A RANGE-WIDE META-ANALYSIS OF WILD TURKEY NESTING PHENOLOGY AND SPRING SEASON OPENING DATES

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Abstract: Timing of nesting is an important consideration when setting opening dates for spring male-only wild turkey (*Meleagris gallopavo*) hunts. We conducted a meta-analysis in which we used mean dates of incubation initiation from 58 studies to evaluate *a priori* models hypothesized to predict turkey nesting phenology across the species' range. Models were based on geographic setting, climate, and management activities, and had weak to moderate explanatory power (Range R^2_{adj} = 0.12–0.55). We developed 2 *post hoc* models to better predict mean incubation date, and used one of these to generate a range-wide map predicting timing of nest incubation. A second model selection exercise focused solely on the eastern subspecies of wild turkey, and our best model of incubation date included population status and a cubic term for latitude (n = 41, R^2_{adj} = 0.80). Lastly, we compared incubation initiation dates to opening dates for spring male-only hunting in each jurisdiction. Of 34 states and provinces for which we obtained data, 25 opened spring hunting >2 weeks prior to the mean date of incubation initiation, and 18 of these also allowed fall either-sex hunting. This finding is noteworthy because extended fall seasons and spring hunting during the pre-nesting period can lead to additive and unsustainable levels of female kill.

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Research has indicated that opening spring male-only wild turkey hunting before most females have begun nesting can lead to high rates of illegal female kill, potentially reducing poult recruitment and depressing populations (e.g., Kimmel and Kurzejeski 1985, Vangilder and Kurzejeski 1995, Norman et al. 2001*b*). Further, some researchers report that males gobble more or are more susceptible to calling after females have begun nesting (Bevill 1974, Hoffman 1990, Miller et al. 1997*a*). These facts suggest that opening dates for spring gobbler seasons should coincide with the initiation of incubation by females (Healy and Powell 2000). However, managers often are pressured to set early opening dates for seasons, as many hunters believe that male tur-

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keys call and display more aggressively early in the breeding season and thus may be more responsive to calling. Consequently, accurate knowledge of nesting and gobbling phenology is important for managers setting opening dates for spring gobbler hunting, as opening seasons too early can have negative consequences for turkey populations, while opening seasons too late may lead to reduced hunt quality and dissatisfaction among hunters.

Researchers have studied timing of breeding by wild turkeys at numerous localities across their range, and several authors have investigated factors leading to variation in nesting phenology between years (e.g., Porter et al. 1983, Vangilder and Kurzejeski 1995, Miller et al. 1998, Norman et al. 2001*a*). However, there has been no effort to quantitatively describe or predict spatial patterns in the timing of breeding by wild turkeys across their range. Perhaps the simplest model to predict breeding phenology would be latitude alone. Expanding on this, Hopkins' law of bioclimatics predicts spring phenology based on latitude, longitude, and elevation, and may be a more useful geographic predictor (Hopkins 1938, McCombs 1997, McCombs et al. 1997). Alternatively, factors relating to the progression of seasonal change, particularly those relating to climate or the phenology of development of plant and animal foods, might also serve as good predictors of timing of breeding. Finally, inclusion of biological or management information on the turkey population may also improve models.

Here we present a meta-analysis to improve our understanding of range-wide patterns in the timing of nesting by wild turkeys. We used existing field studies to obtain estimates of the mean date of Initiation of Nest Incubation (INI) at numerous locations across North America, and evaluated factors such as climate and geographic setting as predictors of nesting phenology. We also used our database to evaluate the extent to which states and provinces had timed the opening of spring seasons to coincide with the onset of nesting and thereby reduce exposure of non-incubating hens to risk of illegal kill.

METHODS

We compiled a comprehensive database on wild turkey breeding phenology from published studies, Federal Aid in Wildlife Restoration (Pittman-Robertson) reports, state and federal reports, and through a request to turkey biologists for unpublished data. We then searched each study for an estimate of the interannual mean date of incubation initiation by female turkeys or for raw data sufficient to calculate one. We attempted to standardize the data extracted from each report to the maximum extent possible. We converted calendar dates to the Day of the Year (DoY), calculated as the cumulative number of days since January 1, thereby quantifying breeding phenology on a continuous and standardized numeric scale. We took into account the extra day in February during leap years. Interannual means were calculated as the average of annual means, rather than the average of individual nesting dates. We considered only incubation initiation dates for first nests (vs. renests), and discarded a study if we were unable to obtain a mean date estimated solely from first nest attempts. If authors reported hatching dates we back-calculated the incubation initiation date by assuming a 28-day incubation period (Eaton 1992). If the date of initiation of egg-laying was reported, we added 1 day for each egg plus 2 additional days, the typical interval between the initiation of laying and incubation (Schorger 1966, Eaton 1992).

