Nest survival of wild turkeys Meleagris gallopavo silvestris in a mixed-use landscape: influences at nest-site and patch scales

Authors: Fuller, Angela K., Spohr, Shelley M., Harrison, Daniel J., and Servello, Frederick A.

Source: Wildlife Biology, 19(2) : 138-146

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/11-121

Wildl. Biol. 19: 138-146 (2013)
DOI: 10.2981/11-121

www.wildlifebiology.com

Original article

Nest survival of wild turkeys *Meleagris gallopavo silvestris* in a mixed-use landscape: influences at nest-site and patch scales

Angela K. Fuller, Shelley M. Spohr, Daniel J. Harrison & Frederick A. Servello

Nest survival is a critical factor affecting avian demographics, and can be influenced by nesting chronology, fine scale nest-site selection and broad-scale landscape characteristics. We modeled the relative influences of nest age, temporal variation in nest success and habitat-related covariates at two spatial scales (nest-site and patch scale) on daily nest survival during incubation for eastern wild turkeys *Meleagris gallopavo silvestris* in a mixed-use landscape. Daily survival rate of turkey nests during incubation increased as percent understory cover (vegetation < 1 m tall) increased and decreased with increasing density of woody shrubs and saplings and herbaceous stems < 1 m tall (understory vegetation density) around the nest. We suggest that nest survival may be dependent on a balance of sufficient understory cover around nests to provide concealment for hens and nests, but with understory vegetation density below levels that reduce the hen's ability to detect a predator or to escape after detecting a potential threat. The balance between sufficient understory cover and limited density of understory vegetation occurred where understory (< 1 m tall) cover exceeded 50% and understory vegetation density was < 25 stems/m^2. Models that included variables related to the patch scale (e.g. fragmentation, edge and dominant land-cover class in a patch) did not receive strong support, demonstrating the relative importance of finer scale nest-site variables over patch-scale variables in determining survival of wild turkey nests in our highly variable mixed-use landscape.

Key words: fragmentation, habitat, Meleagris gallopavo silvestris, nest-site selection, nest success, nest survival, wild turkey

Angela K. Fuller, Shelley M. Spohr**, Daniel J. Harrison & Frederick A. Servello***, Department of Wildlife Ecology, University of Maine, 5755 Nutting Hall, Orono, Maine 04469, USA - e-mail addresses: angela.fuller@cornell.edu (Angela K. Fuller); shelleyspohr@yahoo.com (Shelley M. Spohr); harrison@maine.edu (Daniel J. Harrison); fred.servello@maine.edu (Frederick A. Servello)*

Present addresses:
**U.S. Geological Survey, New York Cooperative Fish and Wildlife Research Unit and Department of Natural Resources, Cornell University, Ithaca, New York 14853, USA*
***146 Cook Hill Road, Griswold, Connecticut 06351, USA*
****University of Maine, College of Natural Sciences, Forestry and Agriculture, 101 Winslow Hall, Orono, Maine 04469, USA*

Corresponding author: Angela K. Fuller

Received 14 December 2011, accepted 10 December 2012

Associate Editor: Erlend B. Nielsen

Nest survival is the most important demographic variable influencing annual population change of eastern wild turkeys *Meleagris gallopavo silvestris* in the northeastern United States (Roberts et al. 1995, Roberts & Porter 1996, 1998, Thogmartin & Schaeffer 2000). Average rates of predation on ground nests are generally greater in suburban than in rural woodlots (Wilcove 1985), and predators are consistently responsible for most nest failures (Vangilder et al. 1987, Vander Haegen et al. 1988, Thomas & Litvaitis 1993, Vangilder & Kurzejeski 1995). Predator densities are often greater in suburban areas (Hoffman & Gottschang 1977, Wilcove 1985, Rosenberg et al. 1999) and predation on artificial nests reportedly increases with human housing density (Thorington & Bowman 2003).

Causes of lower nesting success of turkeys in suburban areas may depend on multi-scale processes including differences in fine scale vegetation structure within patches (nest site), effects of broader scale, across-patch habitat composition and fragmentation, or by landscape processes that influence other aspects of the community such as inflated mesocarnivore densities (Thogmartin 1999). Vegetative cover has been positively associated with nest success in turkeys (Seiss et al. 1990, Palmer et al. 1993, Badyaev et al. 1996, Miller 1997); dense vegetation at the nest site provides concealment of hens and eggs and may reduce predation on ground nesting birds (Martin & Roper 1988). Thus, successful nest sites of wild turkeys are typically characterized by providing adequate concealment cover from predators (Lehman et al. 2008). Additionally, vegetation may disperse scents that some predators may use to locate nests (Conover 2007). Miller et al. (2000) reported that preferred habitats of wild turkeys with successful nests were located closer to water (creeks) than expected, and were characterized by sawtimber stands that were farther from roads and road edges. Wild turkey nests in Arkansas were less successful when they were close to roads (Thogmartin 1999). At the patch scale, turkeys often select larger patches (*sensu* Kotliar & Wiens 1990) than available (Thogmartin 1999). Wild turkey hens avoid areas of high edge density that are typically favoured by nest predators (Thogmartin 1999). This may be explained by greater predator diversity and abundance near edges of forest patches (Chalfoun et al. 2002) where fragmented landscapes may result in elevated densities of medium-sized mammalian nest predators (Oehler & Litvaitis 1996).

