Impact of Reproductive Effort on Survival of Rio Grande Wild Turkey Meleagris Gallop Intermedia Hens in Texas

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The southeastern portion of the Edwards Plateau of Texas, historically a stronghold of Rio Grande wild turkeys *Meleagris gallopavo intermedia*, has seen the numbers of turkeys declining since the 1970s. Because hen survival is a key parameter affecting turkey population dynamics, we monitored radio-tagged Rio Grande wild turkey hens on the Edwards Plateau during 2001-2007 to compare survival during the breeding season in areas where turkey abundance has declined vs areas with stable populations. Breeding season survival was best predicted by a model that allowed variation during different periods of the reproductive season (initial nesting during 25 March - 21 April, renesting during 22 April - 12 June and post-nesting during 13 June - 2 July) and differences between stable and declining regions. Model-averaged estimates of breeding season survival were higher in the stable region (0.88; 95% CI: 0.78-0.94) than in the declining region (0.67; 95% CI: 0.55-0.78). Data collected on nests and hens during the intensive monitoring part of the study conducted during 2005-2007 indicated that breeding season survival was negatively affected by the amount of reproductive effort each season, i.e. the number of days a hen spent incubating a nest. Breeding season (25 March - 2 July) survival (0.86) was higher for non-nesting hens than for hens that nested (0.68; average of 15 days spent nesting). Our results suggest that differences in productivity between stable and declining Rio Grande wild turkey populations in the Edwards Plateau of Texas were associated with differences in breeding season survival due to variable reproductive effort, which, when combined with precipitation-dependent boom-bust dynamics common to galliforms in this region, could limit long-term population productivity and maintenance.

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Wildlife conservation is grounded on an understanding of how variation in biotic and abiotic factors influence dynamics of populations of interest.

Identifying demographic patterns is central to understanding how survival and recruitment contribute to life-history variation and population dynamics

in avian populations (Montgomerie & Weatherhead 1988, Martin 1995, Ghalambor & Martin 2001). The interaction between individual reproductive effort and mortality of breeding individuals underlies population dynamics research and management of populations (Stearns 1976). Under this perspective, high mortality of breeding individuals favours increased reproductive effort whereas high mortality of offspring favours lower reproductive efforts (Martin 2002). Determining the relationship between population trajectory and population demography is necessary for conservation planning and implementation of management actions.

The Edwards Plateau of Texas has long been the historic stronghold for Rio Grande wild turkeys *Meleagris gallopavo intermedia* (Walker 1954, Beasom & Wilson 1992). Since the late 1970s, however, surveys conducted by the Texas Parks and Wildlife Department, as well as anecdotal observations by landowners, have documented a decline in wild turkey numbers in the southeastern portion of the Edwards Plateau (Randel et al. 2005, Collier et al. 2007a). As the reason for this decline was unknown, we initiated a research program in 2001 to determine whether population demography differed between areas characterized by stable vs declining turkey abundance.

Variability in abundance of a wide variety of avian populations often is attributed to changes in reproductive output. Based on seven years of research on the reproductive ecology of Rio Grande wild turkeys in this region, we found limited variation between populations classified as stable vs declining in such reproductive parameters as clutch size ($\bar{x} = 10.9 \pm 3.44$ (SE) and $\bar{x} = 10.8 \pm 2.73$ (SE)), daily nest survival (0.92 ± 0.02 (SE) and 0.94 ± 0.005 (SE)), nesting rates (65 and 58%), rates of nest predation (65 and 67%), nest abandonment (18 and 22%) and poult survival (18% survival for first two weeks across sites; Melton 2007, Dreibelbis et al. 2008). Breeding season survival of both male and female Rio Grande wild turkeys was lower than nonbreeding season survival and there was preliminary evidence that differences might exist between populations classified as stable vs declining (Collier et al. 2007a).

