*RESEARCH ARTICLE*

**Multi-Level Modeling of The Factors Influencing Wild Turkey Reproductive Success in The Mid-Atlantic Region**

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**ABSTRACT**

Organisms interact with the environment at multiple spatial and temporal levels in a hierarchical manner. Variation in recruitment is considered a key factor in population growth of wild turkeys (*Meleagris gallopavo silvestris*) prompting biologists to investigate the factors that influence nesting success. We developed a multi-level framework to link the sequential processes affecting wild turkey recruitment during breeding and nesting periods: an individual movement model, a nest-site selection model, and a nest success model. The individual movement model (with hens as the study unit) and the nest-site selection model (with nests as the study unit) used conditional logistic regression to examine how both nest-level factors (e.g., visual obstruction) and landscape-level classifications (e.g., agricultural land use) influenced decision-making during the pre-nesting and nest-initiation periods. To enhance our understanding of nesting behavior, we also fit a known-fate model to quantify daily nest survival probabilities in relation to various predictors, including weather variables, individual hen characteristics, and landscape and nest-level habitat characteristics. These models were applied to a dataset of female wild turkeys, in Pennsylvania, USA. Hens exhibited differing patterns in habitat selection between nest and landscape-level predictors when selecting nest sites. At the nest-level, hens preferred locations with denser understory vegetation and a higher proportion of woody stem plants but avoided areas with invasive woody stem plant species. At the landscape-level, hens favored sites in an agricultural landscape at greater distances from primary roads. Our findings suggest that mowing and haying fields during peak turkey nesting periods could adversely affect nest success rates. Managing early successional vegetation along wooded field edges, fencerows, and forest clearings combined with invasive species control could be effective in enhancing the quality of turkey nesting habitat.

**INTRODUCTION**

Organisms interact with the environment at multiple nested levels, which can be described as hierarchical (Johnson 1980). For example, in Johnson’s orders of habitat selection, an animal’s selection of habitat patches within its home range (3rd order habitat selection) is dependent on the selection processes of the home range itself (2nd order habitat selection) and physical geographic range (1st order habitat selection). Focusing solely on wildlife-habitat relationships at a single level of ecological organization may ignore broader patterns, while creating a false representation of resource availability (Johnson 1980). Multi-level modelling best captures the hierarchical nature in which organisms interact with landscape features, and it can highlight opposing patterns in selection at the different levels (Buderman et al. 2023, Poizat and Pont 1996).

Nesting is a critical avian life history stage because it directly influences reproductive success and population dynamics. Primarily driven by photoperiod, other causal factors exist such as resource availability and social cues between individuals (Farner 1964). Nesting represents a stage of heightened energetic demand as individuals must expend considerable resources into nest-site selection, nest construction, incubation, and parental care (Mainwaring and Hartley 2013, Nilsson et al. 2001). During this time, individuals must consistently balance reproductive effort and other physical demands such as obtaining critical resources, maintaining self-care, all while mitigating predation risk (Fontaine and Martin 2006).

Nesting behavior in avian species exemplifies a multi-level process. For example, the selection of a nest location (4th order habitat selection) is a sequential decision-making process where habitat characteristics at the patch level within the home range (3rd order habitat selection) are assessed after a nesting home range (2nd order habitat selection) was previously established. Further, once a potential nest-site is identified, factors at multiple scales may factor into the decision-making process. For example, nearby understory vegetation (e.g., visual obstruction) and broader landscape features (e.g., developed land use) may influence the probability that a nest-site is used. Even after the nest-site is chosen, habitat evaluation continues. For example, during nest-building and incubation, individuals may periodically take `bouts` off the nest to prospect the surrounding area within the home range and gather essential resources before returning to the site (Croston et al. 2020).

Wild turkeys (*Meleagris gallopavo silvestris*) are a ground-nesting upland gamebird species that are highly sought after across their range. Female turkeys (hens) select nesting sites that are typically shallow depressions they create themselves. Nest-site selection by hens is highly variable, with nests found across a wide range of habitats where turkeys are known to inhabit (Healy et al. 1990). However, studies have shown that hens are more likely to nest in areas with dense ground cover and high visual obstruction, which provide better concealment and protection (Wood et al. 2019). Hens generally lay a clutch of 10 to 12 eggs over a period of approximately two weeks, laying one egg per day (Williams et al. 1972, Williams and Austin 1988). However, egg-laying can be delayed in response to unusual weather conditions. Continuous incubation lasts about 28 days, during which the hen typically leaves the nest once per day to forage for food, although some variability in this behavior may occur. Several factors have been found to influence turkey nest success. For example, prolonged precipitation on cold days during incubation can negatively affect nest survival (Roberts and Porter 1998). Additionally, habitat characteristics at the nest-site, such as the level of visual obstruction, and proximity to landscape features, like roads, can play a significant role in nest success. Prior research indicates that greater amounts of visual obstruction (e.g., visual obstruction) are associated with higher nest survival probabilities (Fuller et al. 2013, Badyaev et al. 1995, Keever et al. 2023, Gonnerman, 2021[unpublished dissertation]).