Many studies have described fine-scale, within-patch characteristics of turkey nesting sites by comparing successful and unsuccessful nests (Seiss et al. 1990, Badayev 1995, Thogmartin 1999, Miller et al. 2000, Nguyen et al. 2004), or have compared habitat characteristics at nest sites with random sites (Lazarus & Porter 1985, Thomas & Litvaitis 1993, Thogmartin 1999). Few studies have examined the effects of patch-scale metrics on nest survival in turkeys (Porter & Gefell 1995, Miller 1997, Thogmartin 1999). Our fragmented mixed-use landscape presented a unique opportunity to evaluate the relative importance of fine scale vegetation characteristics at the nest site vs fragmentation and edge influences at the patch scale, on daily nest survival of turkeys given the predominance of suburban areas, areas with high density of roads and patch-interface edges, and high variability in landscape composition and configuration between home ranges of nesting hens. Thus, we simultaneously examined the relative influences of nest-site and patch-scale variables on daily survival rate of turkey nests during incubation in a fragmented landscape in southeastern Connecticut, USA, where turkeys inhabit a mosaic of suburban areas, state-owned forest lands and agricultural lands.

Material and methods

Study site

We monitored 29 hen turkeys (N=6 in 1996 and N=23 in 1997) during incubation whose spring home ranges were located within Middlesex and New London counties in southeastern Connecticut, where the median human population density across the nine towns intersected by home ranges was 97 humans/km^2 (range: 34-461 humans/km^2; Secretary of the State 1996). Although much of the landscape was suburban (i.e. characterized by dispersed residential areas interspersed with small businesses), there were sizeable patches of undeveloped lands in various stages of forest succession. Overall, percent mature forest cover within home ranges of all monitored turkey hens ranged from 65 to 100%, percent developed land ranged from 0 to 28% and percent agriculture within home ranges ranged from 0 to 30% (Table 1). Forests were highly interspersed with developed lands (Brooks et al. 1993), which were the second leading contributors to edge density after transportation rights-of-way across all of Connecticut (Dickson & McAfee 1988).

Forests were dominated by oak *Quercus* spp.-hickory *Carya* spp. stands, which were commonly associated with yellow poplar *Liriodendron tulipifera*,

Table 1. Variation in patch-scale variables measured at 29 nests of eastern wild turkeys in southeastern Connecticut, USA, 1996-1997. 25% circle = radius of the 25th percentile of observed distances that hens left the nest during each day.

Variable	Mean	SD	Range
Patch density in home ranges	15.99	6.34	29.15
% forested land in home ranges	85.67	8.81	34.50
% developed land in home ranges	7.33	7.01	27.87
% agricultural land in home ranges	4.86	6.16	29.62
Distance from nest to nearest road (m)	248.97	162.82	670.00
Distance from nest to nearest edge (m)	129.83	107.24	500.00
Perimeter of edge in 25% circles	2287.64	800.78	2989.40

elm *Ulmus* spp. and red maple *Acer rubrum*. Common understory species included blueberry *Vaccinium* spp., witch hazel *Hamamelis virginiana*, dogwood *Cornus* spp., common spicebush *Lindera benzoin*, mountain laurel *Kalmia latifolia*, raspberry *Rubus* spp., maple-leaved viburnum *Viburnum acerifolium*, poison ivy *Rhus radicans* and greenbriar *Smilax* spp. (Dickson & McAfee 1988).

Mean winter (December-March) temperatures at a local weather station were -3.2°C in 1996 and 0°C in 1997 (National Oceanic and Atmospheric Administration). Snow depths exceeded 15.2 cm during 39 of 123 days in winter of 1996, but never exceeded 15.2 cm in 1997. Total precipitation during April and May was 31.0 cm in 1996, which was 7.6 cm greater than normal, and 22.3 cm in 1997. Mean daily temperatures in April and May were 9.8°C in 1996 and 8.8°C in 1997.

Capture, telemetry and home-range estimation

We captured female wild turkeys from January to April, 1996-1997, with rocket nets. After capture, we equipped hens with back-pack transmitters (Advanced Telemetry Systems, Isanti, Minnesota, USA) with 12-hour mortality sensors. All captured hens weighed $\geq$ 3.2 kg and weights of transmitter packages ranged from 89 to 93 g. Transmitters averaged 1.95% of body weight (range: 1.4-2.4%). Capture and handling procedures were approved by the Institutional Animal Care and Use Committee, University of Maine, Maine, USA.

