, and total September–June precipitation as an index of cumulative precipitation prior to and during the breeding season.

To further explore the question of whether turkey production responded to seasonality of precipitation, I chose 3 indices of seasonal rainfall: total precipitation during the previous autumn (September–November), winter (December–February), and spring (March–May). I used raw precipitation alone because my initial analysis indicated that it was comparable to PMDI for predicting poult production. I examined these data for the Edwards Plateau only, because sample sizes in this region were the largest among the regions examined, and thus provided the most precise estimates of poult production and allowed us to evaluate poult production by seasonal precipitation (Chapter II).

I obtained PMDI and raw precipitation data for the Edwards Plateau, Low Rolling Plains, North Central, South Central, and Southern Texas climate divisions (http://lwf.ncdc.noaa.gov/oa/climate/onlineprod/drought/xmgrg3.html). The boundaries of these climate divisions matched closely, but not exactly, those of the Edwards Plateau, Rolling Plains, Cross Timbers and Prairies, Post Oak Savannah, and South Texas Plains ecological regions, respectively (Fig. 3.1).

Analysis

Because both climate and production data could be serially correlated, I detrended these data using the first differences method to determine year-to-year change in precipitation and production indices (Ott and Longnecker 2001). Because the detrended

poult production data from some climate divisions were non-normally distributed (Ryan-Joiner 1976), I used Spearman rank correlation (Zar 1999) to evaluate how poult production varied with values for each index of precipitation. Correlations were considered significant if $P \leq 0.05$. I compared the correlation coefficients (r_S) of June PMDI, September–June PMDI, September–June total rainfall, and June total rainfall for each climate division to determine which variable was most correlated with Rio Grande wild turkey production.

I also performed Spearman rank correlation on RGWT production and each index of seasonal precipitation. I then compared r_S of poult production and previous autumn, winter, and spring precipitation using data from the Edwards Plateau to determine whether the correlation between poult production and precipitation varied by season.

RESULTS

June PMDI and September–June raw precipitation were similarly correlated with poult production in all ecological regions (Table 3.2). June precipitation was correlated with poult production in all ecological regions except the Post Oak Savannah, although the relationship typically was weaker than for June PMDI or September–June raw precipitation (Table 3.2). September–June PMDI was correlated with poult production in the Edwards Plateau, Cross Timbers and Prairies, and Post Oak Savannah, but not in the Rolling Plains or South Texas Plains (Table 3.2).

Correlation between poult production and precipitation in the Edwards Plateau varied by season. Correlation was similar for the previous spring and autumn ($r_S = 0.85$ and 0.74, respectively), but was weaker for the previous winter ($r_S = 0.50$).

Table 3.2. Correlations between monthly and 9-month sums of raw precipitation (Precip) and the Modified Palmer Drought Severity Index (PMDI) and Rio Grande Wild Turkey poult production by Texas ecological region (Gould 1975), 1976–2000 (EP = Edwards Plateau, RP = Rolling Plains, CT&P = Cross Timbers and Prairies, POS = Post Oak Savannah, and STP = South Texas Plains). All data were detrended over years.

Region	June				September–June			
	PMDI		Precip		PMDI		Precip	
	r_S	P	r_S	P	r_S	P	r_S	P
EP	0.84	<0.001	0.60	0.002	0.66	<0.001	0.86	<0.001
RP	0.83	<0.001	0.53	0.009	0.27	0.216	0.81	<0.001
CT&P	0.76	<0.001	0.64	0.001	0.48	0.020	0.69	<0.001
POS	0.54	0.008	0.10	0.651	0.43	0.039	0.65	0.001
STP	0.74	<0.001	0.48	0.021	0.31	0.143	0.74	<0.001

DISCUSSION

Rio Grande wild turkey poult production showed a positive correlation with precipitation in Texas during 1976–2000. This correlation was stronger with indices that included multi-month cumulative weather data than with June raw precipitation alone. This lends support to the hypothesis that precipitation influences Rio Grande wild turkey production in Texas, and this influence arises from the cumulative effects of precipitation over several months rather than individual rainfall events.

My findings differed from those of Healy and Nenno (1985) and Roberts and Porter (1998a), who found that poult survival was negatively correlated with spring rainfall in West Virginia and New York, respectively. They attributed their results to exposure-related mortality among poults. Climatic differences could explain this discrepancy, as poult mortality due to wetting and hypothermia probably was of greater significance in these comparatively cool and wet eastern wild turkey habitats than in Texas.

Quail in Texas also have been found to be influenced by weather, including precipitation. Lusk et al. (2002) found that previous autumn rainfall was the most important variable influencing broad-scale northern bobwhite abundance in Texas. In south Texas, northern bobwhite production was found to be sensitive to both precipitation and temperature, and this relationship was most pronounced with spring weather variables (Guthery et al. 2002). Bridges et al. (2001) used 12-month cumulative PMDI, monthly PMDI, and raw precipitation indices to predict changes in northern bobwhite and scaled quail abundance among years in the Edwards Plateau, Rolling Plains, Cross Timbers and Prairies, South Texas Plains, Gulf Prairies and Marshes, and Trans-Pecos ecological regions of Texas. They found that 12-month cumulative PMDI was a highly correlated with northern bobwhite and scaled quail abundance in the Rolling Plains and South Texas Plains ecological regions, but not in the Edwards Plateau, Cross Timbers and Prairies, or Gulf Prairies and Marshes. Only in the South Texas Plains was there a correlation between quail abundance and 12-month (September–August) raw precipitation, and this correlation was weaker than with 12-month PMDI. Northern bobwhite abundance also was correlated with June PMDI, but

not June precipitation, in the Rolling Plains and South Texas Plains ecological regions. Scaled quail abundance was correlated with June PMDI in the Edwards Plateau and South Texas Plains, but with June raw precipitation in the Edwards Plateau only.

I failed to find evidence that PMDI was a better predictor of RGWT production than precipitation alone. Whereas Bridges et al. (2001) concluded that both 12-month cumulative and monthly PMDI measures were much better predictors of quail abundance than precipitation alone, I found that September–June precipitation and June PMDI did a comparable job of predicting changes in poult production among years, and were superior to both June precipitation and September–June cumulative PMDI. This was true despite the assertion that PMDI was better at capturing moisture-induced variability in vegetation dynamics (Palmer 1965).

Because raw precipitation data are more readily available for user-defined geographic areas, wildlife managers probably would find these data more useful for predicting RGWT production in Texas. Further, because PMDI was superior to raw precipitation for quantifying weather effects on vegetation (Palmer 1965), yet no better at predicting RGWT production, it is possible that turkey population dynamics in Texas were not related to vegetation in the same way as were northern bobwhite and scaled quail populations. Thus, the mechanism by which precipitation influences turkey production (e.g., vegetation change) merits further study.

The results of my exploratory analyses suggested that seasonality of precipitation also had a strong effect on RGWT production. Both autumn and spring precipitation were better predictors of poult production than winter precipitation. This supported the

conclusions of Beasom and Pattee (1980), who found strong positive correlations between total rainfall during the previous autumn and spring and RGWT production in the South Texas Plains.

Again, my findings regarding seasonality of precipitation were consistent with research conducted on bobwhites in Texas. Lusk et al. (2002), using a neural-network model, concluded that autumn precipitation was a better predictor of broad scale changes in northern bobwhite abundance in Texas than either spring or winter precipitation. Bridges et al. (2001) also showed that the strength of correlation between PMDI and northern bobwhite abundance varied among seasons in the Edwards Plateau.

MANAGEMENT IMPLICATIONS

Although managers cannot control the weather, understanding how such exogenous variables influence turkey population dynamics is important to understanding the context in which management actions operate. Our results suggest that managers can anticipate Rio Grande wild turkey production based on weather variables, and adjust management recommendations accordingly. Moreover, managers can use their knowledge of existing weather conditions, along with an understanding of how precipitation influences factors thought to limit abundance to judge, *a priori,* the potential efficiency and effectiveness of management practices directed at these limiting factors.

Brood surveys typically require intensive manpower in order to collect sufficient data to provide meaningful results. As the demands on conservation agencies increase, rarely with concomitant increases in agency budgets, managers must seek less-expensive alternatives to traditional practices. Further, brood surveys typically are conducted

during mid- to late-summer, generally after harvest regulations have been made. The close correlation between precipitation and poult production provides managers with a cost effective alternative to brood surveys for determining Rio Grande wild turkey breeding success, at least in Texas.

CHAPTER IV

MEDIUM-SIZED CARNIVORE ABUNDANCE TRENDS IN CENTRAL TEXAS, 1976–2003: EVIDENCE OF MULTI-SCALE ASYNCHRONY AND SPATIAL STRUCTURING

Mammalian carnivores are important components of terrestrial ecosystems (Estes 1996). In central Texas, most species of large carnivores (e.g., black bear [*Ursus americanus*] and gray wolf [*Canis lupus*]) were extirpated or greatly reduced in abundance during historic times (Davis and Schmidly 1994). However, the medium-sized carnivore community has remained relatively robust (Goetze 1995).

In this chapter, I focus on medium-sized carnivores—mammalian carnivores of the orders Didelphimorphia and Carnivora generally weighing <20 kg. Medium-sized carnivores can significantly influence other wildlife populations including neotropical songbirds (Heske et al. 2001), game birds (Miller and Leopold 1992, Rollins and Carroll 2001), small mammals (Henke and Bryant 1999, Hansson 2002), and reptiles (Christiansen and Gallaway 1984). They also may directly or indirectly affect humans by causing property damage (Conover 2001) or by transmitting infectious diseases and parasites (Davis et al. 1981).

Public perception in central Texas is that some medium-sized carnivore species, especially raccoons (*Procyon lotor*) and striped skunks (*Mephitis mephitis*), have increased in abundance during recent years (T. W. Schwertner, personal observation). If true, then increasing medium-sized carnivore abundance could have serious ecological

effects. Hence, my first objective was to identify long-term trends in medium-sized carnivore abundance across central Texas from 1978 though 2003.

Population trends that emerge at such broad scales, however, may not be representative of population dynamics at smaller spatial scales. Population changes at finer scales might be of different magnitudes, or even move in opposite directions, than those at broader scales. Such spatially-structured asynchronous dynamics might partially or completely cancel each other and become masked when viewed at broad scales allowing potentially important ecological effects to go undetected. Therefore, I examined carnivore population data at three scales—regional, county, and more local—to identify population trends and possible spatial structure and asynchrony in medium-sized carnivore abundance.

STUDY AREA

I analyzed data on medium-sized carnivores collected in 38 central Texas counties (Fig. 4.1). The study region encompassed the Edwards Plateau as well the southern portion of the Cross Timbers ecological regions (Gould 1975). Topography ranged from rolling to steep, with mainly shallow rocky soils. Historically, the region was a grassland or open savannah, but woodlands and brushlands presently dominate. Most of the region was rural, although three major cities occur at the periphery (Austin, Travis County; Del Rio, Val Verde County; San Angelo, Tom Green County).

METHODS

Data Collection

From 1978 through 2003, Texas Parks and Wildlife Department conducted annual spotlight surveys to monitor medium-sized carnivore abundance. Surveys were originally designed to monitor these species because of their significance as furbearing animals. However, this survey provides the only long-term continuous set of broad-scale carnivore abundance data in Texas. Surveys were conducted throughout the region during August–October in conjunction with annual white-tailed deer (*Odocoileus virginianus*) surveys (Berger and George 2003).

Permanent survey routes were situated along public and occasionally private roads in rural areas of each county. Although confined to roads and not randomly distributed, transects typically were situated to give even coverage across individual counties. Most routes were 24.1-km long, but length varied among routes (8.0–25.7 km, $\bar{x}$ = 23.3 km). From 1978 through 2003, 192 routes were established in the study area (Fig. 4.1). Most routes were not surveyed continuously during this period, with 24–101 ($\bar{x}$ = 72) being surveyed each year.

Surveys were conducted beginning approximately 1 hour after sunset. Two observers were situated on elevated seats in the back of a pickup truck that was driven along a survey route at 16–24 km/hr. Observers continually scanned the area adjacent to each side of the roadway to the extent of their vision using spotlights (100,000 cp) and recorded the total number of individuals observed of the following species: raccoon, ringtail (*Bassariscus astutus*), Virginia opossum (hereafter opossum; *Didelphis*

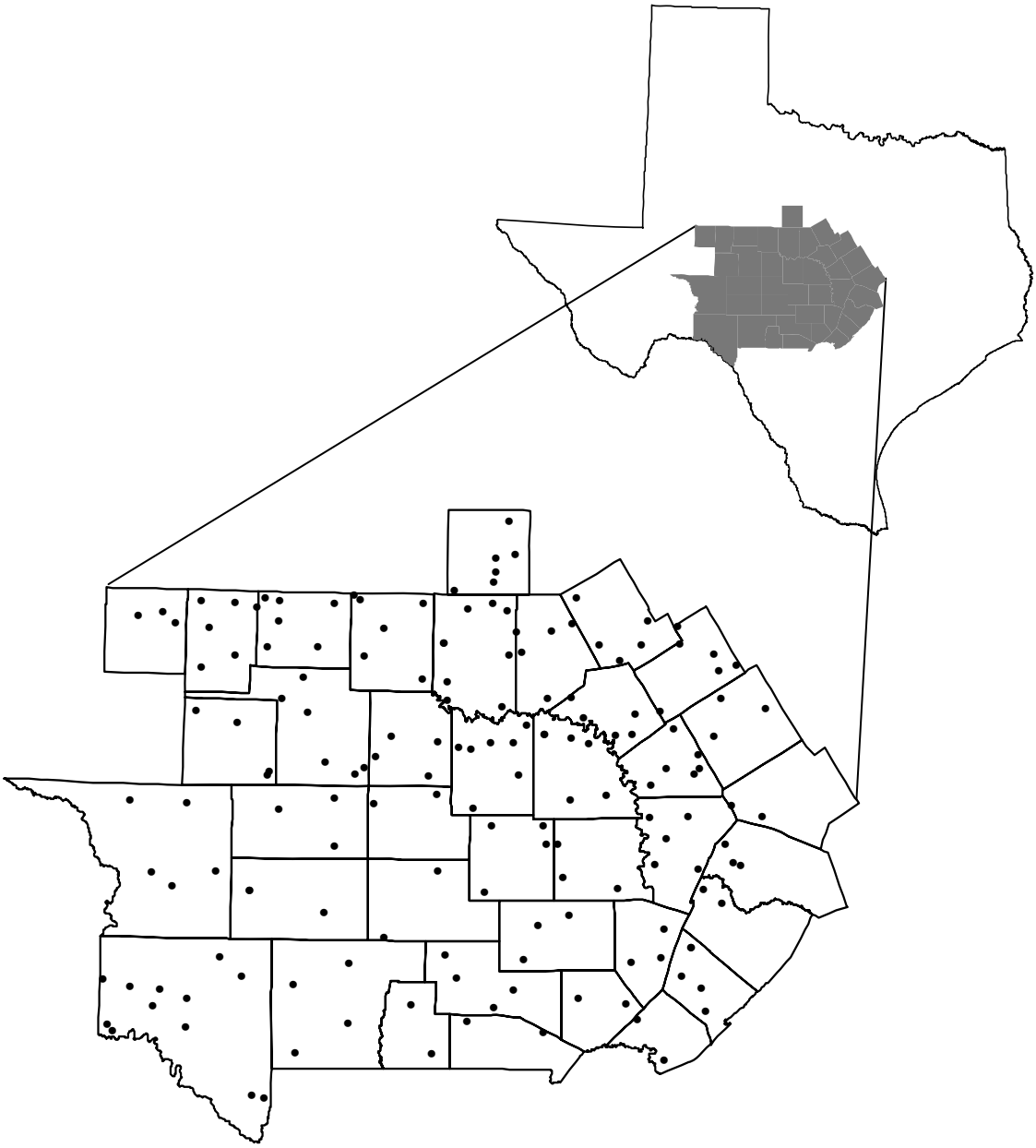


Figure 4.1. County map illustrating the central Texas study area. Circles indicate locations of the 192 spotlight-survey routes where medium-sized carnivore data were collected, 1978–2003.

virginiana), skunk (striped and hog-nosed [*Conepatus mesoleucus*] skunks were not differentiated), gray fox (*Urocyon cinereoargenteus*), red fox (*Vulpes vulpes*), coyote (*Canis latrans*), bobcat (*Lynx rufus*), badger (*Taxidea taxus*), mink (*Mustela vison*), spotted skunk (*Spilogale gracilis* and *S. putorius*), and domestic cat (*Felis domesticus*). A total of 2,130 survey nights was conducted during 1978–2003.

Red fox, coyote, bobcat, badger, mink, and spotted skunk comprised only 1.6% of the total animals identified. Because of their infrequent occurrence and because domestic cats were not recorded prior to 2000, these species were excluded from my analysis.

Analysis

Regional Abundance.— I calculated annual regional abundance (S_{Ri}) of raccoon, ringtail, opossum, skunk, and gray fox as the number of individuals encountered per kilometer on each survey route and averaged across all survey routes in the region as

$$s_{Ri} = \frac{\sum_{j=1}^{n} \left(\frac{x_{ij}}{l_j} \right)}{n_R},$$

where x = the number of individuals of species i sighted on survey route j, l = the length of the survey route, and n_R = the number of routes surveyed throughout the region. To identify trends in regional abundance, I performed simple linear regression (Ott and Longnecker 2001) of S_{Ri} against year for each species after confirming the residuals were normally distributed using a Ryan-Joiner test (Ryan and Joiner 1976).

County-level Abundance.— I calculated annual county-level abundance (S_{Ci}) of each species for each county in the region as

$$s_{Ci} = \frac{\sum_{j=1}^{n} \left(\frac{x_{ij}}{l_j} \right)}{n_C},$$

where n_C = the number of routes surveyed in county C. Results of a Ryan-Joiner test indicated that the residuals for some county data were not normally distributed. Therefore, I tested for abundance trends in each county over time by performing Spearman rank correlation of S_{Ci} against year.

Local Abundance.—I assessed local-level abundance trends by analyzing long-term abundance along individual survey routes. Not all survey routes were suitable for long-term analysis because many routes were surveyed for only a few years or were surveyed only during the early or late years of the survey period. Hence data from these routes would not have been representative of the entire survey period and might have biased estimates of abundance trends. To ensure that I examined only those routes that represented both the early and late years of the survey period, I arbitrarily divided the survey period into 2 phases: 1976–1990 and 1991–2003. Then I selected for analysis only those lines that had been surveyed for ≥9 years (approximately 2/3 of the phase) during each phase of the survey period. I calculated annual local abundance (S_{Li}) of each species along each of the 53 resulting survey routes (hereafter, "long-term routes") as

$$S_{Li} = \frac{x_{ij}}{l_j}.$$

As with the county data, residuals were not normally distributed for some routes, so I used Spearman rank correlation of S_{Li} against year to test for abundance trends. For all statistical tests, I considered results significant where $P \leq 0.10$.

RESULTS

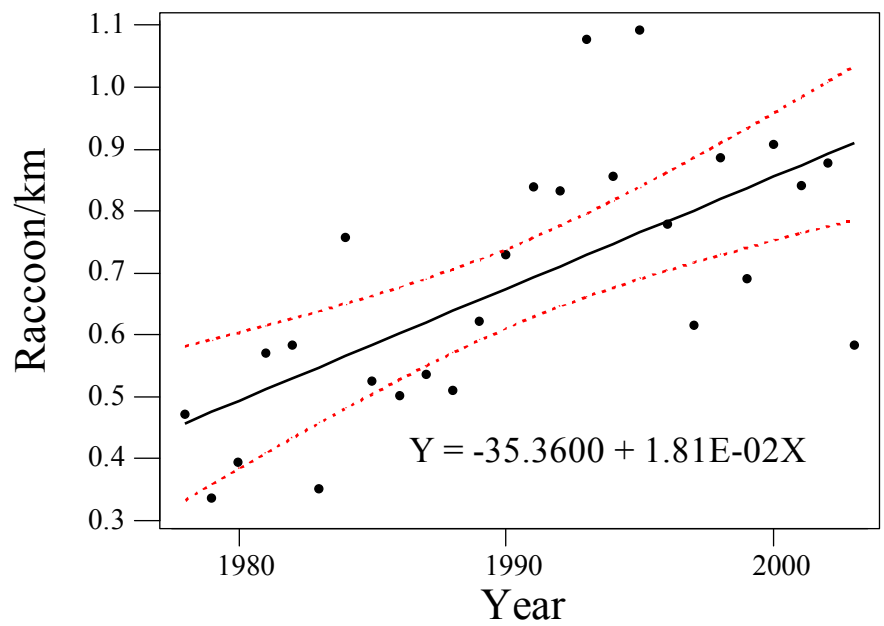
Abundance Trends

Regional Abundance.—Abundance of raccoons and gray foxes increased ($r^2 = 0.45$, $P < 0.001$ and $r^2 = 0.26$, $P = 0.008$, respectively) across central Texas during 1978–2003 (Fig. 4.2). I detected no trends in abundance for ringtail, skunk, or opossum ($P = 0.170$–0.838).

County-level Abundance.—All species exhibited trends in abundance at the county level for at least one county. Raccoon abundance increased in 15 of the 38 counties studied (39%), and did not decrease in any county (Fig. 4.3A). Ringtail abundance increased in seven (18%) counties but decreased in 4 (11%) others (Fig. 4.3B). Opossum abundance increased in 4 (11%), but decreased in 3 (8%) counties (Fig. 4.3C). Skunk abundance showed the least variability among counties, increasing in 2 (5%) while decreasing in 3 (8%) counties (Fig. 4.3D). Finally, gray fox abundance increased in 6 (16%) counties, while decreasing in only 1 (3%; Fig. 4.3E). In all, 27 counties (71%) reported a significant change in abundance of at least one species.

Local Abundance.—At the survey-route level, raccoons again showed a consistent trend of increasing abundance. Raccoon abundance on 18 (34%) long-term routes significantly increased while decreasing on no routes (Fig. 4.3A). Three (6%) survey routes showed significant declines in ringtail abundance, but 9 (17%) showed

A.



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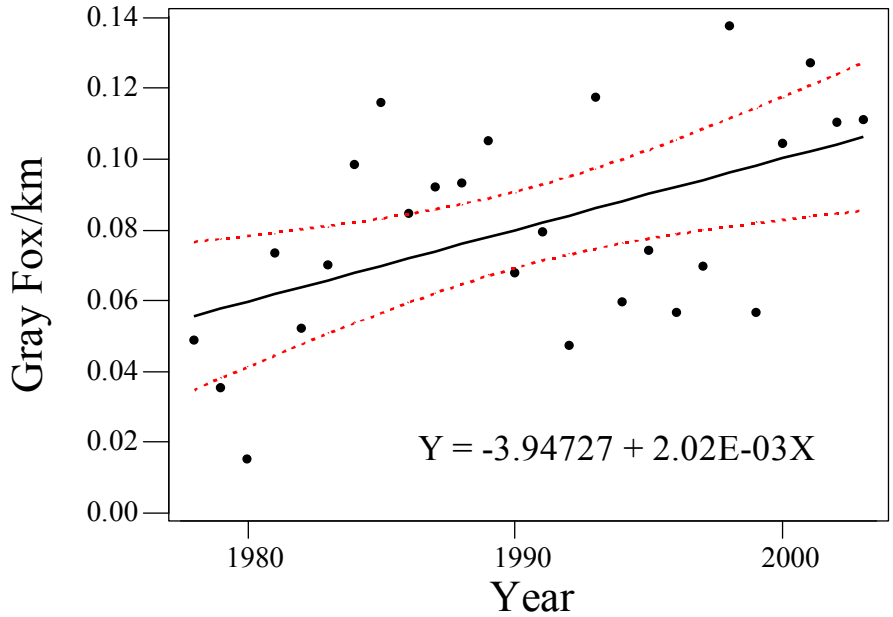


Figure 4.2. Raccoon (A) and gray fox (B) abundance throughout central Texas (Fig. 4.1), showing number observed per kilometer on spotlight surveys, 1978–2003. Solid line is linear regression line and dashed lines indicate 95% confidence bands about the regression line.

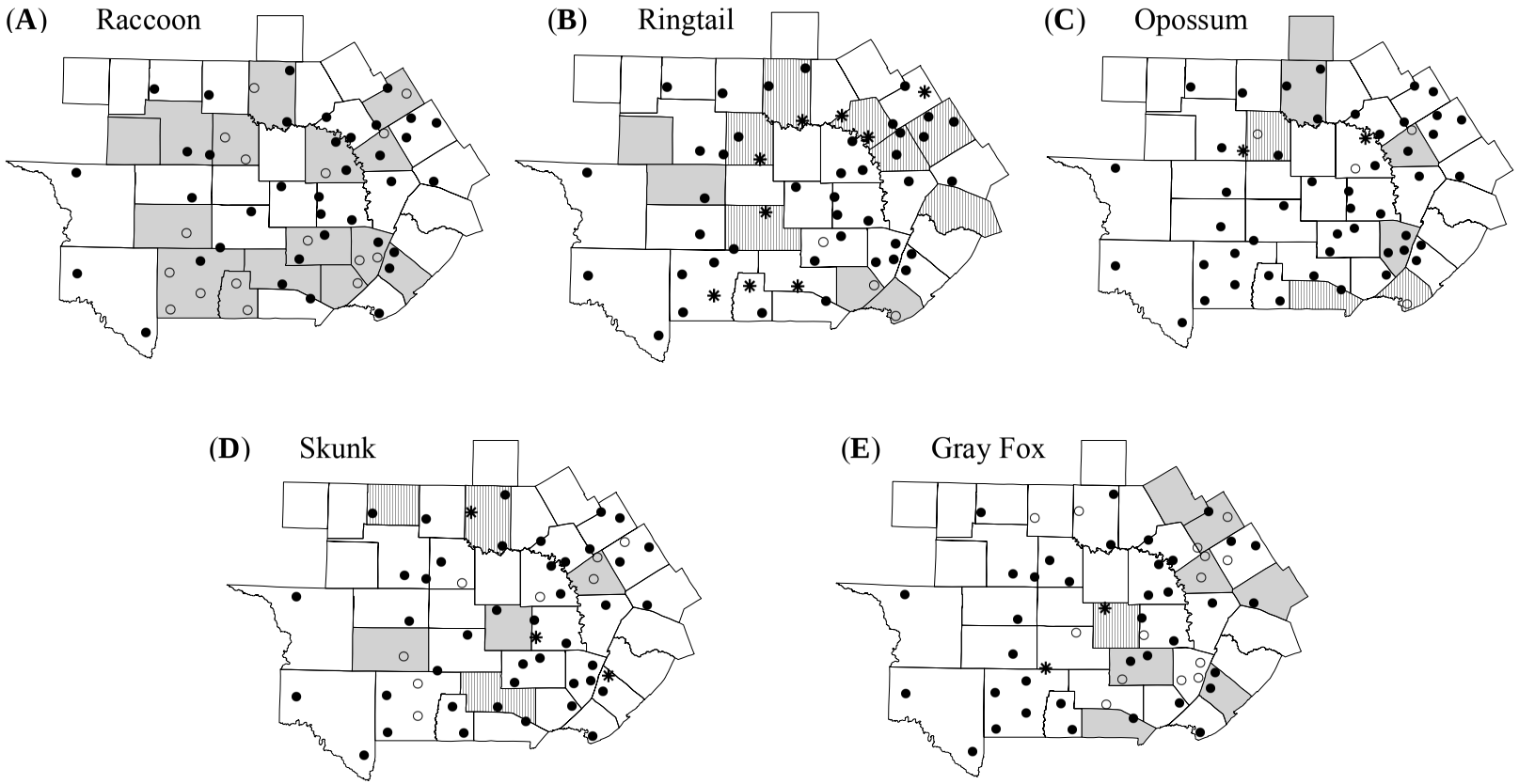


Figure 4.3. County- and local-level trends of raccoon (**A**), ringtail (**B**), opossum (**C**), skunk (**D**), and gray fox (**E**) abundance in central Texas, 1978–2003. Shaded areas indicate counties where abundance increased, cross-hatched areas indicate counties where abundance decreased, and white areas indicated counties where no trend was detected. Open circles (○) indicate long-term survey routes where abundance increased, asterisks (✱) indicate routes where abundance decreased, and closed circles (●) indicate routes where no trend was detected.

increases (Fig. 4.3B). Opossum abundance increased on 4 (8%) routes and decreased on 2 (4%; Fig. 4.3C). Skunk abundance increased on 8 (15%) routes, but decreased on 3 (6%; Fig. 4.3D). Finally, for gray fox, 14 (26%) survey routes exhibited significant increases in abundance while 2 showed decreases (4%; Fig. 4.3E).

DISCUSSION

From 1978 though 2003, medium-sized carnivore populations in central Texas exhibited trends at the local and county level that were not detectable at the regional level. In many cases, these small-scale trends ran counter to those observed at the regional level. Most striking were the results for ringtail, opossum, and skunk, where county and local abundance trends were detected, but no trends were found at the regional level. In all, 23 counties (47%) exhibited abundance trends for at least 1 species that were undetected at the regional level. Moreover, 45% of long-term routes showed a trend for at least one species that was inconsistent with results for the region, whereas 45% exhibited a trend that was inconsistent with results for the county in which the route was located. This suggests that dynamics of medium-sized carnivore populations might be more complex than suggested by broad-scale trends alone, thus reinforcing the importance of addressing multiple spatial scales when investigating potential mechanisms driving carnivore population dynamics.

Inconsistency among spatial scales could lead to misunderstanding about the dynamics of medium-sized carnivore populations. As noted above, the public thought skunk abundance increased, whereas I detected no regional trend. Members of the general public, however, rarely are exposed to broad-scale population data. Instead,

their observations occur at much smaller spatial scales that roughly correspond to our local-level analysis. I did detect trends in abundance at this spatial scale. Thus, controversies between the public and agency personnel could arise from what contradictory conclusions based on observation made at different spatial scales.