In some cases, authors reported median incubation initiation dates, but did not report means or provide the raw data necessary to calculate means. We expected that median incubation initiation dates typically would occur earlier than mean incubation dates, as the distribution of nest initiation dates is often slightly right-skewed for wild turkeys (e.g., Roberts 1993, Kienzler et al. 1995; D. H. Jackson, W. H. Bunger, and T. W. Little, Iowa Department of Natural Resources, unpublished report). To evaluate the necessity of a correction factor to estimate mean nesting dates from median dates, we carried out a Wilcoxon signed rank test (Sokal and Rohlf 1995) of the difference between pairs of mean and median incubation initiation dates from studies for which both parameter estimates were reported or could be calculated. Then, in the event that the difference between mean and median incubation initiation dates differed from zero, we would use the median value of the within-study differences as a correction factor to estimate mean incubation initiation dates for studies reporting only median nesting dates.

We appended a number of covariates to each mean incubation initiation date (Table 1). We recorded whether the research was conducted on an established population or newly-translocated individuals (Status). We recorded the location of each study area in latitude and longitude coordinates (decimal degrees). We estimated elevation for each study as the midpoint between the highest and lowest points on the study area. A Relative Phenologic Index (RPI), which predicts the net delay in spring phenology for a site, was calculated for each study site based on its latitude, longitude, and elevation (Hopkins 1938, McCombs 1997, McCombs et al. 1997). For this we used a reference point at sea level, south of the southernmost study site, and west of the westernmost site (26°00′N, 123°00′W, elevation = 0 m). The RPI for each study site relative to this reference point was calculated by assuming a 4-day delay in growing season phenology for each 1° increase in latitude northwards, each 5° increase in longitude eastwards, and each 122 m increase in elevation (Hopkins 1938). For each study area we obtained 30-year averages (1971–2000) of 3 climatic variables: mean annual snowfall (cm), median date of the last spring frost (DoY date), and median length of the annual frost-free period (Environment Canada 2002, National Oceanic and Atmospheric Administration 2004). In most cases we took values for climate normals from the nearest weather station (within <0.25° latitude and longitude); when multiple stations were approximately

Table 1. List of variables included in models to explain variation in the timing of the mean date of Initiation of Nest Incubation (INI) by wild turkeys.

Variable	Description	Units
Elev	Elevation midpoint of the study area	m
Frostfree	Median annual period between the last spring frost and first fall frost	Days
Hunt	Whether or not the population was open to spring gobbler hunting	Y or N
INI	Mean date of Initiation of Nest Incubation at a location (response variable)	Day of Year
LastFrost	Median date of the last frost each spring	Day of Year
Lat	Latitude of the study area	Decimal Degrees
Long	Longitude of the study area[a]	Decimal Degrees
RPI	Relative Phenologic Index, predicting phenologic delay based on Hopkin's (1938) Bioclimatic Law (reference point = 26.00°N, 123.00°W, elevation = 0 m)	Days
Status	Whether the population was established (E) or represented first-year translocated birds (NT)	E or NT
Snowfall	Mean annual snowfall at a given location	cm

[a] Though sometimes designated as a negative value for locations in the western hemisphere (i.e., west of the Greenwich prime meridian, longitude 0°), for our analyses longitude was always specified as a positive value.

equidistant or were located within a study area values of climate normals were averaged.

We developed a series of *a priori* linear models to explain variability in the timing of incubation initiation across the range of wild turkeys. We did not include geographic variables in models specifying climatic variables; climate is strongly influenced by location and so inclusion of both would likely lead to overfitting or multicolinearity. The response variable was incubation initiation date (INI), and we fit models using JMP statistical software (Version 4.0.4; SAS Institute, Cary, North Carolina, USA). To assess model fit we inspected a residual plot and carried out a goodness-of-fit test on our most complex model (Burnham and Anderson 2002). Models were then evaluated and ranked using information-theoretic model selection techniques (Burnham and Anderson 2002). This approach favors models having greater explanatory power and penalizes models based on complexity, helping to identify the most parsimonious model(s). For reference and to gain an appreciation of the explanatory power of our models, we included a null model (i.e., intercept only) in the set of candidate models. Models within the set were evaluated based on Akaike's Information Criterion adjusted for small sample size (AIC_c), AIC_c differences (Δ_i), explanatory power (R^2_{adj}), and Akaike weights (ω_i). We ordered models from largest to smallest ω_i, and then to identify a 95% confidence set of best models sequentially summed ω_i until $\Sigma\, \omega_i \geq 0.95$.

We applied our best model to a Digital Elevation Map (DEM) encompassing the contemporary range of wild turkeys to create a map of predicted mean incubation initiation dates. The DEM base map was obtained from the USGS global digital elevation database (GTOPO30; USGS EROS Datacenter, Sioux Falls, Missouri, USA), which has a resolution of 30 arc-seconds (approx. 1 km). The range of wild turkeys is highly fragmented, particularly in western North America, but is expanding rapidly. Consequently, we did not restrict model application to the extant species range, but rather applied it across all of southern Canada, the contiguous United States, and northern Mexico. To illustrate any spatial patterns of systematic error we plotted residual errors for each observation on the map.

Of the 5 subspecies, eastern wild turkeys (*M. g. silvestris*) occupy the largest and most contiguous range, and have been most frequently studied. We carried out a second model selection exercise, similar to that described above, but in this case restricted our dataset to eastern wild turkeys. As above, a set of *a priori* models were developed based on factors we suspected might be important within the range of this subspecies, and mean incubation initiation date was the response variable. Data were insufficient to model other subspecies individually.