Variation in nesting behavior and recruitment is considered a key factor in population growth of turkeys prompting wildlife biologists to investigate the factors that influence nesting success. In our study, we developed three models: a nest-site selection model, an individual movement model, and a nest success model to investigate how individual decision-making influences recruitment across multiple levels. Our models will assess: (1) how a suite of individual, nest-level, and landscape-level covariates influence movement and reproduction (2) mismatches in the effect of habitat on individual movement, nest-site selection, and nest survival across multiple levels while accounting for individual-specific variation and, (3) The effect of biologically relevant predictors on daily nest survival probabilities. We applied our modeling framework to a comprehensive dataset of female turkeys from Pennsylvania, Maryland, and New Jersey, which includes spatial data and morphometric measurements. This study offers valuable insights into the conditional processes that shape turkey movement and reproductive success.

**METHODS**

**Study Area**

Our study spans diverse regions across Pennsylvania, Maryland, and New Jersey, strategically selected to capture a wide range of nesting behaviors in varying landscapes (Figure 2.1). In Pennsylvania, the research covers four distinct wildlife management units (WMUs): 2D, 3D, 4D, and 5C. WMU 5C, located in the southeastern part of the state, is a mix of urban and agricultural landscapes. WMU 3D, situated in the northeastern region, features expansive public woodlands surrounded by urban development. WMU 4D, located centrally, consists primarily of public woodlands interspersed with agricultural areas. WMU 2D, in the western portion of the state, is characterized by a diverse landscape that includes urban, forested, and agricultural areas. In Maryland, the study area is divided into two regions: Maryland East and Maryland West. Maryland West encompasses montane forests in the Allegheny Mountains, interspersed with agricultural lands, while Maryland East is dominated by agricultural areas and urban development. In New Jersey, the study spans two regions: New Jersey North and New Jersey South. New Jersey North, located in the northern part of the state, features a combination of forested and agricultural landscapes surrounded by urban development. New Jersey South is situated in the southern portion of the state and consists of patches of pine and deciduous forest mixed with agriculture, surrounded by urban residential areas. This broad geographic scope provides a comprehensive view of nesting behaviors across a wide range of environmental conditions and human influences.

**Field Methods**

***Wild Turkey Capture and Transmitter Programming***

We captured ~25 hens every winter within each of the study areas from 2022-2025 at baited capture locations using rocket nets (Grubb 1988). Upon capture, we collected morphometric measurements from each bird and noted age based upon growth of the ninth and tenth primary feathers and tail fan (Brenneman 1992). Each bird was marked using an aluminum leg band and a subset received an EOBs GPS transmitter with built in ultra-high-frequency (UHF) and accelerometer components (EOBs 2021). We used an ACC informed transmitter schedule in which the transmitter collected locations contingent upon hen activity. Based upon pilot data from a University of Missouri study on captive farm-raised turkeys, we determined an ACC Z-axis variance threshold over 250 standard deviations indicated that the bird was active. During May-July, we collected a GPS fix every 30 minutes if the ACC Z-axis variance threshold was over 250 standard deviations and every 2 hours otherwise.

***Nest Identification and Fate Determination***

We monitored hens three times per week using UHF telemetry and used a combination of accelerometer (ACC) and GPS data to confirm nesting behavior. We were thus able to detect incubation behavior remotely using acceleration data (other examples see Ferraz et al. 2024, Shreven et al. 2021). To determine turkey nesting behavior, we constrained ACC observations to the daylight hours and calculated an average daily z-axis standard deviation value as a proxy for movement patterns. Incubation behavior was determined to occur if the proportion of average z-axis observations was greater than 0.85 for two days in a row (Appendix S1). We determined the termination of a nesting attempt if the daily z-axis standard deviation was less than 0.8 for 3 days in a row (Appendix S2). This allowed us to remotely monitor nesting behavior without disturbing incubation patterns.