Avian reproduction is physiologically and behaviourally expensive, thus optimal life-history strategies must maximize survival of adults relative to reproductive output (Stearns 1976). Mortality of wild turkey hens is typically higher during the breeding season as compared to the rest of the year (Vangilder 1992, Vangilder et al. 1987, Palmer et al. 1993) due to increased predation during reproductive activities (incubation and brooding; Palmer et al. 1993). Loss of hens during reproductive activities influences populations in two ways: reduction in the number of females producing offspring and reduction in population size. Thus, while reproductive parameters were similar between regions characterized by stable vs declining turkey abundance, it is plausible that differences in adult female mortality during the reproductive period could contribute to differences in population size and trajectory. Precocial, ground-nesting species (e.g. belonging to the orders Galliformes and Anseriformes) exhibit both high reproductive output and high mortality of breeding birds, suggesting that an advantageous life-history strategy would be to delay or limit breeding until conditions are optimal for reproduction (Murdoch 1966; but see Jönsson et al. 1991 and Sandercock et al. 2005). Collier et al. (2007a) found that breeding season survival of adult wild turkeys differed between stable and declining populations on the Edwards Plateau of Texas. Because survival of breeding female galliforms is intrinsically tied to recruitment (Stearns 1976, Alerstam & Högstedt 1984, Martin 2002), we hypothesized that population declines in the southeastern portion of the Edward Plateau could be due to comparatively low breeding season survival of females.

We used radio-telemetry to study female Rio Grande wild turkeys captured on the Edwards Plateau before each breeding season to evaluate factors that could contribute to differences in breeding season survival between areas characterized by stable vs declining turkey abundance. Specifically, we evaluated whether precipitation-based environmental variation drove hen nesting intensity, whether hen survival differed between stable and declining populations, how differences between juvenile and adult nesting rates affected hen survival, how reproductive phenology and timing of reproductive events (e.g. nesting, renesting and reproductive senescence) affected hen survival, and which effects increasing the amount of time incubating on a seasonal basis have on mortality.

Species and study area
The breeding season of Rio Grande wild turkeys in Edwards Plateau of Texas begins during late February and continues through mid-July - early August, with the majority of reproductive activities occurring during April through June. After

breeding, hens typically search out clumps of grass or brush offering visual obstruction for use as nest sites (Randel et al. 2005). Clutch sizes average 11 eggs (range: 8-16 eggs; Melton 2007). Hens commonly renest when initial nests are destroyed. Two nesting attempts are common, but we have documented as many as four renesting attempts (five total nesting attempts). Incubation lasts ∼28 days. Poults are restricted to ground roosting at night until approximately two weeks post-hatch when flight feathers replace natal down. Consequently, poult mortality is much higher during this flightless period as young are much more vulnerable to predators (Hubbard et al. 1999b).

We conducted our breeding season study from January 2001 through August 2007 at four research sites on the Edwards Plateau of Texas (Fig. 1). Two sites were located in regions where declines in turkey abundance had occurred (Bandera and Medina counties), and two sites were located in areas where there was no trend in abundance (Kerr and Real counties; Randel et al. 2005, Collier et al. 2007a). Each site was characteristic of Edwards Plateau topography, rolling divides with limestone bedrock and outcrops with rocky soils (Gould 1975). Our study sites (private ranches or public areas) individually ranged from 9.84 to 88.58 km^2, and all were managed for native and exotic ungulate hunting; livestock grazing occurred on three of the sites (Kerr, Medina and Bandera Counties). Limited turkey hunting occurred on one study site (Real County), and while several properties bordering

each site allowed male turkey hunting, harvest was minimal during our study (eight females harvested from >400 radio-tagged individuals).

Methods

We captured wild turkeys in each study region between December and March during 2001-2007, using walk-in funnel traps (Davis 1994, Peterson et al. 2003) or drop nets (Glazener et al. 1964) baited with cracked corn *Zea* spp. and milo *Sorghum* spp. We determined age for captured individuals as juveniles (individuals entering first breeding season) or adults (second year of breeding or older); sex was determined according to primary molt pattern and feather colouration (Pelham & Dickson 1992). Turkeys classified as juveniles were 6-10 months of age at capture. Each individual was weighed and fitted with a uniquely numbered Texas Parks and Wildlife Department aluminum leg band. We radio-tagged turkeys with mortality-sensitive radio-transmitters (69.0-95.0 g; Advanced Telemetry Systems, Isanti, Minnesota, USA), using a modified backpack harness around the wings (Kenward 1987). We tracked radio-tagged individuals daily for the first two weeks postcapture to evaluate capture-related loss and located birds visually twice weekly during this period to ensure that radio-tags remained attached.