Silvy et al. (2000) analyzed furbearer spotlight data from the Edwards Plateau from 1980 through 1999, but failed to detect trends in medium-sized carnivore abundance. It is possible that I was able to detect trends in raccoon and gray fox abundance because I (1) included data from the southern portion of the Cross Timbers as well as the Edwards Plateau, (2) analyzed a larger sample (26 vs. 20 years), and located and analyzed several records not included in the summaries used by Silvy et al. (2000).

Studies conduced elsewhere in the United States also have reported broad-scale trends in medium-sized carnivore abundance. Using fur harvest data, Landholt and Genoways (2000) reported significant increases in raccoon abundance in Nebraska (1941–1997), while skunk numbers declined. Gehrt et al. (2002) used road-kill and spotlight-survey data to determine that raccoon abundance increased in Illinois (1975–1998).

Various authors have suggested explanations for long-term trends in medium-sized carnivore abundance. Rollins and Carroll (2001) hypothesized that declining demand for furs and the concomitant decline in furbearer harvest resulted in increased abundance of medium-sized carnivores, specifically raccoons. Conover (2001) also implicated low fur prices in an increase in raccoon population. These authors presented no evidence to support their claims.

Landscape-scale habitat alteration also has been suggested as a causative mechanism for population changes in medium-sized carnivores (Rollins and Carroll 2001). Raccoons and gray fox are known to respond to landscape-scale phenomena (Pedlar et al. 1997, Dijak and Thompson 2000, Gehring and Swihart 2003), including habitat fragmentation (Oehler and Litvaitis 1996, Gehring and Swihart 2003), urbanization (Prange et al. 2003), rural residential development and human disturbance (Harrison 1997, Kuehl and Clark 2002), land-management practices (Chamberlain et al. 2002), and availability of free water (Gehrt and Fritzell 1998). These hypotheses offer fertile ground for future research.

Because medium-sized carnivore dynamics appear to be, in part, fine-scale phenomena, the effects of carnivore abundance on other components of the ecosystem also might manifest themselves at fine scales. For example, Rollins and Carroll (2001) suggested several possible explanations for the near continent-wide decline in northern bobwhite abundance, including increased medium-sized carnivore numbers. Silvy et al. (2000) failed to find a correlation between medium-sized carnivore and northern bobwhite or scaled quail abundance in the Edwards Plateau of Texas. Because their analyses were conducted at only the regional scale, however, they were not able to address fine-scale relationships. It also is possible the bobwhite decline is the result of multiple factors operating at different scales in different physiographic regions. Whereas increased medium-sized carnivore abundance probably cannot account for the decline in all cases, it might be a driving factor in certain fine-scaled locales. Manipulative experiments could be devised to test this hypothesis.

My results also have implications for monitoring medium-sized carnivore populations. Standard Texas Parks and Wildlife Department procedure is to summarize carnivore data at the regional level. My analysis demonstrates this practice masks small-scale effects, impeding efforts to identify trends in abundance at more local scales. Considerable information is lost when data are aggregated and analyzed at only the regional level. For this reason, I recommend that natural resource agencies monitor medium-sized carnivore abundance and analyze data at multiple scales to better understand the dynamics of these populations.

CHAPTER V

RACCOON ABUNDANCE AND RIO GRANDE WILD TURKEY RECRUITMENT IN CENTRAL TEXAS

Managing wildlife populations requires an understanding of factors influencing those populations, including predation. However, assessing the effect of predation on a species is considered difficult because of the many factors that affect the predation process and the long-time periods required determine relationships (Leopold and Chamberlain 2001). If predation is found to negatively affect population management objectives, it can be mitigated by various management approaches, including direct reduction of predator effects through predator removal (Beasom 1974) and indirect reduction of predator effectiveness through habitat manipulation (e.g., improving prey cover; Jiménez and Conover 2001). Also, to adequately evaluate management alternatives, biologists must consider the full range of possible limiting factors, even for management activities not directly targeting predators. Even in situations where management of predators is not desirable or feasible, predation is an important consideration insofar as it influences populations of the species of interest, and thus, may ultimately influence the outcome of management practices. Finally, predator issues, regardless of biological consequence, tend to be controversial (Kellert 1985, Conover 1994, Messmer et al. 1999, Reiter et al. 1999), and may distract stakeholders from other concerns if the role of predators in the system is not adequately understood and explained.

One way that predators influence prey species is by destroying nests of ground-nesting birds such as wild turkeys, thus potentially limiting recruitment (Miller and Leopold 1992). Nest success has been suggested as one of the most important variables influencing wild turkey population dynamics (Roberts and Porter 1996). In Texas, nest predation accounts for substantial loss of RGWT nests (Cook 1972, Reagan and Morgan 1980, Ransom et al. 1987). Moreover, investigators have identified raccoons as one of the most culpable nest predator of ground-nesting birds in Texas (Hernandez et al. 1997). Although evidence suggests that medium-sized carnivores such as raccoons influence wild turkey population dynamics at small scales (Beasom 1974), their effect on turkey populations at broader spatial scales is less understood. The role of raccoons as RGWT nest predators might be especially important because raccoons often are the most numerous medium-sized carnivores in the predator community and because raccoon abundance has increased in at least part of the wild turkey range in recent decades (Hamilton and Vangilder 1992, Landholt and Genoways 2000, Chapter IV this volume)

Because of their role as nest predators, I hypothesized that raccoons might inhibit RGWT population growth by destroying nests, and thus reducing poult recruitment. My objective was to test this hypothesis by comparing indices of annual raccoon abundance and RGWT production. A negative correlation would be consistent with a prediction that increases in raccoon abundance were associated with lower turkey production.

A second test of my hypothesis was to determine whether RGWT production exhibited long-term decreases in areas where raccoon abundance had increased over the same time period. Analysis of TPWD carnivore survey data indicated that, while overall

raccoon abundance increased throughout central Texas from 1976 through 2003, raccoon abundance trends varied among specific localities depending upon the spatial scale at which abundance was viewed (Chapter IV). These results allowed me to compare RGWT production between areas where raccoon abundance had increased and areas where it had not. If raccoons negatively affected RGWT production, I expected to see that RGWT production had decreased more over time in areas where raccoon abundance had increased compared to areas where it had not.

METHODS

I evaluated RGWT production and raccoon abundance in a 38-county region of central Texas (Figure 4.1). This region was comprised of the Edwards Plateau and the southern portion of the Cross Timbers ecological regions (Gould 1975). Topography ranged from rolling to steep, with primarily shallow, rocky soils. Historically, the region was a grassland or open savannah, but woodlands and brushlands presently dominate.

I used annual poult production, estimated using TPWD's annual brood-count data (Chapter II), as an index of RGWT production. I estimated annual raccoon abundance using data collected during annual TPWD spotlight-furbearer surveys conducted from 1978–2003 (Chapter IV). Individual counties and survey routes were categorized as having raccoon abundance that either increased or remained stable (no counties with decreasing raccoon abundance were identified) from 1978–2003.

Data Analysis

Comparison of Annual RGWT Production and Raccoon Abundance.– Winter and early spring survival of raccoons typically is high in the southern United States

(Chamberlain et al. 1999, Gehrt and Fritzell 1999). Thus, raccoon abundance during autumn should be a good indicator of the following spring population, when raccoons would be expected to most affect turkey production. Moreover, summer RGWT brood counts are estimates of production during spring of the current year. Therefore, I compared RGWT production with the previous autumn's raccoon abundance.

Because both RGWT production and raccoon abundance might be serial correlated, I detrended both data sets using the first differences method (Ott and Longnecker 2001). The results of a Ryan-Joiner test indicated that residuals of raccoon abundance data were normally distributed. Therefore, I compared raccoon abundance and poult proportion using Pearson's product moment correlation (Ott and Longnecker 2001). For all statistical tests, I considered results significant where $P \leq 0.05$. I performed all statistical tests using Minitab (Minitab, Inc., State College, Pennsylvania).

Turkey Production Between Areas Based on Raccoon Trends

I compared RGWT production trends between areas of central Texas that were categorized as having either stable or increasing raccoon abundance. I chose to define these areas at the scale of both county and survey-route (hereafter "local level") because of tradeoffs between the two scales of observation. At the county level, I was able to use the entire turkey brood-count data set, thus increasing the sample size used in the calculation of poult production. However, I consequently included many areas which were distant from raccoon survey routes, and thus were not necessarily represented accurately by the raccoon abundance data. I also conducted analyses using only data from the vicinity of the raccoon survey routes. By doing so, I evaluated RGWT

production in locales which were likely more accurately represented by raccoon abundance data, but some RGWT production information was lost due to a substantially reduced sample size.

County Level. – I compared annual production between counties with different raccoon abundance trends by dividing turkey brood-survey data into 2 groups based on the raccoon abundance trend of the county in which the observation was made. I pooled observations across all counties within each group and determined total number of hens and poults observed per year in each group. I calculated annual RGWT production (p_c) for each group as

$$p_c = \frac{n_{pc}}{(n_{pc} + n_{hc})},$$

where, n_{pc} = number of poults and n_{hc} = number of hens in group c. Regression residuals of production data were normally distributed, so I estimated production trends over time in each group of counties and compared trends between county groups having different raccoon trends using analysis of covariance, with year as the independent variable and county group as the covariate (Ott and Longnecker 2000).

Local Level. – For local-level analysis, I evaluated RGWT production only for areas within <12.3 km of raccoon survey routes. I overlaid a map of the study region with latitude and longitude lines at 5' intervals using ArcView GIS 3.3 (Environmental Systems Research Institute, Inc., Redlands, California, USA) to form a grid corresponding to the 5'×5' system used in recording RGWT brood observations. For grid cells intersected by a spotlight-survey route, I categorized the cell as increasing or stable

in raccoon abundance as determined by its associated survey route. I disregarded cells not intersected by a survey route. I was unable to use data collected prior to 1981 in this analysis because coordinates of turkey observations were not reported prior to that time.

I censored all brood observations not collected in cells intersected by a spotlight-survey route and divided the observations into 2 groups based on the raccoon-abundance trend (increasing or stable) of the cell in which the observation was made. I pooled brood observations across all cells within each group and determined the number of hens and poults observed per year in each group. I calculated annual RGWT poult production (p_r) for each group as

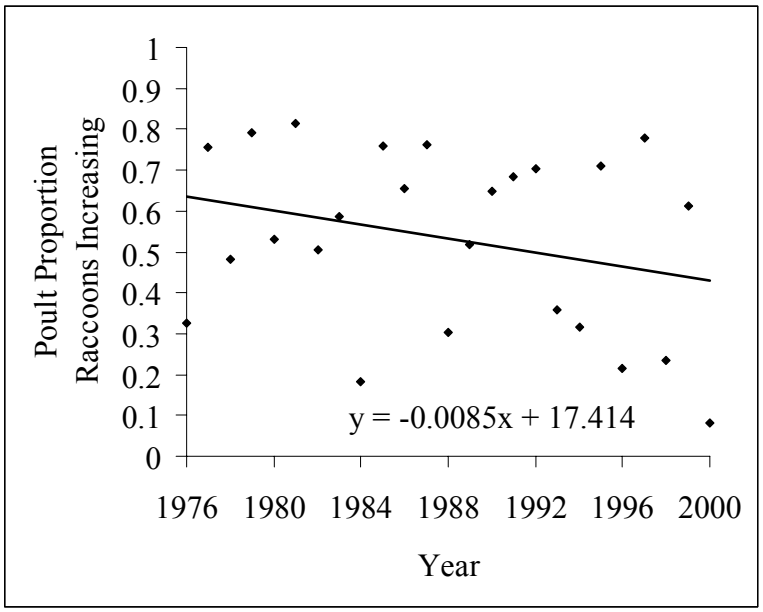
$$p_r = \frac{n_{pr}}{(n_{pr} + n_{hr})},$$

where n_{pr} = number of poults and n_{hr} = number of hens in group r. Regression residuals of production data were normally distributed, so I estimated trends over time in each group of cells and compared trends between cell groups having different raccoon trends and raccoon trends using analysis of covariance, with year as the independent variable and cell group as the covariate (Ott and Longnecker 2000).

RESULTS

I detected no significant correlation ($r = 0.094$, $P = 0.684$) between annual RGWT production and annual raccoon abundance across central Texas. Further, I detected no difference ($t = 0.054$, $df = 46$, $P = 0.9571$) between the slope of the regression line for poult proportion against year for the group of counties with increasing raccoon abundance and that for the group of counties with stable raccoon abundance (Fig. 5.1).

(**A**)



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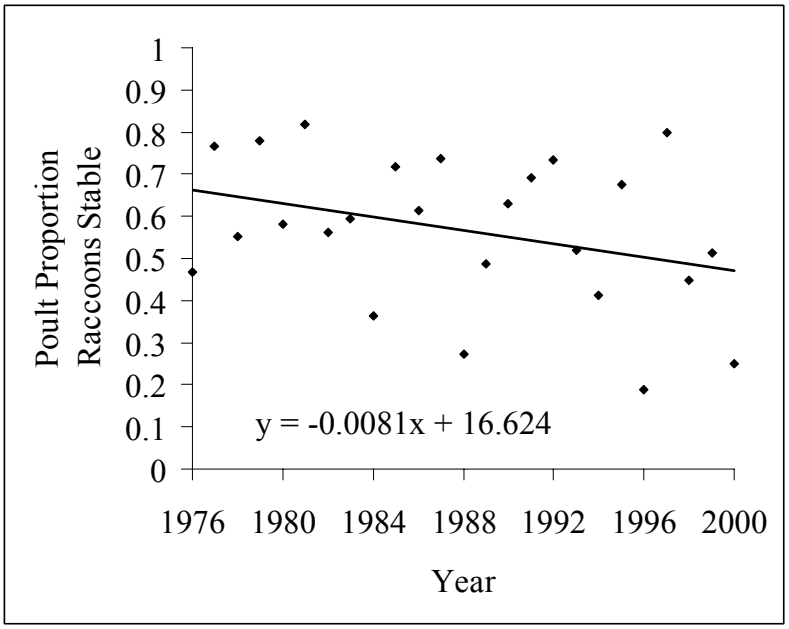


Figure 5.1. Rio Grande wild turkey production in counties where raccoon abundance (**A**) increased and (**B**) remained stable, 1976–2000.

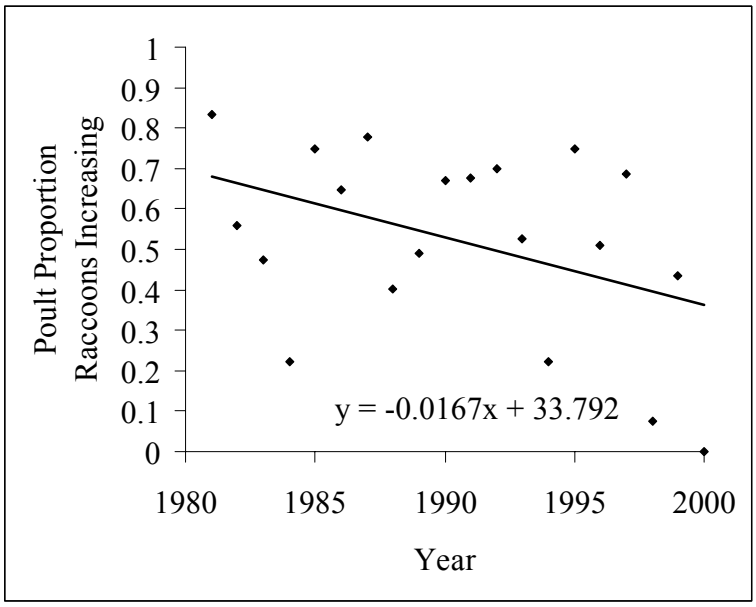
Finally, I detected no difference ($t = 0.429$, $df = 36$, $P = 0.6705$) between the slope of the regression line for poult proportion against year for the group of cells having increasing raccoon abundance and that for the group of cells with stable raccoon abundance (Fig. 5.2). Taken together, the results of the analyses revealed no evidence that turkey production was related to raccoon abundance regardless of the scale at which it was measured.

DISCUSSION

My hypothesis that raccoon densities are associated with RGWT production in central Texas predicted that RGWT production (1) should be correlated with raccoon abundance and (2) should have declined more in areas where raccoon abundance has increased than in areas where raccoon abundance has not increased. However, my analysis did not suggest that either of these phenomena has occurred, weakening the argument that raccoon densities are associated with RGWT production in central Texas.

Although many studies have shown that predators destroy a large proportion of individual turkey nests (Miller and Leopold 1992), few have addressed whether nest predation has significant population-level effects. Those that have addressed whether nest predation is important at the population level typically have done so by evaluating the response of turkey production to intensive predator removal. The results of these studies have been equivocal. Beasom (1974) reported substantially higher poult:hen ratios on his study site in south Texas following intensive predator removal than on an untreated control site. Speake (1980) intensively removed predators for 5 years from his study site in Alabama and reported 55.1% of hens on the experimental site were

(**A**)



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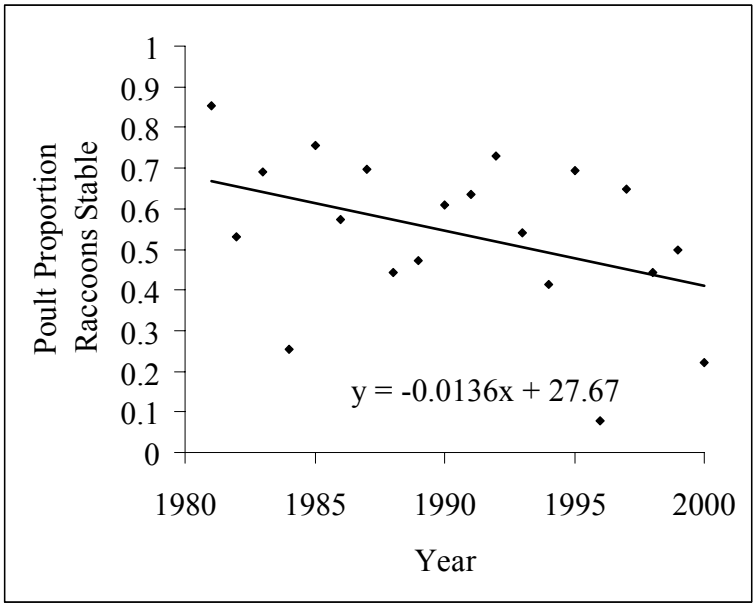

Figure 5.2. Rio Grande wild turkey production in 5′×5′ cells intersected by Texas Parks and Wildlife Department carnivore survey routes where raccoon abundance (**A**) increased and (**B**) remained stable, 1981–2000.

accompanied by poults, whereas 24.4% of hens were accompanied by poults on a site where predators were not removed. However, Guthery and Beasom (1977) conducted a similar study in south Texas and did not conclude that predator removal significantly increased production.

One possible reason my results differed from those reporting significant increases in production following predator removal is these other studies involved large reductions in predator density that probably exceeded the natural level of predator population variability. Speake (1980) removed an average of 318 nest predators—primarily Virginia opossums and raccoons—annually for 5 years from a 4,471-ha-study site in Alabama. Although he did not report a measure of carnivore density, he did state that "almost no predator sign could be found" following removal (Speake 1980:89). Likewise, Beasom (1974) removed 65 raccoons from a 23.3-km^2 experimental site over 2 years, along with 188 coyotes, 120 bobcats, 46 striped skunks, and 38 other medium-sized carnivores. Although he did not report changes in raccoon density over time, it is reasonable to assume that raccoon density may have decreased more than the annual change of 25% that I observed in central Texas (Chapter IV).

Another possible reason that my results differed from published reports is that our study is, to our knowledge, the first to address the association of predator abundance and RGWT production at spatial scales larger than a few square kilometers. Beasom (1974) suggested predator removal experiments had returned conflicting results because of differences in local conditions. Because raccoon and presumably RGWT population dynamics respond to local conditions, spatially asynchronous population dynamics

might result that are undetectable when viewed at the relative broad scales I evaluated. More research focusing on multiple study sites and spatial scales will be necessary to fully elucidate the relationship between RGWT production and predators.

I recognize several shortcomings in my study. First, my results are merely correlative and do not speak directly to cause and effect. However, manipulative experiments designed to reveal cause and effect relationships at the broad scales I treat here are impractical. Thus, analysis of historical data to test *a priori* hypotheses provides the only practical approach to examine the relationship between raccoon abundance and wild turkey predation. Moreover, I do not suggest that my results offer definitive proof that raccoon abundance does not affect turkey production, only that analysis of the available data fails to support the assertion that raccoon abundance and turkey production are related.

Second, the turkey production data used in the analysis suffers from the sampling design employed in its collection. As currently conducted, the TPWD brood survey does not use standard, randomized collection procedures. Instead, it is collected according to a "convenience sampling" (Morrison et al. 2001) scheme, whereby data is collected haphazardly incidental to TPWD personnel's other duties. This results in data that may not be representative of actual turkey production. However, other analysis of this data has shown a statistically significant correlation between precipitation and turkey production (Chapter III). Such a correlation would be unlikely if the production data did not represent, to some degree, an actual underlying biological pattern.

Rio Grande wild turkeys evolved with predation. Whereas abundance of raccoons in central Texas has increased in recent decades, I found no evidence to suggest that either historic levels of inter-annual variation or a long-term increase have been associated with RGWT production. Although managers should be aware of the possibility that raccoon predation could influence RGWT production at fine spatial scales, they should be cautious in concluding that raccoon abundance influences turkey populations at broad scales.

CHAPTER VI

MODEL DESCRIPTION

GENERAL CONCEPTUAL MODEL

Background Information

Mortality in birds often is sex-biased, falling more heavily on one sex than the other. This is particularly true of species which nest on the ground and in which there is little or no parental involvement by the male (Newton 1998). Hens of polygynous gallinaceous species might also be more susceptible to predation than males because males tend to be larger than females, and females may be more active during the breeding season. Wild turkeys fit both these models. Hens appear to be especially vulnerable to predation during the breeding season and thus suffer higher mortality rates, which vary throughout the year (Vangilder 1992).

Wild turkey survival also varies with age. Even among sexually mature birds, younger individuals may be smaller and thus less able to defend themselves against predators, they may be naïve or inexperienced, or the may be forced into suboptimum habitats by more socially dominant individuals (Newton 1998). For this reason, many investigators have treated yearling and adult birds separately when examining survival (e.g., Miller et al. 1995). Moreover, yearling wild turkey hens may be forced to disperse longer distances than older hens (Schmutz and Braun 1989), which may increase their susceptibility to predation, although Miller et al. (1995) found that mortality did not vary with dispersal distance.

Finally, reproductive success in turkey also might vary by age (Newton 1998). Reproductive variables such as clutch size (Reagan and Morgan 1980), nest success (Vangilder et al. 1987), and renest rates (Buford 1993) have been found to vary with age, with adult birds (>1 year of age) enjoying greater success than yearlings.

Description of the General Conceptual Model

I developed a simulation model of Rio Grande wild turkey population dynamics that used difference equations where $\Delta t = 1$, using Stella® (High Performance Systems, inc., Hanover, New Hampshire, USA) modeling software. Because vital rates could differ between yearling and adult hens (as well as their associated offspring) and between males and females, the model was composed of 9 primary submodels (Fig. 6.1). These submodels represented precipitation and 8 age/sex classes: yearling hens, adult hens, poults of yearling hens, poults of adult hens, juveniles of yearling hens, juveniles of adult hens, wintering hatch-year birds, and males. There also were a number of information network modules that calculated various intermediate variables such as density-dependence and harvest.

Entry into the poult classes was driven primarily by yearling and adult hen abundance. As poults mature, they moved into the juvenile classes then into the wintering hatch-year class, where they remained until the breakup of winter flocks in early spring. At this time, they moved into the male and yearling hen classes. Males remained in the male class (which itself was divided into yearling and adult stages) throughout their lifetime. However, females remained in the yearling hen class for 1

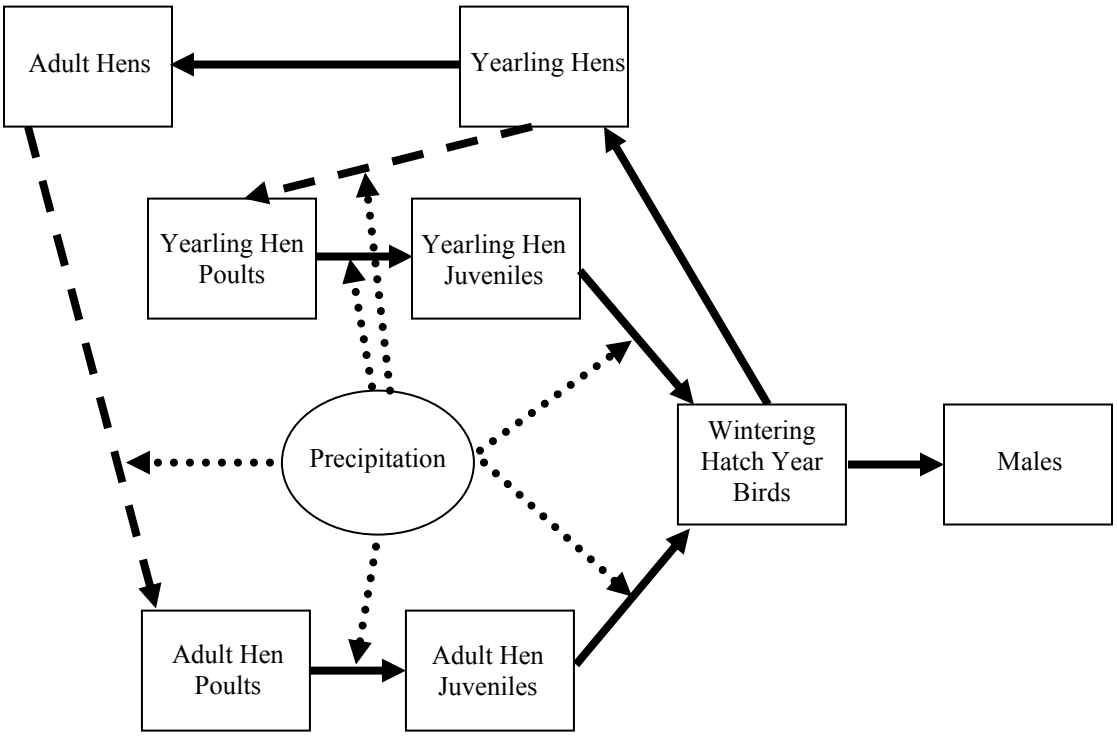

Fig. 6.1. Conceptual diagram of the RGWT population model. Boxes represent age/sex classes. Solid arrows represent movement of turkeys from 1 stage to the next, while dashed lines represent production of poults by hens. Dotted lines represent the influence of precipitation on transfers between various classes.

year, at which time they moved into the adult hen class and remained there throughout their lifetime.

The primary factor driving RGWT population dynamics in the model was precipitation. The important role of precipitation in RGWT production was recognized

by allowing precipitation to influence production of poults by yearling and adult hens, as well as survival of poults and juveniles.

PRECIPITATION SUBMODEL

Background Information

Correlation analysis of precipitation and RGWT production data showed that precipitation was of primary importance in driving RGWT recruitment in the Edwards Plateau (Chapter III). Therefore, it was important that precipitation be realistically represented in the model. My general approach was to design a precipitation submodel that reasonably reproduced the historic precipitation pattern of the Edwards Plateau (Fig. 6.2), using descriptive statistics and relationships among years and months derived from historic data. Because precipitation data were typically reported using English units, and to facilitate future use of the model and data input, precipitation values were initially calculated using English units and then converted to metric for the final output.

The simplest way of simulating precipitation in the stochastic model was to randomly draw monthly precipitation values from a standard sampling distribution (e.g., the normal distribution) using a routine in Stella® (High Performance Systems, inc., Hanover, New Hampshire, USA) based on the mean and standard deviation of historic monthly precipitation data. However, 2 possible characteristics of the data complicated this approach: nonnormality and serial correlation of monthly data.

Prior to designing the submodel, I tested annual and individual monthly precipitation totals for nonnormality using the Ryan-Joiner test (Ryan and Joiner 1976) in Minitab (Minitab, Inc., State College, Pennsylvania). For non-normal data, I determined an

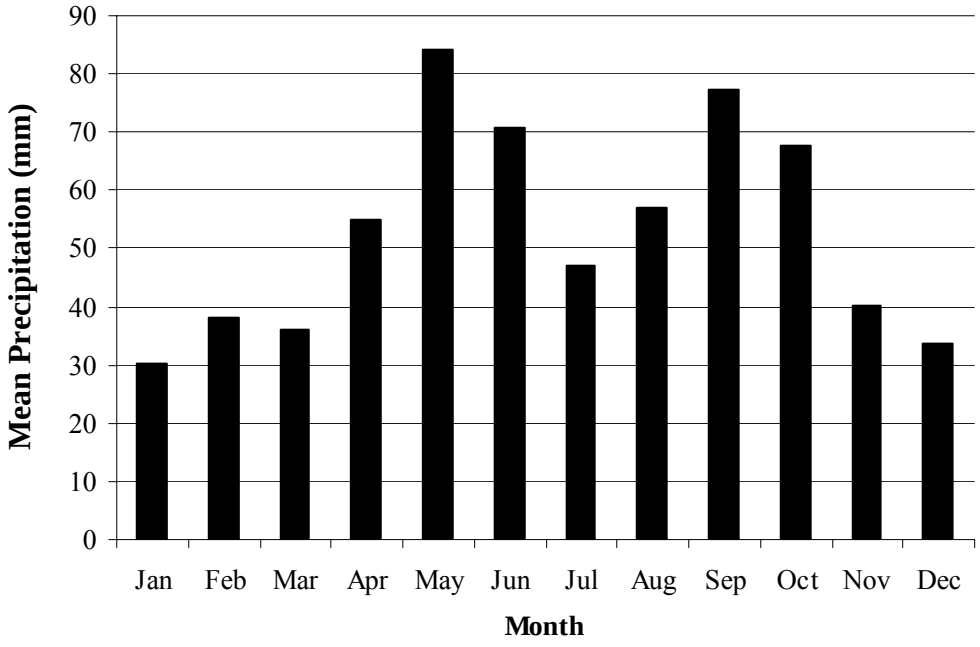

Fig. 6.2. Mean monthly precipitation for the Edwards Plateau of Texas, 1898–2003 (National Climate Data Center). Note the bimodal distribution with peaks in late spring and early autumn.

appropriate transformation that normalized the data and calculated descriptive statistics for the transformed data. I was then able to design a routine that randomly drew a precipitation value in the transformed scale and reverse transformed the output to produce a simulated monthly precipitation total.

