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**Multi-Level Modelling Factors Influencing Wild Turkey Reproductive Success in the Mid-Atlantic Region**

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**ABSTRACT** Organisms interact with their environment at multiple spatial and temporal levels, often in a hierarchical manner. Recognizing that variation in recruitment is considered a key factor in population growth of wild turkeys (*Meleagris gallopavo silvestris*), we developed a multi-level modelling framework to analyze the sequential processes affecting turkey reproductive success during breeding and nesting periods. Specifically, we created a pre-nesting movement model, a nest-site selection model, and a nest success model, which allowed us to explore how fine-scale vegetation metrics, coarse-scale land cover classifications, weather variables, and individual characteristics, influenced reproductive success. These models were applied to a dataset of female turkeys in Pennsylvania, Maryland, and New Jersey USA. At the landscape-scale, hens in Pennsylvania and New Jersey exhibited differing patterns of habitat selection during pre-nesting relative to deciduous forest. Hens in Pennsylvania selected for areas with deciduous forest landcover whereas hens in New Jersey selected for grassland/shrub and wetland, while selecting against developed land use relative to deciduous forest. Further, hens in Maryland selected for mixed forest, wetland and greater distances from primary roads during pre-nesting. During nest-site selection, hens in Pennsylvania selected locations with greatervisual obstruction, and a greater abundance of both ferns and understory woody vegetation, but fewer individual woody stems. Further, in Pennsylvania we detected positive effects on daily nest survival probability for evergreen forest land cover, percent fern, and incubation constancy. In Maryland, during nest-site selection, hens selected for pasture relative to deciduous forest, but nests in this cover type had lower daily nest survival probability. We further found that nest survival decreased with closer proximity to secondary roads in Maryland and to primary roads in New Jersey. When modelling the effects of disease and parasitic infection on daily nest survival probability, we found that coinfection of LPDV and *Eimeria* sp. had a negative effect. Our findings highlight the complexity of understanding turkey reproductive behavior, suggesting that a combination of habitat features, disease dynamics, behavioral factors, and individual traits influence reproductive success.

**KEYWORDS** behavior, disease, habitat selection, *Meleagris gallopavo*, nesting, telemetry, recruitment, survival

Organisms interact with the environment at multiple nested levels, forming a hierarchical structure (Johnson 1980, McGarigal et al. 2016). For example, using 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 broader geographic range (1st order habitat selection) (Johnson 1980). Understanding broader patterns of wildlife-habitat relationships requires research across levels of ecological levels of organization because animals may exhibit selection for different features across different levels (Mayor et al. 2009). Multi-level modelling best captures the conditional nature in which organisms interact with landscape features, and it can highlight opposing patterns in selection across the different levels (Bauder et al. 2018, Buderman et al. 2023, Gigliotti et al. 2023, Poizat and Pont 1996). As with all ecological processes, wildlife-habitat relationships are scale dependent (Wiens 1989); scale is determined by the grain size (e.g., fine or coarse) of a given unit and the spatial extent of the analysis (e.g., spatial or temporal duration at which observations are made). Individuals often perceive habitat at multiple spatial or temporal scales (McGarigal et al. 2016), which can result in responses being linked to different scales of an attribute (Gigliotti et al. 2023, Leblond et al. 2011, Shirk et al. 2014, Thompson and McGarigal 2002). Within a level of selection, individuals may be responding to the landscape at multiple scales (Shirk et al. 2014, Zeller et al. 2017).

Reproduction directly influences recruitment and population dynamics. Nest construction (i.e., nesting behavior) is an example of a reproductive behavior that is exhibited across numerous taxa, including birds, reptiles, fish, insects, and mammals (Hansell 2005, Mainwaring et al. 2023). The nest itself may serve various purposes including display, shelter, and protection of eggs/young (Mainwaring and Hartley 2014, Winkler 2016). However, nesting behavior represents a stage of heightened energetic demands as individuals must expend considerable resources performing nest-site selection, nest construction, egg-laying, incubation, and parental care (Mainwaring and Hartley 2013, Nilsson et al. 2001). Thus, individuals must balance reproductive effort with the normal physical demands of obtaining food and maintaining self-care, all while mitigating the threat of predation (Fontaine and Martin 2006).

Nest-site selection exemplifies a multi-level process. The selection of a nest location (4th order habitat selection) is conditional on the selection of habitat within the home range (3rd order habitat selection), which is conditional on selection of the home range (2nd order habitat selection) itself. Once a potential nest site is identified, factors at multiple spatial scales may have direct effects on fitness. For example, greater vegetation cover in proximity to a nest could positively affect nest success by providing visual and olfactory concealment from predators (Martin and Roper 1988, Martin 1992). At the landscape-scale, nest-site selection patterns may vary in accordance with density-dependence of individuals within a species, resource availability, predator avoidance, or proximity to optimal habitat for offspring (Fontaine and Martin 2006, Thomson et al. 2006, Brown et al. 2004). Considering how a suite of habitat characteristics influences individual decision-making with linkages to reproductive success may aid in the development of habitat management guidelines and its effect on populations.

While the effect of habitat is considered a potential driver of reproductive success, numerous other factors may influence nest survival. For example, abiotic factors such as precipitation, temperature, and wind may cause physical harm to nests and negatively influence offspring body condition and development (Schöll and Hille 2020, Rojas et al. 2019, Engstrom and Evans 1990, Jeanne and Morgan 1992). Furthermore, individual characteristics of the parent, such as disease, parasite load, and age class may interact with weather variables, increasing stress on adults or juveniles due to variability in body condition (Cimadom et al. 2014, Lamarre et al. 2018). These factors can exacerbate the physical demands of nesting, further compromising fitness and altering decision-making. For instance, less time spent on nest during incubation may leave the nest more susceptible to predators as well as abiotic factors such as weather conditions (Skutch et al. 1962, Smith et al. 2012, Parrett et al. 2023).