We monitored hens at least three times/day during $>$ 4 days/week from April-July. We obtained locations of turkeys from the ground using triangulation of at least two bearings with intersecting angles from 30 to 150°. We assumed that incubation was occurring if hens were inactive and at the same location for six readings spaced across two consecutive days of monitoring based on ground visits and locations obtained in close proximity of nests. To avoid research-induced nest abandonment, we did not approach any closer than 15 m from the nest location, took bearings to nests and subsequently returned to the areas to ensure that hens were still nesting and to verify fates of nests by searching areas for nests immediately after hatching or nest failure. We considered an incubation attempt successful if at least one egg hatched (Vangilder et al. 1987). We assumed an incubation period of 28 days (Healy 1992). Lehman et al. (2005) described potential biases associated with rates of overall nest success when excluding nests that fail during the egg-laying period. Therefore, we did not intend for our estimates of nest survival during the incubation period to reflect rates of overall nest survival during both egg laying and incubation. Rather, we restricted our analyses to daily rates of nest survival during incubation to evaluate the relative effects of fine and broader scale landscape characteristics on survival of nests after incubation was initiated.

Additional to evaluating the influence of 4th-order (Johnson 1980) nest-site characteristics, we were interested in whether patch-scale characteristics (3rd-order *sensu* Johnson 1980) within home ranges occupied by nesting hen turkeys influenced their daily survival rates during incubation. Thus, we quantified several potential descriptor variables to define availability at the scale of the spring home range of nesting turkeys, as well as variables to define patch-scale use based on distances to patch transitions from turkey nests. We estimated minimum convex polygon home-range areas (Mohr 1947) during the spring nesting period (6 April - 9 July). Variables at the scale of spring home ranges included the percent forest land, percent developed land, percent agricultural land and patch density (patch types = forest, agriculture/open land, water and development including non-forested land with human-built structures) in home ranges. Patch-scale variables included distance from nest to nearest road and nearest edge (any boundary between any of the four patch types) and the perimeter of edge within the radius of the 25th percentile of observed distances that hens traveled from the nest during each day.

Nest-site and patch-scale measurements

We delineated four patch types within the home ranges of hens: forest, development, agriculture/open land and water. We quantified four variables describing vegetation characteristics adjacent to nest sites (total stems, percent cover above the nest, percent understory cover and understory vegetation density), three metrics describing distance to patch-type transitions (distance from nest to nearest road, distance from nest to nearest edge and perimeter of edge), three variables describing availability of land-cover types (percent forested land, developed land and agricultural land in home ranges) and one variable describing density of our four land-cover patches within spring home ranges. We used FRAGSTATS (McGarigal & Marks 1995) to quantify patch-scale metrics within home ranges that may affect nesting success based on previous studies that examined ground-nesting birds and landscape patterns (e.g. Seiss et al. 1990, Porter & Gefell 1995, Badyaev & Faust 1996, Thogmartin 1999, Miller et al. 2000). We evaluated multicollinearity with a Pearson correlation matrix (r) and because $|r| < 0.70$, we did not consider removing variables. We evaluated patch density (number of patches/unit area) and the percent of each patch type within the home range. We also calculated the distance from each nest to the nearest road (any paved travel lane) and any edge (any boundary between any of the four patch types). To evaluate patch-scale variables with potential to influence survival of nests, we quantified the linear distance of edge perimeters separating our four land-cover classes within mapped circles around all initial nests of radio-marked hens. We calculated circles based on the radius of the 25th percentile of observed distances that hens traveled from the nest during each day.

We measured cover variables around each nest and recorded the total number of understory stems (woody and herbaceous; < 5 cm dbh and ≥ 1 m height) in four 5×0.5 m rectangular plots oriented in each cardinal direction from the edge of the nest bowl. We determined percent total understory cover (< 1 m tall) in four circular plots with a 1-m diameter positioned 1 m from the nest in each cardinal direction as the percent of ground within the circle covered by vegetation (woody and herbaceous) estimated to the nearest five percentage points; the most common species included ferns, grasses, greenbriar, multiflora rose *Rosa multiflora*, *Rubus* spp., rhododendron *Rhododendron* spp. and regenerating hardwood saplings. We measured an index of understory vegetation density (Bakermans et al. 2012) as woody shrubs and saplings and herbaceous stems < 1 m. We measured understory vegetation density in four 1-m diameter circular plots positioned 1 m from the nest bowl in each cardinal direction. Understory vegetation density commonly included ferns, Japanese barberry *Berberis thunbergii*, hardwood saplings, blueberry, *Rubus* spp. and *Viburnum* spp. We averaged the measurements from four plots for both percent understory cover and understory vegetation density. We estimated percent cover above the nest (< 5 cm dbh and ≥ 1 m height) with a spherical densiometer held 30 cm above the nest.