I also tested historic monthly precipitation data (transformed as appropriate) for serial correlation. I performed correlation analysis on total precipitation during consecutive months. I reasoned that months showing no serial correlation could be

modeled independent of each other. However, serially correlated variables would be modeled, in part, on total precipitation during the previous month.

My results indicated that annual precipitation was normally distributed. However, total monthly precipitation was nonnormal ($n = 107$, $P < 0.01$) for all months. Monthly data tended to be skewed right. Square-route transformation normalized total monthly precipitation for February, March, June, September, October, November, and December. Cube-root transformation normalized January, April, May, and July data.

I was unable to determine an appropriate transformation for normalizing August precipitation data. However, visual evaluation of the data indicated a small number (7 of 107) of extreme observations caused the data to be extremely right skewed (Fig. 6.3). I speculated these observations might have resulted from infrequent high rainfall events. When the extreme values were removed from the data set, square root transformation was sufficient to normalize the remaining data. Further, the extreme values themselves were normally distributed.

To determine whether monthly precipitation was serially correlated, I performed linear regression analysis of total monthly precipitation against the previous month's total. Total monthly precipitation correlated with previous month rainfall for January ($P = 0.065$, $r^2 = 0.032$), February ($P = 0.019$, $r^2 = 0.052$), March ($P = 0.043$, $r^2 = 0.038$), April ($P = 0.001$, $r^2 = 0.098$), and December ($P = 0.006$, $r^2 = 0.06$), but not for any other month ($P = 0.244$–0.603).

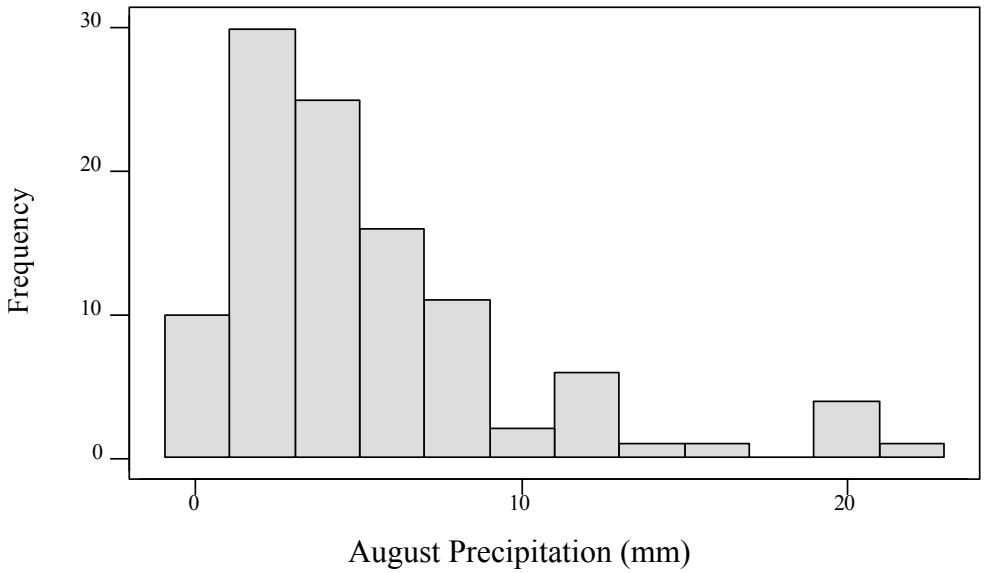

Fig. 6.3. Histogram of historic August precipitation in the Edwards Plateau of Texas, 1898–2001. Note the 7 extreme observations that cause the distribution to be extremely right-skewed.

Conceptual Formulation of the Precipitation Submodel

Simulation of monthly precipitation was performed by a series of converters and information transfers that randomly generated a monthly precipitation total during the time step prior to the beginning of each month (Fig. 6.4). Monthly rainfall for January–April and December (the serially correlated months) was simulated by randomly

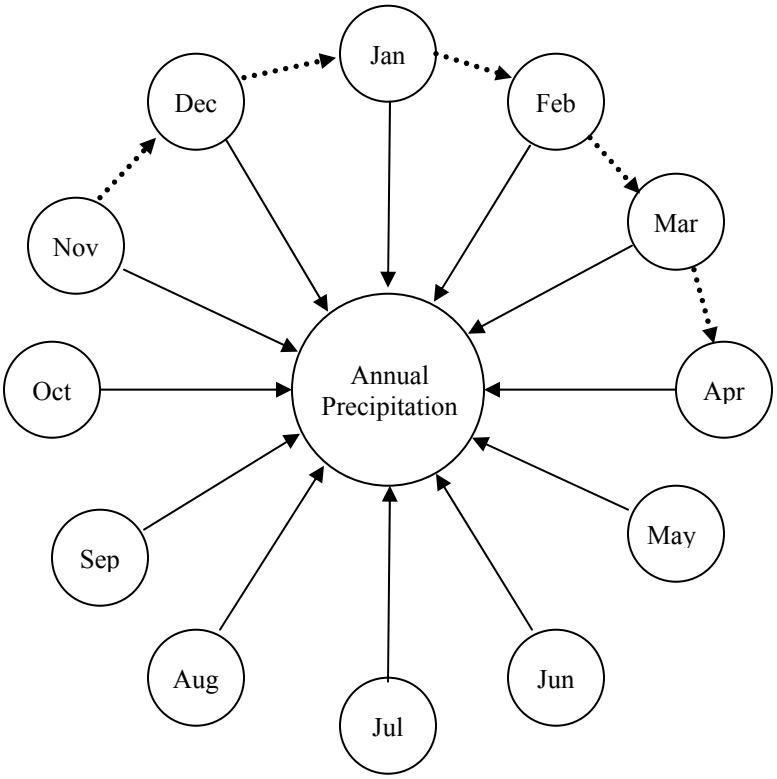

Fig. 6.4. Conceptual diagram of the precipitation submodel. Circles represent monthly and annual precipitation values. Solid lines indicate successive contribution of monthly precipitation to cumulative annual precipitation. Dotted lines indicate the influence of the previous month's total precipitation on monthly rainfall for serially-correlated months.

drawing a value from a normal distribution having a mean predicted by the appropriate regression equation applied to the previous month's square-root or cube-root transformed precipitation, and a standard deviation equal to the square root of the mean squared error derived from the regression analysis. Base precipitation values were then squared or cubed, according to the transformation used, to derive the simulated monthly precipitation. Delay variables were used to hold each month's base precipitation value until needed for calculation of the subsequent month's value.

Monthly rainfall for May–July and September–November was simulated by drawing a random variable from a normal distribution having a mean and standard deviation equal to that of the square-root or cube-root transformed historic data. These values were then squared or cubed, as appropriate, to derive the simulated monthly precipitation.

Simulation of August precipitation was complicated by the presence of extreme values in the historic data and, therefore, involved a 2-step process. First, a random value of 0–1 was drawn and compared with the historic probability of an extreme August precipitation event (7/107 = 0.065) to determine if the current year's precipitation should include an extreme August precipitation value. If the random value >0.065, it was considered a "typical" August (not characterized by an extreme rainfall event) and August precipitation was simulated by drawing a random value from a normal distribution having a mean and standard deviation equal to that of the square root transformed historic data for typical Augusts and squaring it. Otherwise, August was considered extreme and August precipitation was represented by a random value drawn

from a normal distribution having a mean and standard deviation equal to that of the historic extreme August precipitation observations.

Cumulative monthly precipitation for both January–December and September–August annual periods were calculated using state variables. Because certain variables of the turkey population model were driven by cumulative September–June rainfall as a percent of normal rainfall for the period (see Chapter III), an additional state variable was used to track "expected" cumulative rainfall, based on historic data.

Quantitative Specification of Precipitation Submodel

During the first time step of each simulation run, January precipitation was modeled by drawing a normally distributed random variable from a distribution having a mean and standard deviation equal to that of historic January precipitation. Thereafter, because January, February, March, April, and December precipitation correlated with previous month precipitation, I modeled precipitation for those months by drawing a normally-distributed random variable from a distribution having a mean defined by the following regression equations:

$$Jan^{1/3} = 0.804062 + 0.128796Dec^{1/2}$$

$$Feb^{1/2} = 0.838982 + 0.297577Jan^{1/3}$$

$$Mar^{1/2} = 0.972856 + 0.167907Feb^{1/2}$$

$$Apr^{1/3} = 1.020730 + 0.218180Mar^{1/2}$$

$$Dec^{1/2} = 0.773149 + 0.294082Nov^{1/2},$$

Table 6.1. Standard deviation (transformed) of historic monthly precipitation in the Edwards Plateau of Texas, 1989–2003.

Month	Transformed precipitation standard deviation	
	Inches	Millimeters
Jan	0.3575	9.0805
Feb	0.4617	11.7272
Mar	0.3991	10.1371
Apr	0.2689	6.8301
May	0.2587	6.5710
Jun	0.4908	12.4632
Jul	0.3469	8.8113
Aug	0.5027[a]	12.7686[a]
	0.8555[b]	21.7297[b]
Sep	0.5736	14.5694
Oct	0.5771	14.6583
Nov	0.4509	11.4529
Dec	0.4881	12.3977

[a]Value used for "typical" precipitation.

[b]Value used for "extreme" precipitation.

Table 6.2. Selected mean historic monthly precipitation (transformed) in the Edwards Plateau of Texas, 1898–2003.

Month	Transformed mean precipitation	
	Inches	Millimeters
May	1.4556	36.9722
Jun	1.5775	40.0685
Jul	1.1598	29.4589
Aug	1.2197[a]	30.9804[a]
	7.3370[b]	186.3598[b]
Sep	1.6329	41.4757
Oct	1.5052	38.2321
Nov	1.1419	29.0043

[a]Value used for "typical" precipitation.
[b]Value used for "extreme" precipitation.

and a standard deviation equal to that of the historic monthly data (Table 6.1). For all other months, I modeled precipitation by drawing a normally-distributed random variable from a distribution having a mean and standard deviation equal to that of the appropriately transformed historic monthly precipitation data (Tables 6.1 and 6.2).

Precipitation Submodel Evaluation

I evaluated the precipitation submodel by executing a simulation of 5,200 time steps to simulate 100 years of precipitation. I tested simulated January–December and September–August precipitation for normality using a Ryan-Joiner test and compared simulated January–December and September–August mean annual precipitation with historic January–December and September–August mean annual precipitation using a Student's *t*-test (Ott and Longnecker 2001). I used Levine's test to test for equality of variance between simulated and historic data (Minitab, Inc., State College, Pennsylvania).

Both January–December and September–August simulated precipitation were normally distributed ($P > 0.1$ and $P = 0.076$, respectively). Simulated mean annual precipitation did not differ significantly from historic precipitation for either January–December ($P = 0.44$) or Sep–Aug ($P = 0.87$). Levine's test indicated January–December and September–August simulated and historic precipitation had equal variance ($P = 0.129$ and $P = 0.256$, respectively).

DENSITY-DEPENDENCE MODULE

Background Information

Populations cannot increase without limit. This was explicitly recognized by P. F. Verhulst (Begon et al. 1996) in the development of the logistic growth equation, where rate of increase is inversely related to density. Many previous wild turkey population models have failed to account for density-dependent population growth (Suchy et al. 1983, Vangilder and Kurzejeski 1995, Rolley et al. 1998), because no data existed

concerning the relationship between rate of increase and population density. Nevertheless, I regarded density-dependence as a necessary component of my model for 3 reasons. First, although some turkey populations may be maintained at low levels relative to carrying capacity (*K*) by density-independent factors, the development of a broadly-applicable simulation model required that I provide for the possibility that density-dependence might operate in some populations under examination. Second, the stochastic nature of my model made it likely that occasional combinations of highly favorable driving variable values (e.g., several successive years of above average rainfall) would occur that would drive the total population to unrealistic levels, thus inflating the mean population level attained over numerous runs of the model (McCallum 2000). Finally, in the absence of density-dependence, simulations would likely result in higher mean population levels than would be attained if density-dependence were operating (Vangilder and Kurzejeski 1995:37). Because low population levels are usually of most concern to turkey managers, a density-dependent model should provide more conservative results than one that is density-independent.

Incorporation of density-dependence into a population model required some understanding of the functional relationship between rate of increase and population density (Newton 1998). The basic logistic growth equation (Verhulst 1838) assumed a linear relationship, where maximum per capita population growth occurred at a population of 0 and per capita growth ceased at *K*. Gilpin and Ayala (1973) considered simple linear density-dependence to be an oversimplification of the Lotka-Volterra competition model (a 2-species extension of the logistic growth equation). They

suggested an alternative, the θ-logistic model, to account for nonlinear density dependence. In the θ-logistic model, an additional parameter (the exponent θ) is incorporated in the model to describe the shape of the population-growth curve. By varying θ, the population density (relative to K) at which density dependence acts most strongly can by varied. In the θ-logistic model, values of $\theta < 1$ result in density dependence acting most strongly at densities closer to 0 than would be the case for simple linear density dependence, while values of $\theta > 1$ result in density dependence acting at densities closer to K (Fig. 6.5). Hence, whereas linear density-dependence ($\theta = 1$) results in population growth rate being highest at $0.5K$, alternate values of θ shift the point of maximum population growth to the left or right of this point (Fig. 6.6; Gilpin and Ayala 1973).

Gilpin and Ayala (1973) speculated that invertebrate populations should display $\theta < 1$, while vertebrate populations should have $\theta > 1$. More recent work has shown that θ varies by taxa along a continuum, analogous to the r-/K-selection continuum (Begon et al. 1996), but that the vertebrate-invertebrate dichotomy proposed by Gilpin and Ayala (1973) does not apply as cleanly as they suggested. In general, θ tends to be positively correlated with onset of reproduction and adult survival, and negatively correlated with reproductive rates along what Saether et al. (2002:2070) called the "slow-fast continuum" of life history traits. Fowler (1981) showed that large mammals tended to exhibit nonlinear density-dependence, where density-dependence was most pronounced at densities near K, a situation indicative of relatively large values of θ. In

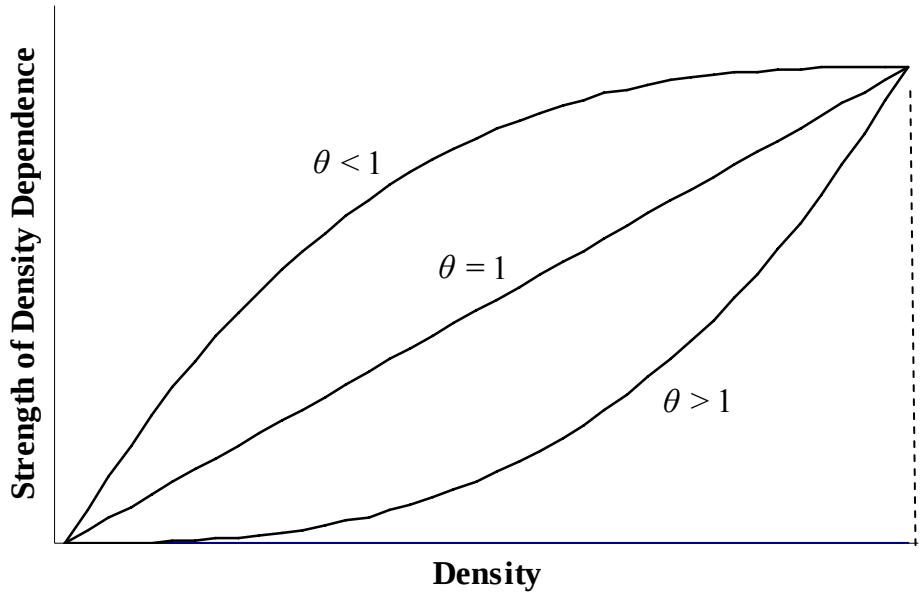

Fig. 6.5. Relationship of density-dependence to density for 3 values of θ. Dashed line represents carrying capacity (K). Where, $\theta = 1$, density dependence is linear. Where $\theta > 1$, density dependence acts more strongly at densities closer to K. Where $\theta < 1$, density dependence acts more strongly at densities closer to 0.

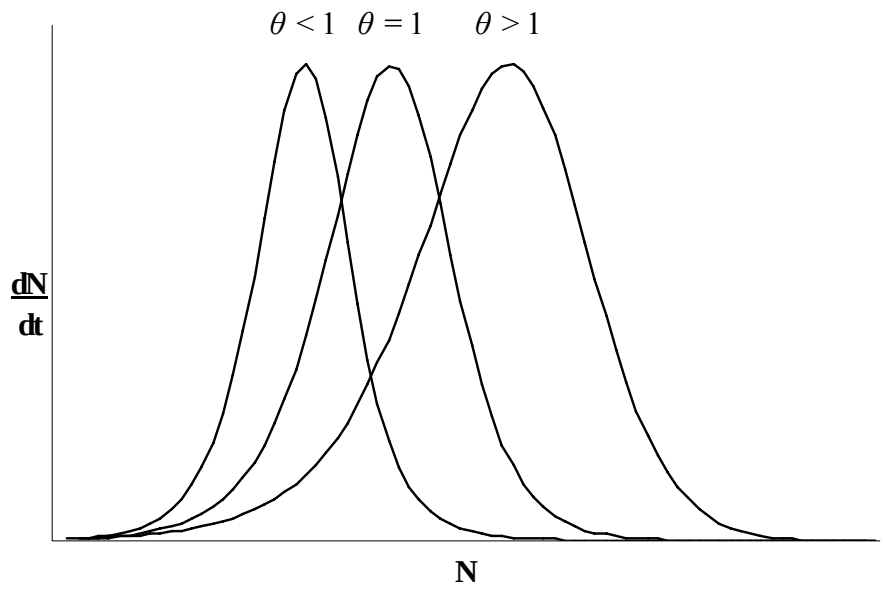

Fig. 6.6. Population growth (*dN/dt*) as a function of population size (*N*) for 3 values of θ. As θ increases, the point of maximum growth approaches *K* (modified from Gilpin and Ayala 1973).

birds, Saether and Engen (2002) found that θ was highly variable, ranging from 0.15 to 11.17 in the 11 species they studied, and negatively correlated with a species intrinsic rate of growth (*r*).

Although density-dependence in wild turkeys is poorly understood, there is some evidence to suggest that, if it acts at all, it should act most strongly on reproduction and recruitment, rather than adult mortality. I identified 4 factors that potentially could

contribute to density-dependence acting more heavily on reproduction than mortality in wild turkeys. They were

1. Increased nest loss at high densities.
2. Inhibition of reproduction due to nutritional stress.
3. Susceptibility of poults to starvation.
4. Inhibition of reproduction by behavioral responses to high densities.

Density-dependent Nest Loss.— Wild turkey hens are known to select nest sites based on vegetational characteristics (Lazarus and Porter 1985, Lutz and Crawford 1987). Moreover, habitat characteristics at the nest site affect nest success and hence reproduction (Baker 1979, Seiss et al. 1990), primarily by influencing the probability of nest predation (Badyaev 1995). Hence by selecting nest sites with abundant lateral and overhead vegetative cover (Porter 1992), hens reduce the chance that their nest will be depredated.

Although attacks on nests, often by animals that are inefficient predators of adult hens (e.g. Virginia opossum [*Didelphis virginiana*]), usually result in the loss of the entire clutch, they are less likely to result in the death of the hen (Ransom et al. 1987, Smith-Blair 1993). Therefore, use of suboptimal nesting habitat should have a stronger affect on reproductive output than adult mortality.

Although wild turkey are not considered territorial birds (Eaton 1992), exploitative competition (Drickamer et al. 2002) for nest sites does occur because occupation of a nest site by a hen precludes its use by other hens. Moreover, hens actively avoid each other during nesting (Healy 1992a). Therefore, availability of nest sites could become

limited at high densities. If we assume that wild turkey hens sequentially select and occupy available nest sites in order from high to low quality, then as population density increased, a larger proportion of hens would nest at sites of low quality. This sequential occupation of sites would lead to a decline in reproductive success due to decreased nest success as density increases (Newton 1998, Nummi and Saari 2003) and hens are forced to nest at sites that offer less protection against predators.

Nutritional Inhibition of Reproduction.— Nutritional stress, such as might occur at high densities, has a greater influence on reproduction than mortality. Blankenship (1992) reported that wild turkeys can survive long periods of nutritional stress. However, nutritional stress resulting from below-average rainfall has been reported to suppress gonadal development in RGWT hens in south and central Texas (Pattee and Beasom 1979, Davis 1994). Porter et al. (1983) also reported that breeding success was related to spring physiological condition resulting from the severity of the previous winter. Therefore, when food resources are limited by high-densities, many hens may survive, yet fail to breed.

Poult Susceptibility to Starvation.— Successfully hatching a brood is no guarantee of reproductive success at high densities. Wild turkey poults are more susceptible to starvation than adults because poults have higher nutritional requirements than adults due to rapid growth during the early weeks of life (Blankenship 1992, Hurst 1992). Seven-day old poults must consume approximately 17% of their body weight a day in live insects to meet their amino acid requirements (Hurst and Poe 1985). Hence

starvation might potentially be a major factor in poult mortality at high densities where insect supplies are limited.

Behavioral Response to High Densities.— Healy (1992*a*) speculated that hen and poult behavior might result in reduced poult production at high densities. He presented anecdotal evidence that dominant hens occasionally interfered with nesting behavior of subdominant hens when confined at high densities. Moreover, he noted an instance where an incubating hen was attracted to the calls of another hen's poults, causing her to abandon her own nest. While he admitted that such anecdotal evidence is not proof of density dependent suppression of production, he noted that such behavior would make close association between nesting and brooding hens disadvantageous and might provide a mechanism for density-dependent reproduction.

Conceptual Formulation of the Density-dependence Module

The density-dependence module is a straightforward information network that uses the current density (as a proportion of theoretical maximum density, see below) and θ to calculate a density dependence function (DDF). This function is applied in turn to various reproductive variables in other submodels and acts to suppress reproduction below the optimum level as density increases.

Although the strength of density-dependence is generally referred to in the context of K, in reality using K as a benchmark against which density-dependence is measured was unsuitable for this model. Carrying capacity is an equilibrium value; population density should tend to move toward K in the absence of some perturbation. By definition, in closed populations at equilibrium, recruitment equals mortality. Therefore, in a model in

which recruitment is density-dependent, and assuming mortality >0, recruitment will eventually assume a value equal to mortality and stop declining, thus never reaching 0. Because mortality in my model varied randomly from time-step to time step, setting reproduction equal to mortality at carrying capacity was akin to aiming at a moving target, and presented a near-intractable problem.

A much more parsimonious solution was to model density-dependence not as a function of K in the classical sense, but as a function of a theoretical density at which reproduction equals 0, what I termed "zero-reproduction density" (D_{R0}). This density was theoretical only, because to attain it, mortality would have to equal 0 as well, a situation which would not occur in nature. This was analogous to the von Bertalanffy (1968) growth equation parameter of the hypothetical age at size 0 (hypothetical because it would be <0). Therefore, in all cases $K < D_{R0}$.

DDF was calculated according to the equation

$$DDF = \left(\frac{H}{N_{R0}} \right)^{\theta},$$

where H = the sum of all adult and yearling hens and

$$N_{R0} = D_{R0} \times A,$$

where A = the geographic area of interest. A binary variable, DD_{Switch}, allows the model user to activate/deactivate density-dependence.

Quantitative Specification of Density-dependence Module

Sæther and Engen (2002) studied published demographics of 11 species of birds and reported that θ varied as a function of r. However, they did not report the actual

regression equation. I analyzed the data they presented (Sæther and Engen 2002:1190) using simple linear regression and found that r predicted θ according to the equation

$$\ln\theta = 0.490–0.792r \ (r^2 = .483,\ P = 0.018).$$

I could find no published reports of r for wild turkeys. However, Cobb and Doerr (1997) reported life tables for an eastern wild turkey population perturbed by flooding as well as an unperturbed population. I used the life table presented for the unperturbed population to calculate $r = 0.679$. I then calculated $\ln\theta = 0.490–(0.792 \times 0.679) = –0.04784$, hence $\theta \approx 0.9$. In light of information presented by Sæther and Engen (2002), this value was not unreasonable and was used in the model.

Because of the low turkey populations that predominated in the early 20th Century, turkey research since the advent of modern wildlife science primarily has dealt with increasing turkey populations. Therefore, there has been little work on density-dependence in turkeys, or even involving turkey populations that were near carrying capacity. I could find no published reports that alluded to the maximum density at which turkeys reproduce. Eaton (1992) reported that wild turkey typically occur at densities of 1–5/km^2. Densities of >10/km^2 have been reported for portions of Texas, although most populations existed at much lower densities (National Wild Turkey Federation 2002). I arbitrarily chose D_{R0} = 10 adult females/km^2. Although populations might exist and reproduce at densities greater than this, misestimation of the value should not seriously impair the model, because the area represented by the model (A) determines the number of hens at D_{R0} (H_{R0}), and is itself an arbitrary value. However, the application of the model to a specific population where A is not arbitrary would

require a more accurate estimation of D_{R0}, particularly in situations where limited mobility by turkeys might render the spatial aspect of population dynamics critical (e.g., isolated populations, metapopulations).

Density-dependence Module Verification

To verify the density-dependence module, I executed 3 simulation runs of 5,200 time steps each. I set $\theta = 1.0$, 0.5, and 1.5 for each run, respectively. I plotted *H* against *DDF* for each time step and visually assessed the shape of the relationship. Relationships were consistent with the expected relationship based on Fig. 6.5 (Figs. 6.7, 6.8, and 6.9).

HEN SUBMODELS

Background Information

Hens entered the adult and yearling hen submodels from different sources: the juvenile submodel for yearlings and the yearling submodel for adults. Otherwise the adult and yearling hen submodels had identical structure.

Hen Mortality.—At Week 1 (1 January), RGWT in the Edwards Plateau usually are in large wintering flocks (Thomas et al. 1966). During this period, RGWT hens generally experience some of the lowest mortality rates of the year. This may be due to turkeys being less vulnerable to predators while roosting in trees instead of on the ground as is necessary during incubation and brooding, as well as to enhanced predator detection by large wintering flocks (Haucke 1974). Moreover, winter weather across most of the RGWT range in Texas is relatively mild compared to that of the eastern

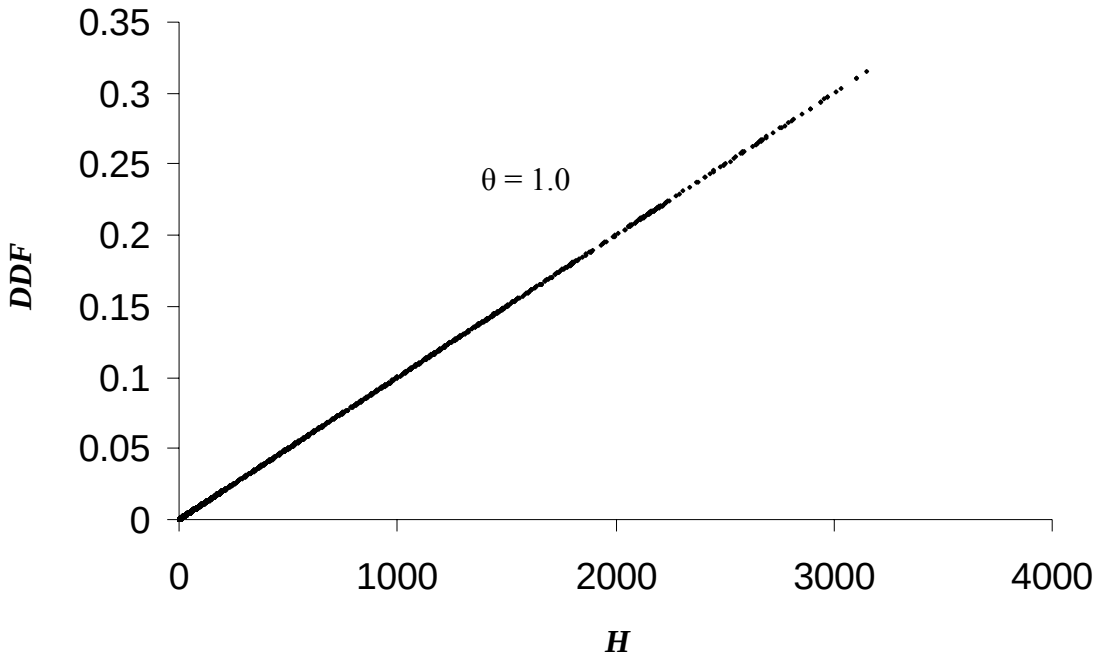

Fig. 6.7. Results of simulation run of 5,200 time steps showing the relationship between *DDF* and *H*, for $\theta = 1.0$.

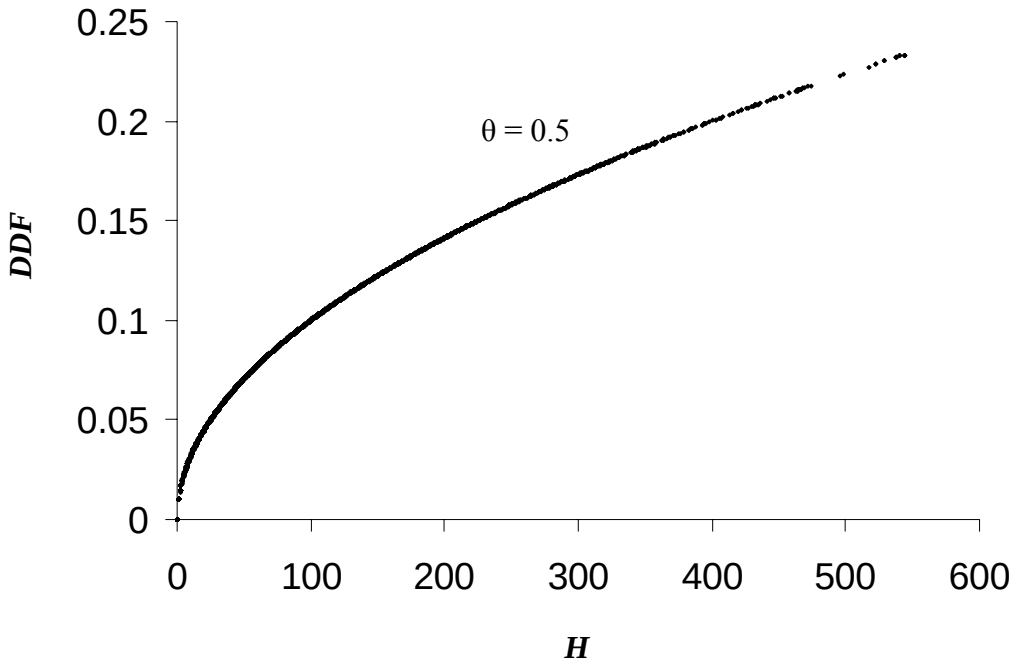

Fig. 6.8. Results of simulation run of 5,200 time steps showing the relationship between *DDF* and *H*, for $\theta = 0.5$.