We revisited nest sites within 3 days of the estimated termination of the nesting attempt and classified nests into the following categories, (1) *“hatched”*, if at least one egg hatched from a clutch, (2) “*abandoned”*, if a nest was uncovered with eggs cold to the touch, (3) “de*predated”*, if the eggs were missing or at least one has been cracked or damaged (not from the process of hatching) and (4) “*unknown”*, if a nest attempt was made but we were unable to determine why it failed and (5) *“unconfirmed”* for nests we were not allowed to access or the fate couldn’t be determined (i.e., may have been a success or a failure). If a nest was depredated, we attempted to determine the predator responsible by using clues at the kill site. If eggs looked to have beak size holes, we classified the predator as “*avian.”* If there was evidence for crushed eggs, scat, scent trails, or fresh tracks around the nest bowl, we classified the predator as “*mammalian.*” If a snake was observed at the nest, we classified the cause as “*reptile.”* If a nest was destroyed due to anthropogenic disturbance, we classified the fate by the practice used to destroy it (e.g., haying; “*human-agricultural*” or yard maintenance; *“human-residential”*). If a landowner’s pet destroyed a nest, it was marked as “*other-mammalian.*”

**Data Management**

We selected covariates based on three levels of interest: individual, nest-level, and landscape-level (Table 2.1). Individual covariates were defined as characteristics that varied according to an individual hen's behavior or body condition. Nest-level covariates referred to attributes or measurements in the immediate vicinity of an individual’s nest. Finally, landscape-level covariates encompassed broader landscape and weather characteristics.

**Individual Covariates**

At each capture event, we obtained important individual information about each hen within our study. To test hypotheses about how age and body condition influence recruitment, we included a binary covariate for turkey age using two classes: *adult* and *juvenile*. Relationships with body condition on decision-making were further investigated through the inclusion of disease covariates. In collaboration with the University of Pennsylvania’s Wildlife Futures program, hens were tested at capture for lymphoproliferative disease virus (hereafter LPDV), reticuloendotheliosis virus (hereafter REV) and avian pox. We classified infection with LPDV, REV, and avian pox as separate categorical predictors to gauge the effects of each disease on decision-making and nest success during reproduction. A coinfection status term describing individuals infected with both LPDV and REV was also included to determine if these diseases are compounding factors influencing decision-making and daily nest success during reproduction.

We derived additional individual-level information using GPS and ACC data sources. Nest incubation date (Julian Date) was included to determine if the day of incubation had an impact on daily nest success. We identified nest recesses by creating a 20m buffer around each nest that was representative of the GPS error. GPS error was calculated by placing transmitters in 6 different habitat types (e.g., steep wooded), obtaining three locations at each (per burst) and then averaging out the mean standard deviation across all habitats. Hen locations outside of the buffer during an individual’s incubation period were categorized as a nest recess. The continuous time spent in a recess was calculated as the difference between the timepoint of the first location in a sequence of locations outside of the buffer and the last location in the sequence before the hen returned to the buffered area. Cumulative distance traveled during incubation was calculated as the sum of the Euclidean distances between each location after leaving the buffer and before returning.

**Nest-Level Covariates**

In Pennsylvania, we performed vegetation surveys at each nest-site and at four generated nests 100m away from the nest in each of the four cardinal directions to assess how fine-scale vegetation influences decision-making during nest-site selection and daily nest survival probabilities. We conducted a vegetation survey within 3 days of a hen leaving the nest (e.g., fledge or termination) to avoid large-scale seasonal changes in vegetation structure. We classified our survey sites as a 26 ft radius around the nest bowl (Brose et al. 2008). A woody stem basal area density was collected for all small trees using a 10 basal area factor prism. We estimated the percent ground coverage using quadrants in each plot using variables such as low woody vegetation, fern, grass/forbs, litter, bare ground, and boulders. A robel pole was then used to estimate visual obstruction (Robel et al. 1970), which was used as a proxy for the visual vulnerability of nest-sites to potential predators. We did not collect microscale vegetation data in Maryland and New Jersey. Due to the high level of correlation among our microscale characteristics, we used pairwise Pearson correlations among nest-site predictors to reduce the set of possible predictor variables.

**Landscape-Level Covariates**

We obtained weather covariates from Daymet to determine how climate characteristics influence daily nest success. Daymet is an open-source database that contains daily climate observations in the form of 1km x 1km resolution rasters (Thornton et al. 2022) and is used to detect dynamic patterns across short temporal scales. We paired each nest site with the closest weather station and extracted minimum and maximum temperature and cumulative precipitation at a daily scale for 30 days prior to nest initiation through the termination of incubation.

We used remotely sensed land cover data from the 2021 National Land Cover Database (NLCD; Dewitz et al. 2023) to assess its role in pre-nesting decision-making and its potential influence on daily nest survival probabilities. The NLCD provides land cover information as grid cells with a 30m x 30m spatial resolution, which we refined into biologically relevant cover types. Specifically, we distinguished three forest categories: “Deciduous Forest,” “Evergreen Forest,” and “Mixed Forest” to capture different forest compositions. A “Developed” category was created by combining developed open space, low-intensity, medium-intensity, and high-intensity urban areas. An “Agriculture” cover type was derived by merging pasture/hay and cultivated crop land. Finally, a “Grassland/Shrub” category was formed by combining shrub/scrub and grassland classifications. We used the `sf ` (Pebesma & Bivand, 2023) and `terra` (Hijmans, 2024) R packages to extract and process the land cover data. Elevation data was sourced via a digital elevation model using the `FedData` package (Bocinsky, 2024), and road data were obtained using the `tigris` package (Walker, 2024) for Maryland and New Jersey. For Pennsylvania, we accessed road data from the Pennsylvania Spatial Data Access (PASDA). To gain deeper insights into how wild turkey landscape perception is influenced by road structures, we calculated the Euclidean distance from each nest and GPS location to the nearest road, distinguishing between two road types: primary roads (defined as state and federal roads) and secondary roads (defined as municipal and logging roads).