Wild turkeys (*Meleagris gallopavo silvestris*) are a uniparental ground-nesting upland gamebird species that are hunted throughout their range (Healy 1992). Female turkeys (hereafter hens) select nesting sites that are typically shallow depressions in the ground they create themselves. Nest-site selection by hens is highly variable, with nests found across a wide range of habitats (Healy 1992). However, studies have shown that hens are more likely to nest in areas with dense ground cover that provides visual obstruction for concealment and protection (Byrne 2013, Keever et al. 2023, Little et al. 2016, Wood et al. 2019). Hens generally lay a clutch of 10–12 eggs over approximately two weeks, laying one egg per day (Little et al. 2014, Williams and Austin 1988). Continuous incubation lasts 25–29 days, during which the hen typically leaves the nest once per day to forage for food, although some variability in this behavior may occur (Healy 1992). During incubation, turkeys are considered central place foragers meaning that they must acquire resources in the surrounding landscape and return to the nest between movement bouts (i.e., recesses) off the nest.

Several abiotic and biotic factors have been identified that may influence nest survival in turkeys. For instance, prolonged climatic conditions such as precipitation on cold days have been shown to negatively influence nest survival (Roberts and Porter 1998). In addition, the wet-hen hypothesis posits that hens exposed to precipitation may experience greater predation risk via easier olfactory detection by mammalian predators (Lehman et al. 2008, Lowrey et al. 2000, Palmer et al. 1993, Roberts et al. 1995, Roberts and Porter 1998). Prior research has emphasized the importance of nest-site selection, particularly vegetative characteristics in proximity of the nest (Badyaev et al. 1995, Fuller et al. 2013, Keever et al. 2023) and habitat features at the landscape scale (Pollentier et al. 2017, Thogmartin et al. 1999) that affect nest survival. Variability in vegetation and landscape features may influence individual behavior during incubation, such as greater distance traveled which has been linked to higher daily nest survival (Bakner et al. 2019).

Turkeys spend part of the year in large social groups often at the human-wildlife interface in proximity to poultry farms. These behaviors present two major concerns for disease dynamics in turkeys including increased risk for pathogen transmission within flocks and potential exposure to pathogens from domestic poultry. Lymphoproliferative disease virus (LPDV) is an avian oncogenic retrovirus that has been linked to cause mortality in domestic turkeys but has been documented to cause minimal mortality in wild populations (Biggs et al. 1978, Macdonald et al. 2022). Disease surveillance studies have found prevalence rates of LPDV between 26–83% in the eastern United States (Alger et al. 2017, Macdonald et al. 2022, [Shea 2021], Thomas et al. 2015) and Pennsylvania has a prevalence rate of 70% (Koch et al*. In Prep*). While previous research linking LPDV to recruitment is sparse, Shea (2021) found hens infected with LPDV laid fewer eggs, suggesting population-level effects. In addition, turkeys are susceptible to a wide range of parasite taxa including protozoans, trematodes, cestodes, acanthocephalans, nematodes, and arthropods (Davidson and Wentworth 1992, Hafez and Shehata 2024). Importantly, coinfections of multiple pathogen types simultaneously in the same host may actually have more severe impacts on wildlife and should be investigated when possible (Jolles et al. 2008). As a result, factors such as habitat, weather, individual characteristics, behavior, disease, and parasites may interact in complex ways to influence turkey reproductive success.

Variation in nesting behavior and recruitment is considered a key factor influencing turkey population growth, which has prompted researchers to investigate factors that may influence reproductive success. In our study, we developed three models: a pre-nesting movement model, a nest-site selection model, and a nest success model to investigate how individual decision-making influences reproductive success across multiple levels. Our models assessed: (1) how a suite of individual, nest, landscape and weather covariates influence movement and nesting (2) mismatches in the effect of habitat on pre-nesting movement, nest-site selection, and nest survival, and (3) the effects of LPDV and parasitic infection on daily nest survival probability. We applied our modeling framework to hens monitored in Pennsylvania, Maryland, and New Jersey.

**METHODS**

**Study Area**

Our study areas spanned diverse regions across Pennsylvania, Maryland, and New Jersey with different landscape compositions (Figure 1). In Pennsylvania, our study areas were wildlife management units (WMUs) 2D, 3D, 4D, and 5C. WMU 5C, located in the southeastern part of the state, was a mix of urban, agricultural, and forested landscapes. 3D, situated in the northeastern region, featured expansive public forests surrounded by urban development. 4D, located centrally, consisted primarily of public forests interspersed with agricultural areas. 2D, in the western portion of the state, was characterized by a diverse landscape that includes urban, forested, and agricultural areas. Pennsylvania study areas were largely characterized by both Appalachian northern hardwood and central oak-pine forests with overstory species including northern red oak (*Quercus rubra*), white oak (*Quercus alba*), scarlet oak (*Quercus coccinea*) black oak (*Quercus velutina*) sugar maple (*Acer saccharum*), American beech *(Fagus grandifolia*), and eastern white pine (*Pinus strobus*) (2015-2025 Pennsylvania Wildlife Action Plan).

In Maryland, the western study area (Maryland West) encompassed montane forests in the Allegheny Mountains, interspersed with agricultural lands, whereas Maryland East consisted of a mix of agricultural areas, forests, wetlands, and urban development. Oak-hickory forest largely encompassed our Maryland West study area with dominant overstory species including a closed canopy of white oak, northern red oak, scarlet oak, black oak, and chestnut oak (*Quercus montana*) (Maryland State Wildlife Action Plan, 2015). Commercial loblolly pine (*Pinus taeda*) plantations encompassed much of forest cover in Maryland East with other dominant overstory trees including white oak, southern red oak (*Quercus falcata*), northern red oak, black oak, scarlet oak, and Virginia pine (*Pinus virginiana*) (Maryland State Wildlife Action Plan, 2015).