To assess the extent to which opening dates for spring gobbler hunting seasons are synchronized with initiation of nesting we compared mean incubation initiation dates to spring 2004 opening dates for hunting in each state or province. In cases where we obtained >1 estimated incubation initiation date for a jurisdiction we took the average of the differences between the incubation initiation dates and the opening date of hunting. We accounted for the fact that 2004 was a leap year in our calculations, and considered the location of study sites for states having different opening dates in different management regions.

RESULTS

Our final dataset comprised interannual mean incubation initiation dates from 58 locations in 33 states plus Ontario (Figure 1). We were able to obtain estimates of both mean and median incubation initiation dates from 18 studies. Median incubation initiation dates occurred 1.5 days earlier than mean incubation initiation dates ($P = 0.033$), and we used this difference as a correction factor for 10 studies reporting only median nesting dates. Studies included all 5 subspecies of wild turkey, and mean incubation initiation dates ranged from 14 April in coastal Georgia to 7 June for newly translocated turkeys in central Ontario (DoY 104–158; mean = DoY 129 [9 May]). Elevation midpoints of study sites ranged from 4–2,630 m. The 7 sites having elevations >1,200 m were located in the western United States (AZ, CO, NM, OR, SD, WY), while sites below 120 m elevation were concentrated in the Southeast (FL, GA, MS, NC, SC, TX, VA).

All of our *a priori* models had some ability to

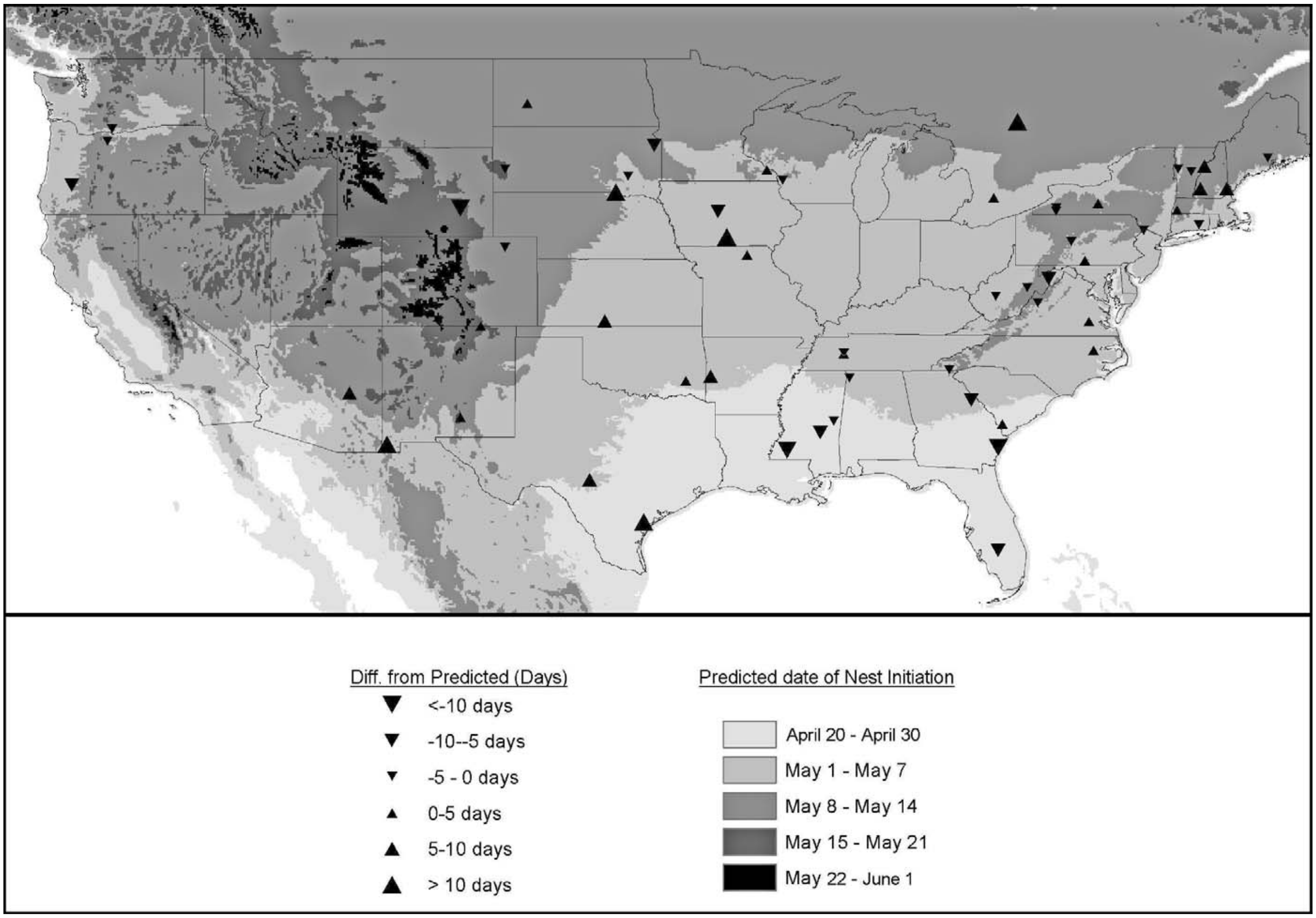

Fig. 1. Predicted Initiation of Nest Incubation (INI) dates for established wild turkey populations, developed by applying the model 16 (Table 3) to a Digital Elevation Model (DEM) of North America. Triangles represent the locations of studies used in our meta-analysis; negative Differences from Predicted (i.e., residual errors) indicate that the actual INI date at that location was earlier than predicted.