We monitored radio-tagged individuals ≥3 times per week from January through August throughout the study (2001-2007) using triangulation, homing and visual observation (White & Garrott 1990) employing vehicle-mounted 4-element Yagi antennas or 3-element handheld Yagi antennas. We increased radio tracking to ≥5 times per week beginning 1 April to monitor reproductive activities (Randel et al. 2005, Melton et al. 2008). During this period, we monitored all individuals until transmitter failure, mortality or emigration to properties with access restrictions. During the seven years of radio-tracking, we did not observe any adult or juvenile radio-tagged individuals moving between study populations, thus we considered each population demographically distinct.
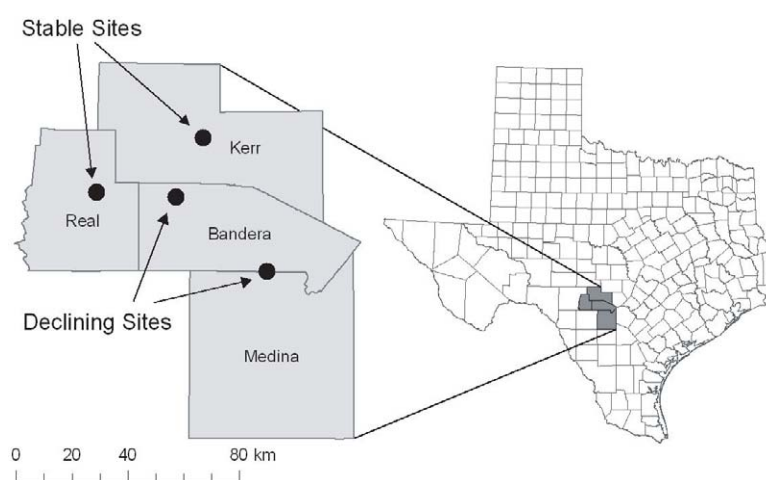

Figure 1. Study site locations in the Edwards Plateau of Texas, USA. The black areas shown on the state map represent the four counties (Kerr, Real, Bandera and Medina) in the southeastern Edwards Plateau in which research on Rio Grande wild turkey survival was conducted during 2001-2007.

We used data from 2001 through 2007 collected as part of a larger study on Rio Grande wild turkey population dynamics (Collier et al. 2007a,b, Randel et al. 2005, Melton et al. 2008, Dreibelbis et al. 2008) to evaluate spatial, seasonal and annual variation in hen survival. Randel et al. (2005) evaluated basic reproductive parameters for hens (e.g. nest success); however, we collected more intensive reproductive data (e.g. nest survival, clutch size and poult survival) during 2005-2007 based on additional research objectives. For each hen we determined date of initiation based on hen movement patterns (Ransom et al. 1987, Paisley et al. 1998, Nguyen et al. 2004) and located nests <3 days after hens had begun incubating to determine nest location and approximated nest age in days by floating eggs (Westerskov 1950). We monitored nesting hens by triangulation ≥3 times weekly from a distance of ≥100 m to prevent nest disturbance and assumed that the nest was still active if hen locations remained constant. We approached the nest to determine fate only when the hen was no longer in the general area of the nest and used these data to determine the time hens spent incubating. In addition, we used motion activated trail cameras (Game Spy 100 and Outfitter Cam, Moultrie Feeders, Alabaster, Alabama, USA) to assist with documentation of nest fate on 21 of 47 and 31 of 71 active nests during 2006-2007, respectively (Dreibelbis et al. 2008).