Modeling nest survival

We used the nest-survival model (Dinsmore et al. 2002) in program MARK (White & Burnham 1999) to evaluate daily nest survival probabilities as a function of biologically relevant covariates. We used the logit-link function, which bounds estimates of daily survival rate in the (0, 1) interval (Lebreton et al. 1992). We standardized 25 April as day one of the nesting season and sequentially numbered all subsequent nest-check dates. We did not standardize covariates because their unstandardized ranges did not prevent numerical optimization of the likelihood. We pooled subadult and adult females because mean annual survival rates of nests were not different between yearling and adult hens in previous studies (Rumble & Hodorff 1993), and because they were similar among age classes during companion studies (Spohr et al. 2004). We used an information-theoretic approach for model selection using Akaike's Information Criterion adjusted for small sample size (AIC_c; Burnham & Anderson 2002).

Previous avian nest-survival studies have commonly reported temporal trends in nest survival during the nesting season (Klett & Johnson 1982) and associated this with consequences for fitness of the nesting female (Grüebler & Naef-Daenzer 2010). Thus, we used a two-step modeling approach (Dinsmore & Dinsmore 2007) to evaluate three hypotheses regarding temporal variation in daily survival of nests during incubation, including a constant survival model, quadratic trend model (i.e. curvilinear changes in daily survival; Dinsmore et al. 2002) and a linear trend model. Support for the quadratic trend model would be consistent with changing conditions either late or early in the incubation period. Rumble and Hodorff (1993) observed increased nesting success of turkeys later in the season, whereas Hatchwell (1991) reported declining success of nesting seabirds as the season progressed. For the linear time trend model, we hypothesized that daily nest survival could increase with later initiation of incubation because vegetation increases in height and diversity as the season progresses, potentially resulting in greater concealment of nests and hens from predators. Early nesters initiate egg laying before spring green-up, so we also hypothesized that those nests might be easier for predators to locate.

After selecting the best model describing temporal trends (Dinsmore & Dinsmore 2007) using an information-theoretic approach, we added covariates describing habitat features at our two spatial scales as well as the effect of nest age and year. We hypothesized that daily nest survival would decrease during incubation because olfactory cues are more pronounced the longer a nest is active as a result of scent trails left by the hen (Erckmann 1981, Spohr et al. 2004), which may increase the chance of being detected by predators such as raccoon *Procyon lotor*, opossum *Didelphis virginiana*, red fox *Vulpes vulpes* and coyote *Canis latrans* that use olfaction as one means to locate nests (Grant & Morris 1971, Wells & Lehner 1978, Bowman & Harris 1980).

Metrics associated with the patch scale were divided into models describing composition, density of different patch types or extent of edge. Metrics describing composition included percent developed land in home range, percent forest land in home range, percent agricultural land in home range and patch density (patch types = forest, development, agriculture/open land and water) in the home range. Models describing edge included distance from nest to nearest road, distance from nest to nearest edge, and perimeter of edge within the radius of the 25th percentile of observed distances that hens left the nest each day. Habitat characteristics corresponding to the nest site were described by variables measuring hen concealment, nest concealment or total concealment. Variables associated with hen concealment included total stems and percent cover above the nest. Variables describing nest concealment included percent understory cover and understory vegetation density. The total concealment model included all four variables associated with cover around the nest site.

We reported AIC_c values (the second-order AIC for small sample size) and Akaike weights (w_i) from program MARK, and made inferences from these models following the guidelines of Burnham & Anderson (2002) for selecting the best model.

To evaluate the effects of percent understory cover and understory vegetation density on turkey nests, we plotted daily nest-survival rates during incubation across the range of percent understory cover observed during our study at three values of understory vegetation density (based on the mean, 90th and 10th percentiles of observed values), representing levels of low density (11/m^2), mean density (34/m^2) and high density (69/m^2) of understory vegetation.

Results

Modeling nest survival

The median date for onset of incubation was 11 May in 1996 (range: 24 April - 9 June) and 6 May in 1997 (range: 22 April - 5 June). The constant daily survival model ($K = 1$, $\Delta AIC_c = 0$, $w_i = 0.57$) performed better than the linear trend ($K = 2$, $\Delta AIC_c = 1.46$, $w_i = 0.28$) or quadratic trend ($K = 3$, $\Delta AIC_c = 2.63$, $w_i = 0.15$) models and carried 57% of the weight of evidence as the top model. Although the linear trend model was competitive with a $\Delta AIC_c < 2$, the confidence interval on the coefficient included zero. Therefore, all subsequent results are presented using the model that treated daily nest survival as constant throughout the incubation period. There were two equivalent competing models which included the nest concealment global model ($\Delta AIC_c = 0.00$) with four variables (total stems, percent cover above the nest, percent understory cover and understory vegetation density) and the two variable (percent understory cover and understory vegetation density) nest-concealment model ($\Delta AIC_c = 0.01$; Table 2). All of the 10 patch-scale models performed relatively poorly with ΔAIC_c values > 7 (see Table 2). The total concealment model had four covariates; however, the 95% confidence interval on β included zero for two of the covariates (total stems and percent cover above the nest), which suggested that those covariates had a minor influence on daily nest survival. We chose the model with fewer parameters because it was only 0.01 ΔAIC_c units from the top model and was more parsimonious. This model assumed constant daily survival and represented covariates associated with hen concealment, indicating that daily survival rate during incubation increased with increasing percent cover around the nest (percent understory cover: $\beta = 3.93$, SE = 1.36 on a logit scale) and decreased with increasing understory vegetation density around the nest (understory vegetation density: $\beta = -0.04$, SE = 0.01 on a logit scale). The logistic regression equation for the hen concealment model of daily nest survival (S) was logit(S) = 2.88 + 3.93 x percent understory cover + -0.037 x understory vegetation density. Percent understory cover averaged 50% (SE = 5) around successful nests (minimum = 4%, maximum = 74%) and 37% (SE = 8) around unsuccessful nests (minimum = 6%, maximum = 88%), whereas understory vegetation density averaged 25.6/m^2 (SE = 5.15) around successful nests (minimum = 4.7/m^2, maximum = 66.3/m^2) and 41.9/m^2 (SE = 8.9) around unsuccessful nests (minimum = 10.6/m^2, maximum = 128.4/m^2).