In New Jersey, New Jersey South was situated in the southern portion of the state and consisted of pine and deciduous forest interspersed with agriculture, surrounded by urban residential areas. New Jersey South consisted of a combination of oak-hickory and loblolly pine-shortleaf pine forest cover types (Bechtold, Patterson, and U.S. Forest Service, 2018). Within these two groups pitch pine (*Pinus rigida*), sugar maple, and Atlantic white-cedar (*Chamaecyparis thyoides*) represented the most common overstory trees respectively (Bechtold, Patterson, and U.S. Forest Service, 2018).

**Field Methods**

Wild Turkey Capture and Transmitter Programming

We captured hens December-March 2022–2023 in Pennsylvania, 2023–2024 in Maryland, and 2024 in New Jersey using rocket and drop nets (Bailey et al. 1980, Glazener et al. 1964). Upon capture, we noted age from each hen based upon growth of the ninth and tenth primary feathers (Pelham and Dickson 1992). Blood and fecal samples were collected from hens to assess infection status for LPDV and to determine the occurrence of three gastrointestinal focal parasites: nematodes such as *Capillaria* sp. (i.e., threadworms) and Ascarids(i.e., roundworms), as well as coccidian infection caused by *Eimeria* sp. (i.e., protozoans) at the individual scale. Each bird was marked using an aluminum leg band and a subset of individuals received a radio transmitter with built in ultra-high-frequency (UHF), global positioning system (GPS) and accelerometer (ACC) components (Bird 1A, E-obs digital telemetry, Munich, Germany). We set our transmitters to collect a GPS fix every 30 minutes during the months April–July which largely encapsulated nesting behavior in the region. Further, we collected ACC observations through bursts of 10Hz every 2 minutes for all three axes (X, Y, and Z) for a total of 120 ACC samples (40/axis). We monitored nesting hens using triangulation via UHF three times per week and downloaded GPS and ACC data from a Basestation (E-obs digital telemetry, Munich, Germany) twice per week.

Nest Identification and Fate Determination

We used the ACC data to confirm incubation behavior. We first calculated the standard deviation of the z-axis observations per burst for each hen. If the standard deviations were consistently less than 15 for at least a day we assumed incubation behavior was occurring. Alternatively, if the values were consistently greater than 15 for one full day we assumed that incubation had ceased. This allowed us to remotely monitor hen behavior without disturbing incubation patterns (Ferraz et al. 2024, Schreven et al. 2021). 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) “depredated”, if the eggs were missing or at least one had been cracked or damaged (not from the process of hatching), (4) “unknown”, if a nest attempt was made but we were unable to determine why it failed and (5) *“*unconfirmed” for nests we were unable to access or the fate could not be determined (i.e., may have been a success or a failure).

To post-hoc estimate initiation and termination of incubation behavior, we used ACC observations for each individual collected during daylight hours 50 days prior to the date a nest was field checked and three days after (54 days). We first calculated the standard deviation of the z-axis observations per burst and then calculated the daily proportion of those values that were less than 15. The start date of incubation was the first day that the daily proportion was greater than 0.85 for two days in a row. The termination of a nesting attempt was defined as the first day when daily proportion was less than 0.85 for three days in a row, following the identification of an incubation start date.

**Environmental and Individual Variables**

We selected covariates to be used in our analyses based on three scales of interest: individual, nest, and landscape (Table 1). Individual covariates were characteristics that varied according to an individual hen’s behavior or body condition. Nest covariates were habitat attributes in the vicinity of nest sites. Some nest covariates (I.e. ferns) may be representative of other ecological characteristics during certain times of the year. Landscape covariates encompassed broader landscape features, cover types, and coarsely derived weather variables that we believed could potentially influence daily nest survival probability. We standardized all continuous predictors within each analysis to a mean of zero and standard deviation of one. Not all covariates were used in each model (Table 2).

Individual Covariates

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*. We classified infection with LPDV as categorical predictor and modelled the effect of focal gastrointestinal parasites including *Capillaria* sp., *Eimeria* sp., and Ascaridson nest survival. To gauge the effects of coinfection with LPDV and parasites on nest survival, we included interaction effects between LPDV and presence of each of the three parasites.

Nest incubation date (Calendar Day) was included to determine if the day of the year when a hen began incubating had an impact on daily nest survival probability. We calculated incubation constancy by creating a 29 m 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 calculating the mean error across all habitats. We calculated the proportion of time a hen spent on the nest by calculating the number of locations that were inside of an individual’s nesting buffer and dividing the resultby the total number of locations collected during an individual’s incubation period.

Nest Covariates

In Pennsylvania, we gathered information about habitat attributes in the proximity of nests at each observed nest location and at four potential nests 100 m away from the observed nest in each of the four cardinal directions. We used these data to assess how fine-scale vegetation was related to nest-site selection and daily nest survival. We conducted a vegetation survey within three days of a hen leaving the nest (e.g., hatch or termination) to avoid seasonal changes in vegetation structure. We created 7.9 m (26 ft) radius survey plots to estimate percent ground cover in proximity to the nest bowl, estimating ground coverage of understory woody vegetation (i.e., plants that have a structural woody stem) ferns, and grass/forbs within each stratum containing an observed nest site and 4 paired potential sites. At the nest bowl, we used a Robel pole (Robel 1970) to measure the amount of visual obstruction of a nest, which was meant to capture how a predator would view the nest horizontally. Visual obstruction was quantified as the average visual obstruction reading in all four cardinal directions in which understory vegetation obscured an observer’s line of sight. In addition, we conducted a woody stem count noting all woody stems greater than 4.5’ tall but less than 4’’ DBH within a survey plot. To calculate basal area (proxy for canopy cover), we used a variable radius plot and a 10 BAF prism.