predict mean incubation initiation date across the range of wild turkeys, and all models in the 95% confidence set (models 1–5) accounted for >50% of variation in INI date (Table 2). Latitude, longitude, and elevation, and interactions between latitude and both longitude and elevation all appeared to be important predictors of mean incubation initiation date. Population status (established or newly translocated) was an important predictor of incubation initiation date, with newly translocated turkeys typically nesting 10–15 days later than established populations. Presence or absence of spring hunting appeared to explain some variability in mean incubation initiation date, though most studies of nonhunted populations were of recently translocated birds. Climatic variables we tested accounted for up to 25% of the variation in mean incubation initiation date. Our model specifying the Hopkins RPI index (model 8) also had some explanatory power (R^2_{adj} = 0.26). However, the coefficient for RPI indicated that it provided a >5-fold overestimate of phenologic delays for wild turkeys ($\beta_{RPI} = 0.18 \pm 0.040$).

Based on results from our *a priori* model fitting and selection, we developed 2 *post hoc* models combining explanatory power, ecological insight, and parsimony (models 16 and 17; Table 3). Both models included population status, and the model including latitude, longitude, and elevation accounted for approximately half of the variation in mean incubation initiation date (model 16; $R^2_{adj} = 0.49$). We applied this model to a DEM of North America to create a map predicting the timing of mean incubation initiation for established populations across the range of wild turkeys (Figure 1). The second *post hoc* model (model 17) included median date of the last spring frost and population status, and was able to account for much of the variation in mean incubation initiation date ($R^2_{adj} = 0.47$).

Our database included estimated incubation initiation dates for 41 populations of eastern wild turkeys. Model selection indicated that, after controlling for population status, a cubic polynomial term for latitude was the best predictor of the timing of incubation initiation for eastern wild turkeys (Table 4; Figure 2). Length of the frost-free period and date of the last spring frost also were good predictors of incubation initiation date (Table 4).

Comparing nesting dates to 2004 spring gobbler season opening dates indicated that of 34 states and provinces for which we obtained data, all but one (CT) opened their hunting season earlier than the mean in-

Table 2. Fit of *a priori* models conceived to explain range-wide variation in the timing of Initiation of Nest Incubation (INI) by wild turkeys (n = 58).

No.	Model (*a priori*)	SSE	K	AIC$_c$	Δ_i	R^2	R^2_{adj}	ω_i
1	INI = 58.0 + 1.12(*Lat*) + 0.30(*Long*) − [0.090(*Lat* − 39.02) × (*Long* − 88.80)] + ϵ	2229.9	5	222.8	0.0	0.55	0.52	0.41
2	INI = 69.73 + 0.97(*Lat*) + 0.24(*Long*) − 0.00059(*Elev*) − [0.065(*Lat* − 39.02) × (*Long* − 88.80)] − [0.00080(*Lat* − 39.02) × (*Elev* − 572.38)] + ϵ	2052.9	7	223.1	0.3	0.59	0.55	0.35
3	INI = 59.78 + 1.11(*Lat*) + 0.28(*Long*) + 0.00060(*Elev*) − [0.088(*Lat* − 39.02) × (*Long* − 88.80)] + ϵ	2225.5	6	225.2	2.4	0.55	0.52	0.12
4	INI = 108.11 + 0.59(*Lat*) + 0.0058(*Elev*) + {*Status*: [NT or E] ± 7.57} + ϵ[a]	2393.1	5	226.9	4.1	0.52	0.49	0.05
5	INI = 58.47 + 1.22(*Lat*) + 0.25(*Long*) + 0.00079(*Elev*) − [0.076(*Lat* − 39.02) × (*Long* − 88.80)] − [0.00022(*Lat* − 39.02) × (*Elev* − 572.38)] − [0.00014(*Long* − 88.80) × (*Elev* − 572.38)] − [0.000042(*Lat* − 39.02) × (*Long* − 88.80) × (*Elev* − 572.38)] + ϵ	1996.5	9	227.0	4.2	0.60	0.54	0.05
6	INI = 101.40 + 0.68(*Lat*) + 0.0011(*Elev*) − [0.0015(*Lat* − 39.02) × (*Elev* − 572.38)] + ϵ	2533.3	5	230.2	7.4	0.49	0.46	0.01
7	INI = 94.57 + 0.84(*Lat*) + 0.0051(*Elev*) + {*Hunt*: [N or Y] ± 3.18} + ϵ[b]	3101.3	5	241.9	19.1	0.37	0.34	0.00
8	INI = 110.77 + 0.18(*RPI*) + ϵ	3622.3	3	246.2	23.4	0.27	0.26	0.00
9	INI = 93.98 + 0.82(*Lat*) + 0.0046(*Elev*) + ϵ	3523.9	4	247.0	24.2	0.29	0.26	0.00
10	INI = 144.51 − 0.095(*Frostfree*) + ϵ	3704.5	3	247.5	24.7	0.25	0.24	0.00
11	INI = 108.89 + 0.17(*LastFrost*) + ϵ	3709.0	3	247.6	24.8	0.25	0.24	0.00
12	INI = 96.78 + 0.81(*Lat*) − 0.032(*Long*) + 0.0050(*Elev*) + ϵ	3516.3	5	249.2	26.4	0.29	0.25	0.00
13	INI = 96.29 + 0.82(*Lat*) + ϵ	3962.2	3	251.4	28.6	0.20	0.19	0.00
14	INI = 124.84 + 0.044(*Snowfall*) + ϵ	4279.9	3	255.9	33.1	0.14	0.12	0.00
15	INI = 128.46 + ϵ (null model)	4946.4	2	262.1	39.3	0.00	0.00	0.00