**Statistical Analysis**

We developed three models to examine nest-site selection, individual movement, and nest success, and then compared the effect sizes across these ecological processes to assess the synchrony or mismatch between them. All models were fitted in R (R Core Team 2024) using the `R2Jags` package (Sue and Yajima 2024). For each model, we applied Markov Chain Monte Carlo (MCMC) methods to estimate posterior distributions of all parameters. Simulations were run with 40,000 iterations per model, using a single chain for each parameter and a thinning interval of 3. We visually inspected the convergence of the chains to determine satisfactory convergence.

***Nest-Site Selection Model***

We modeled nest-site selection of hens using matched conditional logistic regression (Thurjfell et al. 2014, Fortin et al. 2005, Muff et al. 2019) in a Bayesian framework. Conditional logistic regression is likelihood-equivalent to a Poisson distribution with stratum-specific fixed intercepts, which can be implemented using a random effect with a large, fixed variance (Warton and Shepperd 2010) and allows for more efficient estimation of random effects. We modeled nest-site selection, where an individual hen at nest attempt *n* had *j* nests available to her during the decision-making process. We modeled nest-site selection as

(1)

where was a stratum-specific intercept where the stratum defines the paired used and available nests, was a vector of coefficient that describe the effects of on-ground vegetation measurements, landscape characteristics, and individual covariates. The probability a nest was used conditional on our stratum can be calculated as .

We used low information priors for each coefficient, such that . Our stratum-specific intercept was modeled as a random effect . Following Muff et al. (2019), we fixed the variance at a high value (e.g., 106) to avoid shrinkage when estimating the values of our stratum-specific random effect.

***Individual Movement Model***

We modeled individual movements during a hen’s pre-nesting period using conditional logistic regression, or a step-selection function, in a Bayesian framework. We paired 10 “available” steps from the observed distribution of step lengths and turning angles from all individuals with each “used” step using the ‘amt’ package (Signer et al. 2019). We modeled individual movement during incubation with a slight adjustment to equation (1) by conditioning our availability distribution to an individual hen *n* at a discrete point in time *t* where

(2)

was a stratum-specific intercept where the stratum defines the paired used and available locations, was a vector of coefficient that describe the effects of landscape characteristics and individual covariates. The probability a location was used conditional on our stratum can be calculated as . We followed the same specifications for modeling our parameters as the nest-site selection process.

***Nest Survival Model***

We fit a Bayesian known-fate model to determine if daily nest survival varied as a function of time-dependent weather covariates, landscape characteristics, on-ground vegetation measurements and individual covariates. We combined nests with fates labeled as "Abandoned" and "Depredated" into a single "Failed" category, represented by a value of "0," while nests that successfully hatched were assigned a value of "1." Encounter histories for each individual were created from the onset of incubation to the termination of the nesting attempt. We modeled nest fate *y* of each nest *i*, individual hen k, on day *j* as a Bernoulli distribution where if and the nest survived if a nest failed:

Daily nest survival probability was modeled as a function of microscale, macroscale, and individual covariates using the cloglog link as

*,* (3)

where vectorcontainedtime-varying, nest-level covariates for each nest that we believed effected nest survival (e.g., daily precipitation). The intercept and coefficients,β0 and **β**,were modeled as and respectively. was a vector of coefficients that describe the effects of time-dependent climate variables, on-ground vegetation measurements, landscape characteristics, and individual covariates. We included a random effect to account for individual variation in nest success within our study, and this was modeled as   
*.* Accounting for individual variation allowed us to gauge how nest success rates varied among hens in our study which is useful for informing population-level reproductive dynamics (Byrne et al. 2022). We modeled the variance associated with our random effect as .

**Results**

We captured a total of # turkeys between 2022 and 2025 and equipped # of them with GPS-ACC transmitters across three states. Within our sample, # individuals were classified as juveniles and # as adults. During the study, we collected # GPS locations and # tri-axial accelerometer measurements from these individuals during both the pre-nesting and nesting periods. The telemetry error was calculated to be 29 meters, and # individuals were excluded from the analysis due to capture-related mortality.