Landscape Covariates

We used remotely sensed land cover data from the 2019 National Land Cover Database (NLCD; Dewitz et al. 2021) to assess its role in pre-nesting movement, nest-site selection, and daily nest survival probability. The NLCD portrays land cover information as grid cells with a 30 m × 30 m spatial resolution, which we refined into biologically relevant land cover types. We created three forest categories: “Deciduous Forest,” “Evergreen Forest,” and “Mixed Forest” to capture different forest cover compositions. A “Developed” category was created by combining developed open space, low-intensity, medium-intensity, and high-intensity urban areas. We created separate “Pasture/Hay” and “Crop” cover types to portray differing agricultural landscapes. A “Grassland/Shrub” category was formed by combining shrub/scrub, barren, and grassland classifications. Finally, a “Wetland” category was created by merging open water, with woody and open herbaceous wetlands. We used the sf (Pebesma & Bivand, 2023) and terra (Hijmans, 2024) R packages to extract and process the land cover data. Road data were obtained using the tigris package (Walker, 2024) for Maryland and New Jersey. For Pennsylvania, we accessed road data from Pennsylvania Spatial Data Access (PASDA) (Pennsylvania Spatial Data Access, 2024). We calculated the Euclidean distance from the 30 m × 30 m grid cell in which the nest occurred to the nearest road, distinguishing between two road types: primary roads which were defined as highways, accessways, state, and federal roads and secondary roads which were defined as county, municipal, and township roads.

We obtained weather covariates from Daymet (Thornton et al. 2022) using the R package daymetr to determine how weather characteristics influenced daily nest survival probability. We extracted daily precipitation (mm) and daily minimum temperature (°C) for each each day within a nesting attempt to determine the effects of each on daily nest survival probability. We calculated a three-day moving average for both weather variables to account for uncertainty in how weather conditions influence nest failure on the day of, one day before, and two days before the termination of the nesting attempt. We also included an interaction effect between daily precipitation and daily minimum temperature to gauge if lower temperatures and precipitation have compounding effects on nest survival.

**Statistical Analysis**

We developed three models to examine pre-nesting movement, nest-site selection, and nest success, and compared the effect sizes across these ecological processes to assess synchrony or mismatch. All models were fitted in R (R Core Team 2024) using the nimble package (de Valpine et al. 2024). For each model, we applied Markov Chain Monte Carlo (MCMC) methods to estimate posterior distributions of all parameters. We visually inspected the convergence of the chains to determine satisfactory convergence and used 90% Bayesian credible intervals when evaluating uncertainty associated with our estimates. We included predictors within our model that contained a Pearson’s correlation value less than 0.7. We a priori hypothesized that the majority of GPS and nest locations within our study would be located in deciduous forest land cover, so we compared the effect of all categorical landscape covariates relative to deciduous forest.

Pre-Nesting Movement Model

We modeled individual movements during a hen’s pre-nesting period using conditional logistic regression, also referred to as a step-selection function (Fortin et al. 2005, Thurjfell et al. 2014, Muff et al. 2019). 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, Muff et al. 2019). We calculated nest initiation (i.e., onset of laying) by subtracting the estimated clutch size of each hen from the estimated date of incubation initiation. To ensure that our pre-nesting period didn’t contain nest-site selection behavior, we buffered each nest initiation date by subtracting 5 days from the estimated date of nest initiation. Our pre-nesting period was defined as the 2-week interval prior to laying. We generated ten “available” steps for each observed step using the observed distribution of step lengths and turning angles from all individuals using the ‘amt’ package (Signer et al. 2019). Each set of one used location and ten available locations formed a stratum within the conditional logistic regression. Then we removed all steps within a stratum of used and available steps if the used step had an open water classification. If an available step had an open water classification, we removed it from the existing stratum. Each used or available observation *j*, at time *t*, for hen *n*, was assumed to arise from a Poisson distribution

(1)

in which was a stratum-specific intercept, and was a vector of coefficients that described the effects of the covariates (Muff et al. 2019). 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 set the variance at 106 to avoid shrinkage when estimating the values of our stratum-specific random effect. We sampled 40,000 iterations and deleted the first 10,000 iterations, using a single chain for each parameter and a thinning interval of 1.

Nest-Site Selection Model

We modeled nest-site selection of hens using a conditional logistic regression (Thurjfell et al. 2014, Fortin et al. 2005, Muff et al. 2019), where each stratum contained the observed nest and the four paired potential nest sites. We modeled the relative probability a nest-site was used as

where *n* represented an individual hen, *j* represented each used or available nest location, was a stratum-specific intercept, and was a vector of coefficients that describes the effects of the covariates . 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 set the variance at 106 to avoid shrinkage when estimating the values of our stratum-specific random effect. We sampled 30,000 iterations and removed the first 10,000 iterations in the nest-site selection model, using a single chain for each parameter and a thinning interval of 3.

Nest Success Model

We developed two known-fate models to compare the effects of various predictors on daily nest survival probability: a habitat and weather model, which examined the influence of nest, landscape, age, and weather variables, and a disease model, which assessed the impact of LPDV and parasite taxa. We reclassified nests denoted as abandoned or depredated to a response variable of zero, while nests that successfully hatched at least one offspring were assigned a value of one. We removed nests where the fate was unknown from the analysis. Encounter histories for each individual were created from the onset of incubation to the termination of the incubation period. We modeled the fate of each individual hens nesting attempt *n* on day *k* as a Bernoulli distribution where

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where the fate of the nest was conditional on whether the nest survived the previous interval. Daily nest survival probability was modeled as a function of time-dependent weather variables, landscape metrics, nest covariates, and individual characteristics as

Where was a vector of coefficients that describes the effects of biologically relevant covariatesfor each nest. We used the complementary log-log (cloglog) link and low-information priors for each coefficient, such that . We sampled 20,000 iterations and removed the first 3,000 samples in both known fate models, using a single chain for each parameter and a thinning interval of 3. In Pennsylvania, the reference level in the disease model was no LPDV infection and absence of the three parasites, and in Maryland it was no LPDV infection.