[a] *Status* is a categorical variable: If *Status* = NT, then add 7.57 days. If status = E, then subtract 7.57 days.
[b] *Hunt* is a categorical variable: If *Hunt* = N, then add 3.18 days. If Hunt = Y, then subtract 3.18 days.

cubation initiation date (Table 5). Four northeastern states opened seasons during the week preceding the mean incubation initiation date (ME, NY, PA, and VT), and another 4 states (MA, NH, WI, and WV) opened seasons 8–14 days prior to the INI date. On average, the remaining 25 jurisdictions (74%) opened hunting 28 days prior to the mean incubation initiation date, with 3 opening hunting ≥40 days prior (FL, SC, and TX).

DISCUSSION

Through our review of existing field studies, we were able to construct a database of estimates of the timing of nesting by wild turkeys across most of the species' range. Using this, we identified geographic and climatic factors that related to regional variability in turkey nesting phenology. Managers may find the associated models and figures useful when making decisions regarding opening dates for spring hunting seasons. If the figures are deemed too general, readers can use the formulae and estimates presented in Tables 3–5 to obtain more precise estimates for a locality (see Table 1 for details on measurement units).

Our best models accounted for 50–80% of the variation in timing of incubation by wild turkeys (Tables 2–4). We presume that there were other important drivers of nesting phenology that we could not test, such as vegetation cover (e.g., Lazarus and Porter 1985, Day et al. 1991, Vander Hagen et al. 1991). Another potentially important factor is the effect of hunting on timing of nesting. However, because very few studies we reviewed were of unhunted wild turkey populations, our test of this relationship was inconclusive. We also expect that some portion of the residual error in our models resulted from inaccuracy in estimation of mean incubation initiation dates during field studies. Though we made every effort to standardize the data extracted, studies we reviewed used a variety of methods to measure reproductive phenology. Further, 60% of the estimates we obtained were derived from ≤3 years monitoring, and many studies were based on small numbers of individual turkeys in any one year. Since reproductive phenology is highly variable across

Table 3. *Post hoc* models explaining range-wide variation in the timing of Initiation of Nest Incubation (INI) by wild turkeys (n = 58). Values for AIC differences (Δ_i) were calculated based on the best model in the *a priori* set (Table 2).

No.	Model (*post hoc*)	SSE	K	AIC$_c$	Δ_i	R^2	R^2_{adj}
16	INI = 116.53 + 0.57(*Lat*) − 0.091(*Long*) + 0.0070(*Elev*) + {*Status*: [NT or E] ± 7.83} + ϵ[a,b]	2332.6	6	227.9	5.1	0.53	0.49
17	INI = 115.90 + 0.16(*LastFrost*) + {*Status*: [NT or E] ± 7.46} + ϵ[a]	2515.6	4	227.4	4.6	0.49	0.47

[a] *Status* is a categorical variable: If *Status* = NT, then add the indicated number of days. If status = E, then subtract the indicated number of days.
[b] See also Figure 1.

Table 4. Fit of *a priori* models explaining variation in the timing of Initiation of Nest Incubation (INI) by the eastern subspecies of wild turkeys (n = 41).