Statistical analyses

For analysis, we considered our known-fate data as ragged telemetry data (Rotella et al. 2004), because our interest was to model changes in survival probabilities over time and across the range of individual-level data (Dinsmore et al. 2002, Rotella et al. 2004). Thus, we estimated probability of daily survival for Rio Grande wild turkey hens during the breeding season using the nest survival approach (Dinsmore et al. 2002), which is a general model for known-fate data as implemented in program MARK (White & Burnham 1999). This approach to analyzing known-fate data has increased recently (Hartke et al. 2006, Mong & Sandercock 2007) given its flexibility and ability to incorporate groups and individual covariates that vary over time (Rotella et al. 2004). When estimating survival, we based encounter histories on reproductive phenology. We coded our encounter histories for each hen in the data set using a 118-day period equivalent to the breeding season (25 March - 20 July) based on our seven years of radio-tracking data. We entered each

radio-tagged hen into the data set at the start of the breeding season (if alive) on 25 March each year (k = 1). We recorded the last day each radio-tagged hen was known to be alive (l), the final date that either 1) we checked the hen and found mortality had occurred, or 2) a transmitter failure occurred or the hen was lost (e.g. censoring), or 3) the hen was still alive at the end of the study (m), the fate of the hen where 1 = mortality and 0 = survived to the end of each breeding season or were censored (f), and the number of unique individual birds that had the same exact encounter history (n). We used an information theoretic approach to model selection and assessed model strength based on AIC_c and Akaike's weights (w_i; Burnham & Anderson 2002). When we found evidence of model selection uncertainty ($w_i < 0.8$; Mong & Sandercock 2007), we used multimodel inference and provided model-averaged estimates of survival (Burnham & Anderson 2002).

We developed models (Table 1) for the entire period (2001-2007) which focused on broad-scale assessment of trends in survival. Production in gallinaceous birds in the semi-arid regions of Texas typically is characterized by regular boom-bust cycles (e.g. in quails; Bridges et al. 2001, Hernández & Peterson 2007, Lusk et al. 2007). During our study, we characterized 2001 and 2007 as good years for Rio Grande turkey production based on precipitation amount and timing in the region (Schwertner et al. 2005, Texas Parks and Wildlife Department, unpubl. data). To evaluate whether survival would decline based on increased reproductive activities (such as days incubating and nesting attempt; Miller et al. 1995), we developed competing models; one model with good years (2001 and 2007) vs poor years (2002-2006) for comparison with models evaluating variation across all years and a model with no variation among years (see Table 1). Based on work by Melton (2007), we divided the breeding season into three unequal segments based on nesting chronology of hens on the Edwards Plateau to evaluate seasonal variation in survival due to hen nesting frequency (number of hens actively nesting at any given time). The first period was from 25 March to 21 April (28 days), which represented 61% (63/103) of initial nesting attempts (Melton 2007). The second period was from 22 April to 12 June (51 days), which represented fewer initial nestings (39%; 40/103), but a majority (89%; 53/59) of renesting attempts for hens available to renest. The third and final period was from 13 June to 2 July (38 days), representing breeding senescence when hen nesting/renesting

Table 1. Candidate models used to examine the effects of region (stable or declining), age (juvenile or adult), and temporal changes (based on three delineated periods of breeding activity: initial nesting: 25 March - 21 April; renesting period: 22 April - 12 June; and post-nesting: 13 June - 2 July) in breeding chronology on daily survival of radio-tagged Rio Grande wild turkey hens on the Edwards Plateau of Texas between 2001 and 2007. Numbers in each model (1, 2, 3) denote the above-mentioned breeding period and models which differ by region or year are denoted at the end of each equation, otherwise we did not consider effects of region or year within each model.