**RESULTS**

We obtained data from 127 hens and 158 nesting attempts in Pennsylvania, 87 hens and 102 nesting attempts in Maryland, and 12 hens and 12 nesting attempts in New Jersey. The median dates of incubation by year were estimated as 18 May in 2022 and 19 May in 2023 in Pennsylvania, 8 May 2022, and 9 May 2023 in Maryland, and 27 April 2024 in New Jersey. Mean incubation constancy was 0.81 in Pennsylvania (n = 127), 0.83 in Maryland (n = 102), and 0.81 in New Jersey (n = 12).

**Pre-Nesting Movement Model**

We obtained 43,562 GPS locations during the pre-nesting period in Pennsylvania. Hens selected against all cover types including mixed forest (-0.05; CI = -0.08– -0.02), evergreen forest (-0.18; CI = -0.25– -0.10), crop (-0.41; CI = -0.46– -0.37), pasture (-0.47; CI = -0.51– -0.44), grassland/shrub (-0.24; CI = -0.32– -0.17), and wetland (-0.40; CI = -0.48– -0.32) relative to deciduous forest (Figure 2). Hens also selected for areas that were further from primary roads (0.18; CI = 0.13–0.23; Figure 2) during pre-nesting. We collected 33,435 GPS locations during the pre-nesting period in Maryland. Hens exhibited differing selection patterns as compared to the deciduous forest reference level (Figure 2). Hens selected for mixed forest (0.07; CI = 0.02–0.12), while selecting against evergreen forest (-0.16; CI = -0.23– -0.10), crop (-0.41; CI = -0.47– -0.35), pasture (-0.21; CI = -0.27– -0.14), developed (-0.70; CI = -0.78– -0.62), and grassland/shrub (-0.27; CI = -0.38– -0.17). In addition, hens selected for greater distances from primary roads (0.16; CI = 0.008–0.28). We obtained 3,617 GPS locations during the pre-nesting period in New Jersey. Hens exhibited varying levels of selection of landscape variables compared to the deciduous forest reference level (Figure 2). Hens selected for grassland/shrub (0.19; CI = 0.08–0.31), and wetland (0.40; CI = 0.29–0.52). However, hens selected against developed land use (-0.66; CI = -0.99– -0.36), pasture (-1.31; CI = -2.49– -0.25), and greater distances from secondary roads (0.08; CI = 0.006– 0.17).

**Nest-Site Selection**

At the nest-scale, hens in Pennsylvania selected for greater fern cover (0.30; CI = 0.04– 0.56), woody vegetation (0.55; CI = 0.27–0.84), and higher visual obstruction (1.38; CI = 1.13–1.64) in proximity to the nest (Figure 3). However, hens selected against greater woody stem counts (0.51; 90% CI = -0.79– -0.24). At the landscape-scale hens selected against nest locations in mixed forest (-0.86; CI = -1.50– -0.24) as compared to deciduous forest (Figure 3). In Maryland, hens selected for nest locations within pasture (1.06; CI = 0.05–2.17) relative to deciduous forest (Figure 3). In New Jersey, as compared to deciduous forest, we failed to detect an effect of landscape variables on the relative probability a nest location was used (Figure 3).

**Nest Success**

In our habitat and weather model for Pennsylvania (Figure 4) we detected positive relationships between daily nest survival and percent fern (0.06; CI = 0.002–0.13), incubation constancy (0.13; CI = 0.06–0.21) and evergreen forest (0.48; CI = 0.12–0.88). In our habitat and weather model for Maryland (Figure 4) we detected positive effects on daily nest survival probability for the juvenile age class (0.32; CI = 0.11–0.53) and greater distances to secondary road structures (0.07; CI = 0.005–0.15). Additionally, in Maryland we detected a negative effect for use of pasture (-0.32; CI = -0.60– -0.04) on nest survival. In our Maryland disease model (Figure 5), we failed to detect an effect of LPDV (-0.03; CI = -0.16–0.08) on nest survival. In our Pennsylvania disease model (Figure 5), when factoring in coinfection, we detected a negative effect for LPDV × *Eimeria* sp. (-0.41; CI = -0.81– -0.05) on nest survival.

**DISCUSSION**

We completed the first wild turkey field research project in Pennsylvania in over a decade, as well as landmark studies in New Jersey and Maryland. We used a multi-level modelling approach to examine the influence of habitat on three sequential processes affecting hen decision-making and reproductive success. By investigating these factors across multiple levels, we directly compared the effects of nest- and landscape-scale habitat on hen decision-making during the pre-nesting and nest-site selection stages, as well as the linkages of those decisions to reproductive success. Additionally, we evaluated the effects of weather, behavioral metrics, infection with LPDV and parasites, as well as individual covariates on nest survival. Collectively, our findings underscore the complexity of understanding turkey reproductive behavior and the factors influencing reproductive success in the region.