At high understory vegetation density and low levels of percent understory cover (< 12%), the daily survival rate was < 0.65, but increased to 0.85 at 36% understory cover (Fig. 1). Daily survival rates between nests with high and low understory vegetation density differed the most at the lowest levels of percent understory cover (see Fig. 1), suggesting that high understory vegetation density around a nest

Table 2. Model selection results for covariates influencing daily survival rate of wild turkey nests in Connecticut, USA, 1996-1997. Only models with $\Delta AIC_c < 10$ are reported here. Deviance = the difference in -2 log-likelihood of the current model and -2 log-likelihood of the saturated model. Nest-site global model = percent understory cover + understory vegetation density + total stems + percent cover above the nest. Edge global model = distance from nest to nearest road + distance from nest to nearest edge + perimeter of edge in 25% circles. 25% circle = radius of the 25th percentile of observed distances that hens left the nest during each day.

Model	Deviance	AIC_c	ΔAIC_c	K	w_i
Nest site	66.63	76.80	0.00	5	0.45
Percent understory cover + understory vegetation density	70.74	76.81	0.01	3	0.44
Total stems + percent cover above nest	77.53	83.60	6.80	3	0.01
Total stems	79.71	83.75	6.95	2	0.01
Understory vegetation density	79.77	83.81	7.01	2	0.01
Edge global	75.81	83.92	7.12	4	0.01
Percent understory cover	79.97	84.00	7.20	2	0.01
Constant daily survival - $S_{(\cdot)}$	82.98	84.99	8.19	1	0.01
Distance from nest to nearest road	81.61	85.65	8.85	2	0.01
Perimeter of edge in 25% circles	82.33	86.37	9.57	2	0.00
Percent forested land in home ranges	82.41	86.45	9.65	2	0.00
Nest age	82.42	86.46	9.66	2	0.00
Year	82.47	86.50	9.70	2	0.00
Percent developed land in home ranges	82.55	86.58	9.78	2	0.00

does not substitute for dense understory cover. Increased visual and movement obstruction around the nest, which was associated with increased understory vegetation density, greatly reduced rates of nest survival.

Discussion

Wild turkey nest survival was most strongly influenced by habitat structure adjacent to the nest.

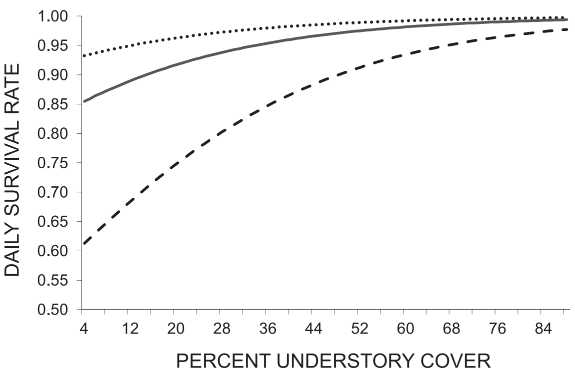

Figure 1. Predicted daily survival rate (S) of eastern wild turkey nests with differing amounts of percent understory cover around the nest at three values of understory vegetation density (< 1 m tall) representing the mean ($34/m^2$; solid line), 10th ($11/m^2$; dotted line) and 90th ($69/m^2$; dashed line) percentiles of our observed data. Estimates from the most parsimonious model where logit(S) = 2.88 + 3.93 x percent understory cover + -0.037 x understory vegetation density.