Model notation	Number of parameters	Deviance	AIC$_c$[a]	w_i
S [Juv(1) = Ad(1); Juv(2) = Ad(2); Juv(3) = Ad(3)] Different by region	6	730.49	0	0.339
S [Juv(1) = Ad(1); Juv(2) ≠ Ad(2); Juv(3) = Ad(3); Juv(2) = Juv(3)] Different by region	6	730.53	0.041	0.332
S [Juv(1) = Ad(1); Juv(2) ≠ Ad(2); Juv(3) = Ad(3); Juv(2) = Juv(3); Ad(1) = Ad(2)] Different by region	4	735.13	0.646	0.246
S [Juv(1) = Ad(1); Juv(2) ≠ Ad(2); Juv(3) = Ad(3)] Different by region	8	729.49	3.010	0.075
S [Juv(1) = Ad(1); Juv(2) = Ad(2); Juv(3) = Ad(3)] 2001 = 2007, 2002 = 2003 = 2004 = 2005 = 2006 (Good versus bad years)	6	738.52	8.030	0.02
S (Constant)	1	748.81	8.320	<0.01
S [Juv(1) = Ad(1); Juv(2) = Ad(2); Juv(3) = Ad(3)]	3	747.77	11.28	<0.01
S [Juv(1) = Ad(1); Juv(2) ≠ Ad(2); Juv(3) = Ad(3)]	4	747.07	12.58	<0.01
S[Juv(1) ≠ Ad(1); Juv(2) ≠ Ad(2); Juv(3) = Ad(3)] Different by region	5	746.65	14.17	<0.01
S [Juv(1) = Ad(1); Juv(2) = Ad(2); Juv(3) = Ad(3)] Different by year	18	720.75	14.29	<0.01

[a] Minimum -2lnL = 730.4868.

attempts declined. We also developed models to evaluate whether there was evidence for regional differences in seasonal survival. In addition, as we hypothesized that juveniles were more likely to nest a single time and then forego renesting attempts (hence reducing overall mortality risk associated with nesting), so we evaluated models to test for this contingency. We used the delta method to calculate standard errors for the model-averaged estimates from the 2001 through 2007 data (Seber 1982).

We used data collected from 2005 to 2007 to evaluate hen and nest-specific effects on daily survival of hens. We developed a candidate model set (Table 2) to evaluate individual-level factors which we hypothesized would explain variation in hen survival. As nesting has been shown to influence hen survival (Martin 1995, Miller et al. 1998), we evaluated impact of the number of days spent incubating using an approach akin to nest-age models

(Dinsmore et al. 2002). For each individual in our study, in addition to the information required by program MARK, we included covariates for hen age (Juvenile = 1, Adult = 2), hen age since initial capture (0-7 years), nesting event (nested that year = 1, did not nest that year = 0), and the cumulative (total) number of days a hen spent incubating within a breeding season, followed by 118 individual covariates for the number of days spent actively nesting and the number of nesting attempts by that hen. We labeled the covariate for days nesting (DN) and nesting attempt (NA) as DN1, DN2,…, DN118 and NA1, NA2,…, NA118 for use in the design matrix in MARK (Dinsmore et al. 2002). As an example (following Dinsmore et al. 2002), we coded an encounter history (Appendix I) for a single hen for one season, where the commented section included the bird's unique information, followed by values for k, l, m, f, and the number of birds with that

Table 2. Candidate models used to examine the effects of nest and hen-specific information on daily survival of radio-tagged Rio Grande wild turkey hens on the Edwards Plateau of Texas during 2005-2007.

Model notation	Number of parameters	Deviance	AIC$_c$[a]	w_i
S Days on nest	2	237.11	0	0.420
S [Juv (Days on nest) ≠ Ad (Days on nest)]	3	235.82	0.71	0.297
S [Stable (Days on nest) ≠ Declining (Days on nest)]	3	236.28	1.17	0.236
S [Nest attempt]	2	242.53	5.42	0.028
S (Constant)	1	247.89	8.78	<0.01
S [Hen age]	2	246.77	9.66	<0.01
S [Age since capture]	2	246.80	9.69	<0.01
S [Cumulative days on nest]	2	247.61	10.50	<0.01
S [Nested]	2	247.88	10.77	<0.01

[a] Minimum -2lnL = 237.1138.

unique encounter history and our individual covariates. Because of our *a priori* expectation of age and regional variation, we incorporated both into the best fitting model, after analyzing our initial model set, in an attempt to optimize model selection procedures (Norman et al. 2004). If addition of these variables, however, did not change $AIC_c \geq 2$ units, we considered that model non-competitive and focused interpretation on the best fitting model without inclusion of age or regional variation (Burnham & Anderson 2002:131). In addition, for the data collected from 2005 though 2007, we computed odds ratios estimating the likelihood of nest initiation between study regions, hen ages and good vs poor precipitation years to evaluate our use of these variables in our candidate models.