We observed differences in hen landscape selection across each state, and the resulting effect on daily nest survival. Our pre-nesting movement model results showed that hens primarily favored forested landscapes, including mixed, deciduous, and evergreen forests, as well as wooded wetlands. This pattern is expected, particularly for early nesting attempts, as acorns and other hard mast species are essential food sources for turkeys during the winter months (Healy 1992, Hurst 1992, Steffen et al. 2002). The selection for conifers (mixed and evergreen forests) in Maryland and New Jersey during pre-nesting may represent a behavioral adaptation that aids in thermoregulation during colder temperatures and high winds (Gonnerman et al. 2022, Healy 1992, Vander Haegen et al. 1989), but we failed to detect this relationship in Pennsylvania, perhaps due to lower availability of mixed and evergreen land cover relative to deciduous forest in the state. Wunz and Hayden (1975) noted that terrain may play a role in explaining turkey winter survival in Pennsylvania, as individuals in deeper valleys have access to spring seeps, plowed roads, and cleared hillsides which help support wintering individuals. Although we failed to identify selection for conifers in Pennsylvania during pre-nesting, we observed a positive effect of evergreen forest on daily nest survival in Pennsylvania. Previous studies have found the Merriam’s wild turkey (*Meleagris gallopavo merriami*) having greater nest success in coniferous forests in the western United States (Lutz and Crawford 1987, Wakeling et al. 1998). In Maryland, we found that during nest-site selection hens selected nest locations in pasture relative to deciduous forest, but there was a negative effect on daily nest survival; previous studies have found mowing and haying have led to considerable anthropogenic destruction of nests in agricultural landscapes (Crawford et al. 2021, Paisley et al. 1998, Tyl et al. 2023). Additionally, we observed negative effects for developed land use relative to deciduous forest across the three states on the relative probability a location would be used during pre-nesting. The negative relationship with developed suggests an overall avoidance for areas with greater human population density. Wright and Speake (1975) observed that turkeys also avoided areas with greater human recreational activity during the summer months.

The relationships between turkeys and road structures are complex as hens may perceive roads differently based on differing levels of anthropogenic disturbance (Adey et al. 2024, Butler et al. 2005, McDougal et al. 1990). To reflect this, we attempted to discern differences between primary and secondary roads across the three processes to account for differences in vehicular traffic, speed, and anthropogenic disturbance. We detected positive relationships for the effect of greater distances to primary roads in Pennsylvania and Maryland during the pre-nesting period. The avoidance of roads during pre-nesting may represent a behavioral response to avoid frequently traveled road structures (Erlexben et al. 2010, McDougal et al. 1990) while also avoiding mammalian edge predators, such as coyote (*Canis latrans*), red fox (*Vulpes vulpes*), and gray fox (*Urocyon cinereoargenteus*; Lombardi et al. 2017, Way et al. 2004). In addition, we further found that nest survival decreased with closer proximity to secondary roads in Maryland and to primary roads in New Jersey. Our findings are comparable to Thogmartin et al. (1999) in Arkansas in which nest success decreased closer to roads.

Previous studies have shown that rain and cold weather reduce nest survival by increasing stress on hens during incubation, which lowers incubation constancy and increases predation risk (Lehman et al. 2008; Palmer et al. 1993; Roberts and Porter 1998; Yarnall et al. 2020). However, we failed to detect any relationships supporting the wet-hen hypothesis in the Mid-Atlantic region. Instead, our results align with Boone et al. (2024), who found no linkage between precipitation during incubation and nest survival. Unlike Boone et al. (2024), our study did not assess weather effects during the pre-nesting period, nor did we examine anomalies in weather patterns or long-term trends. Boone et al. (2024) reported that January precipitation positively affected nest success, suggesting that precipitation during pre-nesting may increase body condition leading to greater nest success. Thus, understanding how precipitation and temperature during pre-nesting as well as anomalies may be important for understanding how weather influences nest survival in northern regions.

We observed selection for specific vegetative attributes in proximity to nest sites in Pennsylvania. We found a negative relationship between nest-site selection and woody stem density near the nest site. Since previous studies have suggested that predation is the main influence on nest-site selection (Murphy, 1983, Martin 1992, 1993a), potentially a higher density of woody stems in proximity to a nest may hinder escape routes therefore decreasing adult survival (Fuller et al. 2013, Mangelinckx et al. 2020, Schooley et al. 1996, Wiebe et al. 1998). However, our results are similar to other studies that have reported greater use of areas with visual obstruction and percent woody vegetation in proximity to the nest, which offers concealment from predators (Wood et al. 2019, Yeldell et al. 2017). We observed positive relationships between percent fern cover and the relative probability of nest site selection, as well as on nest survival. We believe this demonstrates that turkeys preferred areas with a more open canopy and greater nest survival was also associated with these areas. This is supported by the presence of focal fern species such as hay-scented fern (*Dennstaedtia punctilobula*), New York fern (*Thelypteris noveboracensis*), and bracken fern (*Pteridium aquilinum*) which are typically associated with reduced canopy closure and landscape disturbance (I.e., windthrow) (de la Cretaz and Kelty 1999, Engelman et al. 2006). However, we failed to detect an effect of basal area on nest-site selection possibly because restricting potential nest locations to within 100 m limited variability between used and potential sites. We recognize that the phenology of vegetation growth may mean that the effect of vegetation measurements upon nest-site selection and the termination of the nest attempt may be confounded because vegetation at hatched nests has had the full period of the nesting cycle to grow relative to failed nests (McConnell et al. 2017, Ringleman and Skaggs 2019).

We examined the influence of individual characteristics and decision-making during incubation on daily nest survival probability. We found a positive effect of incubation constancy in Pennsylvania demonstrating that a greater time spent in proximity to a nest increased daily nest survival. This is aligned with previous avian studies demonstrating that time spent off the nest is an important predictor in reproductive success (Parret et al. 2023, Smith et al. 2012). Our average incubation constancy values aligned with previous work on wild turkeys (84%; Bakner et al. 2019), but were lower than those found for other Galliformes, such as greater sage grouse (96%, *Centrocercus urophasianus;* Coates and Delahanty 2011), greater prairie chicken (95%, *Tympanuchus cupido;* Winder et al. 2016) and white-tailed ptarmigan (95%, *Lagopus leucura*; Wiebe and Martin 2000). High incubation constancy allows females to preserve optimal thermal conditions within the nest that facilitate reproductive success (Afton and Paulus 1992). Further, individuals with higher incubation constancy values may have shorter incubation durations, thus decreasing predation risk (Aldrich and Raveling 1983). We found that juveniles in Maryland had greater daily nest survival rates than adults but acknowledge our small sample size of juveniles within this category (*n* = 18). This contradicts the findings of previous studies where older hens had greater daily nest survival probabilities (Keever et al. 2023, Pollentier et al. 2014).