Further, models with covariates performed better than unstructured models of simple nest survival. In the best approximating model, the nest-site covariate, percent understory cover around nests, was 27% greater around successful than unsuccessful nests. Thorny vegetation dominated the species composition of understory cover around successful nests, and most commonly included greenbriar, multiflora rose, barberry and *Rubus* spp. Nest obscurity (e.g. dense vegetation surrounding the nest) may reduce predator foraging efficiency and increase nesting success by impeding movement of potential nest predators (Bowman & Harris 1980, Hines & Mitchell 1983, Lehman et al. 2008) because of disrupted visual and olfactory reception (Conover 2007), or by increasing search time. Coyotes were one of the major predators on hens and nests in our mixed-use landscape (Spohr et al. 2004), and the dense understory cover at successful nest sites may have inhibited their ability to locate nests (Lehman et al. 2008). Lehman et al. (2008) suggest that hens that are wet produce strong odours, which allows coyotes to use olfaction to find nesting females. Therefore, precipitation was their best predictor of nest survival, but the authors noted an interaction between precipitation and the amount of concealment cover around nests, whereby the effects of precipitation were reduced as shrub cover increased. Previous studies have demonstrated that lateral and vertical concealment is important in nest-site selection of wild turkeys (Lazarus & Porter 1985, Wertz & Flake 1988, Schmutz et al. 1989, Badyaev 1995, Nguyen et al. 2004, Lehman et al. 2008). Only

Lehman et al. (2008) considered effects of vegetation across multiple scales on survival of nests, but their study addressed the Merriam's *M. g. merriami* subspecies in a semi-arid environment, which may not reflect ecological relationships of other subspecies in more mesic landscapes of eastern North America that are characterized by dense understory and overstory of a diversity of deciduous shrubs and trees. Thus, our study was unique in evaluating habitat relationships of eastern wild turkeys in mesic, mixed-use landscapes by simultaneously evaluating the relative influences of nest-site and patch-scale characteristics on daily nest survival during incubation.

Although nest concealment was important to nest survival, hens may also require unobstructed escape routes from predators (Speake et al. 1975). Vegetation cover enhances nest concealment, but a high density of vertical stems may be detrimental if they restrict the ability of the hen to detect an approaching predator and to flee (Lima 1987, Schooley et al. 1996, Arenz & Leger 1999, Blumstein et al. 2004). We observed that nest survival was negatively associated with understory vegetation density (< 1 m) surrounding the nest, and that density was 39% greater around unsuccessful than successful nests. Thus, our results are consistent with those of Pöysä (1994), who noted a trade-off between the probability of being detected and the probability of being surprised and unable to flee.

Patch-scale variables were not strongly supported, and cumulatively those models accumulated < 2% of the weight of evidence as top models. It appears that factors related to concealment and escape from predators were more important directly surrounding the nest than the extent of fragmentation across patches within the home range of the hen in affecting the survival of nests. Although nest survival was not influenced by the extent of fragmentation at the scales that we measured, overall rates of nest success across our entire mixed-use study area were generally lower than reported in adjacent states (Spohr et al. 2004). Fragmentation may have a minor influence on forest-dependent species until the background forest matrix is reduced to < 30% of the landscape (Andrén 1994), whereas the percent forest in home ranges of wild turkeys that we monitored averaged 86%. Thus, we recommend that managers interested in increasing reproductive success of wild turkeys focus on maintaining understory (< 1 m) cover > 50% and woody and herbaceous stem (< 1 m) densities < 25 stems/m^2, rather than attempting to influence landscape composition and configuration in areas where forests remain a dominant feature in the landscape.

Acknowledgements - we thank D. May, former director of the Connecticut Wildlife Division (CWD), Connecticut Department of Environmental Protection, who was an enthusiastic supporter of this project and helped initiate this research. We also thank many supportive staff of CWD, especially H. Kilpatrick and M. Gregonis, and the many landowners who allowed access to their properties. Financial assistance was provided by the Connecticut Chapter of the National Wild Turkey Federation, Wildlife Forever, The University of Maine and Connecticut's Department of Environmental Protection (Federal Aid in Wildlife Restoration project number R-49-W-21). This is scientific contribution number 3308 of the Maine Agricultural and Forest Experiment Station. This work is based upon research supported in part by McIntire-Stennis Grant MEO-9660-05 from the USDA National Institute of Food and Agriculture.

References

Andrén, H. 1994: Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. - Oikos 71: 355-366.

Arenz, C.L. & Leger, D.W. 1999: Thirteen-lined ground squirrel (Sciuridae: *Spermophilus tridecemlineatus*) antipredator vigilance decreases as vigilance cost increases. - Animal Behavior 57: 97-103.

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

Badyaev, A.V. & Faust, J.D. 1996: Nest site fidelity in female wild turkey: potential causes and reproductive consequences. - Condor 98: 589-594.

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

Bakermans, M.H., Rodewald, A.D. & Vitz, A.C. 2012: Influence of forest structure on density and nest success of mature forest birds in managed landscapes. - Journal of Wildlife Management 76: 1225-1234.

Blumstein, D.T., Runyan, A., Seymour, M., Nicodemus, A., Ozgul, A., Ransler, F., Im, S., Stark, T., Zugmeyer, C. & Daniel, J.C. 2004: Locomotor ability and wariness in Yellow-bellied Marmots. - Ethology 110: 615-634.