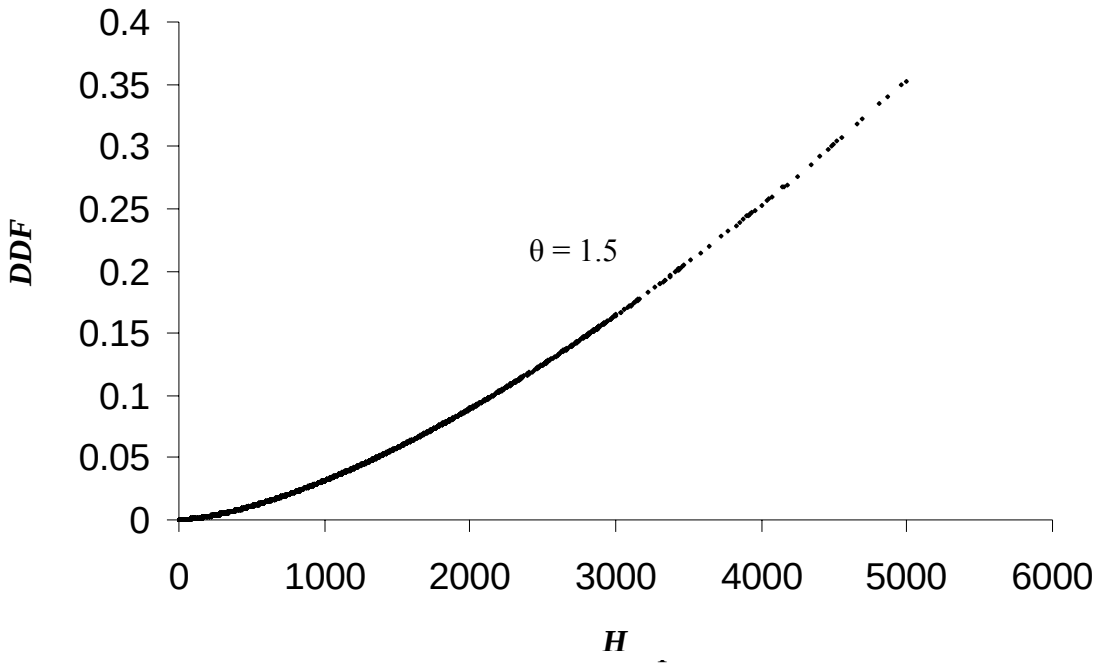

Fig. 6.9. Results of simulation run of 5,200 time steps showing the relationship between *DDF* and *H*, for $\theta = 1.5$.

turkey in the northern United States, where severe winter weather may cause substantial mortality of adult birds (Porter et al. 1983).

Hennan and Lutz (2001) reported a winter survival rate of 0.790 for RGWT hens in south-central Kansas. This extrapolates to a weekly survival rate of 0.9862 over the 17-week period. In South Dakota, Lehman et al. (2000) found that RGWT had a winter survival rate of 0.974 (0.998 weekly survival rate). This high survival rate was despite severe winter weather typical of the region. Finally, Hohensee and Wallace (2001) reported a RGWT hen winter survival rate of 1 in northcentral Texas. Although it is unlikely that birds in this region actually experienced no mortality during the winter, this does suggest that winter survival was high.

In early spring, winter flocks begin to break up and hens disperse for breeding and subsequent nesting. Thomas et al. (1966) reported that spring dispersal generally began in late February in the Edwards Plateau, and was completed by late April. Davis (1994) reported that birds in central Texas began breeding in early March and continued through May. Spring dispersal is accompanied by an increase in hen mortality. Hennan and Lutz (2001) reported an average daily survival rate over 2 years of 0.9973 during spring dispersal, while Miller et al. (1995) reported a seasonal survival rate during spring dispersal of 0.8757. These rates extrapolate to weekly rates of 0.9814 and 0.9939, respectively.

Rio Grande wild turkey hens tend to experience the highest mortality rates during the 4-week period when they are incubating nests, when they are most vulnerable to predation. Hennan and Lutz (2001) reported an average daily survival rate of 0.9968

(weekly rate of 0.9778) for incubating RGWT. Likewise, Miller et al. (1995) reported RGWT hens incubating first nests experienced 0.742 survival during the incubating period (0.9281/week). However, hens incubating subsequent nests experienced much higher survival rates (0.9828/week).

After hatching, hens generally accompany their brood for ≥4 months (Healy 1992*b*). I could find no published studies that reported separate survival rates for hens brooding poults (0–2 weeks old) versus hens brooding juveniles (2–16 weeks old). However, Miller et al. (1995) reported a weekly survival rate during brood-rearing of 0.9975. Also, Hohensee and Wallace (2001:88) reported that survival of RGWT hens in northcentral Texas was "essentially 100%" during all seasons outside of dispersal and nesting, supporting Miller et al.'s (1995) claim of high survival during this period.

Hens not engaged in some phase of reproduction (dispersal, laying, incubating, or brood rearing) generally have high survival. Hennan and Lutz (2001) reported average daily survival rates for non-breeding RGWT hens of 0.9963 (0.9748/week), while Miller et al. (1995) reported seasonal rates of 0.8897 (0.9947/week) and Hohensee and Wallace (2001) reported 100% survival of non-reproducing hens.

Reproduction.— Schmutz and Braun (1989) suggested that yearling hens might initiate nests later in the season than adults, and they attributed this difference to greater dispersal distances among yearlings. However, they reported different mean nest initiation dates in only 1 of 2 years. Buford (1993) found no difference in nest initiation dates between yearling and adult hens in Kansas, and Davis (1994) stated that breeding peaked at the same time for the 2 age classes in south and central Texas.

Most studies of RGWT have reported near 100% of adult hens attempt to nest. Yearling hens, however, tend to nest at lower rates. Keegan and Crawford (1993) found that 94% of yearling hens in their study in Oregon attempted to nest, while the yearling hen nesting rate in Colorado was 95% (Schmutz and Braun 1989). Both of these studies were conducted outside the historic RGWT range. In Kansas, Buford reported a yearling nesting rate of 90%.

Hatching success is defined as the proportion of eggs that hatch in successful nests, and encompasses "egg fertility, embryo viability, and partial predation" (Vangilder 1992). Hatching success in wild turkeys generally is high. Cook (1972) reported overall hatching success of 0.90 in the Edwards Plateau, but did not differentiate between hen age classes or nesting attempts. In south Texas, hatching success across hen-ages classes averaged 0.89. Keegan and Crawford (1999) reported similarly hatching nest success. Although their study differentiated between yearling and adult nests, they found no significant difference in hatching success between them. They also reported that hatching success for second nest attempts averaged approximately 50% that of initial nests.

Wild turkey hens often will attempt to renest following the loss of their first nest (Vangilder 1992). Buford (1993) reported renesting rates in Kansas of 56% for adult hens and 64% for yearlings. Reagan and Morgan (1980) reported similar renesting rates for the 2 ages classes, with an adult rate of 54% and a yearling rate of 50%.

Schmutz and Braun (1989) reported that adult birds had average clutch sizes (for first nests) of 11.3 eggs, while yearling bird clutches averaged 10.4 eggs. Likewise, Buford

(1993) reported adult first nest clutch sizes of 10.5 and 10.4 eggs, respectively. Conversely, Reagan and Morgan (1980) reported that adult hens in the Edwards Plateau laid smaller clutches during their first nesting attempt than did yearlings (9.9 versus 11.0). Finally, Hohensee and Wallace (2001) reported that adult hen clutch size averaged 9.9 eggs in north Texas. They did not report on any yearling nests.

When wild turkeys renest following the loss of their initial nest, clutch sizes are generally smaller for the second clutch. Two studies have reported explicitly on second nest clutch size for Rio Grande wild turkeys in Texas. In Kansas, adult hens averaged 9.4 eggs per clutch while yearlings averaged 9.6 eggs (Buford 1993). In the Edwards Plateau, the average clutch size for second nests was 9.4 for adults and 8.3 for yearlings (Reagan and Morgan 1980).

The proportion of nests that successfully hatch ≥1 poult varies widely among published studies of wild turkey reproduction. I examined nest-loss rates of both adult and yearling hens from 15 published studies covering Rio Grande, eastern, Florida (*M. g. osceola*), and Merriam's (*M. g. merriami*) wild turkeys, because I wanted to evaluate as completely as possible the full range of wild turkey nest loss rates in order to quantify nest loss as a stochastic variable

Nesting success is difficult to measure during the laying phase. Although researchers usually attempt to determine the onset of nesting (e.g., by the onset of localized hen movements during radio-tracking), nests may be destroyed before nesting activity is identified. Thus, nests might go unnoticed and bias an estimate of nest loss

Table 6.3. Combined nest loss rates for yearling and adult wild turkey hens during laying reported in the literature.

Source	Subspecies	Weekly nest loss rate[a]
Campo 1983	Eastern	0.0249
Vangilder et al. 1987	Eastern	0.1056
Vander Haegen et al. 1988	Eastern	0.0000
Davis et al. 1995	Eastern	0.0955
Leif 2000	Eastern	0.1592
Ransom et al. 1987	Rio Grande	0.0000
Williams and Austin 1981	Florida	0.2320
Lutz and Crawford 1987	Merriam's	0.0000

[a]Reported rates were extrapolated to weekly rates.

during laying. On the other hand, reduced activity accompanying incubation makes nests easier to locate and monitor during this period, thus increasing the likelihood of an accurate estimate of nesting attempts and nest loss. Because not all nests are found during laying there are fewer published studies reporting nest loss during laying than nest loss during incubation. Of those studies that did examine nest loss during laying, none differentiated between yearling and adult loss rates. Therefore, I report combined

Table 6.4. Reported nest loss rates during incubation for yearling wild turkey hens.

Source	Subspecies	Weekly nest loss rate[a]
Glidden and Austin 1995	Eastern	0.0810
Porter et al. 1983	Eastern	0.0791
Vangilder et al. 1987	Eastern	0.2562
Vander Haegen et al.1988	Eastern	0.1835
Seiss et al. 1995	Eastern	0.1694
Roberts et al. 1995	Eastern	0.2201
Lopez 1996	Eastern	0.2928
Godfrey and Norman 2000	Eastern	0.1784
Vangilder et al. 2000	Eastern	0.1544
Lehman et al. 2000	Eastern/Rio Grande	0.0980
Williams and Austin 1981	Florida	0.0810
Lutz and Crawford 1987	Merriam's	0.0791

[a]Reported rates were extrapolated to weekly rates.

yearling and adult rates for loss during the laying period (Table 6.3), but differentiate rates by age classes for loss during incubation (Tables 6.4 and 6.5).

Nest loss rates during the laying period were generally slightly lower (range: 0.0000–0.2320) than during the incubation period for either yearling hens (range: 0.0694–0.2928) or adult hens (range: 0.0717–0.2773). This may be due to possible bias

Table 6.5. Reported nest loss rates during incubation for adult wild turkey hens.

Source	Subspecies	Weekly nest loss rate[a]
Glidden and Austin 1995	Eastern	0.2254
Porter et al. 1983	Eastern	0.0717
Vangilder et al. 1987	Eastern	0.2562
Vander Haegen et al. 1988	Eastern	0.0894
Davis et al. 1995	Eastern	0.1069
Roberts et al. 1995	Eastern	0.1412
Godfrey and Norman 2000	Eastern	0.0971
Ransom et al. 1987	Rio Grande	0.2778
Lutz and Crawford 1987	Merriam's	0.0694

[a]Reported rates were extrapolated to weekly rates.

in estimating laying-nest-loss rates mentioned earlier. Alternatively, higher nest loss rates during incubation may be attributable to the hens spending more time on the nest during this period, especially at night (Healy 1992*a*), and thus being more susceptible to predation (Miller and Leopold 1992).

General Relationship Between Precipitation and Turkey Production.— My analysis of Texas Parks and Wildlife Department poult production data from the Edwards Plateau for 1976–2000 indicated a strong correlation between September–June precipitation and Rio Grande wild turkey recruitment (see Chapter III). Subsequently, I

performed polynomial regression of Edwards Plateau poult proportion against raw September–June precipitation. Because raw precipitation was not normally distributed, I normalized the data using a square-root transformation.

I analyzed the relationship using the quadratic-fitted line-plot analysis in Minitab. Results indicated a strong curvilinear relationship between square root of the precipitation and poult proportion ($r^2 = 0.812$, $P < 0.001$; Fig. 6.10).

Although I did not include a recruitment variable in the simulation model per se, I surmised the relationship between precipitation and recruitment resulted from a strong influence of precipitation on reproductive variables that drive recruitment: nest success, poult mortality, and juvenile mortality. I further reasoned the shape of the relationship between precipitation and the various recruitment variables would be similar to that between precipitation and recruitment.

I chose not to define reproductive variables using the actual regression equation derived from my regression analysis. Such precision was unwarranted because the relationship between my reproductive variables and recruitment was unclear and probably imperfect. However, visual analysis of the regression plot suggested the relationship followed a monotonically ascending trajectory up to approximately 60 cm annual precipitation, and then assumed an approximately flat trajectory thereafter (Fig 6.11). Therefore, I chose to simulate the effect of precipitation on reproductive variables based on this general relationship.

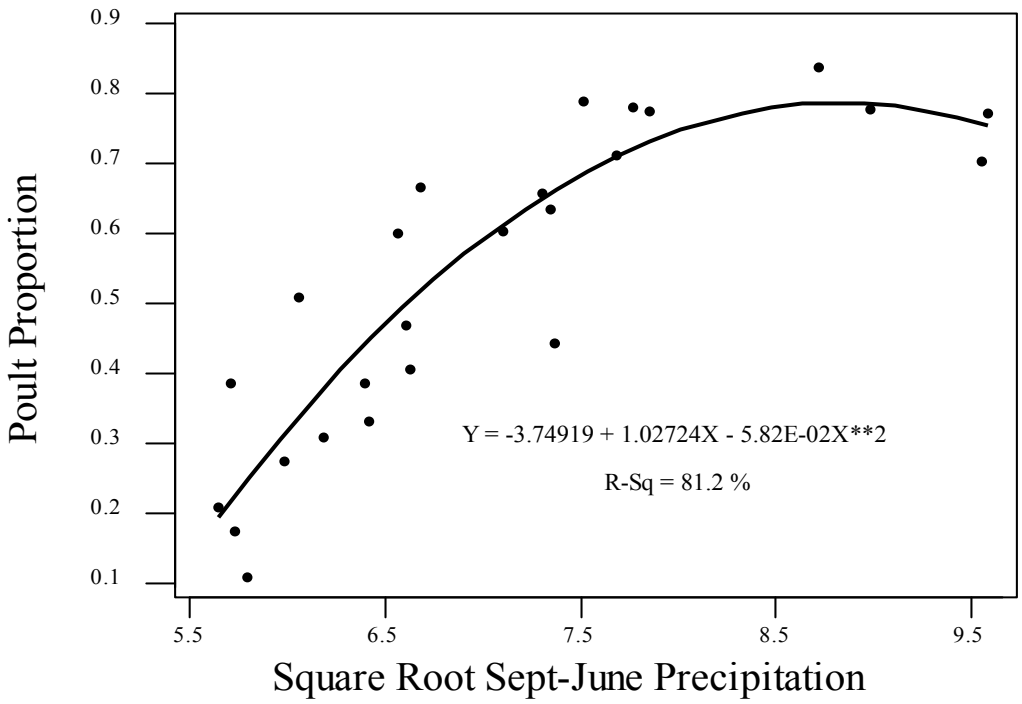

Fig. 6.10. Polynomial regression of poult proportion against total September–June raw precipitation (square-root transformed) for the Edwards Plateau, 1976–2000.

Conceptual Formulation of the Hen Submodels

The yearling and adult-hen submodels each consisted of 9 stages representing reproductive status (Fig. 6.12). Hens progressed through the reproductive stages on an annual cycle. After beginning the year in the wintering stage, all hens entered the breeding population simultaneously. Henceforth, the proportion of hens in each stage was determined by reproductive status, hen mortality, and reproductive success.

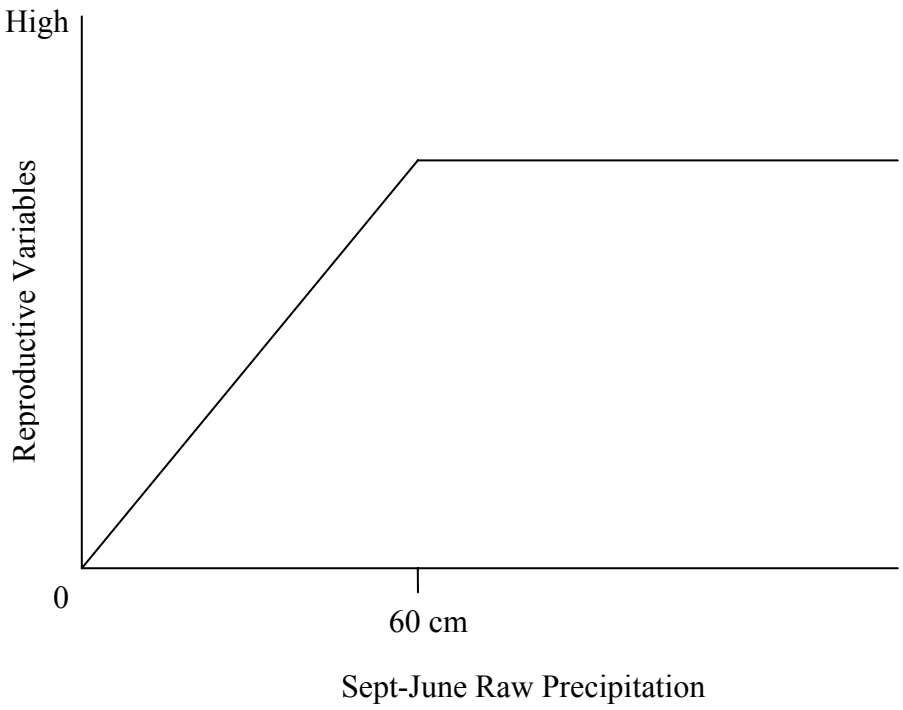

Fig. 6.11. Generalized relationship between September–June raw precipitation and reproductive variables.

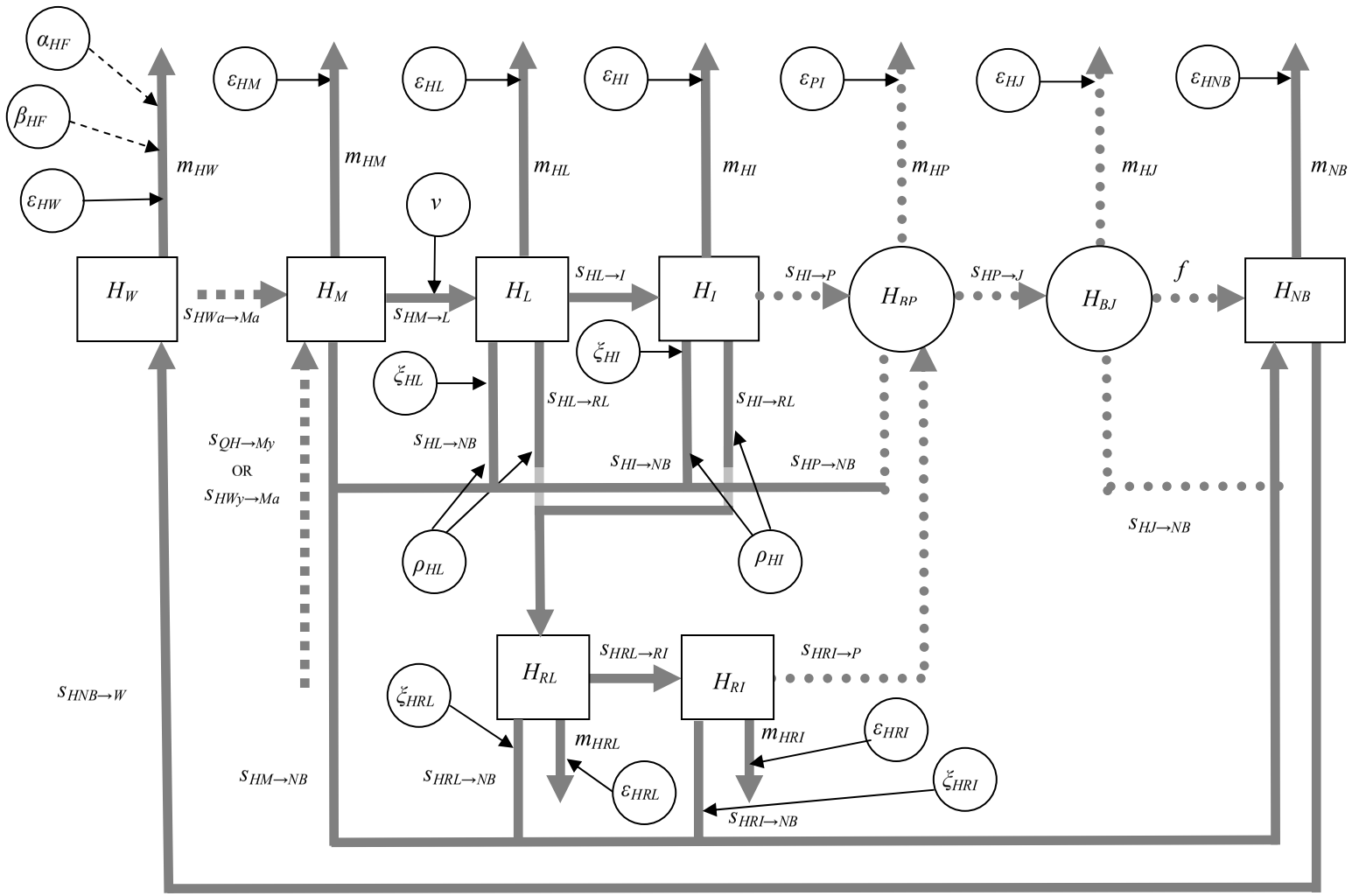

Figure 6.12. Conceptual diagram of hen submodel showing key parameters. Boxes indicate state variables (stocks) while circles indicate information variables. Black lines represent information transfer (dashed black lines represent optional harvest information). Solid gray lines represent material transfers; dashed gray lines represent 3 alternative pathways into the mating stage: from juvenile, yearling, and adult hens.

Description of the Hen Submodel

Each hen (yearling and adult) submodel consisted of 7 state variables representing different reproductive stages (Fig. 6.12). These variables were: H_W, H_M, H_L, H_I, H_{RL}, H_{RI}, and H_{NB}. The submodel also consists of 2 auxiliary variables (H_{BP} and H_{BJ}) representing brooding hens as a function of total broods. When used in the model description, lower case subscripts (e.g., y = yearling) denote variables that refer to specific age classes. When lower case subscripts are absent, variables refer to all age classes.

Week 1 represents early January, a time when RGWT are grouped in winter flocks. Therefore, at Week 1 the hen population is represented by the state variable H_W (Fig. 6.12). Hens represented by this variable are subjected to mortality, represented by the flow variable m_{H_W}, which subtracts hens from H_W each time step. Variable m_{H_W} is the sum of both natural and hunting mortality, and is calculated by 1 of 2 equations, depending on whether hunting mortality is operating. If hunting mortality is not operating, either because the hen harvest option has been deactivated or because the current time step falls outside the user-defined hen hunting season, m_{H_W} is defined according to the equation

$$m_{H_W} = H_W \times \varepsilon_{H_W},$$

where ε_{H_W} = wintering hen weekly mortality rate (proportion of wintering yearling hens dying from time step t to time step $t+1$). Conversely, if the hen harvest option has been activated and the current time step falls within the hen hunting season, m_{H_W} is defined according to the equation

$$m_{H_W} = (H_W \times \varepsilon_{H_W}) + \left(\frac{\alpha_{H_F}}{\beta_{H_F}} \right),$$

where α_{H_F} = the total fall harvest of hens during the current year and β_{H_F} = the length of the fall hen season, in weeks.

At the beginning of the mating season, which coincides with the spring break-up of winter flocks (Week 9; Thomas et al 1966, Davis 1994), all surviving wintering hens enter the mating hen stock (H_M) via the flow $s_{H_{W \to M}}$. At this time, hens are recruited to the next oldest age class, with wintering hatch-year hens (H_{W_j}) entering the mating yearling hen (H_{M_y}) stage via the flow variable $s_{Q_W \to H_{M_y}}$, and wintering yearling hens (H_{W_y}) entering the mating adult hen (H_{M_a}) stage via the flow variable $s_{H_{W_y \to M_a}}$ (Fig. 6.12). Wintering adult hens reenter H_{M_a} via $s_{H_{W_a \to M_a}}$.

Variable H_M represents those hens available for breeding during the current year. Hens leave H_M by 1 of 3 processes. Each time step, hens may (1) die, (2) begin laying, or (3) leave the breeding population without laying. Mortality is represented by the flow variable m_{H_M}, which is the number of mating hens dying during the current time step, and is calculated according to the equation

$$m_{H_M} = H_M \times \varepsilon_{H_M},$$

where ε_{H_M} = the weekly mortality rate of mating hens. Laying is represented by movement of a portion of H_M into the H_L (laying hens) state variable via the $s_{H_{M \to L}}$ flow

variable. The proportion passing into the H_L population each time step is determined by the equation

$$s_{H_{M\rightarrow L}} = \mathrm{H_M} \times v,$$

where v = nesting rate = the proportion of H_M nesting during the current time step. Variable v is a graphical function that enables the user to define nesting rate as a function of week and thus vary the value by week throughout the season.

Hens do not remain eligible for breeding indefinitely. At the end of the mating season (Week 21; Davis 1994), all surviving yearling hens remaining in H_M move out via the $s_{\mathrm{H_{M\rightarrow NB}}}$ flow variable and into H_{NB} (Fig. 6.12) to become part of the year's non-breeding hen population.

The state variable H_L represents those hens currently in the laying stage of reproduction (Fig. 6.12). H_L is a conveyer variable with a transit time of 2 weeks, the approximate duration of the laying period in wild turkeys (Healy 1992a). As a conveyor variable, H_L maintains each cohort of hens entering it as a discrete unit for the duration of the transit time, applying all driving variables to each cohort separately. Each time step, a portion of hens is subtracted from each cohort in H_L by either death or nest loss, with or without renesting. These processes are combined in the conveyor outflow variable e_{H_L}, calculated using the equation

$$e_{H_L} = m_{H_L} + s_{H_{L\rightarrow NB}} + s_{H_{L\rightarrow RL}}.$$

Further,

$$m_{H_L} = H_L + \varepsilon_{H_L},$$

where ε_{H_L} = the weekly mortality rate of laying hens and $s_{H_{L\rightarrow NB}}$ = the number of laying hens that lose their nest during the current time step but do not attempt a second nest and thus move into the nonbreeding population =

$$(H_L \times (1-\xi_{H_L})) - s_{H_{L\rightarrow RL}},$$

where $1-\xi_{H_L}$ = the proportion of hens which lose there nest, but survive, during each week of the laying period. $s_{H_{L\rightarrow RL}}$ = the number of laying hens that lose their nest during the current time step and attempt a second nest

$$= H_L \times \rho_{H_L},$$

where ρ_{H_L} = the renest rate of laying hens. Finally, all yearling hens that survive the laying period with their nest intact move out of H_L via the $s_{H_{L\rightarrow I}}$ flow variable and begin the incubation stage, represented by the state variable H_I.

The structure of that portion of the hen submodel representing the incubation stage (Fig. 6.12) is similar to that representing the laying stage. The conveyor variable H_I has a transit time of 4 time steps, representing the approximately 4-week incubation period of wild turkeys (Healy 1992a). Each time step, hens leave H_I via the flow variable e_{H_I}, due to either mortality or nest loss, with or without renesting, according to the equation

$$e_{H_I} = m_{H_I} + s_{H_{I\rightarrow NB}} + s_{H_{I\rightarrow RL}}.$$

The variables involved in this equation are the same as for e_{H_l}, but have values specific to the incubating period and its associated material transfers. Those hens that survive and keep their nest throughout the entire incubation period are considered to hatch their clutch and move out of H_I via flow $s_{H_{I\rightarrow P}}$. They temporarily cease to be tracked by the

model as discrete units using state variables. Instead, because the number of brooding hens is, by definition, equal to the number of broods, the total number of hens with broods is represented by the information variables H_P (hens with poults) and H_J (hens with juveniles), depending on the life stage of their respective broods. Thus $H_P = \sum P_i$, where P_i = the total number of broods containing poults, and $H_J = \sum J_i$, where J_i = the total number of broods containing juveniles. For further discussion, see Brood Submodels section.