We investigated the effect of LPDV and three prevalent parasites on nest survival using an exploratory approach. Our study failed to detect effects on nest survival attributable to LPDV or each parasite taxa alone. We observed a high prevalence of LPDV in our study area (Koch et al. In Prep, Macdonald et al. 2022, Thomas et al. 2015), which could explain the lack of variability in nest survival within our sample of infected and non-infected hens potentially obscuring effects. Previous studies have indicated that while LPDV can impact body condition, it does not appear to strongly influence reproductive success or overall survival. This is supported by the results of previous studies where LPDV accounts for minimal morbidity and mortality in turkey populations (Allison et al. 2014, Macdonald et al. 2022). However, we detected a negative effect when accounting for coinfection with LPDV and *Eimeria* sp.on nest survival. While at least seven *Eimeria* speciesare known to parasitize domestic and wild turkeys (Chapman 2008) clinical cases of coccidiosis have only been documented in domestic pen-raised birds. However, infection of *Eimeria* sp*.* in wild turkeys potentially could lead to reduced physical condition (Davidson and Wentworth 1992, Hill et al. 2005, Kozicky 1948) which during nesting could exacerbate the energetic cost of reproduction. Infection with LPDV may result in immunosuppression, further allowing *Eimeria* sp. to establish and replicate faster within a host (Niedringhaus et al. 2019). Thus, our results suggest that while infection with LPDV alone may not have a significant impact on reproductive success, coinfection with additional parasites may amplify the effects of the disease potentially leading to reduced reproductive success.

**MANAGEMENT IMPLICATIONS**

Our results suggest that land managers should embrace complexity when it comes to turkey management, focusing on both nest- and landscape-scales. At the nest-scale in Pennsylvania, our results suggest habitat management that prioritize growth of understory woody vegetation that provide visual obstruction, albeit with fewer individual woody stems. Our results suggest that turkey nest survival is higher in disturbed landscapes with lower canopy closure. At the landscape-scale in Maryland, we found that hens selected for pasture when placing nests, and that this decision had a negative effect on nest survival. Our results suggest that landowners use caution, if possible, when mowing or haying agricultural fields during the summer months, particularly during peak nesting which occurs between May-July. Additionally, our results suggest that future research evaluating the effect of coinfection with LPDV and parasites on decision-making during incubation may be helpful in linking viral and parasitic effects to turkey reproductive success.

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**ETHICS STATEMENT**

All capture and handling was completed under the Pennsylvania State University Institutional Animal Care and Use Committee (Protocol # PROTO202202180).

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Figure Captions

Figure 1. Our study area spans four Wildlife Management Units—2D, 3D, 4D, and 5C—in Pennsylvania, USA (2022–2023); one region—South—in New Jersey, USA (2024); and two regions—East and West—in Maryland, USA (2023–2024).

Figure 2. Estimates and 90% Bayesian credible intervals for the effect of landscape covariates on pre-nesting habitat selection based on GPS locations obtained from 127 wild turkey hens in Pennsylvania (2022-2023), 87 hens in Maryland (2023-2024), and 12 hens in New Jersey (2024). Deciduous forest land cover was the reference category.

Figure 3. Estimates and 90% Bayesian credible intervals for the effect of landscape (circle) and nest (triangle) covariates on nest-site selection based on 158 wild turkey nesting attempts in Pennsylvania (2022-2023), 99 nesting attempts in Maryland (2023-2024), and 12 nesting attempts in New Jersey (2024). Deciduous forest land cover is set as our reference category.

Figure 4. Estimates and 90% Bayesian credible intervals for the effect of weather variables (diamond), landscape variables (circle), nest covariates (triangle), and individual covariates (square) on daily nest survival probability based on 158 wild turkey nesting attempts in Pennsylvania (2022-2023), 102 nesting attempts in Maryland (2023-2024) and 12 nesting attempts in New Jersey (2024). No used nests were located within our wetland cover type in Pennsylvania and New Jersey. Deciduous forest land cover is set as our reference category. There were zero used nests within the wetland cover type in New Jersey, so it was excluded from the model.

Figure 5. Estimates and associated 90% Bayesian credible intervals from disease known fate models vary as a function of disease covariates in 68 wild turkey hens and 83 nesting attempts in Pennsylvania and 84 hens and 102 nesting attempts in Maryland. Hens that were not infected with LPDV or each of the three parasites are set as the reference level in the Pennsylvania model. Hens that were not infected with LPDV in Maryland were set as the reference level in the Maryland model.

Table 1. Percent land cover type is shown within four Wildlife Management Units—2D, 3D, 4D, and 5C—in Pennsylvania, USA (2022–2023); One region—South—in New Jersey, USA (2024); and two regions—East and West—in Maryland, USA (2023–2024).

|  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| *Study Area* | *%*  *Developed* | *%*  *Deciduous*  *Forest* | *%*  *Mixed Forest* | *%*  *Evergreen*  *Forest* | *%*  *Grassland*  *Shrub* | *%*  *Wetland* | *%*  *Crop* | *%*  *Pasture* |
| PA 2D | 10.3 | 47.2 | 13.9 | 10 | 2.6 | <1 | 9.2 | 13.9 |
| PA 3D | 13.1 | 57.2 | 11.0 | 2.2 | 1.5 | 7.3 | 4.0 | 1.0 |
| PA 4D | 8.8 | 54.3 | 10.9 | 2.7 | 1.6 | <1 | 11.7 | 8.5 |
| PA 5C | 27.8 | 28.8 | 4.9 | <1 | 1.6 | 1.9 | 18.0 | 15.5 |
| MD East | 7.9 | <1 | 3.3 | 6.9 | <1 | 42.9 | <1 | 25.3 |
| MD West | 10.2 | 51.8 | 10.4 | 1.2 | 2.1 | 1.3 | 5.9 | 15.3 |
| NJ South | <1 | 9.1 | 8.5 | 5.9 | 2.1 | 33.6 | 13.3 | <1 |