***Nest-Site Selection***

We monitored a total of # nesting attempts and collected vegetation measurements at # survey plots for this analysis. Our dataset included # initial attempts, # second attempts, and # third attempts. The earliest nest attempt we observed occurred on (insert date), while the latest termination of incubation took place on (insert date). Nesting propensity, defined as the proportion of hens that initiated a nest, was calculated to be # for juveniles and # for adults across the study area. Of the sampled nests, # were in agricultural areas, # in deciduous forest, # in mixed forest, # in evergreen forest, # in shrub/grassland, and # in developed cover types.

Hens exhibited differing patterns in habitat selection between nest and landscape-level predictors when selecting nest sites (Figure 2.3). At the nest-level, hens preferred locations with denser understory vegetation and a higher proportion of woody stem plants but avoided areas with invasive woody stem plant species. At the landscape-level, hens favored sites in agricultural and grassland/shrub landscapes at greater distances from primary roads. Hens also chose nest-sites further from developed land-use as it was highly correlated with our agriculture category. We found that forest cover types, elevation, and distance from secondary roads had minimal impact on hen landscape perception during nest-site selection.

***Individual Movement***

We obtained \_#\_ GPS locations from \_#\_ hens during the pre-nesting period. Of these locations, \_#\_ were in agriculture, \_#\_ were in developed, \_#\_ were in mixed forest, \_#\_ were in deciduous forest, \_#\_ were in evergreen forest, and \_#\_ were in grassland/shrub cover types. The average step length was \_#\_m over this period.

***Nest Success***

**References**

Ardia, D.R., Pérez, J.H., Chad, E.K., Voss, M.A. and Clotfelter, E.D. (2009), Temperature and life history: experimental heating leads female tree swallows to modulate egg temperature and incubation behaviour. Journal of Animal Ecology, 78: 4-13. <https://doi.org/10.1111/j.1365-2656.2008.01453.x>

Badyaev, A. V., Martin, T. E., & Etges, W. J. (1996). Habitat sampling and habitat selection by female wild turkeys: ecological correlates and reproductive consequences.  *The Auk*, *113*(3), 636-646.

Bakner, N. W., Schofield, L. R., Cedotal, C., Chamberlain, M. J., & Collier, B. A. (2019). Incubation recess behaviors influence nest survival of Wild Turkeys. *Ecology and Evolution*, *9*(24), 14053-14065.

Bocinsky RK (2024). FedData: Functions to Automate Downloading Geospatial Data Available from Several Federated Data Sources\_. R package version 4.0.1, https://CRAN.R-project.org/package=FedData>.

Boone, W. W., Moorman, C. E., Moscicki, D. J. Collier, B. A., Chamberlain, M. J., Terando, A. J., and Pacifici, K. 2023. Robust assessment of associations between weather and eastern wild turkey nest success. Journal of Wildlife Management e22524. https://doi.org /10.1002/jwmg.2252

Brenneman, R. Aging spring turkeys. NWTF Wildlife Bulletin No. 19, NWTF, Edgefield, South Carolina, USA. (1992): 2pp.

Brose, P. H, K. W. Gottschalk, S. B. Horsley, P. D. Knopp, J. N. Kochenderfer, B. J McGuinness, G. W. Miller, T. E. Ristau, S. H. Stoleson, and S. L. Stout. Prescribing regeneration treatments for mixed oak forests in the Mid-Atlantic Region. U. S. Department of Agriculture, Forest Service, Northern Research Station, General Technical Report NRS-33. 108pp.

Byrne, M. E., Cohen, B. S., Collier, B. A., & Chamberlain, M. J. (2022). Nest site fidelity and nesting success of female Wild Turkeys. *Wildlife Society Bulletin*, *46*(2), e1279.

Carlson, A., and Moreno, J. 1981. Central Place Foraging in the Wheatear Oenanthe oenanthe: An Experimental Test. *Journal of Animal Ecology*, *50*(3), 917–924. https://doi.org/10.2307/4146

Casalena, M. J., Schiavone, M. V., Bowling, A. C., and Gregg, I. D. 2015. Understanding the new normal: wild turkeys in a changing northeastern landscape. Proceedings of the National Wild Turkey Symposium 11:45-57.

Croston, R., Hartman, C. A., Herzog, M. P., Casazza, M. L., Feldheim, C. L., & Ackerman, J. T. (2020). Timing, frequency, and duration of incubation recesses in dabbling ducks. *Ecology and evolution*, *10*(5), 2513-2529.