The state variables H_{RL} (renesting laying hens) and H_{RI} (renesting incubating hens) represent those yearling hens that attempt a second nest following loss of their first nest in either the laying or incubating stages (Fig. 6.12). The structure of these state variables is identical to H_L and H_I respectively, with 2 exceptions. First, driving variables are specified with values applicable to hens attempting second nests, versus first nest hens. Second, hens that lose their second nest are not allowed subsequent attempts. Although third nesting attempts are known to occur in wild turkeys (Buford 1993), the rarity of such events led me to exclude the possibility of >2 nesting attempts to avoid over complicating the model. Therefore, all renesting hens that lose their nest but survive are moved via $s_{H_{RL \to NB}}$ or $s_{H_{RI \to NB}}$ into the nonbreeding hen population (H_{NB}) for the remainder of the year. Renesting hens that survive the laying and incubation periods with nests intact are considered to hatch their clutch and move out of H_{RI} via flow $s_{H_{RI \to P}}$. They are combined with successful first-nest hens to be represented by the information variable H_P.

Hens that are not in 1 of the reproductive stages are considered nonbreeding and are represented by the state variable H_{NB} (Fig. 6.12). During each time step (except during the wintering period), hens enter the nonbreeding stage via 2 mechanism. First, hens may enter via the flow variable f, which represents those hens raising at least 1 offspring to 16 weeks of age during the current time step. Alternatively, hens ending reproductive effort but surviving (e.g., following nest loss) and are moved directly to H_{NB} via flow variables subscripted $_{\rightarrow NB}$ (e.g., $s_{H_{RL\rightarrow NB}}$)

Hens leave H_{NB} each time step due to mortality via $m_{H_{NB}}$ according to the equation

$$m_{H_{NB}} = H_{NB} \times \varepsilon_{H_{NB}},$$

where $\varepsilon_{H_{NB}}$ = the weekly mortality rate of nonbreeding hens.

During Week 45 (the beginning of the wintering period), all hens are subtracted from H_{NB} and added to H_W. To account for hens that might conclude breeding during the winter, all hens entering the nonbreeding population between Week 45 and Week 9 are moved directly to H_W.

Quantitative Specification of the Yearling Hen Submodel

For model evaluation and sensitivity analysis, I specified the mortality variables using values reported in the literature (Table 6.6). When more than 1 source reported values, I specified the variable using the mean of all reported values.

I specified those reproductive parameters held constant during simulations (e.g., hatching success), in a manner similar to mortality variables, by using values reported in the literature (Table 6.7). However, nest survival (ξ) was not held constant. It varied

Table 6.6. Values used to specify mortality parameters in the model, derived from empirical data reported in the literature.

Variable[a]	Value	Source
ε_{H_M}	0.01235[b]	Miller et al. 1995, Hennen and Lutz 2001[c]
ε_{H_L}	0.01235[b]	Miller et al. 1995, Hennen and Lutz 2001
$\varepsilon_{H_{RL}}$	0.0186	Hennen and Lutz 2001
ε_{H_I}	0.0471[b]	Miller et al. 1995, Hennen and Lutz 2001
$\varepsilon_{H_{RI}}$	0.01720	Miller et al. 1995
ε_{H_P}	0.0025	Miller et al. 1995
ε_{H_J}	0.0025	Miller et al. 1995
$\varepsilon_{H_{NB}}$	0.0102[b]	Miller et al. 1995, Hennen and Lutz 2001, Hohensee and Wallace 2001
ε_{H_W}	0.0051[b]	Hennen and Lutz 2001, Hohensee and Wallace 2001, Lehman et al. 2001

[a]Miller et al. (1995), Keegan and Crawford (1999), and Hennen and Lutz (2001) reported no difference between yearling and adult RGWT hen mortality rates; therefore, stage-specific rates were set equal for both age classes.

[b]Mean of reported values.

[c]Miller et al. (1995) and Hennen and Lutz (2001) referred to this period as "dispersal."

Table 6.7. Values used to specify certain parameters variables in the model, derived from empirical data reported in the literature.

Variable	Value	Source
$\rho_{H_{Ly}}$	0.57[a]	Reagan and Morgan 1980, Buford 1993
$\rho_{H_{La}}$	0.55[a]	Reagan and Morgan 1980, Buford 1993
$\rho_{H_{Iy}}$	0.57[a]	Reagan and Morgan 1980, Buford 1993
$\rho_{H_{La}}$	0.55[a]	Reagan and Morgan 1980, Buford 1993
$\upsilon_{\mu_{y1}}$	10.46[a]	Reagan and Morgan 1980, Schmutz and Braun 1989, Buford 1993
$\upsilon_{\mu_{a1}}$	10.31[a]	Reagan and Morgan 1980, Schmutz and Braun 1989, Buford 1993, Hohensee and Wallace 2001
$\upsilon_{\mu_{y2}}$	8.93[a]	Reagan and Morgan 1980, Buford 1993
$\upsilon_{\mu_{a2}}$	9.20[a]	Reagan and Morgan 1980, Buford 1993
$\upsilon_{\sigma_{y1}}$	2.34[a]	Reagan and Morgan 1980, Schmutz and Braun 1989, Buford 1993
$\upsilon_{\sigma_{a1}}$	2.08[a]	Reagan and Morgan 1980, Schmutz and Braun 1989, Buford 1993
$\upsilon_{\sigma_{y2}}$	1.42[a]	Reagan and Morgan 1980, Buford 1993
$\upsilon_{\sigma_{a2}}$	2.12[a]	Reagan and Morgan 1980, Buford 1993

[a]Mean of reported values.

[b]Keegan and Crawford (1999) reported that renest hatchability was approximately ½ that of 1st nests.

each time step as a function of (1) precipitation (according to the general relationship shown in Fig. 6.6), (2) stochasticity, and 3) density-dependence.

I modeled ξ based on the estimated range of plausible ξ's, the range of historic precipitation in central Texas, and the presumed relationship between them. Examination of 1896-2001 Edwards Plateau precipitation revealed a minimum annual precipitation of 23 cm, or 43% of the long-term mean. I assumed this precipitation total would coincide with minimum ξ. I also assumed that maximum ξ would occur at the plateau of the precipitation-recruitment relationship (60 cm; Fig. 6.6) which corresponds to 112% of long-term mean annual rainfall.

To approximate the minimum and maximum possible values for ξ, I used published values from the literature. Because published data regarding ξ was limited, I used a single value (ξ_L) for all laying nest survival variables (yearling and adult first and second nests), 1 value (ξ_{I_y}) for incubating yearling first and second nests, and 1 value (ξ_{I_a}) for incubating adult first and second nests.

Each time step, ξ for each class was estimated using a 3-step process. First, a base value (ξ') was determined as a function of precipitation (Eqs. 6.1–6.3). Next, an intermediate value (ξ'') was generated by drawing a random value from a normal distribution having a mean equal to ξ'. Finally, ξ'' was adjusted according to total turkey density by multiplying it by *DDF* to attain ξ.

I calculated the nest survival mean (ξ_μ) and standard deviation (ξ_σ) for each class and estimated the minimum and maximum values as a 99% confidence interval of ξ_μ

($\xi_\mu \pm 3\xi_\sigma$), using data reported in the literature (Table 6.8). I then fit a line to the 2 Cartesian coordinates defined by 43% and 112% of long-term mean annual precipitation (x-values) and estimated maximum and minimum ξ (y-values) and calculated slope and y-intercept. The resulting equations were

$$\xi_L' = 0.4533118 + 0.00488114P, \quad 6.1$$

$$\xi_{Iy}' = 0.380528 + 0.005531P, \quad 6.2$$

and

$$\xi_{Ia}' = 0.358438 + 0.005728P, \quad 6.3$$

where P = cumulative precipitation to date since September.

Table 6.8. Estimated wild turkey nest survival rates, from the literature.

Variable	Value[a]
ξ_{L_μ}	0.92285
ξ_{L_σ}	0.08655
ξ_{Ia_μ}	0.85166
ξ_{Ia_σ}	0.08230
ξ_{Iy_μ}	0.83509
ξ_{Iy_σ}	0.07224

[a]Sources: Glidden and Austin 1975, Campo 1983, Porter et al. 1983, Williams and Austin 1984, Ransom et al. 1987, Vangilder et al. 1987, Vander Haegen et al. 1988, Seis et al. 1990, Davis et al. 1995, Porter 1995, Roberts, Coffey, and Porter 1995, Lopez 1996, Godfrey and Norman 2000, Lehman et al. 2000, Leif 2000, Vangilder 2000.

HARVEST MODULES

Background Information

Fall-hen harvest has been permitted in several Texas counties since the 1980's (R. MacDonald, Texas Parks and Wildlife Department, personal communication). Although research in some states has suggested moderate hen harvest, particularly of eastern wild turkey, is not detrimental to the turkey populations (Little et al. 1990, Kurzejeski and Vangilder 1992), the full effect of fall-hen harvest in most regions of the country remains poorly understood (Kurzejeski and Vangilder 1992). To my knowledge, there has been no published research regarding the effect of hen harvest on RGWT populations.

An important charge of the Wildlife Division of TPWD has been to expand hunter opportunity and simplify hunting regulations (TPWD Commission Chairman Charges to Committees http://www.tpwd.state.tx.us/publications/agency_reports/pdf_docs/chairman_charges_2003_09.pdf.). One of the ways in which this objective has been pursued has been the liberalization of hunting regulations, including lengthening hunting seasons and enlarging bag limits. However, these changes typically have been made without careful evaluation of their effects on RGWT populations. Thus, my model was designed to account for varying degrees of harvest, in order to test the population-level effects of specific management strategies.

Conceptual Formulation and Description of the Harvest Modules

Hen Harvest Module.– The hen-harvest module is an information network used to calculate fall adult and yearling hen harvest. The module requires user-parameterization of 6 driving variables:

1. $\varphi_{H_{FB}}$ = the week in which the fall hen hunting season begins.
2. $\varphi_{H_{FE}}$ = the week in which the fall hen hunting season ends.
3. γ_{H_F} = the week in which the model determines the hen population upon which the fall hen harvest is based.
4. ψ_{H_F} = the ratio of yearling to adult female harvest rates.
5. ι_{H_F} = a binary variable indicating whether fall hen harvest is allowed. A value of 1 = yes, 2 = no.
6. ζ_{H_F} = the proportion of the total fall hen population to be harvested.

If ι_{H_F} is set to 0 (harvest disallowed), $\alpha_{F_H} = 0$ and fall hen harvest does not occur. Conversely, if ι_{F_H} is set to 1 (harvest allowed), $\alpha_{H_{Fy}}$ (total yearling hens to be harvested) is calculated according to the equation

$$\alpha_{H_{Fy}} = \zeta_{H_F} \times \left(\frac{\dfrac{H_y \psi_{H_F}}{H_a}}{\left(\dfrac{H_y \psi_{H_F}}{H_a} \right) + 1} \right) \times H \ ,$$

where H = total yearling and adults hens in the population, H_a = the total adult hens in the population and H_y = the total yearling hens in the population. Likewise, total adult hen fall harvest ($\alpha_{H_{Fa}}$) is calculated as

$$\alpha_{HFa} = \zeta_{HF} \times \left[1 - \left(\frac{\frac{H_y \psi_{HF}}{H_a}}{\left(\frac{H_y \psi_{HF}}{H_a} \right) + 1} \right) \right] \times H \ .$$

The model calculates $\alpha_{H_{Fy}}$ and $\alpha_{H_{Fa}}$ every time step. However, only the values calculated during $t = \gamma_{H_F}$ are applied to the population.

Male Harvest Module.– The gobbler harvest modules calculates fall and spring harvest mortality of yearling and adult males. The module requires user parameterization of 14 driving variables:

1. $\varphi_{M_{FB}}$ = the week in which the fall male hunting season begins.
2. $\varphi_{M_{FE}}$ = the week in which the fall male hunting season ends.
3. γ_{M_F} = the week in which the model determines the male population upon which the fall male harvest is based.
4. $\varphi_{M_{SB}}$ = the week in which the spring male hunting season begins.
5. $\varphi_{M_{SE}}$ = the week in which the spring male hunting season ends.
6. γ_{M_S} = the week in which the model determines the male population upon which the spring male harvest is based.
7. ψ_{M_F} = the ratio of jake (yearling male) to gobbler (adult male) fall harvest rates.
8. ψ_{M_S} = the ratio of jake to gobbler spring harvest rates.
9. ι_{Mj_F} = a binary variable indicating whether fall jake harvest is allowed. A value of 1 = yes, 2 = no.

10. ι_{Mj_S} = a binary variable indicating whether spring jake harvest is allowed. A value of 1 = yes, 2 = no.

11. ι_{Ma_F} = a binary variable indicating whether spring gobbler harvest is allowed. A value of 1 = yes, 2 = no.

12. ι_{Ma_S} = a binary variable indicating whether spring gobbler harvest is allowed. A value of 1 = yes, 2 = no.

13. ζ_{M_F} = the proportion of the total fall male population to be harvested.

14. ζ_{M_S} = the proportion of the total spring male population to be harvested.

The model can be parameterized to allow no male harvest, gobbler harvest only, or gobbler and jake harvest, during either the spring season, fall season or both. When male harvest during a particular season is allowed, jake harvest (α_{My}) is calculated according to the equation

$$\alpha_{My} = \zeta_M \times \left(\frac{\frac{M_y \psi_M}{M_a}}{\left(\frac{M_y \psi_M}{M_a} \right) + 1} \right) \times M$$

where M = the total population of jakes and gobblers. Gobbler harvest (α_{Ma}) is calculated according to the equation

$$\alpha_{Ma} = \zeta_M \times \left[1 - \left(\frac{\frac{M_y \psi_M}{M_a}}{\left(\frac{M_y \psi_M}{M_a} \right) + 1} \right) \right] \times M \ . \qquad 6.4$$

As with the hen harvest module, harvest totals are calculated every time step, but only the value calculated when $t = \gamma_{M_F}$ or γ_{M_S} is applied to the populations during the fall or spring hunting season, respectively. When gobbler, but not jake, harvest is allowed, $\psi_M = 0$ and Equ. 6.4 collapses to $\alpha_M = \zeta_M \times M$.

Quantitative Specification of the Harvest Modules

Harvest parameters were initially specified consistent with current regulations and harvest levels in the Edwards Plateau in 2004. For details on the parameterization of the module, see Chapter VIII.

Verification of the Harvest Modules

The primary verification of the hen harvest module was to ensure that the various equations functioned as intended mathematically. To this end, I analytically solved the equations for 1 time step and compared my results with those of the simulation. Identical results indicated that the module was performing properly.

BROOD SUBMODELS

Background Information

Mortality rates of turkey hens vary depending on whether the hen is accompanied by a brood (Miller et al. 1995, Hennan and Lutz 2001). Therefore, mortality of individual poults or juveniles in a brood and its consequent effect on brood size and possible brood extinction is an important determinant of whether a hen is accompanied by a brood and her resulting probability of survival.

Although little is know about Rio Grande wild turkey poult survival, survival of eastern wild turkey poults has been reported widely in the literature. Throughout their

range, poult survival is typically low. In Wisconsin, Paisley et al. (1998) reported a poult survival rate to 16 days of 0.538. In Missouri, Vander Haegen et al. (1988) reported survival to 2 weeks as 0.38, while Vangilder and Kurzejeski (1995) reported a survival rate of 0.525 for the same time period. Glidden and Austin (date) reported survival rate to 2 weeks of 0.43 while working in New York. Finally, for birds in the southeastern United States, Speake (1980) stated that Alabama poult survival to 2 weeks was 0.287, whereas eastern wild turkey poults in Texas experienced survival rates to 2 weeks of 0.442 (Campo et al. 1984).

Survival of hatch-year birds increases substantially following 2 weeks, as young birds become sufficiently developed to fly into and roost in trees (Healy 1992:56). In Wisconsin, eastern wild turkey juveniles experienced survival rates of 0.880 for the period 2–4 weeks of age. Vangilder and Kurzejeski (1995) reported survival 0–4 weeks as 0.450; the same birds had survival rates for 0–2 weeks of 0.525. By factoring out 0–2 week mortality, this results in a 2–4 week survival rate of 0.857.

The probability that a series of independent binary random events, such as death of an individual, will occur declines as the number of events in the series increases (Williams et al. 2002). Hence, if the probability of survival of a poult/juvenile is at all independent of that of its brood mates (i.e., death of 1 brood member does not necessarily mean death of the entire brood), then the probability that an entire brood is lost ("brood extinction") is in part a function of brood size.

This leads to 2 conclusions. First, the total number of poults/juveniles in the population may not accurately reflect the effect of their presence on overall hen survival

if the number of broods, and thus the proportion of brooding hens in the population, is unknown. Second, because brood extinction and the resulting movement of hens from the brooding to the non-brooding populations is a function of brood size, size of individual broods or the proportion of total broods in each size class must be known to accurately model the effects of broods on hen survival. Further, although total number of juveniles in the population is necessary to estimate recruitment, this value can be derived if the number of broods and the number of individuals in each brood is known. Therefore, to adequately capture the effect of broods numbers and brood size on turkey population dynamics, I chose to model the poult/juvenile portion of the turkey population using broods as my modeling unit instead of individual birds.

Because mortality rates differ between yearling and adult hens, I modeled broods of yearling hens and broods of adult hens using separate submodels. Because survival of young birds ≤ 2 weeks old (hereafter "poults") and that of those 3–16 weeks old (hereafter "juveniles") differed substantially (Healy 1992), I also modeled these 2 groups using separate submodels. Hence, I used 4 submodels to simulate poult/juvenile population dynamics: Yearling Hen Poult Broods, Yearling Hen Juvenile Broods, Adult Hen Poult Broods, and Adult Hen Juvenile Broods.

Conceptual Formulation and Description of the Brood Submodels

Yearling Hen and Adult Hen Poult Brood Submodels. – Each Poult Brood Submodel is based on 2 state variables, P_1 and P_2 representing poults in the 1-week and 2-week age classes, respectively. Variables P_1 and P_2 are 1-dimension array variables with 20 array elements representing brood sizes of 1–20. The value of each element in

each variable thus represents the total number of broods of a given size and age belonging to yearling hens.

Entry of broods into the submodel is via the flow variable h into P_1, where

$$h = \sum_{i=1}^{20} c_b ,$$

c_b = the number of broods of size b calculated as

$$c_b = (s_{H_{1\to P}} \times \kappa_{b1}) + (s_{H_{1\to P}} \times \kappa_{b2}),$$

where κ_{b1} = the proportion of broods in each brood size class b for first nests and κ_{b2} = the proportion of broods in each brood size class b for second nests

Although Buford (1993) reported clutch size of Rio Grande wild turkey was normally distributed, little is known about the statistical distribution of wild turkey brood size at hatching. I tested brood size data collected in the southern Edwards Plateau (Dustin Jones, unpubl. data) using a Ryan-Joiner test (Minitab, Inc., State College, Pennsylvania) and found it to be normally distributed (R = 0.9793, P >0.1, N = 15). Therefore, I assumed brood size at hatching to be normally distributed and calculated κ_b using a normal probability density function (Williams et al. 2002). κ_b is a 1-dimensional array variable with 20 array elements representing the proportion of first nest broods in each of 20 size classes (b = 1…20), and is calculated according to the equation

$$\kappa_b = \frac{1}{\sqrt{2\pi\upsilon_\sigma}} \exp\left[-\frac{1}{2}\left(\frac{b-\upsilon_\mu}{\upsilon_\sigma} \right)^2 \right],$$

where υ_σ = the estimated population standard deviation of brood sizes at hatching,

and υ_μ = the mean brood size at hatching.

In turn,

$$\upsilon_\mu = \omega_\mu \tau,$$

where ω_μ = mean clutch size immediately prior to hatching, and

τ = proportion of eggs hatching in each clutch (hatching success).

Because I considered poult mortality within broods to be independent events, I modeled poult mortality within each brood as a series of independent Bernoulli trials (Williams et al. 2002) resulting in either survival or death of poult in a brood, according to equation 6.1 (modified from Ott and Longnecker 2001:146).

$$P(d) = \frac{b!}{d!(b-d)!} \varepsilon_p{}^d (1-\varepsilon_p)^{b-d} \qquad 6.5$$

where

P(d) = the proportion of all broods of size *b* that loses *d* poults.

b = brood size =the number of trials,

ε_p = poult mortality rate = probability of "success" of one trial,

and *d* = the number of mortalities = the number of "successes" in *b* trials.

Because brood extinction was a special case that incorporated both mortality of all poults in a brood ($d = b$) and hen mortality, I used equation 6.5 to calculate $P(d)$ only for cases where $d < b$.

Brood extinction ($d = b$) could result from 3 events: death of the hen and resulting death of the poults, death of all poults but survival of the hen, or death of both the hen and of all poults due to independent events. Thus, I calculated poult brood extinction

rates (λ_p) as the combined probability of death of the hen and death of all poults in a brood, where these are non-mutually-exclusive events (Zar 1999), according to the equation

$$\lambda_p = \varepsilon_{H_P} + \varepsilon_p^{\,b} - (\varepsilon_{H_P} \times \varepsilon_p^{\,b}),$$

where μ_{HP} = the mortality rate of hens accompanied by poults and μ_p= the mortality rate of poults. Thus broods were removed from P via flow variable e, representing the number of broods lost between time step t and $t + 1$, as a function of λ_p.

At the end of each time step, broods moved from P_1 to P_2. Because poult mortality altered brood size, surviving broods were reapportioned among size classes upon transfer. Therefore, flow from P_1 to P_2 was governed by the equation

$$P_{2,b,t} = \sum_{d=i}^{d+b} (P(d) \times B_{1,b+d,t-1}), b < d < 20,$$

where $B_{2,b,t}$ = the number of poults in broods of size b at age 2 weeks at time t, and $B_{1,b,t-1}$ = number of poults in broods of size b of age 1 week at time $t - 1$.

Yearling Hen and Adult Hen Juvenile Brood Submodels.– Juvenile brood submodels were extensions of the poult-brood submodels. Juvenile mortality decreases significantly after 2 weeks of age, attaining adult levels at 16 weeks of age; therefore, age 2–16 weeks was the time period simulated by the juvenile models.

After 16 weeks, surviving juveniles are split into 2 groups (male and female) based on the user-specified sex ratio (χ), and moved into the Winter Hatch Year Bird Submodel. Male and female juvenile birds are tracked as state variables (Q_M and Q_H, respectively) throughout the winter, with birds being removed from each stock by

natural mortality via the flow variables m_J, as a function of hatch-year winter mortality ($\varepsilon_{H_{Wj}}$ and $\varepsilon_{M_{Wj}}$) At the end of the wintering period, males and females enter their respective yearling populations via flow variables $s_{Q_H \rightarrow H_{My}}$ and $s_{Q_M \rightarrow My}$.

Quantitative Specification of the Brood Submodels

Yearling Hen and Adult Hen Poult Brood Submodels. – For model evaluation and sensitivity analysis, I specified ω_μ, ω_σ, τ, and ε_{Hp} using values reported in the literature (Table 6.9). When more than 1 source reported values, I specified the variable using the mean of all reported values.

Porter (1992:206) described 3 habitat elements vital to poult survival: insect production, foraging cover, and escape cover. All these elements depend on vegetation condition or structure, which in turn depends upon weather conditions. Moreover, poult survival is an important variable contributing to recruitment. Because recruitment is moisture-dependent, it might be assumed that poult survival is influenced, in part, by precipitation. Therefore, I modeled ε_p as a function of precipitation.

To approximate the minimum and maximum possible values for ε_p, I used published values from the literature (Table 6.9). Each time step, ε_p for each class was estimated using the same 3-step process I used to approximate other precipitation-dependent variables. First, a base value (ε_p') was determined as a function of precipitation (Eqs. 6.1–6.3). Next, an intermediate value (ε_p'') was generated by drawing a random value from a normal distribution having a mean equal to ε_p'. Finally, ε_p'' was adjusted according to total turkey density by multiplying it by (1 – *DDF*) to attain ε_p.

Table 6.9. Reproductive parameter values used in specifying the poult brood submodels.

Variable[a]	Value	Source
τ_1	0.90 [b]	Cook 1972, Ransom et al. 1987[c]
τ_2	0.45 [b]	Cook 1972, Ransom et al. 1987, Keegan and Crawford 1999[c]
ε_{H_P}	0.0025	Miller et al. 1995 [c]
$\omega_{\mu_{y1}}$	10.46	Reagan and Morgan 1980, Schmutz and Braun 1989, Buford 1993
$\omega_{\mu_{y2}}$	8.93	Reagan and Morgan 1980, Buford 1993
$\omega_{\mu_{a1}}$	10.31	Reagan and Morgan 1980, Schmutz and Braun 1989, Buford 1993, Hohensee and Wallace 2001
$\omega_{\mu_{a2}}$	9.20	Reagan and Morgan 1980, Buford 1993
$\omega_{\sigma_{y1}}$	2.34	Reagan and Morgan 1980, Schmutz and Braun 1989, Buford 1993
$\omega_{\sigma_{y2}}$	1.42	Reagan and Morgan 1980, Buford 1993
$\omega_{\sigma_{a1}}$	2.08	Reagan and Morgan 1980, Schmutz and Braun 1989, Buford 1993
$\omega_{\sigma_{a2}}$	2.12	Reagan and Morgan 1980, Buford 1993

[a]Subscripts are defined as follows: y = yearling, a = adult, 1 = first nest, 2 = second nest, and H_P = hen with poults.

[b] Mean of reported values.

[c]Authors reported no difference between adult and yearling rates.

I calculated the poult mortality mean (ε_{p_μ}) and standard deviation (ε_{p_σ}) and estimated the minimum and maximum values as a 99% confidence interval of ε_{p_μ} ($\varepsilon_{p_\mu} \pm 3\ \varepsilon_{p_\sigma}$), using data reported in the literature (Table 6.10). I then fitted a line to the 2 Cartesian coordinates defined by 43% and 112% of long-term mean annual precipitation (x-values)

Table 6.10. Parameter values used to specify brood submodels, from the literature.

Variable	Value[a]
ε_{P_μ}	0.2123
ε_{P_σ}	0.0636
ε_{J_μ}	0.1790
ε_{J_σ}	0.0689
ε_{Q_H}	0.0077[b]
ε_{Q_M}	0.0077[b]
ε_{H_J}	0.0025
χ	0.5

[a]Sources: Glidden and Austin 1985, Speake 1980, Little and Varland 1981, Campo et al. 1984, Metzler and Speake 1985, Speake et al. 1985, Vander Haegen et al. 1988, Williams and Austin 1988, Miller et al. 1995, Vangilder and Kurzejeski 1995, Newton 1998:244, Paisley et al. 1998, Hubbard et al. 1999, Thogmartin and Johnson 1999, Hennen and Lutz 2001, Hohensee and Wallace 2001, Lehman et al 2001.

[b]Juvenile mortality during the winter was not reported in the literature. On the assumption that juvenile mortality would be somewhat greater than yearling mortality, I estimated juvenile mortality by multiplying the reported yearling mortality by 1.5.

and estimated maximum and minimum ε_p (y-values) and calculated slope and y-intercept to determine the relationship between precipitation and ε_p. The resulting equation was

$$\varepsilon_p' = 0.640752 - 0.005529P.$$

Yearling Hen and Adult Hen Poult Brood Submodels. – As with the poult submodels, I specified certain variables (ε_{Q_M}, ε_{Q_H}, ε_{H_J}, χ) using values reported in the literature (Table 6.10). When more than 1 source reported values, I specified the variable using the mean of all reported values. I modeled juvenile (≤16 weeks of age) mortality rate (ε_J) as a function of precipitation using the same 3-step process as for ε_P (Table 6.11), with the regression equation for ε_J' being

$$\varepsilon_J' = 0.625073 - 0.005581P.$$

Verification of the Brood Submodels

The primary verification of the brood submodels was to ensure that the various equations functioned mathematically as intended. To this end, I analytically solved the equations for 1 time step and compared my results with those of the simulation. Identical results indicated that the submodels were performing properly.

MALE SUBMODEL

Background Information

Male wild turkey population parameters have received much less research attention than either female or juvenile parameters, perhaps because males are perceived as less important to overall population dynamics than either females or young. Godwin et al. (1991) reported that survival rates adult and yearling eastern wild turkeys did not differ significantly during 5 years of monitoring. Moreover, gobbler survival did not vary

among seasons, except for decreased survival during the spring hunting season due to hunter kill. This suggested that there would be no seasonal variability in survival in an unhunted population.

I located only 1 published account of Rio Grande wild turkey gobbler survival. In south Texas, wild turkey gobblers had a weekly survival rate 0.0097755 (Watts 1969).

Conceptual Formulation and Description of the Male Submodel

The Male Submodel is composed of 2 state variables representing jakes (M_y) and gobblers (M_a). Entry into the submodel is via the material transfer $s_{Q_M \rightarrow My}$, which represents the maturation of juvenile males and subsequent movement into the yearling male population at the end of the wintering period (Week 9). During the same time step, all yearling males are transferred to the adult male population via the material transfer $s_{M_{y \rightarrow a}}$.

During each time step, males are removed from the population due to natural and harvest mortality via the material transfers m_{Mj} and m_{Ma}, defined according to the equation

$$M_M = (M \times \varepsilon_M) + \left(\frac{\alpha_M}{\beta_M}\right).$$

Quantitative Specification of the Male Submodel

Godwin et al. (1991) reported that male mortality rates did not vary among seasons. Therefore, although I designed the model to accommodate time-specific male

mortality rates, I initially specified male mortality rates as 0.009775 (Watts 1969), held constant throughout the year.

Verification of the Male Submodel

The primary evaluation of the male submodel was to ensure that the various equations functioned mathematically as intended. To this end, I analytically solved the equations for 1 time step and compared my results with those of the simulation. Identical results indicated that the submodels were performing properly.

MODEL EVALUATION

Grant et al. (1997) suggested comparing model output to *a priori* expectations of model behavior as 1 means of model evaluation. Following specification of the model, I executed 100 simulation runs of 5,200 time steps (representing 100 years). Because the model was specified with empirically derived estimates of wild turkey demographic parameters (albeit from a variety of sources, locations, and subspecies), I expected the simulations would not tend toward extinction or unreasonably high population, but should generally maintain a long-term equilibrium, allowing for occasional extreme outcomes resulting from the stochastic nature of the model.

In general, the model performed as expected. Fig. 6.13 shows the outcome of 5 simulations chosen randomly from the 100 test runs to illustrate the long-term equilibrium exhibited by the model.