Table 2. Covariates used in models for pre-nesting movement, nest-site selection, and daily nest survival probability of wild turkey hens monitored in Pennsylvania (2022-2023), Maryland (2023-2024) and New Jersey (2024). Each covariate is presented with the models in which it was used, however not every covariate was present in every model.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| *Covariate* | *Model* | *Source* | *Scale* | *Description* | *State* |
| Wetland | Pre-Nesting Movement, Nest-Site Selection, Nest Success | NLCD  30m x 30m Raster | Landscape | Woody Wetlands, Emergent Herbaceous Wetlands cells | Pennsylvania, Maryland, New Jersey |
| Developed | Pre-Nesting Movement, Nest-Site Selection, Nest Success | NLCD  30m x 30m Raster | Landscape | Developed Open Space, Developed Low Intensity, Developed Medium Intensity, Developed High Intensity cells | Pennsylvania, Maryland, New Jersey |
| Pasture | Pre-Nesting Movement, Nest-Site Selection, Nest Success | NLCD  30m x 30m Raster | Landscape | Pasture/Hay cells | Pennsylvania, Maryland, New Jersey |
| Crop | Pre-Nesting Movement, Nest-Site Selection, Nest Success | NLCD  30m x 30m Raster | Landscape | Cultivated Crop cells | Pennsylvania, Maryland, New Jersey |
| Deciduous Forest | Pre-Nesting Movement, Nest-Site Selection, Nest Success | NLCD  30m x 30m Raster | Landscape | Deciduous Forest cells | Pennsylvania, Maryland, New Jersey |
| Evergreen Forest | Pre-Nesting Movement, Nest-Site Selection, Nest Success | NLCD  30m x 30m Raster | Landscape | Evergreen Forest cells | Pennsylvania, Maryland, New Jersey |
| Mixed Forest | Pre-Nesting Movement, Nest-Site Selection, Nest Success | NLCD  30m x 30m Raster | Landscape | Mixed Forest cells | Pennsylvania, Maryland, New Jersey |
| Grassland/Shrub | Pre-Nesting Movement, Nest-Site Selection, Nest Success | NLCD  30m x 30m Raster | Landscape | Barren, Shrub/Scrub, Grassland/Herbaceous cells | Pennsylvania, Maryland, New Jersey |
| Distance to Primary Road | Pre-Nesting Movement, Nest-Site Selection, Nest Success | NLCD  30m x 30m Raster | Landscape | Distance from a grid cell to the nearest state/federal road | Pennsylvania, Maryland, New Jersey |
| Distance to Secondary Road | Pre-Nesting Movement, Nest-Site Selection, Nest Success | NLCD  30m x 30m Raster | Landscape | Distance from a grid cell to the nearest local/municipal road | Pennsylvania, Maryland, New Jersey |
| Daily Precipitation | Nest Success | Daymet  1km x 1km Raster | Landscape | Daily precipitation (mm) averaged across a 3 day rolling average | Pennsylvania, Maryland, New Jersey |
| Daily Minimum Temperature | Nest Success | Daymet  1km x 1km Raster | Landscape | Daily Minimum Temperature (°C) averaged across a 3 day rolling average | Pennsylvania, Maryland, New Jersey |
| Visual Obstruction | Nest-Site Selection, Nest Success | Field Sampled | Nest | Visual obstruction reading in all 4 cardinal directions averaged | Pennsylvania |
| Percent Woody Vegetation | Nest-Site Selection, Nest Success | Field Sampled | Nest | Includes shrubs, vines, trees less than 6ft tall, down woody debris, and branches of taller trees in plot | Pennsylvania |
| Percent Fern | Nest-Site Selection, Nest Success | Field Sampled | Nest | Live green ferns | Pennsylvania |
| Percent Grass/Forb | Nest-Site Selection, Nest Success | Field Sampled | Nest | Live grass/shrub species | Pennsylvania |
| Woody Stem Count | Nest-Site Selection, Nest Success | Field Sampled | Nest | Count of number of woody stems that are at least 4.5’ tall but < 4” DBH | Pennsylvania |
| Basal Area | Nest-Site Selection, Nest Success | Field  Sampled | Nest | Basal area using a 10 BAF prism (ft2/ acre) | Pennsylvania |
| LPDV Infection Status | Nest Success | Lab  Sampled | Individual | Blood sample tested positive for LPDV | Pennsylvania, Maryland |
| *Capillaria* sp. | Nest Success | Lab  Sampled | Individual | Fecal sample tested positive for *Capillaria* sp*.* | Pennsylvania |
| *Eimeria* sp. | Nest Success | Lab Sampled | Individual | Fecal sample tested positive for *Eimeria* sp. | Pennsylvania |
| Ascarids | Nest Success | Lab Sampled | Individual | Fecal sample tested positive for Ascarids | Pennsylvania |
| Nest Incubation Date | Nest Success | ACC Data | Individual | The Julian date in which a hen began incubating | Pennsylvania, Maryland, New Jersey |
| Age Class | Nest Success | Field Sampled | Individual | The age class of the hen (Adult or Juvenile) | Pennsylvania, Maryland, New Jersey |
| Incubation Constancy | Nest Success | GPS Data | Individual | The proportion of time a hen spent on the nest during incubation using GPS data | Pennsylvania, Maryland, New Jersey |