Clark, A. B., & Wilson, D. S. (1985). The Onset of Incubation in Birds. *The American Naturalist*, *125*(4), 603–611. http://www.jstor.org/stable/2461276

Coe, B.H., Beck, M.L., Chin, S.Y., Jachowski, C.M.B. and Hopkins, W.A. (2015). Local variation in weather conditions influences incubation behavior and temperature in a passerine bird. J Avian Biol, 46: 385-394. https://doi.org/10.1111/jav.00581

Dewitz, J. 2023. National Land Cover Database (NLCD) 2021 Products: U.S. Geological Survey data release, [https://doi.org/10.5066/P9JZ7AO3.](https://doi.org/10.5066/P9JZ7AO3. )

*E-OBS System Manual*, 2021. [https://documentcloud.adobe.com/spodintegrationindex.html](https://documentcloud.adobe.com/spodintegrationindex.html )

Muff, S., Signer, J., & Fieberg, J. (2020). Accounting for individual‐specific variation in habitat‐ selection studies: Efficient estimation of mixed‐effects models using Bayesian or frequentist computation. *Journal of Animal Ecology*, *89*(1), 80-92.

Farner, D. S. (1964). The photoperiodic control of reproductive cycles in birds. *American Scientist*, *52*(1), 137–156. http://www.jstor.org/stable/27838920

Ferraz, G., Pacheco, C., Fernández-Tizón, M. *et al.* Using GPS and accelerometer data to remotely detect breeding events in two elusive ground-nesting steppe birds. *Anim Biotelemetry* **12**, 30 (2024). https://doi.org/10.1186/s40317-024-00385-y

Fontaine, J.J. and Martin, T.E. 2006. Parent birds assess nest predation risk and adjust their reproductive strategies. Ecology Letters, 9: 428-434. [https://doi.org/10.1111/j.1461-0248.2006.00892.x](https://doi.org/10.1111/j.1461-0248.2006.00892.x )

Fortin, D., Beyer, H. L., Boyce, M. S., Smith, D. W., Duchesne, T., & Mao, J. S. (2005). Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. *Ecology*, *86*(5), 1320-1330.

Fuller, A. K., Spohr, S. M., Harrison, D. J., and Servello., F. A. (2013). “Nest Survival of Wild Turkeys *Meleagris Gallopavo Silvestris* in a Mixed‐use Landscape: Influences at Nest‐site and Patch Scales.” *Wildlife Biology* 19, no. 2. 138–4. <https://doi.org/10.2981/11-121>.

Gottdenker, N. L., Streicker, D. G., Faust, C. L., & Carroll, C. R. (2014). Anthropogenic land use change and infectious diseases: a review of the evidence. *EcoHealth*, *11*, 619-632.

Grant, T. A., Shaffer, T. L., Madden, E. M., & Pietz, P. J. (2005). Time-specific variation in passerine nest survival: new insights into old questions. *The Auk*, *122*(2), 661-672.

Grubb, T. G. 1991. “Modifications of the Portable Rocket-net Capture System to Improve Performance.” United States, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station

Hijmans R (2024). *terra: Spatial Data Analysis*. R package version 1.8-6, <https://github.com/rspatial/terra>.

Johnson, D. H. 1980. The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. Ecology, 61(1), 65–71. [https://doi.org/10.2307/1937156](https://doi.org/10.2307/1937156 )

Johnson, V. M., Harper, C. A., Applegate, R. D., Gerhold, R. W., & Buehler, D. A. (2022). Nest site selection and survival of wild turkeys in Tennessee. *Journal of the Southeastern Association of Fish and Wildlife Agencies*, *9*, 134-143.

Keever, A.C., Collier, B. A., Chamberlain, M. J., and Cohen, B. S. 2023. “Early Nest Initiation and Vegetation Density Enhance Nest Survival in Wild Turkeys.” *Ornithology* 140, no. 1: ukac050. <https://doi.org/10.1093/ornithology/ukac050>.

Lohr, A. K., Martin, J. A., Wann, G. T., Cohen, B. S., Collier, B. A., & Chamberlain, M. J. (2020). Behavioral strategies during incubation influence nest and female survival of Wild Turkeys. *Ecology and Evolution*, *10*(20), 11752-11765.

Lowrey, D. K., G. A. Hurst, S. R. Priest, and B. S. Weemy. 2001. Selected weather variables on predation of wild turkey females and nest success. Proceedings of the National Wild Turkey Symposium 8:173-178.

McGarigal, K., Wan, H. Y., Zeller, K. A., Timm, B. C., & Cushman, S. A. (2016). Multi-scale habitat selection modeling: a review and outlook. *Landscape ecology*, *31*, 1161-1175.

Mayor, S. J., Schneider, D. C., Schaefer, J. A., & Mahoney, S. P. (2009). Habitat selection at multiple scales. *Ecoscience*, *16*(2), 238-247.