No.	Model (*a priori*)	SSE	K	AIC_c	Δ_i	R^2	R^2_{adj}	ω_i
18	INI = 126.88 + 0.15(*Lat*) + 0.0044(*Lat* − 39.27)^2 + 0.036(*Lat* − 39.27)^3 + {*Status*: [NT or E] ± 5.56} + ε[a,b]	665.7	6	128.7	0.0	0.82	0.80	0.81
19	INI = 159.18 − 0.15(*Frostfree*) + {*Status*: [NT or E] ± 7.80} + ε[a]	858.4	4	133.8	5.1	0.76	0.75	0.06
20	INI = 101.11 + 0.28(*LastFrost*) + {*Status*: [NT or E] ± 7.88} + ε[a]	871.7	4	134.4	5.7	0.76	0.75	0.05
21	INI = 92.49 + 1.04(*Lat*) − 0.0022(*Elev*) − [0.0025(*Lat* − 39.27) × (*Elev* − 351.79)] + {*Status*: [NT or E] ± 6.28} + ε[a]	766.5	6	134.5	5.8	0.79	0.76	0.05
22	INI = 80.35 + 1.32(*Lat*) + {*Status*: [NT or E] ± 6.10} + ε[a]	925.9	4	136.9	8.2	0.74	0.73	0.01
23	INI = 81.13 + 1.14(*Lat*) + 0.11(*Long*) − 0.0054(*Elev*) − [0.036(*Lat* − 39.27) × (*Long* − 82.27)] − [0.0030(*Lat* − 39.27) × (*Elev* − 351.79)] − [0.00034(*Long* − 82.27) × (*Elev* − 351.79)] − [0.000040(*Lat* − 39.27) × (*Long* − 82.27) × (*Elev* − 351.79)] + {*Status*: [NT or E] ± 6.66} + ε[a]	614.4	10	138.3	9.6	0.83	0.79	0.01
24	INI = 80.97 + 1.28(*Lat*) + 0.0023(*Elev*) + {*Status*: [NT or E] ± 6.23} + ε[a]	912.3	5	138.9	10.2	0.75	0.73	0.01
25	INI = 86.43 + 1.10(*Lat*) + 0.042(*Long*) − 0.0017(*Elev*) − [0.015(*Lat* − 39.27) × (*Long* − 82.27)] − [0.0024(*Lat* − 39.27) × (*Elev* − 351.79)] + {*Status*: [NT or E] ± 6.33} + ε[a]	759.8	8	140.2	11.5	0.79	0.75	0.00
26	INI = 111.99 + 0.22(*RPI*) + {*Status*: [NT or E] ± 7.94} + ε[a]	1020.5	4	140.9	12.2	0.72	0.70	0.00
27	INI = 82.24 + 1.27(*Lat*) − 0.010(*Long*) + 0.0023(*Elev*) + {*Status*: [NT or E] ± 6.30} + ε[a]	912.1	6	141.7	13.0	0.75	0.72	0.00
28	INI = 129.39 + 0.048(*Snowfall*) + {*Status*: [NT or E] ± 8.33}+ ε[a]	1381.1	4	153.3	24.6	0.62	0.60	0.00
29	INI = 63.0 + 1.65(*Lat*) + ε	1608.8	3	157.1	28.4	0.55	0.54	0.00
30	INI = 63.01 + 1.65(*Lat*) − 0.00017(*Elev*) + ε	1608.7	4	159.6	30.9	0.55	0.53	0.00
31	INI = 127.78 + ε (null model)	3601.9	2	187.8	59.1	0.00	0.00	0.00

[a] *Status* is a categorical variable: If *Status* = NT, then add the indicated number of days. If status = E, then subtract the indicated number of days.
[b] See also Figure 2.

individuals and between years (see below), long-term monitoring and large samples are required to obtain a reliable estimate of the interannual mean incubation initiation date.

Inclusion of interaction terms between latitude and longitude and latitude and elevation yielded models that more fully accounted for variation in mean INI date (Table 2; models 1, 2, 3, 5, and 6). However, elevation of study sites increased from east to west, leading to a poor ability to discriminate statistically between effects of elevation and longitude, likely accounting for the observed interaction between latitude and longitude. The interaction between latitude and elevation, which suggests turkeys nest later as elevation increases in the South, but earlier at higher elevations in the North, is counterintuitive. It may be that, due to severity of conditions at higher elevations, turkeys on northern sites made greater use of lowlands and riparian areas (e.g, Schmutz and Braun 1989). If this was the case, our method of estimating study area elevations as the midpoint between the highest and lowest points would overestimate the mean elevation at which turkeys occurred on northern sites. Consequently, we suspect that these interactions were spurious and chose to base our *post hoc* model relating INI date to geographic setting (model 16; Figure 1) or the first order model (model 12).

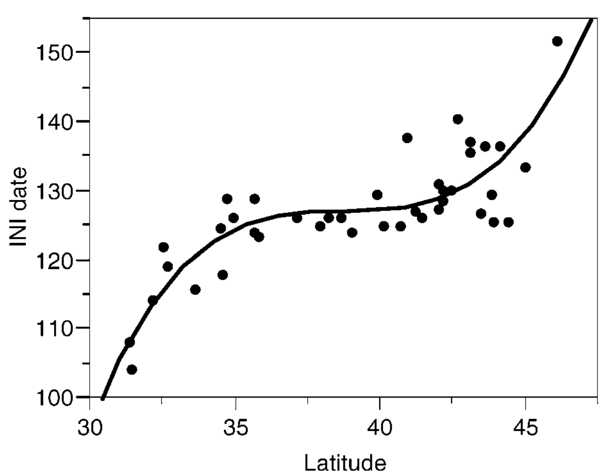

Fig. 2. Cubic fit of latitude as a predictor of the mean date of incubation initiation for established populations of eastern wild turkeys (see Table 4, model 18).

Our map of nesting dates (Figure 1) should have value as a predictor of nesting phenology, though 2 caveats are necessary. Accuracy of estimated incubation initiation dates can be gauged for localities proximate to the study sites used to develop the model, but many areas are distant from any of these study sites. Greater uncertainty must be associated with these unverified estimates. Also, examination of the map reveals some pattern in the spatial distribution of errors, in that the model generally predicted early in the Southwest and late in the Southeast. We urge that individuals using this map pay attention to patterns in the surrounding residual errors when estimating nesting dates.