While few empirical estimates of demographic parameters exists for wild turkey, I did have historical poult production data for wild turkeys in the Edwards Plateau. This provided an opportunity to compare simulated model results against actual turkey

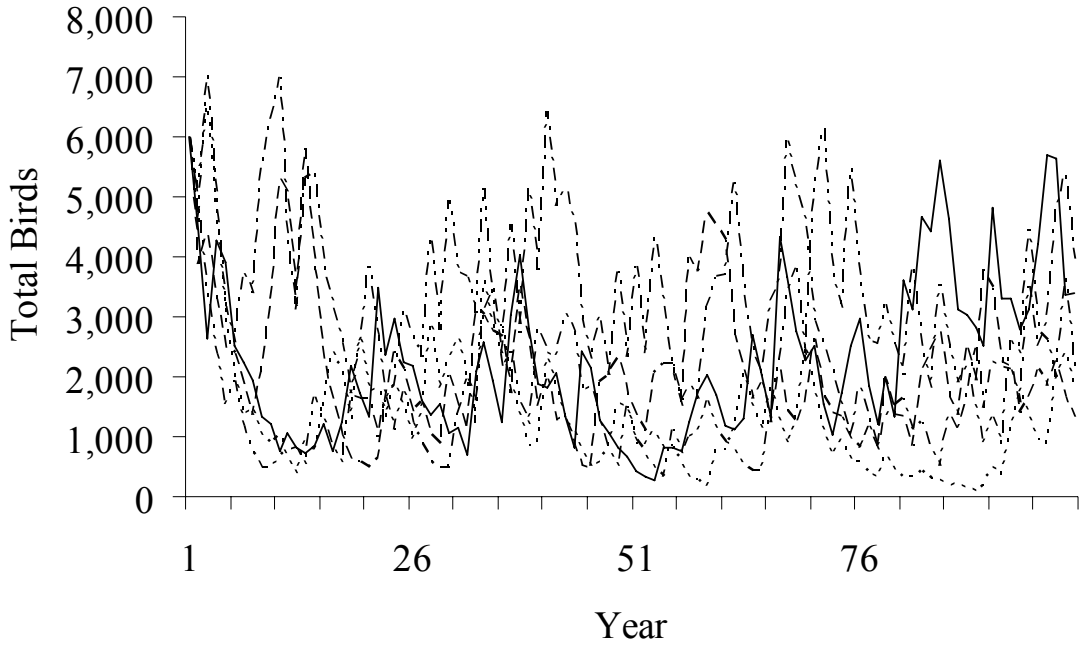

Fig. 6.13. Results of 5 simulations of 5,200 time steps of the wild turkey model as initially specified, showing the total number of birds at Week 1 for each of 100 years.

population performance, in order to assess whether the model performed realistically. I performed a simulation run of 100 years and calculated poult proportion for Week 32 (late summer, when TPWD brood counts are performed). The results of a Ryan-Joiner test (Ryan-Joiner 1976) showed that both real and simulated poults per hen were non-normal. Therefore, I compared the median real and simulated poults per hen using a Mann-Whitney test (Zar 1999). Further, I normalized both datasets using cube-root transformation and compared transformed real and mean simulated poults per hen using a 2-sample t-test, and variance using Levine's test (Ott and Longnecker 2001). All tests

were performed using Minitab for Windows 12.2 (Minitab, Inc., State College, Pennsylvania).

I detected no difference in median poults per hen ($P = 0.659$), mean transformed poults per hen ($P = 0.620$), or transformed poults per hen variance ($P = 0.659$). Based on these findings and a visual assessment of the data (Fig. 6.14), I concluded that the model was realistically simulating wild turkey poult production.

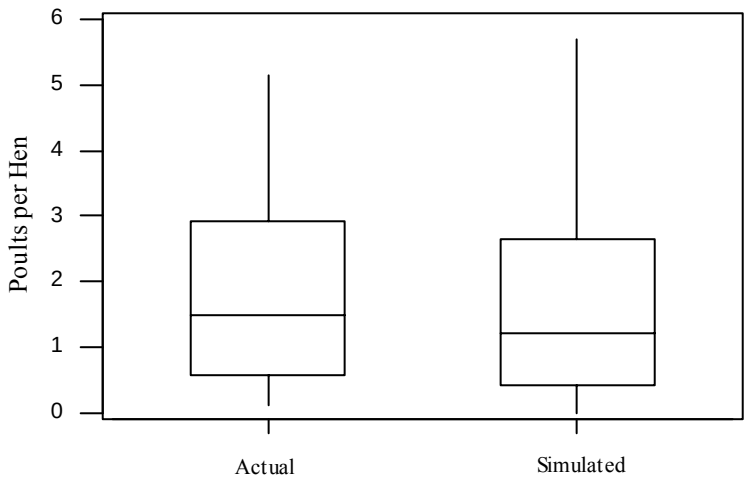

Fig. 6.14. Boxplots of actual (Edwards Plateau) and simulated poults per hen.

CHAPTER VII

SENSITIVITY ANALYSIS

Sensitivity analysis is a technique to determine the sensitivity of model output to particular parameters (Grant et al. 1997). Selected parameter values are varied 1 at a time by a specific amount and the simulation output is compared to baseline (performed using unvaried parameters) results. For stochastic models such as mine, results can be compared statistically. Sensitivity analysis allows the modeler to identify those parameters that most influence the model, to: (1) evaluate the results of the model based on the degree of confidence in estimates of important parameters (Grant et al. 1997), and (2) determine those parameters most important in the biology of the species, insofar as the model accurately simulates the biology, thus informing management decisions (Boyce 2001).

METHODS

I performed sensitivity analysis by varying the baseline value of 26 model parameters by +10% and –10% (Table 7.1). I assumed that any factor that altered or led to misestimation of a parameter would act equally on yearling and adults; therefore, I varied yearling and adult parameters in tandem.

Power analysis using variance estimates derived from the baseline model suggested that 300 runs of the model would be necessary to detect ≥10% change in median ending population. Therefore, I performed 300 simulation runs of 25 years each for each parameter. I tested for differences between the ending populations and baseline simulations using a Kruskal-Wallis test (Ott and Longnecker 2001).

Table 7.1. Results of sensitivity analysis of 26 model parameters varied ±10%, showing median ending population after 25 years (*N* = 300) and its difference from median ending population of the baseline (unvaried) model.

Parameter		Median ending population	% Difference from baseline
Theta**	+10%	3245	+10%
	–10%	2388	–19%
1st Clutch Size**	+10%	3313	+12%
	–10%	2948	–20%
Renest Clutch Size	+10%	2782	–6%
	–10%	2767	–6%
Hatchability**	+10%	3139	+6%
	–10%	2570	–13%
Hatchability (Renest)	+10%	3078	+4%
	–10%	2912	–1%
Laying Renest Rate	+10%	2977	+1%
	–10%	2813	–5%
Incubating Renest	+10%	2949	+0%
Rate	–10%	2888	–2%
Nesting Proportion	+10%	—[a]	—
	–10%	2686	–9%

Table 7.1. Continued.

Parameter		Median ending population	% Difference from baseline
Proportion Females at 16-weeks**	+10%	3287	+11%
	–10%	2520	–15%
Incubating Nest Survival	+10%	3085	+5%
	–10%	2851	+3%
Laying Nest Survival	+10%	3350	+14%
	–10%	2762	–6%
Poult Survival*	+10%	3497	+19%
	–10%	2674	–9%
Juvenile Survival**	+10%	3056	+4%
	–10%	2615	–11%
Laying Nest Survival (Renest)	+10%	3174	+8%
	–10%	2762	–6%
Incubating Nest Survival (Renest)	+10%	2880	–2%
	–10%	2883	–2%
Mating Hen Mortality	+10%	2902	–2%
	–10%	3038	+3%
Laying Hen Mortality	+10%	2788	–5%
	–10%	3045	+3%
Incubating Hen Mortality	+10%	2770	–6%
	–10%	2939	+0%

Table 7.1. Continued.

Parameter		Median ending population	% Difference from baseline
Laying Hen Mortality (Renest)	+10%	2742	–7%
	–10%	2778	–6%
Incubating Hen Mortality (Renest)	+10%	2825	–4%
	–10%	2690	–9%
Hens w/Poults Mortality	+10%	2842	–4%
	–10%	3112	+6%
Hens w/Juveniles Mortality	+10%	2745	–7%
	–10%	3004	+2%
Nonbreeding Hen Mortality*	+10%	2544	–14%
	–10%	2985	+1%
Wintering Hen Mortality	+10%	2500	–15%
	–10%	2921	–1%
Male Mortality	+10%	2642	–10%
	–10%	2802	–5%
Wintering Juvenile Mortality	+10%	2671	–9%
	–10%	2726	–8%

*Median ending population is significantly different from baseline value ($P < 0.01$)

**Median ending populations is significantly different from baseline value ($P < 0.001$)

[a] Baseline value of nesting proportion = 1.0. Therefore, it could not be altered by +10%.

RESULTS

Mean ending population values differed significantly ($P < 0.01$) from the baseline simulation for the following 7 parameters: θ, clutch size of first nests, hatchability, proportion of females at 16-weeks of age, poult survival, juvenile survival, and nonbreeding hen mortality (Table 7.1). No other parameters produced a significantly different median ending population when varied ±10%.

DISCUSSION

The model proved to be most sensitive to clutch size and poult survival. There is a great deal of published data regarding both of these variables (e.g., Reagan and Morgan 1980, Hubbard et al 1999), although most is limited to EWT. Moreover, clutch size especially is relatively easy to measure. Therefore, I feel confident that my baseline estimation of these parameters is reasonable, and that estimation for further simulations will not present a substantial problem.

This is not the case with θ. Varying θ caused the third largest change in median ending population. However, little is known about the shape of the density-dependence function in wild turkeys. My estimate of 0.9 for the baseline value was based on theory derived from other species and limited empirical data. These results underscore the importance of this poorly understood phenomenon in game birds, and suggests that substantial effort should be invested in investigating the role of density-dependence in regulating turkey populations. Again, this paucity of information suggests further study is needed.

Proportion of juvenile females at 16-weeks proved to be an important variable. Although Newton (1998) suggested that most birds produced young at a 1:1 ratio, field data in the Rolling Plains of Texas suggested that sex ratio in wild turkeys occasionally is skewed (John Brunjes, Texas Tech University, personal communication). I am unaware of any treatment of wild turkey sex ratios in the literature.

Nonbreeding hen mortality rate was an important variable. This is surprising, as mortality rate of nonbreeding females tends to be low (Miller et al. 1995, Hennan and Lutz 2001, Hohensee and Wallace 2001). However, hens spend a significant portion of their time in this stage, and lengthy exposure to mortality might enhance the overall significance of this period.

Finally, hatchability and juvenile survival played significant roles in determining the outcome of simulations. While hatchability is fairly easy to measure, juvenile survival is much harder and does not appear extensively in the literature. It is often assumed to be similar to adult survival. While this might be true, my analysis suggests that this assumption is critical and should be well-founded if it is to be relied upon.

CHAPTER VIII

EVAULATION OF FALL HEN HARVEST IN TEXAS AND SIMULATION OF ALTERNATIVE MANAGEMENT STRATEGIES

An important goal of wildlife management is preventing overexploitation of hunted populations (Robinson and Bolen 1984). Like the physician's stricture to "do no harm," this principle is embodied in such ideas as maximum sustained yield, adaptive harvest management, and "wise use" (Walter 2001).

Traditionally, harvest regulations have been set to protect populations from overharvest. In species having sexual-dimorphic adults (e.g., pheasants), harvest is often limited to males to reduce negative population effects (Strickland et al. 1994). However, harvest of females typically is allowed when it is considered to present minimal risk to the viability of the population. For example, several states allow hunting of wild turkey hens in the fall, on the assumption that removal of some females outside the breeding season is not detrimental to the population (Vangilder 1994).

In Texas prior to the early 1990's, turkey harvest was restricted to gobblers only. However, various counties were opened to either-sex hunting between 1990 and 1995 (Robert MacDonald, TPWD, personal communication), and RGWT hens are currently legal game during the fall hunting season in 84 of the 146 counties having a fall turkey hunting season (Jefferson 2004). Yet the consequences of harvesting RGWT hens in Texas have not been investigated.

My objective was 3-fold. First, using TPWD harvest data as an index of turkey abundance, I compared counties having an either-sex fall hunting season with counties

having gobbler-only fall hunting to determine if either-sex hunting had caused a decline in turkey abundance. I hypothesized that, if hen-harvest negatively affected turkey populations, then harvest-per-unit-effort trends should have declined significantly more in either-sex counties than in gobbler-only counties. Second, I examined existing data to estimate the current level of RGWT harvest in the Texas Hill Country (see Chapter IV for description of the region). I focused on this region because: (1) it is the region of Texas with this largest turkey population and highest turkey harvest, (2) TPWD currently allows either-sex fall turkey harvest in much of the region, and (3) data were available from field studies to parameterize the simulation model used in part of this analysis. Finally, I simulated various levels of turkey harvest, including the estimated current harvest rate, to evaluate population-level consequences of different management strategies.

METHODS

Comparison of Abundance Trends Between Zones

Although no annual abundance data exist for wild turkey in Texas, the harvest survey does provide an index of turkey abundance in the form of harvest per unit effort. Although recognized as imperfect (Healy and Powell 1999), harvest per unit effort is considered a reliable indicator of turkey abundance (Lint et al. 1995). I hypothesized negative population effects of either-sex harvest would be manifested as a difference in slope of the abundance trend between the 2 zones. Therefore, I performed simple linear regression for each zone, using year as the independent variable and harvest per hunter day as the dependent variable, then compared the slopes of the regression lines using the

"Comparison of Regression Line" function in Statistix 7 (Analytical Software, Tallahassee, Florida, USA).

Estimate of Hill Country Turkey Abundance

There is no TPWD survey in place to estimate RGWT density in Texas. However, I used 2 sources of RGWT abundance to estimate the Hill Country turkey population. Since 1979, the National Wild Turkey Federation (NWTF) has published an estimate of wild turkey abundance in Texas (National Wild Turkey Federation 2002). This estimate is based on input provided by TPWD Turkey Program Staff. Along with this estimate is published a map of the wild turkey's range in Texas, with areas categorized into 4 ranges of density estimates (0–1.9 birds/km^2, etc.). This map (Fig. 8.1) was updated in 2004 using density estimates provided by TPWD field personnel. To calculate statewide turkey populations based on this data, I multiplied the median density value in each category by the total land area occupied by the category. To estimate Hill Country populations, I assumed that densities indicated by the various categories were reflective of actual relative abundance across the state. Therefore, I multiplied the proportion of occupied turkey range in the Hill Country, weighted according to relative density, by the total wild turkey abundance estimates derived by the 2 methods.

Harvest Rate Estimation

Harvest estimates were based on data collected by TPWD since 1986 using a mail-out harvest questionnaire (Purvis 2004). Date were aggregated into 2 groups ("zones") based on whether the RGWT fall hunting season in the county of origin allowed gobbler-only or either-sex harvest (Fig. 8.2). Hen versus gobbler harvest was not

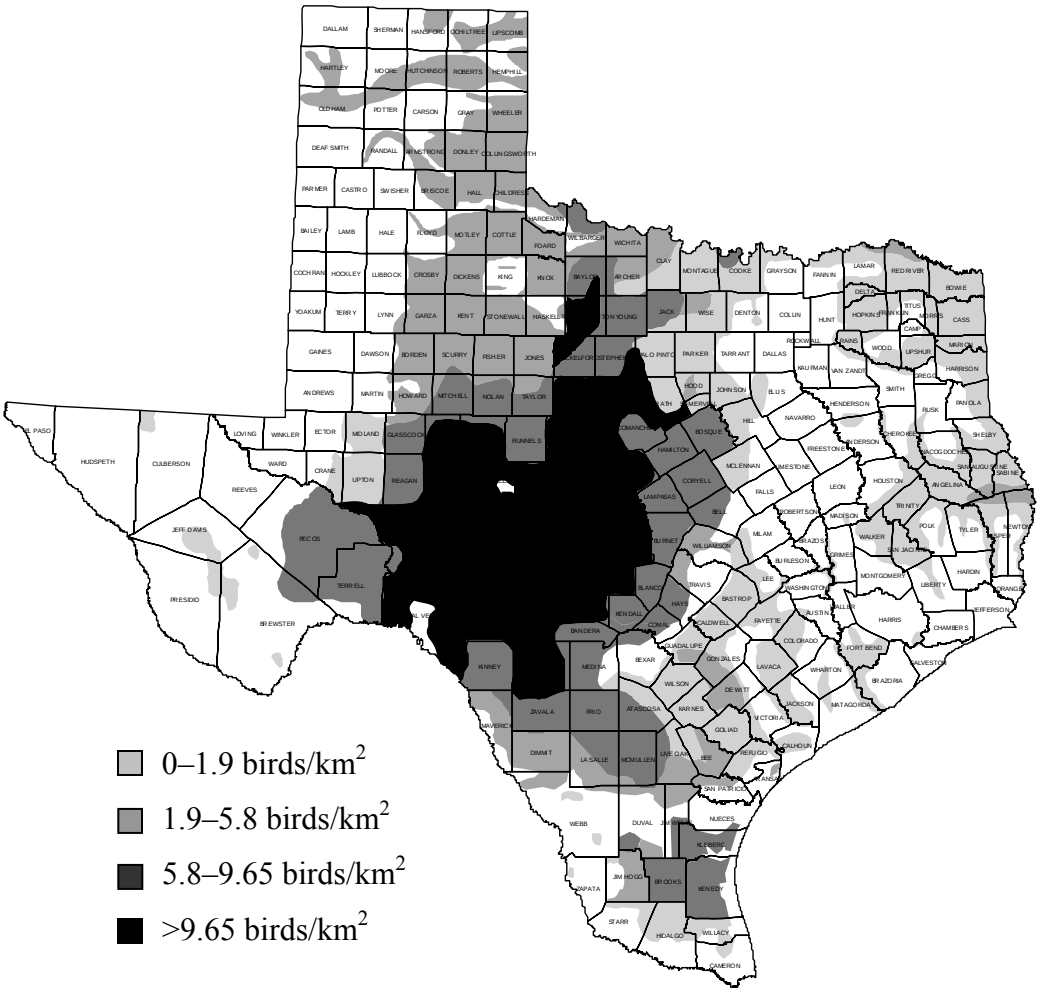

Fig. 8.1. Map of Texas indicating wild turkey range and estimated density, based on expert opinion of TPWD field staff, 2004.

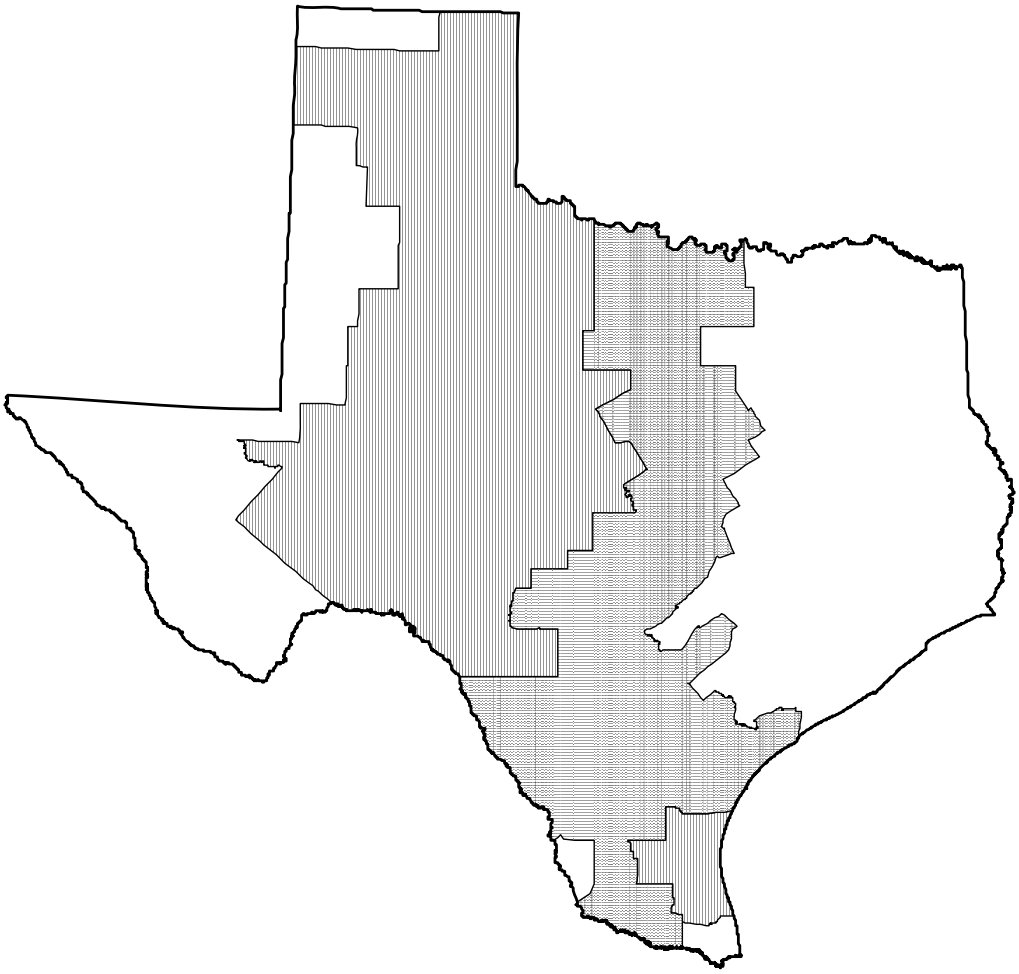

Fig. 8.2. Map of Texas showing Rio Grande wild turkey harvest zones. Vertical lines indicate either-sex fall harvest. Horizontal lines indicate gobbler-only fall harvest.

estimated explicitly in the survey. In order to estimate the hen harvest in counties with either-sex regulations, I assumed that the ratio of spring to fall gobbler harvest was the same in both zones (Eq. 8.1).

$$\frac{G_{S_{go}}}{G_{F_{go}}} = \frac{G_{S_{es}}}{G_{F_{es}}} \quad , \qquad 8.1$$

where $G_{S_{go}}$ = mean spring gobbler harvest in the gobbler-only zone, 1986–2003, $G_{F_{go}}$ = mean fall gobbler harvest in the gobbler-only zone, 1986-2003, G_{Ses} = mean spring gobbler harvest in the either-sex zone, 1986–2003, and $G_{F_{es}}$ = mean fall gobbler harvest in the either sex zone, 1986–2003. Because $G_{S_{go}}$, $G_{F_{go}}$, and G_{Ses}, where known from the survey, I solved for $G_{F_{es}}$, and derived the proportion of the fall harvest composed of gobblers ($PG_{F_{es}}$) as

$$PG_{F_{es}} = \frac{G_{F_{es}}}{T_{F_{es}}}$$

and, thus, the proportion of the fall harvest composed of hens ($PH_{F_{es}}$) as

$$PH_{F_{es}} = 1 - PG_{F_{es}}.$$

I then multiplied the estimated total fall harvest in the Hill Country, derived from the harvest survey, by $PH_{F_{es}}$ to determine the hen harvest rate of the region as a proportion of the total population. Because I assumed hens and gobblers occurred in the population at a 1:1 ratio, I multiplied this value by 2 to derive the harvest rate as a proportion of the hen population.

Simulation of Harvest Strategies

I simulated the population effects of different hen harvest strategies by reparameterizing several variables in the simulation model using values derived from the Edwards Plateau field study (Table 8.1). Because of inconsistencies in data collection, field data collected in years 2 and 3 of the study were of insufficiently fine temporal scale to be used in the model. Therefore, only data collected during year 1 were used in the simulation. Also, I set adult and yearling hen values equal, because small sample sizes of yearling hens precluded precise estimates of yearling reproductive variables. Except for the harvest variables, values of all parameters were retained at baseline values. I arbitrarily set the initial population level at 6,000 individuals. I simulated 7 levels of harvest: no harvest; gobbler harvest only; either-sex at the current estimated hen harvest rate; and either-sex with hen harvest of 5%, 10%, 15%, and 20% of the fall hen population. For all strategies except no harvest, gobbler harvest was set equal to 0.058 (spring and fall season), the estimated actual rate. Hen harvest rates for current, 5%, 10%, 15%, and 20% hen harvest strategies were set equal to 0.034, 0.05, 0.10, 0.15, and 0.20, respectively. Season beginning and ending weeks were set to approximate 2004 season dates in the Hill Country: spring season begin Week 14 (2 Apr), spring season end Week 19 (7 May), fall season begin Week 45 (5 Nov), and fall season end Week 52 (24 Dec). For each strategy, I performed 300 simulations of 25-year duration and recorded the final mid-winter (1 Jan) population value after 25 years as well as the number of simulation runs that resulted in population extinction (final value = 0), which I converted to extinction probability by dividing the number of extinctions by the

Table 8.1. Values assigned to adult and yearling hen reproductive and mortality parameters for all harvest simulations.

Adult hens		Yearling hens	
Variable[a]	Value	Variable	Value
$\omega_{\mu_{a1}}$	8.96	$\omega_{\mu_{y1}}$	8.96
$\omega_{\sigma_{a1}}$	3.14	$\omega_{\sigma_{y1}}$	3.14
$\omega_{\mu_{a2}}$	8.67	$\omega_{\mu_{y2}}$	8.67
$\omega_{\sigma_{a2}}$	3.31	$\omega_{\sigma_{y2}}$	3.31
τ_{a1}	0.90	τ_{y1}	0.90
τ_{a2}	0.84	τ_{y2}	0.84
$\rho_{H_{La}}$	0.53	$\rho_{H_{Ly}}$	0.53
$\rho_{H_{Ia}}$	0.53	$\rho_{H_{Iy}}$	0.53
ν_a	0.66	ν_y	0.66
$\varepsilon_{H_{Ma}}$	0.03632	$\varepsilon_{H_{My}}$	0.03632
$\varepsilon_{H_{La}}$	0.05267	$\varepsilon_{H_{Ly}}$	0.05267
$\varepsilon_{H_{Ia}}$	0.01710	$\varepsilon_{H_{Iy}}$	0.01710
$\varepsilon_{H_{RLa}}$	0.052671[b]	$\varepsilon_{H_{RLy}}$	0.052671[b]
$\varepsilon_{H_{RIa}}$	0.01710[b]	$\varepsilon_{H_{RIy}}$	0.01710[b]
$\varepsilon_{H_{Pa}}$	0.05132	$\varepsilon_{H_{Py}}$	0.05132
$\varepsilon_{H_{Ja}}$	0.00001[c]	$\varepsilon_{H_{Jy}}$	0.00001[c]
$\varepsilon_{H_{NBa}}$	0.00838	$\varepsilon_{H_{NBy}}$	0.00838
$\varepsilon_{H_{Wa}}$	0.00757	$\varepsilon_{H_{Wy}}$	0.00757

[a]For definition of variable, see Chapter VI and Appendix.

[b]Insufficent sample size precluded estimating mortality rates of renesting hens. Therefore, first nest values were used.

[c]Actual data indicated $\varepsilon_{H_J} = 0$. However, to avoid division by 0 errors, calculations were performed using a value of 0.00001.

number of simulation runs. Because final population values were not normally distributed, I compared the median final values among the 7 harvest strategies using a Kruskal-Wallis test (Ott and Longnecker 2001) and a comparison of mean ranks procedure with an experiment-wise error rate of $P = 0.05$ (Daniel 1990, Analytical Software 2000) using Statistix 7 (Analytical Software, Tallahassee, Florida, USA). I compared the extinction probability for each harvest strategy to that of the no harvest strategy using the test for differences between 2-proportions function in Minitab for Windows 12.2 (Minitab, Inc., State College, Pennsylvania).

RESULTS

Comparison of Abundance Trends Between Zones

Analysis of population trends in the 2 zones revealed a population index that was significantly higher in the either-sex zone than in the gobbler-only zone ($P < 0.0001$; Fig. 8.3). However, there was no significant difference in the slopes of the trend lines ($P = 0.7764$).

Estimate of Hill Country Turkey Abundance

The published estimated wild turkey population for Texas was approximately 600,000 birds (National Wild Turkey Federation 2002). The estimate based on field staff estimates of range and density was 2,050,870. Because of the wide variation between the 2 estimates, I chose to use the National Wild Turkey Federation's more conservative estimate for all analyses.

Of the 386,952 km^2 of occupied turkey range in Texas, approximately 149,486 km^2 (37%) occurred in the Hill Country. However, much of this range supported higher

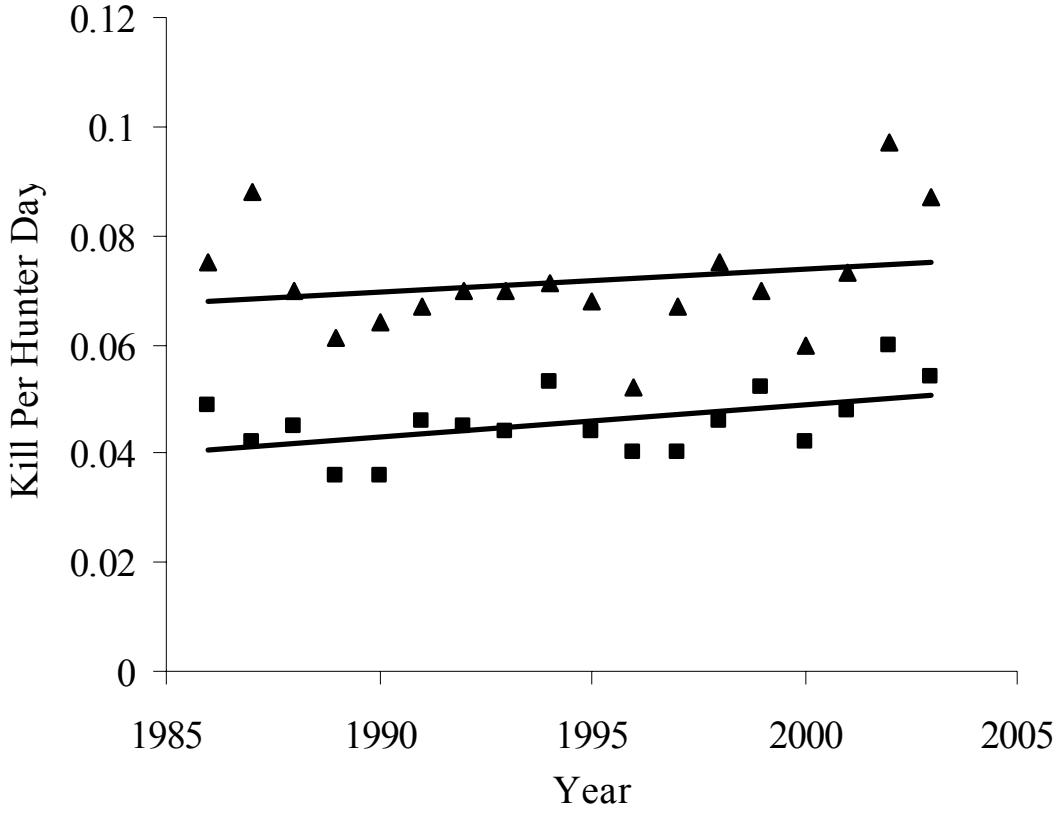

Fig. 8.3. Wild turkey abundance, as indexed by combined spring and fall harvest per hunter day trends for 2 turkey harvest zones in Texas, 1986–2003. Squares (■) indicate data from gobbler-only zones, triangles (▲) indicate data from either-sex zone.

turkey densities than the rest of the state. Thus, when weighted for relative densities based on the opinion of field staff, the Hill Country accounted for approximately 56% of the actual turkey population of Texas. Based on the NWTF's report of 600,000 birds statewide, this resulted in an estimated Hill Country population of about 336,000 birds.