Results

We captured and radio-tagged 304 Rio Grande wild turkey hens between 2001 and 2007, with more hens captured in the region characterized by stable (170) vs declining (134) turkey abundance. Due to mortalities, transmitter failures or transmitter loss before the breeding season, 241 individual hens were radio-tagged and available during ≥ 1 breeding season. We tracked 55, 73, 91, 34, 56, 55 and 45 hens during the reproductive season in the years of 2001-2007, respectively. We tracked 135 hens for one year, 61 for two, 32 for three, 10 for four, and three for five. No hens were tracked consecutively for > 5 breeding seasons, although several hens were recaptured after transmitter failure and were re-entered in the data set the year following capture.

The odds of a Rio Grande wild turkey hen initiating a nest during 2007 (i.e. a good year) were 4.55 (95% CI: 1.78-11.66) times higher than the odds of a hen initiating a nest during 2005-2006 (i.e. poor years). We found no evidence of differences in odds of a hen initiating a nest between stable vs declining regions (odds ratio: 1.51; 95% CI: 0.587-3.857) and no difference in the odds of adult hens initiating more nests than juveniles during good vs poor years (odds ratio: 2.92; 95% CI: 0.907-3.69).

The best-approximating model indicated that hen survival varied according to a 3-period trend within the breeding season (see Table 1). Model averaged daily survival estimates (with unconditional standard errors) for the first period (daily survival within the initial nesting period; 25 March - 21 April) were 0.9992 (0.00058) and 0.9971 (0.00093) for stable and declining regions, respectively. Daily survival estimates for the second (daily survival within the renesting period; 22 April - 12 June) and third (daily survival within the senescence period; 13 June - 20 July) were 0.9986 (0.00061) and 0.9990 (0.00040) for the stable, and 0.9968 (0.0010) and 0.9961 (0.00099) for the declining regions, respectively. Model-averaged breeding season survival was much higher for birds in the stable region (0.88; 95% CI: 0.78-0.94) than for birds in the declining region (0.67; 95% CI: 0.56-0.78).

Using data collected during the intensive reproductive study focused on nest and hen-specific variation (2005-2007), we documented 31 mortality events and the best fitting model was one in which hen survival was associated with the number of days spent incubating (see Table 2). While we tested for both age and regional differences based on this model, none were evident based on the AIC_c values. Based on our fixed breeding period of 118 days, hens that did not nest (e.g. DN = 0) had a daily survival estimate of 0.99, with an expected breeding season survival of 86%. The number of non-nesting juveniles and adults varied during 2005-2007 across the total number of hens radio-tracked for breeding season (Table 3). Average number of days per nesting attempt during this period was 13 (SE = 1.01) for the stable region vs 18 (SE = 1.24) for the declining region. Juvenile and adult hens in the stable region spent an average of 22.31 (SE = 10.12) and 21.26

Table 3. Percentage of Rio Grande wild turkey hens (N) that nested according to age class (Juvenile or Adult) of a total of 156 radio-tagged hens tracked on the Edwards Plateau of Texas during 2005-2007.

Population status	Age class	Year 2005 % (N)	Year 2006 % (N)	Year 2007 % (N)	Pooled % (N)
Stable	Juvenile	47 (30)	100 (1)	50 (2)	48.5 (33)
	Adult	68.8 (16)	84.8 (26)	88.9 (18)	81.7 (60)
Declining	Juvenile	0 (0)	40 (15)	100 (4)	52.6 (19)
	Adult	60 (10)	33 (12)	85 (20)	64.3 (42)

(SE = 11.96) total days on nests, whereas juvenile and adult hens in the declining region spent 16.50 (SE = 15.96) and 28.56 (SE = 14.71) total days on nests.