Table 5. Mean date of initiation of nest incubation, opening dates for 2004 spring gobbler season, and information on fall turkey hunting for each of 34 jurisdictions for which we obtained nesting data.

State or province	*n*[a]	Mean INI date (DoY)[b]	Spring opening date (DoY)[c]	Difference (days)	Fall hunting[d]
Alabama	1	4/28 (118)	4/1 (92)	26	MO
Arizona	1	5/19 (139)	4/23 (114)	25	ES
Arkansas	1	5/7 (127)	4/3 (94)	33	MO
Colorado	2	5/12 (132)	4/10 (101)	31	ES
Connecticut	1	5/6 (126)	5/5 (126)	0	ES
Florida	1	4/19 (109)	3/6 (66)	43	MO
Georgia	2	4/20 (110)	3/20 (80)	30	NFH
Iowa	2	5/10 (130)	4/12 (103)	27	ES
Kansas	1	5/10 (130)	4/14 (105)	25	ES
Maine	1	5/6 (126)	5/3 (124)	2	ES
Massachusetts	1	5/10 (130)	4/26 (117)	13	ES
Minnesota	1	5/8 (128)	4/14 (105)	23	ES
Mississippi	3	4/24 (114)	3/20 (80)	34	ES
Missouri	1	5/5 (125)	4/19 (110)	15	ES
New Hampshire	3	5/16 (136)	5/3 (124)	12	ES
New Jersey	1	5/7 (127)	4/19 (110)	17	ES
New Mexico	2	5/22 (142)	4/15 (106)	36	ES
New York	3	5/9 (129)	5/1 (122)	7	ES
North Carolina	2	5/5 (125)	4/10 (101)	24	NFH
North Dakota	1	5/15 (135)	4/10 (101)	34	ES
Oklahoma	1	5/5 (125)	4/6 (97)	28	ES
Ontario	2	5/17 (137)	4/25 (116)	21	NFH
Oregon	2	5/2 (122)	4/15 (106)	16	ES
Pennsylvania	2	5/7 (127)	5/1 (122)	5	ES
South Carolina	1	5/2 (122)	3/15 (75)	47	NFH
South Dakota	4	5/11 (131)	4/10 (101)	30	ES
Tennessee	2	5/2 (122)	4/3 (94)	28	ES
Texas	2	5/9 (129)	3/27 (87)	42	ES
Vermont	2	5/8 (128)	5/1 (122)	6	ES
Virginia	2	5/6 (126)	4/10 (101)	25	ES
Washington	1	5/4 (124)	4/15 (106)	18	ES
West Virginia	4	5/6 (126)	4/26 (117)	9	ES
Wisconsin	1	5/7 (127)	4/14 (115)	12	ES
Wyoming	1	5/4 (124)	4/10 (101)	23	ES

[a] Number of studies used to calculate mean nesting date.
[b] 15 days were subtracted from mean incubation initiation dates for newly translocated populations.
[c] 2004 was a Leap Year, so DoY corresponding to calendar dates is 1 greater than for non-Leap Years.
[d] NFH = No Fall turkey Hunting, ES = Either Sex fall hunt, MO = Male Only fall hunt.

Our modeling efforts were most successful when restricted to the eastern subspecies of wild turkey. This may be due in part to the reduced variability in environmental factors such as elevation, moisture, and vegetation types within the region occupied by this subspecies. We also had more complete and even data coverage for eastern wild turkeys than for other subspecies. Our best model included a cubic polynomial term for latitude and a term for population status (Table 4). This indicated that, while relatively constant around 5–9 May in the Mid-Atlantic States, incubation initiation date increased sharply from south to north in both the Southeast and Northeast (Figure 2). Reasons for this pattern might include the transition from coastal plain to more mountainous terrain in the Southeast, and the rapid increase in the prevalence of persistent snow cover in the Northeast. Median date of the last spring frost and median length of the frost-free period also were good predictors of timing of incubation for this subspecies. Interestingly, neither elevation nor longitude emerged as important predictors of nesting phenology for eastern turkeys, possibly because this subspecies occupies a narrower range of these features than does the species as a whole. It may also be the case that the smaller size of eastern mountains means that most turkeys inhabiting mountainous terrain can still make extensive use of lowlands, thereby avoiding any effect of elevation on nesting phenology (e.g., Fleming and Porter 2001).

There is considerable interannual variation in mean nest initiation dates for turkeys, with ranges of 19–28 days being observed in studies spanning ≥5 years (e.g., Vangilder and Kurzejeski 1995, Hubbard 1997, Miller et al. 1998, Thogmartin and Johnson 1999, Norman et al. 2001*a*). This variability in breeding phenology has been related to metrics of winter severity, including mean March temperature, number of subfreezing days, and snow depth (Vangilder and Kurzejeski 1995, Norman et al. 2001*a*). Thus, though photoperiod cues physiological pathways that prepare turkeys for breeding, there is still considerable plasticity in timing of reproduction. Presumably this behavioral flexibility is beneficial in turkey restoration efforts, as even when individuals are translocated over large distances they soon modify their breeding phenology to coincide with conditions at the release site.