Harvest Rate Estimation

Mean spring and fall gobbler harvest in the gobbler-only zone during 1986–2003 was 11,086 and13,997, respectively. Spring gobbler harvest in the either-sex zone during the same period averaged 12,340. Using these values, I estimated fall gobbler harvest in the either-sex zone to be approximately 15,580, representing 64% of the total fall harvest of 24,288 in the either-sex zone. Thus hen harvest equaled approximately 36% of fall either-sex harvest. When applied to the total fall harvest of 15,950 birds in the Hill Country, the resulting hen harvest equaled 5,742, or 1.7% of the total estimated population of the region. Assuming a 1:1 sex ratio in the region, this represented a fall hen harvest rate of 3.4% of the hen population.

Simulation of Harvest Strategies

Median total population after 25 years for gobbler-only harvest and either-sex at the current level of hen harvest were not significantly different from that of a non-harvested population. All other harvest strategies resulted in significant declines in median population, with median population 35%–86% less than the unhunted population (Table 8.2). Only harvest strategies involving hen harvests ≥15% of fall hen population resulted in extinction probability significantly greater than that of the unhunted population (Table 8.2).

Table 8.2. Median mid-winter (1 Jan) population after 25 years and extinction probability for 300 runs each of 7 simulated harvest strategies. Extinction P-value represents the results of 2-proportion test to determine whether the extinction probability differed from that under the no harvest strategy.

Harvest Strategy	Median Ending Population	Difference From No Harvest	Extinction Probability	Extinction P-value
None	1199A[a]	—	0.007	—
Gobbler Only	1440A	+20%	0.007	1.000
Either Sex – Actual Rate	1078A	–10%	0.007	1.000
Either Sex – 5% Hen Harvest	785B	–35%	0.003	0.315
Either Sex – 10% Hen Harvest	410C	–66%	0.023	0.201
Either Sex – 15% Hen Harvest	331C	–72%	0.073	<0.0001
Either Sex – 20% Hen Harvest	168D	–86%	0.170	<0.0001

[a]Median values with the same letter are not significantly (experiment-wise $P > 0.05$) different.

DISCUSSION

Comparison of abundance index trends between gobbler-only and either-sex fall hunting zones showed no difference in the slope of the abundance trend lines, suggesting the current level of hen harvest did not negatively affect turkey abundance. Other authors also have suggested that hen harvest rates of <5% do not negatively affect abundance. Vangilder and Kurzejeski (1995) developed a simulation model of eastern wild turkey population dynamics in Missouri that showed an average increase of 140% in the mean population after 25 years when fall hen harvest =5%. However, mean population after 25 years declined for fall hen harvest values ≥10%. Suchy et al. (1983) simulated fall either-sex harvest of eastern wild turkey in Iowa and determined that fall hen harvest rates of 5–10% were sustainable, and that actual population response depended in part on the degree to which harvest mortality was additive.

Fall hen harvest in the Hill Country accounts for approximately 3.4% of the total hen population. This result is consistent with the <5% hen harvest rate reported for private lands in Missouri with hunter densities of 3.8 to 5.0 hunters/km^2 by Kurzejeski and Vangilder (1994). The Hill Country also is predominately private land, with comparatively low hunter densities (0.3 hunters/km^2; T. W. Schwertner, unpublished data).

The results of the simulation suggested also that current levels of harvest did not negatively affect the wild turkey population. However, my model did respond more strongly to fall hen harvest than did those of Kurzejeski and Vangilder (1995) and Suchy et al (1983), with significant declines in the total population occurring with fall hen

harvest rates of ≥5%. Moreover, fall hen harvest rates ≥15% resulted in notable risk of extinction. One reason might have been that my model was parameterized using nesting rates that seemed somewhat low (Table 8.1). Although the model has been shown to be relatively insensitive to variation in nesting rates (Chapter VII), and I cannot rule out the possibility that this value represents the actual nesting rate of hens at the field site, it has been suggested that such low rates might have resulted from investigators having difficulty gaining access to birds on private land and thus not observing nesting attempts (N. J. Silvy, Texas A&M University, personal communication).

I acknowledge some serious shortcomings in my analyses, foremost being a lack of empirical data regarding turkey abundance and harvest, and reliance on multiple assumptions. Although I attempted to formulate logical assumptions regarding turkey harvest, the fact remains that the actual abundance of RGWT in Texas is far from certain and harvest rates are hardly more so. Moreover, the dynamic interplay among variables that eventually results in actual harvest is unclear. For instance, I assumed the harvest rate of gobblers during the fall would be the same in both gobbler-only and either-sex, but this admittedly seems highly unlikely. Nevertheless, although many of the assumptions made herein are little more than educated guesses, the fact that the estimated harvest rates and simulation results align reasonably well with each other and the results of other investigators is encouraging.

Another problem with the analysis was the fact that assignment of counties to harvest zones was not random and resulted in the zones being stratified, with the either-sex zone lying generally north and west of the gobbler-only zone. Thus, the possibility arises that

zone specific effects (e.g., climate) might affect abundance and mask effects of harvest. Therefore, inferences might not apply outside the zones in question.

Finally, the model was parameterized with only 1 year's data. These limited data may not adequately represent RGWT demography in the Hill Country. I am working closely with project investigators to ensure that data collected during the final 2 years of the study will be suitable for incorporation into the model, and this should produce more robust results.

Under the current harvest management scheme, fall hen harvest does not appear to pose a threat to RGWT abundance. However, simulation results suggest that rates slightly higher than those currently observed would likely cause the population to decline significantly. Moreover, RGWT abundance and harvest estimates are based on data that might be inadequate to confidently predict the consequences of harvest. I strongly encourage TPWD to step up efforts to measure RGWT density, harvest, and other demographic parameters. State wildlife officials also should consider using the simulation model, parameterized with relevant data, to test the sustainability of fall hen harvest in other regions with current or proposed either-sex seasons.

CHAPTER IX

SUMMARY AND CONCLUSION

Given the significance of Rio Grande wild turkey (RGWT) as a game bird in Texas, surprisingly little research has been done on the subspecies in the state. In fact, my work, along with concurrent studies in the Rolling Plains (by Texas Tech University) and south Texas (by Texas A&M University-Kingsville), is the first major study of RGWT in Texas since the work of Sam Beasom (1973) and Bruce Baker (1979) in the early 1970's. Hence, the research described herein was not only long-overdue, but revealed significant new perspectives on RGWT biology and management, especially in central Texas.

Brood counts as currently conducted by Texas Parks and Wildlife Department (TPWD) appear to have little power to detect biologically-significant inter-annual variation or long-term trends in RGWT production. This suggests TPWD should reevaluate the manner in which it assesses RGWT demographics. That being said, the strong relationship between brood-count data and precipitation, an independent variable, suggests the brood count, despite inherent design flaws and low statistical power, does indeed provide a meaningful index to RGWT production. However, an estimate of turkey abundance, rather than recruitment, would be more relevant to making decisions regarding harvest management. Thus, replacing the current brood-count methodology with some method of abundance estimation, instead of just revamping the brood count, should be seriously considered.

Precipitation long has been considered important in wild turkey dynamics. However, conventional wisdom among many turkey biologists has been that spring precipitation affected turkey populations negatively, suppressing production by facilitating predation and increasing poult mortality due to hypothermia. While logical in the cool and/or wet environs of eastern North America, there was little data to support this assumption in the arid regions inhabited by RGWT in Texas. On the contrary, early work by Beasom (1973) suggested a positive relationship between turkey production and precipitation, and work on other galliformes in Texas such as quail (Bridges et al. 2001) revealed a similar relationship. This is unsurprising, as it is generally accepted that, at least in arid environments, precipitation is critical to producing cover and food required for game bird production. My research bears this out. I found a significant positive relationship between precipitation and RGWT production, up to approximately 60 cm, where the relationship leveled out.

Interestingly, production appeared to decline slightly at precipitation >72 cm (Fig. 6.10), although limited data prevented drawing any conclusions about the relationship. While it is certainly dangerous and unwise to extrapolate the relationship beyond the data, the possibility exists that high levels of precipitation might reduce turkey productivity. If this is the case, then in areas where annual precipitation event routinely exceeds 90 cm (the highest annual precipitation recorded in my study) high precipitation levels might negatively affect turkey production. This would reconcile the alternative views of the production-precipitation relationship, and is an area of study that is ripe for

further investigation, perhaps using a meta-analysis of existing studies across the range of the wild turkey.

Another school of thought holds that predation significantly limits turkey populations. However, my analysis revealed no relationship between turkey production and predator abundance. Of course, "absence of evidence is not evidence of absence" — a relationship might well exist despite my inability to identify it with the available data. Also, my study sought a relationship at broad spatial scales. Because I found predator dynamics fluctuate asymmetrically at different spatial scales, broad-scale phenomena might be masked. Predators might significantly effect turkey populations at the local level; my research does not speak to that. However, I urge caution to managers who would suggest that predation significantly limits turkey populations or is the cause of broad-scale decline, such as in the southern Edwards Plateau.

I developed a detailed, mechanistic wild turkey population model. Unlike similar models, mine explicitly considered density-dependence and the relationship between population density and how strongly density-dependence acts. I originally implemented density-dependence simply as a measure to reduce biologically unreasonable model behavior. Refinement of the density-dependence module to include θ was a novel approach that, to my knowledge, had not previously been applied to wild turkey population studies. The effect on model behavior was unexpected and significant. I found that density dependence and the shape of the density-dependence relationship was an important determinant of model behavior. Because density dependence has heretofore not been widely considered in wild turkey management, this necessitates a

shift in the way we think about turkey population dynamics. I suggest that we explicitly consider density dependence as an important component of wild turkey population behavior. Density dependence might be especially important in areas where wild turkey populations are spatially restricted by dispersal barriers, thus coupling density dependence with metapopulation dynamics. For example, many TPWD biologists have stated that eastern wild turkey populations in east Texas appear to be declining, as recently-restored populations disappear from local areas, despite apparently favorable habitat conditions (Nathan Garner, TPWD, personal communication). Because much of east Texas is highly fragmented, I suggest that many of these populations might have been established in habitat fragments that were favorable, but of insufficient size to support long-term viable populations. Moreover, dispersal barriers might prevent recolonization of patches once subpopulations have gone extinct – a classic metapopulation scenario (Hanski and Gilpin 1997). In cases such as this, an understanding of population dynamics at high densities is critical.

Another example is that of the southern Edwards Plateau. Research on some declining sites suggests that turkey ranges are smaller than on stable sites, while availability of arthropods per unit area also is less than on stable sites (Schaap 2005). Although the difference in arthropod availability is slight, when coupled with the restricted ranges, total arthropods available to individual birds are substantially less on declining than on stable sites. While not direct evidence of density dependence due to food limitation, it is indicative of a population that is crowded into a small space with

limited food resources, suggests density dependence as a possible mechanism for the population decline, and warrants further study.

Sensitivity analysis of the population model revealed 2 other parameters that significantly influence model behavior but are poorly understood: brood sex ratio and juvenile survival. Brood sex ratio is widely assumed to be 1:1. However, I could find no research that addresses sex ratio in turkeys. Anecdotal evidence suggests that sex ratio in RGWT may vary considerably from 1:1. Ideally, future research will reveal a realistic picture of sex ratio in juvenile turkeys, the mechanisms that drive sex ratio, and possible management actions. At the least, it will place sex ratio in the category of weather: a factor that is not susceptible to management action but which should be understood in order to anticipate population consequences of management actions.

Survival of juvenile turkeys >2 weeks of age also emerged as an important but poorly-understood parameter. This is understandable, given the difficulty associated with studying the ecology of this age class. Small initial body size and fast growth make study using radio telemetry difficult, as radio attachment and retention is problematic. Some ecologists would argue that a detailed understanding of poult mortality is unimportant, as long as we understand the juvenile mortality rate over the entire period. However, this discounts the possibility of juveniles having habitat requirements that vary during the time period between 2 weeks of age and recruitment. This would prevent managers from applying management practices that address critical stages of juvenile life cycle. Fortunately, major research has been proposed that would address poult

ecology and brood sex ratio, shedding much-needed light on this important subject. I strongly encourage its support and continuation.

Finally, I used my model to assess the possible outcome of different fall-hen-harvest strategies. Current hen harvest appears not to be limiting turkey populations where fall-hen harvest is legal. Based on available evidence, extending fall harvest into additional Texas counties in the Cross Timbers and eastern Edwards Plateau should not result in negative population-level consequences, given a critical assumption: population parameters and hen-harvest rate in the newly-opened areas are similar to those used to parameterize the model. Unfortunately, neither of these assumptions has been validated, as the data necessary to do so do not exist. The region's proximity to urban areas would suggest, at least, the harvest rate may be higher than in more remote areas.

The opening to hunting of these additional areas appears to have been politically-motivated out of a desire to increase "hunter opportunity." There was no *a priori* biological justification to do so (T. W. Schwertner, TPWD, unpublished data). Lack of contravening data was viewed by decision-makers as sufficient justification for the change. While the ethics of this type of decision making are debatable, it is not necessarily bad from a population standpoint. Assessment of the turkey population following implementation of the regulation should reveal the consequences of the move. Should these consequences prove negative, however, it would suggest that populations in these regions cannot sustain fall-hen harvest, and TPWD must be willing to take the politically unpalatable step of rescinding the regulation and once again prohibiting fall-hen harvest.

LITERATURE CITED

Analytical Software. 2000. Statistix 7 user's manual. Analytical Software, Tallahassee, Florida, USA.

Anderson, D. R. 2001. The need to get the basics right in wildlife field studies. Wildlife Society Bulletin 29:1294–1297

Badyaev, A. 1995. Nesting habitat and nesting success of eastern wild turkeys in the Arkansas Ozark Highlands. Condor 97:221–232.

Baines, D. 1991. Factors contributing to local and regional variation in black grouse breeding success in northern Britain. Ornis Scandinavica 22:264–269.

Baker, B. W. 1979. Habitat use, productivity, and nest predation of Rio Grande turkeys. Dissertation, Texas A&M University, College Station, Texas, USA.

Bartush, W. S., M. S. Sasser, and D. L. Francis. 1985. A standardized turkey brood survey method for northwest Florida. Proceedings of the National Wild Turkey Symposium 5:173–181.

Beasom, S. L. 1973. Ecological factors affecting wild turkey reproductive success in south Texas. Dissertation, Texas A&M University, College Station, Texas, USA.

_____. 1974. Intensive short-term predator removal as a game management tool. Proceedings of the North American Wildlife Conference 39:230–240.

_____, and O. H. Pattee. 1980. The effect of selected climatic variables on wild turkey productivity. Proceedings of the National Wild Turkey Symposium 4:127–135.

_____, and D. Wilson. 1992. Rio Grande turkey. Pages 306–330 in J. D. Dickson, editor. The wild turkey: biology and management. Stackpole Books, Mechanicsburg, Pennsylvania, USA.

Begon, M., J. L. Harper, and C. R. Townsend. 1996. Ecology: individuals, populations, and communities. Third edition. Blackwell Science, Oxford, England, United Kingdom.

Belovsky, G. E., and J. B. Slade. 1995. Dynamics of two Montana grasshopper populations: relationships among weather, food abundance, and intraspecific competition. Oecologia 101:383–396.

Berger, M. E., and R. R. George. 2003. Operation plan: fiscal year 2004, Wildlife Division. PWD PL W7000-170 (8/03) Texas Parks and Wildlife Department, Austin, Texas, USA.

Blankenship, L. H. 1992. Physiology. Pages 84–100 *in* J. D. Dickson, editor. The wild turkey: biology and management. Stackpole Books, Mechanicsburg, Pennsylvania, USA.

Boyce, M. S. 2001. Population viability analysis: development, interpretation, and application. Pages 123–136 *in* T. M. Shenk and A. B. Franklin, editors. Modeling in natural resource management: development, interpretation, and application. Island Press, Washington, D.C., USA.

Bridges, A. S., M. J. Peterson, N. J. Silvy, F. E. Smeins, and X. B. Wu. 2001. Differential influence of weather on regional quail abundance in Texas. Journal of Wildlife Management 65:10–18.

Buford, D. J. 1993. Reproductive ecology of Rio Grande wild turkeys in south central Kansas. Thesis, Texas Tech University, Lubbock, Texas, USA.

Cable, D. R. 1975. Influence of precipitation on perennial grass production in the semidesert southwest. Ecology 56:981–986.

Campbell, H., D. K. Martin, P. E. Ferkovich, and B. K. Harris. 1973. Effects of hunting and some other environmental factors on scaled quail in New Mexico. Wildlife Monographs 34:1–49.

Campo, J. J. 1983. Brood habitat use, reproduction, and movement of recently restocked eastern wild turkeys in east Texas. Dissertation, Texas A&M University, College Station, Texas, USA.

_____, C. R. Hopkins, and W. G. Swank. 1984. Mortality and reproduction of stocked eastern turkeys in east Texas. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 38:78–86.

Carr, J. T. 1967. The climate and physiography of Texas. Texas Water Resources Board Report 53. Austin, Texas, USA.

Chamberlain, M. J., L. M. Conner, and B. D. Leopold. 2002. Seasonal habitat selection by raccoons (*Procyon lotor*) in intensively managed pine forests of central Mississippi. American Midland Naturalist 147:102–108.

_____, K. M. Hodges, B. D. Leopold, and T. S. Wilson. 1999. Survival and cause-specific mortality of adult raccoons in central Mississippi. Journal of Wildlife Management 63:880–888.

Chesness, R. A., M. M. Nelson, and W. H. Longley. 1968. The effect of predator removal on pheasant reproductive success. Journal of Wildlife Management 32:683–697.

Christiansen, J. L., and B. J. Gallaway. 1984. Raccoon removal, nesting success, and hatchling emergence in Iowa turtles with special reference to *Kinosternon flavescens* (Kinosternidae). Southwestern Naturalist 29:343–348.

Cobb, D. T., and P. D. Doerr. 1997. Eastern wild turkey reproduction in an area subjected to flooding. Journal of Wildlife Management 61:313–317.

Conover, M. R. 1994. Perceptions of grass-roots leaders of the agricultural community about wildlife damage on their farms and ranches. Wildlife Society Bulletin 22:94–100.

_____. 2001. Effect of hunting and trapping on wildlife damage. Wildlife Society Bulletin 29:521–532.

Cook, R. L. 1972. A study of nesting turkeys in the Edwards Plateau of Texas. Proceedings of the Annual Conference of the Southeastern Association of Game and Fish Commissioners 26:236–244.

Crouch, W. B., III, and P. W. C. Paton. 2002. Assessing the use of call surveys to monitor breeding Anurans in Rhode Island. Journal of Herpetology 36:185–192.

Daniel, W. W. 1990. Applied nonparametric statistics. Houghton-Mifflin, Boston, Massachusetts, USA.

Davis, B. D. 1994. Breeding chronology in Rio Grande turkey hens. Final Report, Federal Aid Project W-126-R-2, Texas Parks and Wildlife Department, Austin, Texas, USA.

Davis, J. R., H. R. Barnhill, D. C. Guynn, Jr., R. E. Larkin, and W. M. Baughman. 1995. Wild turkey nesting ecology in the lower coastal plain of South Carolina. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 49:454–465.

Davis, J. W., L. H. Karstad, and D. O. Trainer. 1981. Infectious diseases of wild mammals. Second edition. Iowa State University Press, Ames, Iowa, USA.

Davis, W. B., and D. J. Schmidly. 1994. The mammals of Texas. Texas Parks and Wildlife Press, Austin, Texas, USA.

DeArment, R. 1969. Turkey hen:poult ratios as an index to reproductive trends. Proceedings of the National Wild Turkey Symposium 1:27–31.

Dijak, W. D., and F. R. Thompson. 2000. Landscape and edge effects on the distribution of mammalian predators in Missouri. Journal of Wildlife Management 64:209–216.

Drickamer, L. C., S. H. Vessey, and E. M. Jakob. 2002. Animal behavior: mechanisms, ecology, evolution. Fifth edition. McGraw-Hill, New York, New York, USA.

Eaton, S. W. 1992. Wild turkey. *In* A. Poole, P. Stettenheim, and F. Gill, editors. The birds of North America 22:1–28. Academy of Natural Sciences and American Ornithologists Union, Philadelphia, Pennsylvania and Washington, D. C., USA.

Estes, J. A. 1996. Predators and ecosystem management. Wildlife Society Bulletin 24:390–396.

Fowler, C. W. 1981. Density dependence as related to life history strategy. Ecology 62:603–610.

Frampton, G. K., P. J. Van Den Brink, and P. J. L. Gould. 2000. Effects of spring drought and irrigation on farmland arthropods in Britain. Journal of Applied Ecology 37:865–883.

Gehring, T. M., and R. K. Swihart. 2003. Body size, niche breadth, and ecologically scaled responses to habitat fragmentation: mammalian predators in an agricultural landscape. Biological Conservation 109:283–295.

Gehrt, S. D., and E. K. Fretzell. 1998. Resource distribution, female home range dispersion and male spatial interactions: group structure in a solitary carnivore. Animal Behaviour 55:1211–1227.

_____, and E. K. Fritzell. 1999. Survivorship of a nonharvested raccoon population in south Texas. Journal of Wildlife Management 63:889–894.

_____, G. F. Hubert, Jr., and J. A. Ellis. 2002. Long-term population trends of raccoons in Illinois. Wildlife Society Bulletin 30:457–463.

Gerard, P. D., D. R. Smith, and G. Weerakkody. 1998. Limits of retrospective power analysis. Journal of Wildlife Management 62:801–807.

Gibbs, J. P., and S. M. Melvin. 1997. Power to detect trends in waterbird abundance with call-response surveys. Journal of Wildlife Management 61:1262–1267.

Gilpin, M. E., and F. J. Ayala. 1973. Global models of growth and competition. Proceedings of the National Academy of Sciences 70:3590–3593.

Glazener, W. C., D. Ransom, Jr., J. R. Cary, and O. J. Rongstad. 1990. Demographic analysis of a Rio Grand wild turkey population. Southwestern Naturalist 35:23–27.

Glidden, J. W., and D. E. Austin. 1975. Natality and mortality of wild turkey poults in southwestern New York. Proceedings of the National Wild Turkey Symposium 3:48–54.

Godfrey, C. L., and G. W. Norman. 2000. Reproductive ecology and nesting habitat of eastern wild turkeys in western Virginia. Proceedings of the National Wild Turkey Symposium 8:203–210.

Godwin, K. D., G. A. Hurst, and R. L. Kelley. 1991. Survival rates of radio-equipped wild turkey gobblers in east-central Mississippi. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 45:218–226.

Goetze, J. R. 1995. Distribution, natural history, and biogeographic relationships of mammals on the Edwards Plateau of Texas. Dissertation, Texas Tech University, Lubbock, Texas, USA.

Gore, H. G. 1969. Exploitation and restoration of turkey in Texas. Proceedings of the Annual Conference of the Southeastern Association of Game and Fish Commissioners 23:37–45.

Gould, F. W. 1975. Texas plants: a checklist and ecological summary. Texas A&M University, Agricultural Experiment Station, College Station, Texas, USA.

Graham, G. L, and R. R. George. 2002. Operational plan: fiscal year 2003. Texas Parks and Wildlife Department, Austin, Texas, USA.

Grant, W. E., E. K. Pedersen, and S. L. Marin. 1997. Ecology and natural resource management: systems analysis and simulation. John Wiley and Sons, New York, New York, USA.

Guthery, F. S., and S. L. Beasom. 1977. Responses of game and nongame wildlife to predator control in south Texas. Journal of Range Management 30:404–409.

_____, J. L. Lusk, D. R. Synatzske, J. Gallagher, S. J. DeMaso, R. R. George, and M. J. Peterson. 2002. Weather and age ratios of northern bobwhites in south Texas. Proceedings of the National Quail Symposium 5:99–105.

Hamilton, D. A., and L. D. Vangilder. 1992. Furbearer populations, animal rights and wild turkey production. Special Report, Missouri Department of Conservation, Columbia, Missouri, USA.

Hanski, I. W., and M. E. Gilpin. 1997. Metapopulation biology: ecology, genetics, and evolution. Academic Press, San Diego, California, USA.

Hansson, L. 2002. Dynamics and trophic interactions of small rodents: landscape or regional effects on spatial variation? Oecologia 130:259–266.

Harrison, R. L. 1997. A comparison of gray fox ecology between residential and undeveloped rural landscapes. Journal of Wildlife Management 61:112–122.

Haucke, H. H. 1974. Characteristics of roosts of the Rio Grande turkey (*Meleagris gallopavo intermedia*) in south Texas. Thesis, Texas A&M University, College Station, Texas, USA.

Healy, W. M. 1992*a*. Behavior. Pages 46–65 in J. D. Dickson, editor. The wild turkey: biology and management. Stackpole Books, Mechanicsburg, Pennsylvania, USA.

_____. 1992*b*. Population influences: environment. Pages 129–143 *in* J. D. Dickson, editor. The wild turkey: biology and management. Stackpole Books, Mechanicsburg, Pennsylvania, USA.

_____, and E. S. Nenno. 1985. Effect of weather on wild turkey poult survival. Proceedings of the National Wild Turkey Symposium 5:91–101.

_____, and S. M. Powell. 1999. Wildl turkey harvest management: biology, strategies, and techniques. U.S. Fish and Wildlife Service, Biological Technical Publication BTP-R5001-1999, Washington D.C., USA.

Heddinghaus, T. R., and P. Sabol. 1991. A review of the Palmer Drought Severity Index and where do we go from here? Proceedings of the Conference on Applied Climatology 7:242–246.

Henke, S. E., and F. C. Bryant. 1999. Effects of coyote removal on the faunal community in western Texas. Journal of Wildlife Management 63:1066–1081.

Hennen, R. S., and S. Lutz. 2001. Rio Grande turkey female survival in southcentral Kansas. Proceedings of the National Wild Turkey Symposium 8:117–122.

Hernandez, F., D. Rollins, and R. Cantu. 1997. Evaluating evidence to identify ground-nest predators in west Texas. Wildlife Society Bulletin 25:826–831.

Heske, E. J., S. K. Robinson, and J. D. Brawn. 2001. Nest predation and neotropical songbirds: piecing together the fragments. Wildlife Society Bulletin 29:52–61.

Hohensee, S. D., and M. C. Wallace. 2001. Nesting and survival of Rio Grande turkeys in northcentral Texas. Proceedings of the National Wild Turkey Symposium 8:85–91.

Hubbard, M. W., D. L. Garner, and E. E. Klaas. 1999. Wild turkey poult survival in southcentral Iowa. Journal of Wildlife Management 63:199–203.

Hurst, G. A. 1992. Foods and feeding. Pages 66–83 *in* J. D. Dickson, editor. The wild turkey: biology and management. Stackpole Books, Mechanicsburg, Pennsylvania, USA.

_____, and W. E. Poe. 1985. Amino acid levels and patterns in wild turkey poults and their food items in Mississippi. Proceedings of the National Wild Turkey Symposium 5:133–143.

Jefferson, J., editor. 2004. Texas Parks and Wildlife outdoor annual: hunting and fishing regulations. Texas Monthly Custom Publishing, Austin, Texas, USA.

Jiménez, J. E., and M. R. Conover. 2001. Ecological approaches to reduce predation on ground-nesting gamebirds and their nests. Wildlife Society Bulletin 29:62–69.

Johnson, D. L., and A. Worobec. 1988. Spatial and temporal computer analysis of insects and weather: grasshoppers and rainfall in Alberta. Memoirs of the Entomological Society of Canada 146:33–48.

Keegan, T. W., and J. A. Crawford. 1999. Preproduction and survival of Rio Grande wild turkeys in Oregon. Journal of Wildlife Management 63:204–210.

Kellert, S. R. 1985. Public perceptions of predators, particularly the wolf and coyote. Biological Conservation 31:167–189.

Kennamer, J. E., D. H, Arner, C. R. Hopkins, and R. C. Clanton. 1975. Productivity of the eastern wild turkey in the Mississippi Delta. Proceedings of the National Wild Turkey Symposium 3:41–47.

_____, and M. C. Kennamer. 1995. Status and distribution of the wild turkey in 1994. Proceedings of the National Wild Turkey Symposium 7:203–211.

Krebs, C. J. 1994. Ecology: the experimental analysis of distribution and abundance. Fourth edition. Harper Collins, New York, New York, USA.

Kuehl, A. K., and W. R. Clark. 2002. Predator activity related to landscape features in northern Iowa. Journal of Wildlife Management 66:1224–1234.