Bowman, G.B. & Harris, L.D. 1980: Effect of spatial heterogeneity on ground-nest depredation. - Journal of Wildlife Management 44: 806-813.

Brooks, R.T., Kittredge, D.B. & Alerich, C.L. 1993: Forest resources of southern New England. - Resource Bulletin NE-127. USDA Forest Service, Northeastern Forest Experiment Station, Radnor, Pennsylvania, USA, 71 pp.

Burnham, K.P. & Anderson, D.R. 2002: Model Selection and Multi-Model Inference: A Practical Information-

Theoretic Approach. 2nd edition. - Springer-Verlag, New York, New York, USA, 488 pp.
Chalfoun, A.D., Ratnaswamy, M.J. & Thompson III, F.R. 2002: Songbird nest predators in forest-pasture edge and forest interior in a fragmented landscape. - Ecological Applications 12: 858-867.
Conover, M.R. 2007: Predator-Prey Dynamics: The Role of Olfaction. - CRC Press, Boca Raton, Florida, USA, 264 pp.
Dickson, D.R. & McAfee, C.L. 1988: Forest statistics for Connecticut: 1972 and 1985. - Resource Bulletin NE-105. USDA Forest Service, Northeastern Forest Experiment Station, Broomall, Pennsylvania, USA, 102 pp.
Dinsmore, S.J. & Dinsmore, J.J. 2007: Modeling avian nest survival in program MARK. - Studies in Avian Biology 34: 73-83.
Dinsmore, S.J., White, G.C. & Knopf, F.L. 2002: Advanced techniques for modeling avian nest survival. - Ecology 83: 3476-3488.
Erckmann, W.J., Jr. 1981: The evolution of sex-role reversal and monogamy in shorebirds. - PhD dissertation, University of Washington, Seattle, USA, 319 pp.
Grant, P.R. & Morris, R.D. 1971: The distribution of *Microtus pennsylvanicus* within grassland habitat. - Canadian Journal of Zoology 49: 1043-1052.
Grüebler, M.U. & Naef-Daenzer, B. 2010: Fitness consequences of timing of breeding in birds: date effects in the course of a reproductive episode. - Journal of Avian Biology 41: 282-291.
Hatchwell, B.J. 1991: An experimental study of the effects of timing of breeding on the reproductive success of common guillemots *Uria aalge*. - Journal of Animal Ecology 60: 721-736.
Healy, W.M. 1992: Behavior. - In: Dickson, J.G. (Ed.); The Wild Turkey: Biology and Management. Stackpole, Harrisburg, Pennsylvania, USA, pp. 46-65.
Hines, J.E. & Mitchell, G.J. 1983: Gadwall nest-site selection and nesting success. - Journal of Wildlife Management 47: 1063-1071.
Hoffman, C.O. & Gottschang, J.L. 1977: Numbers, distribution, and movements of a raccoon population in a suburban residential community. - Journal of Mammalogy 58: 623-636.
Johnson, D.J. 1980: The comparison of usage and availability measurements for evaluating resource preference. - Ecology 61: 65-71.
Klett, A.T. & Johnson, D.H. 1982: Variability in nest survival rates and implications to nesting studies. - Auk 99: 77-87.
Kotliar, N.B. & Wiens, J.A. 1990: Multiple scales of patchiness and patch structure: A hierarchical framework for the study of heterogeneity. - Oikos 59: 253-260.
Lazarus, J.E. & Porter, W.F. 1985: Nest habitat selection by wild turkeys in Minnesota. - Proceedings of the National Wild Turkey Symposium 5: 67-81.
Lebreton, J.D., Burnham, K.P., Clobert, J. & Anderson, D.R. 1992: Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. - Ecological Monographs 62: 67-118.
Lehman, C.P., Flake, L.D., Rumble, M.A., Shields, R.D. & Thompson, D.J. 2005: Pre-incubation movements of female wild turkeys relative to nest initiation in South Dakota. - Wildlife Society Bulletin 33: 1062-1070.
Lehman, C.P., Rumble, M.A., Flake, L.D. & Thompson, D.J. 2008: Merriam's turkey nest survival and factors affecting nest predation by mammals. - Journal of Wildlife Management 72: 1765-1774.
Lima, S. 1987: Distance to cover, visual obstructions, and vigilance in house sparrows. - Behaviour 102: 231-238.
Martin, T.E. & Roper, J.J. 1988: Nest predation and nest-site selection of a western population of the Hermit Thrush. - Condor 90: 51-57.
McGarigal, K. & Marks, B.J. 1995: FRAGSTATS: Spatial pattern analysis program for quantifying landscape structure. - PNW-GTR-351. USDA Forest Service, Pacific Northwest Research Station, Portland, Oregon, USA, 132 pp.
Miller, D.A. 1997: Habitat relationships and demographic parameters of an eastern wild turkey population in central Mississippi. - PhD dissertation, Mississippi State University, Starkville, Mississippi, USA, 307 pp.
Miller, D.A., Leopold, B.D., Hurst, G.A. & Gerard, P.D. 2000: Habitat selection models for eastern wild turkeys in central Mississippi. - Journal of Wildlife Management 64: 765-776.
Mohr, C.O. 1947: Table of equivalent populations of North American small mammals. - American Midland Naturalist 37: 223-249.
Nguyen, L.P., Hamr, J. & Parker, G.H. 2004: Nest site characteristics of eastern wild turkeys in central Ontario. - Northeastern Naturalist 11: 255-260.
Oehler, J.D. & Litvaitis, J.A. 1996: The role of spatial scale in understanding responses of medium-sized carnivores to forest fragmentation. - Canadian Journal of Zoology 74: 2070-2079.
Palmer, W.E., Hurst, G.A., Stys, J.E., Smith, D.R. & Burk, J.D. 1993: Survival rates of wild turkey hens in loblolly pine plantations in Mississippi. - Journal of Wildlife Management 57: 783-789.
Porter, W.F. & Gefell, D.J. 1995: Influences of weather and land use on wild turkey populations in New York. - Proceedings of the National Wild Turkey Symposium 7: 75-80.
Pöysä, H. 1994: Group foraging, distance to cover and vigilance in the teal, *Anas crecca*. - Animal Behavior 48: 921-928.
Roberts, S.D., Coffey, J.M. & Porter, W.F. 1995: Survival and reproduction of female wild turkeys in New York. - Journal of Wildlife Management 59: 437-447.
Roberts, S.D. & Porter, W.F. 1996: Importance of demographic parameters to annual changes in wild turkey abundance. - Proceedings of the National Wild Turkey Symposium 7: 15-20.
Roberts, S.D. & Porter, W.F. 1998: Relation between