Even with this flexibility in breeding phenology, our analyses indicated that newly translocated turkeys typically delayed nesting by 10–15 days (Tables 2–4). Of note, this effect was evident in a study comparing reproduction between translocated and established turkeys inhabiting the same area during the same years; on average, translocated individuals nested 10 days later than local birds (Benner 1989; but see Lehman et al. 2001). Three studies we reviewed followed individual turkeys for >1 breeding season after translocation. Weaver (1989) monitored 1 individual in consecutive years, and it nested 24 days earlier during its second year post-translocation. The 2 remaining studies pooled second year post-release turkeys with additional newly translocated individuals during the second year of monitoring, potentially weakening any trend in timing of breeding relative to time since release. However, both studies reported that mean nesting dates occurred earlier in the second year of study (Nguyen 2001, Shields 2001). Thus, there is some evidence that delayed breeding of translocated turkeys is limited to the year of release. Combining this observation with the facts that relocated populations all nested late regardless of the direction of translocation, and that established turkeys exhibit considerable variability in nesting phenology, we doubt that delayed nesting resulted from translocated turkeys being inflexible in their nesting phenology and poorly adapted to local seasonal cues (e.g., photoperiod). Rather, we suspect delays resulted from proximate factors such as increased time spent searching unfamiliar areas for breeding sites or mates, disrupted dominance hierarchies, or poor physical condition due to inexperience with the distribution and variety of local foods (e.g., Porter et al. 1983, Badyaev et al. 1996).

Finally, though the influence of daily weather on gobbling rates is relatively well understood, there is still uncertainty as to the effects of a number of important ecological and management factors on patterns of gobbling by male turkeys (Hoffman 1990, Kienzler et al. 1995, Miller et al. 1997*b,* Norman et al. 2001*b*). We originally designed this study to include analyses of gobbling phenology and interactions between gobbling, hunting, and nesting. However, our review of existing studies yielded only a handful of reliable estimates of gobbling chronology, few of which were accompanied by information on nesting, so we were forced to abandon this topic. However, our review made clear the need for research comparing gobbling chronology to nesting phenology, and comparing gobbling behavior between hunted and unhunted turkey populations.

Timing of Opening Dates for Spring Hunting

Setting season opening dates to coincide with the initial peak in gobbling may lead to high levels of illegal female kill (Kimmel and Kurzejeski 1985, Vangilder and Kurzejeski 1995, Miller et al. 1997*b,* Healy and Powell 2000, Norman et al. 2001*b*). This is a critical concern for managers, as harvests of even 10% of females can depress turkey populations (Healy and Powell 2000), and harvests are typically greatest during the opening days of spring seasons (Miller et al. 1997*b,* Norman et al. 2001*b*; J. Pack, West Virginia Division of Natural Resources, unpublished data). Because female wild turkeys are less vulnerable to harvest following initiation of incubation, the onset of nesting behavior is recommended as a biological benchmark for setting opening dates for spring gobbler seasons (Healy and Powell 2000, Norman et al. 2001*b*). However, only 1 state for which we obtained estimates of nesting chronology delayed hunting until the mean incubation initiation date, and only 26% of states met the less conservative criterion of delaying hunting until the onset of laying by most females (approx. 2 weeks preceding mean incubation initiation date) (Table 5). Fall and spring harvests of female turkeys may be additive in their impact on populations (Vangilder and Kurzejeski 1995, Rolley et al. 1998, Pack et al. 1999), so jurisdictions having restricted (e.g., male-only) or no fall turkey hunting seasons can perhaps afford to be more liberal in regulating spring harvests. However, 18 of 25 states (72%) that opened spring hunting >2 weeks prior to the mean incubation initiation date also allowed fall either-sex turkey hunting (Table 5).

While our comparison of opening dates and timing of nesting suggests that many management agencies do not consider nesting phenology and related illegal harvest issues when setting spring wild turkey hunting seasons, a number of other factors must also be taken into account. Other steps can be taken to limit harvests, for example restricting bag limits or the number of licenses available, and non-biological factors, including hunt quality and social and political expectations, are important considerations. For example, it is desirable to offer hunting opportunities during periods when males are gobbling vigorously and responsive to calling (Norman et al. 2001*b*). Consequently, managers must strive to set season opening dates that achieve a balance between the desire to maximize both quality and quantity of hunting opportunities, and the need to ensure harvest sustainability (e.g., Wright and Vangilder 2000). Towards this end, there is a need for research to improve our understanding of temporal patterns in gobbling propensity, effects of hunting and social factors on gobbling behavior, and seasonal trends in the susceptibility of males to calling. Further, greater knowledge of the interactive effects of breeding phenology and timing of spring hunting seasons on female kill, and the consequences of such loss of females for populations, is necessary for informed wild turkey management. In light of current limits to our understanding of these factors, it is apparent that many states, particularly those also allowing extended fall either-sex turkey hunting, are accepting higher risks when setting opening dates for spring gobbler seasons. Managers in these jurisdictions should carefully monitor wild turkey populations, as these may suffer from reduced female survival and consequently impaired population growth or even population decline, ultimately affecting harvests and hunt quality.

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