Discussion

Our results indicate that differences in breeding season survival of female Rio Grande wild turkeys on regions of the Edwards Plateau of Texas that exhibited stable vs declining turkey abundance since the late 1970s are due to the amount of time each hen spends incubating. Variation in hen survival was best accounted for by partitioning the breeding season into general periods of nesting activity (initial nesting, renesting and post-nesting periods; Melton 2007). Differences in breeding season survival over these periods were largely attributable to our regional classification, as those regions characterized by historically stable populations had much higher breeding season survival (0.88) than locations where abundance had declined since the late 1970s (0.67). Our definition of the breeding season (25 March - 20 July; 118 days), based on seven years of data, was shorter than the breeding season defined by Miller et al. (1995), who included the pre-breeding dispersal period through the end of brooding activities (15 March - 15 August; 154 days). Using the period from Miller et al. (1995), and assuming the daily survival from our study, survival in our declining region (0.59) was similar to the survival (0.62) documented by Miller et al. (1995), whereas our estimate for the stable region (0.87) was much higher. Survival of hens during the breeding season in our stable region is among the highest reported for Rio Grande wild turkeys (Miller et al. 1995), but is similar to values reported for eastern wild turkeys *M. g. silvestris* (e.g. 0.81 (Palmer et al. 1993), 0.74-0.86 (Roberts et al. 1995) and 0.72 (Wright et al. 1996)).

Life-history theory predicts that in variable environments, such as the semiarid regions of Texas (Riskind & Diamond 1988), limiting or foregoing reproduction (i.e. the environmental constraint hypothesis; Gasparini et al. 2006) may in turn decrease mortality risk (Stearns 1976). Exposure of turkeys to potential causes of mortality is highest during the reproductive season due to nesting activities (Vangilder 1992, Vangilder et al. 1987, Vander Haegen et al. 1988, Palmer et al. 1993). Speake (1980) identified the period of incubation and the first two weeks of brooding as the most likely time

for hen predation to occur; however, Hubbard et al. (1999a) and Vangilder & Kurzejeski (1995) found no relationship between eastern wild turkey hen survival and nest-specific activities. We found that differences in hen survival within a study area, but not between regions, were attributable to hen-specific characteristics (e.g. days spent incubating).

During good years for reproduction (2001 and 2007), we predicted that the number of breeding individuals would increase, and that survival would subsequently decline (Murdoch 1966, Charnov 1993). Although the number of Rio Grande wild turkey hens that nested during 2005-2007 followed this general pattern, our prediction that hen survival would differ between unproductive and productive seasons was not supported by data. We found that hens were more likely to nest during years with higher precipitation than in years with limited precipitation, as did Miller et al. (1995). Adult females also had a higher probability of nesting than juveniles across all years. Juvenile hens may forego the physiological expense of renesting in favour of increasing their likelihood of survival (Stearns 1976, Martin 2002), and this contention was supported by our modeling results ($w_i = 0.332$). Thus, we suggest that maximizing survival of breeding hens relative to reproductive output on the Edwards Plateau of Texas seems to be driven by the reproductive season phenology; these differences in turn are driven by environmental variation related to precipitation timing and amount (Moran 1953, Miller et al. 1995, Schwertner et al. 2005).

Although further research is needed to determine exactly why these differences in hen survival exist, it is likely that these answers ultimately will be tied to differences in habitat and related land uses as climatic and edaphic factors are essentially identical across our study sites. Because the oak-juniper savannah in the Edwards Plateau is a disturbance-maintained community (Fuhlendorf et al. 2008, Taylor & Smeins 1994), creating and maintaining ample usable space for reproductive activities (Badyaev 1995, Guthery 1997) should diminish nest predation, hence reducing the need for long-distance movements by hens between nesting attempts. Should managers wish to implement habitat management practices designed to increase hen survival during the reproductive season prior to completion of further research, we suggest long-term monitoring of population responses to these habitat changes. Because precipitation cannot be experimentally controlled, but can provide suitable habitat nearly any-

where within our study regions during good years, it is critically important to evaluate management practices in the long term in these semiarid regions so that population responses to habitat manipulation can be differentiated from those caused by the boom-bust dynamics common to galliforms in this region.

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Appendix I.

Example encounter history:/*RGWT-2274-0.204-A*/6 118 118 0 1 2 5 1 52 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 27 28 29 30 31 32 33 34 35 36 37 38 39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 2 0 0 0 0 0;