Kurzejeski, E. W., and L. D. Vangilder. 1992. Population management. Pages 165–184 *in* J. D. Dickson, editor. The wild turkey: biology and management. Stackpole Books, Mechanicsburg, Pennsylvania, USA.

——, L. D. Vangilder, and J. B. Lewis. 1987. Survival of wild turkey hens in north Missouri. Journal of Wildlife Management 51:188–193.

Landholt, L. M., and H. H. Genoways. 2000. Population trends of furbearers in Nebraska. Transactions of the Nebraska Academy of Science 26:97–110.

Lazarus, J. E., and W. F. Porter. 1985. Nest habitat selection by wild turkeys in Minnesota. Proceedings of the National Wild Turkey Symposium 5:67–81.

Lehman, C. P., L. D. Flake, A. P. Leif, and R. D. Shields. 2000. Comparative survival and reproduction of sympatric eastern and Rio Grande wild turkey females in northeastern South Dakota. Proceedings of the National Wild Turkey Symposium 8:123–135.

Leif, A. P. 2000. Survival, reproduction, and home ranges of translocated wild turkeys in South Dakota. Proceedings of the National Wild Turkey Symposium 8:211–220.

Leopold, B. D., and M. Chamberlain. 2001. Predator control: here we go again. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 56: 239–254.

Lint, J. R., B. D. Leopold, and G. A. Hurst. 1995. Comparison of abundance indexes and population estimates for wild turkey gobblers. Wildlife Society Bulletin 23:164–168.

Little, T. W., J. M. Kienzler, and G. A. Hanson. 1990. Effects of fall either-sex hunting on survival in an Iowa wild turkey population. Proceedings of the National Wild Turkey Symposium 6:119–125.

Lopez, R. R. 1996. Population dynamics of eastern wild turkey relocated in the Post Oak Savannah of Texas. Thesis, Texas A&M University, College Station, Texas, USA.

Lougheed, L. W., A. Breault, and D. B. Lank. 1999. Estimating statistical power to evaluate ongoing waterfowl population monitoring. Journal of Wildlife Management 63:1359–1369.

Lusk, J. J., F. S. Guthery, R. R. George, M. J. Peterson, and S. J. DeMaso. 2002. Relative abundance of bobwhites in relation to weather and land use. Journal of Wildlife Management 66:1040–1051.

Lutz, R. S., and J. A. Crawford. 1987. Reproductive success and nesting habitat of Merriam's wild turkeys in Oregon. Journal of Wildlife Management 51:783–787.

Markley, M. H. 1967. Limiting factors. Pages 199–244 *in* O. H. Hewitt, editor. The wild turkey and its management. The Wildlife Society, Washington, D. C., USA.

Marshall, A. J. 1959. Internal and environmental control of breeding. Ibis 101:456–478.

McCallum, H. 2000. Population parameters: estimation for ecological models. Blackwell Science, Oxford, England, UK.

Menzel, K. E. 1975. Population and harvest data for Merriam's turkeys in Nebraska. Proceedings of the National Wild Turkey Symposium 3:184–188.

Messmer, T. A., M. W. Brunson, D. Reiter, and D. G. Hewitt. 1999. Unites States public attitudes regarding predators and their management to enhance avian recruitment. Wildlife Society Bulletin 27:75–85.

Miller, J. E., and B. D. Leopold. 1992. Population influences: predators. Pages 119–128 *in* Dickson, J. G., editor. The wild turkey: biology and management. Stackpole Books, Mechanicsburg, Pennsylvania, USA.

Miller, M. S., D. J. Buford, and R. S. Lutz. 1995. Survival of female Rio Grande turkeys during the reproductive season. Journal of Wildlife Management 59:766–771.

Morrison, M. L., W. M. Block, M. D. Strickland, and W. L. Kendall. 2001. Wildlife study design. Springer-Verlag, New York, New York, USA.

Moss, R. 1986. Rain, breeding success and distribution of capercaillie (*Tetrao urogallus*) and black grouse (*Tetrao tetrix*) in Scotland. Ibis 128:65–72.

National Wild Turkey Federation. 2002. The wild turkey in North America: current status and distribution. National Wild Turkey Federation, Edgefield, South Carolina, USA.

Newton, I. 1998. Population limitation in birds. Academic Press, San Diego, California, USA.

Nummi, P., and L. Saari. 2003. Density-dependent decline of breeding success in an introduced, increasing mute sway *Cygnus olor* population. Journal of Avian Biology 34:105–111.

Oehler, J. D., and J. A. Litvaitis. 1996. The role of spatial scale in understanding responses of medium-sized carnivores to forest fragmentation. Canadian Journal of Zoology 74:2070–2079.

Ott, R. L., and M. Longnecker. 2001. An introduction to statistical methods and data analysis. Fifth edition. Duxbury, Pacific Grove, California, USA.

Pack, J. C., G. W. Norman, C. I. Taylor, D. E. Steffen, D. A. Swanson, K. H. Pollock, and R. Alpizar-Jara. 1998. Effects of fall hunting on wild turkey populations in Virginia and West Virginia. Journal of Wildlife Management 63:964–975.

Paisley, R. N., R. G. Wright, J. F. Kubisiak, and R. E. Rolley. 1998. Reproductive ecology of eastern wild turkeys in southwestern Wisconsin. Journal of Wildlife Management 62:911–916.

Palmer, W. C. 1965. Meteorological drought. Weather Bureau Research Paper Number 45, United States Department of Commerce, Washington, D. C., USA.

Palmer, W. E., S. R. Priest, R. S. Seiss, P. S. Phalen, and G. A. Hurst. 1993. Reproductive effort and success in a declining wild turkey population. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 47:138–147.

Panek, M. 1992. The effect of environmental factors on survival of grey partridge (*Perdix perdix*) chicks in Poland during 1987–89. Journal of Applied Ecology 29:745–750.

Pattee, O. H., and S. L. Beasom. 1979. Supplemental feeding to increase wild turkey productivity. Journal of Wildlife Management 43:512–516.

Pedlar, J. H., L. Fahrig, H. G. Merriam. 1997. Raccoon habitat use at two spatial scales. Journal of Wildlife Management 61:102–112.

Porter, W. F. 1992. Habitat requirements. Pages 202–213 *in* J. D. Dickson, editor. The wild turkey: biology and management. Stackpole Books, Mechanicsburg, Pennsylvania, USA.

_____, G. C. Nelson, and K. Mattson. 1983. Effects of weather conditions on reproduction in a northern wild turkey population. Journal of Wildlife Management 47:281–290.

Prange, S., S. D. Gehrt, and E. P. Wiggers. 2003. Demographic factors contributing to high raccoon densities in urban landscapes. Journal of Wildlife Management 67:324–333.

Purvis, J. 2004. Small game harvest survey results: 1986–87 through 2003–2004. TPWD Report PWD RP W7000-988 (7/04). Texas Parks and Wildlife Department, Austin, Texas, USA.

Ransom, D., Jr., O. J. Rongstad, and D. H. Rusch. 1987. Nesting ecology of Rio Grande turkeys. Journal of Wildlife Management 51:435–439.

Reagan, J. M., and K. D. Morgan. 1980. Reproductive potential of Rio Grande turkey hens in the Edwards Plateau of Texas. Proceedings of the National Wild Turkey Symposium 4:136–144.

Reiter, D. K., M. W. Brunson, and R. H. Schmidt. 1999. Public attitudes toward wildlife damage management and policy. Wildlife Society Bulletin 27:746–758.

Rice, C. G. 2003. Utility of pheasant call counts and brood counts for monitoring population density and predicting harvest. Western North American Naturalist 63:178–188.

Roberts, S. D., J. M. Coffey, and W. F. Porter. 1995. Survival and reproduction of female wild turkeys in New York. Journal of Wildlife Management 59:437–447.

_____, and W. F. Porter. 1996. Importance of demographic parameters to annual changes in wild turkey abundance. Proceedings of the National Wild Turkey Symposium 7:15–20.

_____, and _____. 1998a. Influence of temperature and precipitation on survival of wild turkey poults. Journal of Wildlife Management 62:1499–1505.

_____, and _____. 1998b. Relation between weather and survival of wild turkey nests. Journal of Wildlife Management 62:1492–1498.

Robinson, W. L., and E. G. Bolen. 1984. Wildlife ecology and management. Second edition. Macmillan, New York, New York, USA.

Rolley, R. E., J. F. Kubisiak, R. N. Paisley, and R. G. Wright. 1998. Wild turkey population dynamics in southwestern Wisconsin. Journal of Wildlife Management 62:917–924.

Rollins, D., and J. P. Carroll. 2001. Impacts of predation on northern bobwhite and scaled quail. Wildlife Society Bulletin 29:39–51.

Ryan, T. A., Jr., and B. L. Joiner. 1976. Normal probability plots and tests for normality. Technical Report, Department of Statistics, Pennsylvania State University, State College, Pennsylvania, USA.

Sæther, B-E., and S. Engen. 2002. Pattern of variation in avian population growth. Philosophical Transactions of the Royal Society of London, Series B. 357:1185–1195.

_____, _____, and E. Matthysen. 2002. Demographic characteristics of population dynamical patterns of solitary birds. Science 295:2070–2073.

Schaap, J. N. 2005. Ranges, movements, and spatial distribution of radio-tagged Rio Grande wild turkeys in the Edwards Plateau of Texas. Thesis, Texas A&M University, College Station, Texas, USA.

Schmutz, J. A., and C. E. Braun. 1989. Reproductive performance of Rio Grande wild turkeys. Condor 91:675–680.

Schultz, V., and R. D. McDowell. 1957. Some comments on a wild turkey brood study. Journal of Wildlife Management 21:85–89.

Seiss, R. S., P. S. Phalen, and G. A. Hurst. 1990. Wild turkey habitat and success rate. Proceedings of the National Wild Turkey Symposium 6:18–24.

Shaw, H. G. 1973. The roadside survey for Merriam's turkey in Arizona. Pages 285–293 *in* G. C. Sanderson and H. C. Schultz, editors. Wild turkey management: current problems and programs. University of Missouri, Columbia, Missouri, USA.

Silvy, N. J., M. J. Peterson, J. R. Purvis, and A. S. Bridges. 2000. Relationships of fur market conditions to Texas quail populations. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 54:266–273.

Smith-Blair, A. E. 1993. Rio Grande wild turkey habitat and edge use, survival, and reproductive characteristics in the Texas Rolling Plains. Thesis, Texas Tech University, Lubbock, Texas, USA.

Speake, D. W. 1980. Predation on wild turkeys in Alabama. Proceedings of the National Wild Turkey Symposium 4:86–101.

——, R. Metzier, and J. McGlincy. 1985. Mortality of wild turkey poults in northern Alabama. Journal of Wildlife Management 49:472–474.

Steidl, R. J., J. P. Hayes, and E. Schauber. 1997. Statistical power analysis in wildlife research. Journal of Wildlife Management 61:270–279.

Strickland, M. D., H. J. Harju, K. R. McCaffery, H. W. Miller, L. M. Smith, and R. J. Stoll. 1994. Harvest management. Pages 445–473 *in* T. A. Bookhout, editor.

Research and management techniques for wildlife and habitat. The Wildlife Society, Bethesda, Maryland, USA.

Suchy, W. J., W. R. Clark, and T. W. Little. 1983. Influence of simulated harvest on Iowa wild turkey populations. Proceedings of the Iowa Academy of Science 90:98–102.

Texas Game, Fish, and Oyster Commission. 1945. Wild turkeys. Pages 15–33 *in* Principal game birds and mammals of Texas: their distribution and management. Texas Game, Fish, and Oyster Commission, Austin, Texas, USA.

Texas Parks and Wildlife Department. 1997. Wild turkey distribution in Texas. TPWD Leaflet PWD LF W7000-038 (11/97). Austin, Texas, USA.

_____. 2003. Big game harvest survey results: 1993–94 through 2003–2004. Texas Parks and Wildlife Department, Austin, Texas, USA.

The Wildlife Society. 1995. Journal news. Journal of Wildlife Management 59:196–198.

Thomas, J. W., C. V. Hoozer, and R. G. Marburger. 1966. Wintering concentrations and season shifts in range in the Rio Grande wild turkey. Journal of Wildlife Management 30:34–49.

U.S. Department of Interior – U.S. Fish and Wildlife Service and U.S. Department of Commerce – U.S. Census Bureau. 2001. 2001 survey of fishing, hunting, and wildlife-associated recreation. U.S. Department of Interior, Washington, D.C., USA.

Vander Haegen, W. M., W. E. Dodge, and M. W. Sayre. 1988. Factors effecting productivity in a northern wild turkey population. Journal of Wildlife Management 52:127–133.

Vangilder, L. D. 1992. Population dynamics. Pages 144–164 *in* J. D. Dickson, editor. The wild turkey: biology and management. Stackpole Books, Mechanicsburg, Pennsylvania, USA.

_____, M. W. Hubbard, and D. A. Hasenbeck. 2000. Reproductive ecology of eastern wild turkey females in the eastern Missouri Ozarks. Proceedings of the National Wild Turkey Symposium 8:53–59.

_____, and E. W. Kurzejeski. 1995. Population ecology of the eastern wild turkey in northern Missouri. Wildlife Monographs 130:1–50.

_____, _____, V. L. Kimmel-Truitt, and J. B. Lewis. 1987. Reproductive parameters of wild turkey hens in north Missouri. Journal of Wildlife Management 51:535–540.

von Bertalanffy, L. 1968. General system theory: foundation, development, application. George Braziller, Inc., New York, New York, USA.

Walters, C. 2001. Adaptive management of renewable resources. Blackburn Press, Caldwell, New Jersey, USA.

Watts, C. R. 1969. The social organization of wild turkeys on the Welder Wildlife Refuge, Texas. Dissertation, Utah State University, Logan, Utah, USA.

Welty, J. C., and L. Baptista. 1988. The life of birds. Fourth edition. Saunders College Publishing, New York, New York, USA.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations: modeling, estimation, and decision making. Academic Press, San Diego, California, USA.

Williams, L. E., Jr., and D. H. Austin. 1988. Studies of the wild turkey in Florida. Florida Game and Freshwater Fish Commission Technical Bulletin 10., Tallahassee, Florida, USA.

Wunz, G. A., and W. K. Shope. 1980. Turkey brood survey in Pennsylvania as it relates to harvest. Proceedings of the National Wild Turkey Symposium 4:69–75.

Zar, J. H. 1999. Biostatistical analysis. 4th edition. Prentice-Hall, Inc., Upper Saddle River, New Jersey, USA.

Zwank, P. J., T. H. White, Jr., and F. G. Kimmel. 1988. Female turkey habitat use in Mississippi River batture. Journal of Wildlife Management 52:253–560.

APPENDIX

PARAMETER AND VARIABLE DEFINITIONS

A = geographic area of interest simulated by the model.

α_{H_F} = total fall harvest of hens during the current year.

α_{M_F} = total fall harvest of males during the current year.

α_{M_S} = total spring harvest of males during the current year.

B_J = total broods 3–16 weeks of age.

B_P = total broods ≤2 weeks of age.

B_{ia} = total broods containing juveniles of age class i, accompanied by adult hens.

B_{iy} = total broods containing juveniles of age class i, accompanied by yearling hens.

β_{H_F} = length of the fall hen hunting season, in weeks.

β_{M_F} = length of the fall male hunting season, in weeks.

β_{M_S} = length of the spring male hunting season, in weeks.

χ = sex ratio at 16 weeks of age.

DDF = density dependent factor; factor applied to certain reproductive parameters to reduce reproductive success at high densities.

D_{R_0} = zero-reproduction density; the theoretical density of sexually-mature above which density-dependent factors cause reproduction to cease.

e_{I_a} = total outflow from the incubating adult hen conveyor variable.

e_{I_y} = total outflow from the incubating yearling hen conveyor variable.

e_{L_a} = total outflow from the laying adult hen conveyor variable.

e_{L_y} = total outflow from the laying yearling hen conveyor variable.

$\varepsilon_{H_{La}}$ = weekly mortality rate of mating adult hens.

$\varepsilon_{H_{Ly}}$ = weekly mortality rate of mating yearling hens.

$\varepsilon_{H_{Ma}}$ = weekly mortality rate of mating adult hens.

$\varepsilon_{H_{My}}$ = weekly mortality rate of mating yearling hens.

$\varepsilon_{H_{NBa}}$ = weekly mortality rate of nonbreeding adult hens.

$\varepsilon_{H_{NBy}}$ = weekly mortality rate of nonbreeding yearling hens.

$\varepsilon_{H_{Wa}}$ = weekly mortality rate of wintering adult hens.

$\varepsilon_{H_{Wy}}$ = weekly mortality rate of wintering yearling hens.

ε_j = weekly juvenile mortality rate.

ε_M = weekly male mortality rate.

ε_p = weekly poult mortality rate.

f = the number of hens that successfully raise a brood to 16 weeks of age between time step t and $t + 1$.

γ_{H_F} = week in which hen population is determined for harvest.

γ_{M_F} = week in which fall male population is determined for harvest.

γ_{M_S} = week in which spring male population is determined for harvest.

H = total number of sexually-mature (adult and yearling) hens in the population.

H_{Ia} = total number of adult hens incubating firsts nests.

H_{Iy} = total number of yearling hens incubating second nests.

H_{Ja} = total number of adult hens accompanying broods >2 weeks of age.

H_{Jy} = total number of yearling hens accompanying broods >2 weeks of age.

H_{La} = total number of adult hens laying first nests.

H_{Ly} = total number of yearling hens laying second nests.

H_{Ma} = total number of mating adult hens.

H_{My} = total number of mating yearling hens.

H_{NBa} = total number of nonbreeding adult hens.

H_{NBy} = total number of nonbreeding yearling hens.

H_{Pa} = total number of adult hens accompanying broods ≤2 weeks of age.

H_{Py} = total number of yearling hens accompanying broods ≤2 weeks of age.

H_{R_0} = number of sexually-mature hens in A at D_{R_0}.

H_{RIa} = total number of adult hens incubating second nests.

H_{RIy} = total number of yearling hens incubating second nests.

H_{RLa} = total number of adult hens laying seond nests.

H_{RLy} = total number of yearling hens laying second nests.

H_{Wa} = total number of wintering adult hens.

H_{Wy} = total number of wintering yearling hens.

h = number of broods hatching between time step t and $t + 1$.

ι_{H_F} = a binary variable indicating whether fall hen harvest is allowed.

ι_{Ma_F} = a binary variable indicating whether fall gobbler harvest is allowed.

ι_{Ma_S} = a binary variable indicating whether spring gobbler harvest is allowed.

ι_{Mj_F} = a binary variable indicating whether fall jake harvest is allowed.

ι_{Mj_S} = a binary variable indicating whether spring jake harvest is allowed.

J_{ia} = total broods containing juveniles of age class i, accompanied by adult hens.

J_{iy} = total broods containing juveniles of age class i, accompanied by yearling hens.

κ_{ba1} = proportion of broods hatched by adult hens attempting first nests in size class b.

κ_{by1} = proportion of broods hatched by yearling hens attempting first nests in size class b.

κ_{ba2} = proportion of broods hatched by adult hens attempting second nests in size class b.

κ_{by2} = proportion of broods hatched by yearling hens attempting second nests in size class b.

λ_{pa} = brood extinction rate for poult broods accompanied by adult hens.

λ_{py} = brood extinction rate for poult broods accompanied by yearling hens.

λ_{ja} = brood extinction rate for juvenile broods accompanied by adult hens.

λ_{jy} = brood extinction rate for juvenile broods accompanied by yearling hens.

M = total number of sexually-mature (adult and yearling) males in the population.

$m_{H_{Ia}}$ = number of incubating adult hens dying between time step t and $t + 1$.

$m_{H_{Iy}}$ = number of incubating yearling hens dying between time step t and $t + 1$.

$m_{H_{La}}$ = number of laying adult hens dying between time step t and $t + 1$.

$m_{H_{Ly}}$ = number of laying yearling hens dying between time step t and $t + 1$.

$m_{H_{Ma}}$ = number of mating adult hens dying between time step t and $t + 1$.

$m_{H_{My}}$ = number of mating yearling hens dying between time step t and $t + 1$.

$m_{H_{NBa}}$ = number of nonbreeding adult hens dying between time step t and $t + 1$.

$m_{H_{NBy}}$ = number of nonbreeding yearling hens dying between time step t and $t + 1$.

$m_{H_{Wa}}$ = number of wintering adult hens dying between time step t and $t + 1$.

$m_{H_{Wy}}$ = number of wintering yearling hens dying between time step t and $t + 1$.

v_a = proportion of adult hens that begin laying between time step t and $t + 1$.

v_y = proportion of yearling hens that begin laying between time step t and $t + 1$.

$\omega_{\mu_{a1}}$ = mean clutch size prior to hatching for adult hens attempting first nests.

$\omega_{\mu_{a2}}$ = mean clutch size prior to hatching for adult hens attempting second nests.

$\omega_{\mu_{y1}}$ = mean clutch size prior to hatching for yearling hens attempting first nests.

$\omega_{\mu_{y2}}$ = mean clutch size prior to hatching for yearling hens attempting second nests.

$\omega_{\sigma_{a1}}$ = standard deviation of clutch size prior to hatching for adult hens attempting first nests.

$\omega_{\sigma_{a2}}$ = standard deviation of clutch size prior to hatching for adult hens attempting second nests.

$\omega_{\sigma_{y1}}$ = standard deviation of clutch size prior to hatching for yearling hens attempting first nests.

$\omega_{\sigma_{y2}}$ = standard deviation of clutch size prior to hatching for yearling hens attempting second nests.

P_{ia} = total broods containing poults of age class *i*, accompanied by adult hens.

P_{iy} = total broods containing poults of age class *i*, accompanied by yearling hens.

$\varphi_{H_{FB}}$ = week in which the fall hen season begins.

$\varphi_{H_{FE}}$ = week in which the fall hen season ends.

$\varphi_{M_{FB}}$ = week in which the fall male season begins.

$\varphi_{M_{FE}}$ = week in which the fall male season ends.

$\varphi_{M_{SB}}$ = week in which the spring male season begins.

$\varphi_{M_{SE}}$ = week in which the spring male season ends.

ψ_{H_F} = ratio of yearling to adult hen harvest rates.

ψ_{M_F} = ratio of yearling to adult male fall harvest rates.

ψ_{M_S} = ratio of yearling to adult male spring harvest rates.

Q_H = total wintering hatch year hens.

Q_M = total wintering hatch year males.

$\rho_{H_{Ia}}$ = proportion of adult hens losing their nest during incubation that attempt a second nest.

$\rho_{H_{Iy}}$ = proportion of yearling hens losing their nest during incubation that attempt a second nest.

$\rho_{H_{La}}$ = proportion of adult hens losing their nest during laying that attempt a second nest.

$\rho_{H_{Ly}}$ = proportion of yearling hens losing their nest during laying that attempt a second nest.

$s_{H_{Ia \to NBa}}$ = number of incubating adult hens surviving the loss of a nest and not attempting a second nest between time step t and $t + 1$.

$s_{H_{Ia \to Pa}}$ = number of incubating adult hens hatching their first clutch between time step t and $t + 1$.

$s_{H_{Ia \to RLa}}$ = number of incubating adult hens surviving the loss of a nest and attempting a second nest between time step t and $t + 1$.

$s_{H_{Iy \to NBy}}$ = number of laying yearling hens surviving the loss of a nest and not attempting a second nest between time step t and $t + 1$.

$s_{H_{Iy \to Py}}$ = number of incubating yearling hens hatching their first clutch between time step t and $t + 1$.

$s_{H_{Iy \to RLy}}$ = number of incubating yearling hens surviving the loss of a nest and attempting a second nest between time step t and $t + 1$.

$s_{H_{La \to Ia}}$ = number of laying adult hens surviving and initiating incubation of their first nest between time step t and $t + 1$.

$s_{H_{La \to NBa}}$ = number of laying adult hens surviving the loss of a nest and not attempting a second nest between time step t and $t + 1$.

$s_{H_{La \to RLa}}$ = number of laying adult hens surviving the loss of a nest and attempting a second nest between time step t and $t + 1$.

$s_{H_{Ly \to Iy}}$ = number of laying yearling hens surviving and initiating incubation of their first nest between time step t and $t + 1$.

$s_{H_{Ly \to NBy}}$ = number of laying yearling hens surviving the loss of a nest and not attempting a second nest between time step t and $t + 1$.

$s_{H_{Ly \to RLy}}$ = number of laying yearling hens surviving the loss of a nest and attempting a second nest between time step t and $t + 1$.

$s_{H_{Ma \to La}}$ = number of mating adult hens surviving and attempting a first nest between time step t and $t + 1$.

$s_{H_{Ma \to NBa}}$ = number of mating adult hens surviving but forgoing nesting between time step t and $t + 1$.

$s_{H_{My \to Ly}}$ = number of mating adult hens surviving and attempting a first nest between time step t and $t + 1$.

$s_{H_{My \to NBy}}$ = number of mating yearling hens surviving but forgoing nesting between time step t and $t + 1$.

$s_{H_{NBa \to Wa}}$ = number of nonbreeding adult hens entering the wintering period between time step t and $t + 1$.

$s_{H_{NBy \to Wy}}$ = number of nonbreeding yearling hens entering the wintering period between time step t and $t + 1$.

$s_{H_{RIa \to NBa}}$ = number of incubating adult hens surviving the loss of their second nest between time step t and $t + 1$.

$s_{H_{RIa \to Pa}}$ = number of adult hens hatching their second nest between time step t and t + 1.

$s_{H_{RIy \to NBy}}$ = number of incubating yearling hens surviving the loss of their second nest between time step t and $t + 1$.

$s_{H_{RIy \to Py}}$ = number of yearling hens hatching their second nest between time step t and $t + 1$.

$s_{H_{RLy \to NBa}}$ = number of laying adult hens surviving the loss of their second nest between time step t and $t + 1$.

$s_{H_{RLa \to RIa}}$ = number of adult hens initiating incubation of their second nest between time step t and $t + 1$.

$s_{H_{RLy \to NBy}}$ = number of laying yearling hens surviving the loss of their second nest between time step t and $t + 1$.

$s_{H_{RLy \to RIy}}$ = number of yearling hens initiating incubation of their second nest between time step t and $t + 1$.

$s_{H_{Wa \to Ma}}$ = number of wintering adult hens surviving and moving into the mating adult hen class between time step t and $t + 1$.

$s_{H_{Wy \to Ma}}$ = number of wintering yearling hens surviving and moving into the mating adult hen class between time step t and $t + 1$.

$s_{Q_H \to Hy}$ = number of wintering juvenile hens surviving and moving into the mating yearling hen class between time step t and $t + 1$.

$s_{Q_M \rightarrow My}$ = number of wintering juvenile males surviving and moving into the yearling male class between time step t and $t + 1$.

$s_{My \rightarrow Ma}$ = number of wintering yearling males surviving and moving into the adult male class between time step t and $t + 1$.

$\tau_{\mu_{a1}}$ = hatching success for adult hens attempting first nests.

$\tau_{\mu_{a2}}$ = hatching success for adult hens attempting second nests.

$\tau_{\mu_{y1}}$ = hatching success for yearling hens attempting first nests.

$\tau_{\mu_{y2}}$ = hatching success for yearling hens attempting second nests.

$\upsilon_{\mu_{a1}}$ = mean brood size at hatching for adult females hatching first nests.

$\upsilon_{\mu_{a2}}$ = mean brood size at hatching for adult females hatching second nests.

$\upsilon_{\mu_{y1}}$ = mean brood size at hatching for yearling females hatching first nests.

$\upsilon_{\mu_{y2}}$ = mean brood size at hatching for yearling females hatching second nests.

$\upsilon_{\sigma_{a1}}$ = standard deviation of brood size at hatching for adult females hatching first nests.

$\upsilon_{\sigma_{a2}}$ = standard deviation of brood size at hatching for adult females hatching second nests.

$\upsilon_{\sigma_{y1}}$ = standard deviation of brood size at hatching for yearling females hatching first nests.

$\upsilon_{\sigma_{y2}}$ = standard deviation of brood size at hatching for yearling females hatching second nests.

$\xi_{\mu_{La}}$ = mean weekly adult nest survival (proportion of adult hen nests surviving from time t to $t + 1$), first nest attempt.

$\xi_{\mu_{Ly}}$ = mean weekly yearling nest survival, first nest attempt.

$\xi_{\mu_{Ia}}$ = mean weekly adult nest survival during incubation, first nest attempt.

$\xi_{\mu_{Iy}}$ = mean weekly yearling nest survival during incubation, first nest attempt.

$\xi_{\mu_{RLa}}$ = mean weekly adult nest survival during laying, second nest attempt.

$\xi_{\mu_{RLy}}$ = mean weekly yearling nest survival, second nest attempt.

$\xi_{\mu_{RIa}}$ = mean weekly adult nest survival during incubation, second nest attempt.

$\xi_{\mu_{RIy}}$ = mean weekly yearling nest survival during incubation, second nest attempt.

$\xi_{\sigma_{Ia}}$ = standard deviation of weekly adult nest survival during incubation, first nest attempt.

$\xi_{\sigma_{Iy}}$ = standard deviation of weekly yearling nest survival during incubation, first nest attempt.

$\xi_{\sigma_{RIa}}$ = standard deviation of weekly adult nest survival during incubation, second nest attempt.

$\xi_{\sigma_{RIy}}$ = standard deviation of weekly yearling nest survival during incubation, second nest attempt.

$\xi_{\sigma_{La}}$ = standard deviation of weekly adult nest survival during laying, first nest attempt.

$\xi_{\sigma_{Ly}}$ = standard deviation of weekly yearling nest survival during laying, first nest attempt.

$\xi_{\sigma_{RLa}}$ = standard deviation of weekly adult nest survival during laying.

$\xi_{\sigma_{RLy}}$ = standard deviation of weekly yearling nest survival during laying, second nest attempt.

ζ_{H_F} = proportion of the fall hen population to be harvested.

ζ_{M_F} = proportion of the fall male population to be harvested.

ζ_{M_S} = proportion of the spring male population to be harvested.

VITA

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