Mainwaring M. C., Hartley I. R. 2013The Energetic Costs of Nest Building in Birds. *Avian*  *Biology Research*. 6(1):12-17. doi:[10.3184/175815512X13528994072997](https://doi.org/10.3184/175815512X13528994072997)

MacDonald, E. C., Camfield, A. F., Jankowski, J. E., & Martin, K. (2013). Extended incubation recesses by alpine‐breeding Horned Larks: a strategy for dealing with inclement weather? Journal of Field Ornithology, 84(1), 58-68.

Nilsson, JÅ., Råberg, L. 2001. The resting metabolic cost of egg laying and nestling feeding in great tits. *Oecologia* **128**, 187–192. [https://doi.org/10.1007/s004420100653](https://doi.org/10.1007/s004420100653 )

Nord, A., Sandell, M.I. and Nilsson, J.-Å. (2010), Female zebra finches compromise clutch temperature in energetically demanding incubation conditions. Functional Ecology, 24: 1031-1036. <https://doi.org/10.1111/j.1365-2435.2010.01719.x>

Orians, G. H., and Pearson, N. E. (1979). On the theory of central place foraging. Analysis of ecological systems. *Ohio State University Press, Columbus*, *2*, 155-177.

Parrett, J. P., Johnson, C. B., Gall, A. E., and Prichard, A. K. 2023. Factors influencing incubation behavior and nesting success of yellow-billed loons in Arctic Alaska. *Journal* *of Wildlife Management* 87:e22406. [https://doi.org/10.1002/jwmg.22406](https://doi.org/10.1002/jwmg.22406 )

Pebesma, E., & Bivand, R. (2023). Spatial Data Science: With Applications in R. Chapman and Hall/CRC. <https://doi.org/10.1201/9780429459016>

Pollentier, C. D., Lutz, R. S., & Drake, D. (2017). Female wild turkey habitat selection in mixed forest‐agricultural landscapes. *The Journal of Wildlife Management*, *81*(3), 487-497.

Poizat, G., & Pont, D. (1996). Multi‐scale approach to species–habitat relationships: juvenile fish in a large river section. *Freshwater biology*, *36*(3), 611-622.

Roberts, S. D., and Porter, W. F. 1998. Relation between Weather and Survival of Wild Turkey Nests. *The Journal of Wildlife Management*, *62*(4), 1492–1498. https://doi.org/10.230 7/3802015

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. <https://doi.org/10.2307/3802449>

Robel, R. J., Briggs, J. N., Dayton, A. D., & Hulbert, L. C. (1970). Relationships between visual obstruction measurements and weight of grassland vegetation. *Rangeland Ecology & Management/Journal of Range Management Archives*, *23*(4), 295-297.

Schreven, K. H., Stolz, C., Madsen, J., & Nolet, B. A. (2021). Nesting attempts and success of Arctic-breeding geese can be derived with high precision from accelerometry and GPS- tracking. *Animal Biotelemetry*, *9*, 1-13.

Shea, S. A., Gonnerman, M., Blomberg, E., Sullivan, K., Milligan, P., & Kamath, P. L. (2022). Pathogen survey and predictors of lymphoproliferative disease virus infection in wild turkeys (Meleagris gallopavo). *The Journal of Wildlife Diseases*, *58*(3), 537-549.

Signer, J., Fieberg, J., & Avgar, T. (2019). Animal movement tools (amt): R package for managing tracking data and conducting habitat selection analyses. *Ecology and evolution*, *9*(2), 880-890.

Smith, P. A., Tulp, I., Schekkerman, H., Gilchrist, H. G., & Forbes, M. R. (2012). Shorebird incubation behaviour and its influence on the risk of nest predation. *Animal Behaviour*, *84*(4), 835-842.

Spohr, S. M., Servello, F. A., Harrison, D. J., & May, D. W. (2004). Survival and reproduction of female wild turkeys in a suburban environment. *Northeastern Naturalist*, *11*(4), 363-374.

Su Y, Yajima M (2024). \_R2jags: Using R to Run 'JAGS'\_. R package version 0.8-5, <https://CRAN.R-project.org/package=R2jags>.

Thogmartin, W. E. (1999). “Landscape Attributes and Nest-Site Selection in Wild Turkeys.” *The Auk* 116, no. 4: 912–23. [https://doi.org/10.2307/4089671.](https://doi.org/10.2307/4089671. )

Thornton, M.M., R. Shrestha, Y. Wei, P.E. Thornton, and S-C. Kao. 2022. Daymet: Daily Surface Weather Data on a 1-km Grid for North America, Version 4 R1. ORNL DAAC, Oak Ridge, Tennessee, USA. https://doi.org/10.3334/ORNLDAAC/2129

Thurfjell, H., Ciuti, S., & Boyce, M. S. (2014). Applications of step-selection functions in ecology and conservation. Movement ecology, 2, 1-12.