weather and survival of wild turkey nests. - Journal of Wildlife Management 62: 1492-1498.
Rosenberg, K.V., Lowe, J.D. & Dhondt, A.A. 1999: Effects of forest fragmentation on breeding tanagers: a continental perspective. - Conservation Biology 13: 568-583.
Rumble, M.A. & Hodorff, R.A. 1993: Nesting ecology of Merriam's turkeys in the Black Hills, South Dakota. - Journal of Wildlife Management 57: 789-801.
Schmutz, J.A., Braun, C.E. & Andelt, W.F. 1989: Nest habitat use of Rio Grande wild turkeys. - Wilson Bulletin 101: 591-598.
Schooley, R.L., Sharpe, P.B. & Van Horne, B. 1996: Can shrub cover increase predation risk for a desert rodent? - Canadian Journal of Zoology 74: 157-163.
Secretary of the State 1996: State of Connecticut register and manual. - Hartford, Connecticut, USA, 900 pp.
Seiss, R.S., Phalen, P.S. & Hurst, G.A. 1990: Wild turkey nesting habitat and success rates. - Proceedings of the National Wild Turkey Symposium 6: 18-24.
Speake, D.W., Lynch, T.E., Fleming, W.J., Wright, G.A. & Hamrick, W.J. 1975: Habitat use and seasonal movements of wild turkeys in the southeast. - Proceedings of the National Wild Turkey Symposium 3: 122-130.
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: 363-374.
Thogmartin, W.E. 1999: Landscape attributes and nest-site selection in wild turkeys. - Auk 116: 912-923.
Thogmartin, W.E. & Schaeffer, B.A. 2000: Landscape attributes associated with mortality events of wild turkeys in Arkansas. - Wildlife Society Bulletin 28: 865-874.
Thomas, G.E. & Litvaitis, J.A. 1993: Nesting ecology of wild turkeys in New Hampshire. - Northeast Wildlife 50: 119-126.
Thorington, K.K. & Bowman, R. 2003: Predation rate on artificial nests increases with human housing density in suburban habitats. - Ecography 26: 188-196.
Vander Haegen, W.M., Dodge, W.E. & Sayre, M.W. 1988: Factors affecting productivity in a northern wild turkey population. - Journal of Wildlife Management 52: 127-133.
Vangilder, L.D. & Kurzejeski, E.W. 1995: Population ecology of the eastern wild turkey in northeastern Missouri. - Wildlife Monographs 130: 3-50.
Vangilder, L.D., Kurzejeski, E.W., Kimmel-Truitt, V.L. & Lewis, J.B. 1987: Reproductive parameters of wild turkey hens in north Missouri. - Journal of Wildlife Management 51: 535-540.
Wells, M.C. & Lehner, P.N. 1978: The relative importance of the distance senses in coyote predatory behavior. - Animal Behaviour 26: 251-258.
Wertz, T.L. & Flake, L.D. 1988: Wild turkey nesting ecology in south-central South Dakota. - Prairie Naturalist 20: 29-37.
White, G.C. & Burnham, K.P. 1999: Program MARK: survival estimation from populations of marked animals. - Bird study 46(Suppl.): 120-139.
Wilcove, D.S. 1985: Nest predation in forest tracts and the decline of migratory songbirds. - Ecology 66: 1211-1214.