Tyl, R. M., Rota, C. T., and Lehman, C. P. (2020). “Factors Influencing Productivity of Eastern Wild Turkeys in Northeastern South Dakota.” *Ecology and Evolution* 10, no. 16 8838–8854. <https://doi.org/10.1002/ece3.6583>.

Walker, K. “Tigris: Load Census TIGER/Line Shapefiles,” October 11, 2015. <https://doi.org/10.32614/CRAN.package.tigris>.

Warton, D. I., & Shepherd, L. C. (2010). Poisson point process models solve the" pseudo- absence problem" for presence-only data in ecology. *The Annals of Applied Statistics*, 1383-1402.

Wiens, J. A. (1989). Spatial scaling in ecology. *Functional ecology*, *3*(4), 385-397.

*Wild Turkey in New Jersey*. (2023, August 14). New Jersey Department of Environmental Protection. Retrieved November 20, 2023, from [https://dep.nj.gov/njfw/hunting/wild- turkey-in-new-jersey/](https://dep.nj.gov/njfw/hunting/wild-%20turkey-in-new-jersey/)

Wood, J. D., Cohen, B. S., Conner, L. M., Collier, B. A., & Chamberlain, M. J. (2019). Nest and brood site selection of eastern wild turkeys. *The Journal of Wildlife Management*, *83*(1), 192-204.

**Tables**

Table 2.1. Macroscale, Microscale, and Individual Covariates

|  |  |  |  |
| --- | --- | --- | --- |
| **Covariate** **Source** | **Reference** | **Model** |  |
| ***Landscape-Level***  Daily Precipitation Daymet  Daily Minimum Temperature Daymet | Lowrey et al. 2001  Roberts et al. 1995, Tyl et al. 2020 | Nest Success  Nest Success |  |
| Developed NLCD  Mixed Forest NLCD  Deciduous Forest NLCD  Evergreen Forest NLCD  Agriculture NLCD  Grassland/Shrub NLCD  Elevation DEM  Distance from Primary Road `FedData`  Distance from Secondary Road `FedData` | Spohr et al. 2004  Pollentier et al. 2017  Pollentier et al. 2017  Pollentier et al. 2017  Thogmartin 1999  Pollentier et al. 2017  Thogmartin 1999 (Distance from Road)  Thogmartin 1999 (Distance from Road)  Thogmartin 1999 (Distance from Road) | Nest-Site Selection, Individual Movement, Nest Success  Nest-Site Selection, Individual Movement, Nest Success  Nest-Site Selection, Individual Movement, Nest Success  Nest-Site Selection, Individual Movement, Nest Success  Nest-Site Selection, Individual Movement, Nest Success  Nest-Site Selection, Individual Movement, Nest Success  Nest-Site Selection, Individual Movement, Nest Success  Nest-Site Selection, Individual Movement, Nest Success  Nest-Site Selection, Individual Movement, Nest Success |  |
| ***Nest-Level***  Visual Obstruction Sampled  Percent Woody Vegetation Sampled  Invasive Woody Vegetation Sampled  Native Woody Vegetation Sampled  Basal Area Sampled  Percent Grass Forb Sampled  ***Individual***  Nest Incubation Date ACC  Time Spent Away from Nest GPS  Cumulative Distance Traveled GPS  LPDV Infection Status Sampled  REV Infection Status Sampled  Coinfection Status Sampled  Body Mass at Capture Sampled | Fuller et al. 2013, Tyl et al. 2020  Wood et al. 2019  Wood et al. 2019  Keever et al. 2022  TBD  TBD  Keever et al. 2022  Lohr et al. 2020  Lohr et al. 2020  Shea et al. 2022  Shea et al. 2022  Shea et al. 2022  Badyaev et al. 1996 | Nest-Site Selection, Nest Success  Nest-Site Selection, Nest Success  Nest-Site Selection, Nest Success  Nest-Site Selection, Nest Success  Nest-Site Selection, Nest Success  Nest-Site Selection, Nest Success  Nest Success  Nest Success  Nest Success  Nest Success  Nest Success  Nest Success  Nest Success |  |
| Above are macroscale, microscale, and individual covariates that were used in our modeling process. Each variable is listed with its associated source and references for justification of inclusion. All sampled measurements were collected in a field or laboratory setting. ACC measurements were collected using the ACC component of our transmitters and GPS measurements were collected via the GPS component. | |  |  |

**Figures**

A map of the state of pennsylvania

Description automatically generated

Figure 2.1. Our study took place in Pennsylvania USA in WMUs 2D, 3D, 4D, and 5C. We had 56 capture locations (dark triangles) in total that were evenly distributed through these WMUs.

A graph with red dots and white text

Description automatically generated

Figure 3. Presented are beta estimates and associated 90% credible intervals at the nest and landscape levels for the nest-site selection model.