



Goguen, C. B., and L. D. Murray. 2025. Exotic plants and other habitat characteristics do not impact Veery reproductive success at multiple spatial scales in northeastern Pennsylvania. *Avian Conservation and Ecology* 20(1):8. <https://doi.org/10.5751/ACE-02812-200108>
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Research Paper

Exotic plants and other habitat characteristics do not impact Veery reproductive success at multiple spatial scales in northeastern Pennsylvania

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ABSTRACT. It is expected that birds have evolved nest site preferences that, on average, lead to positive fitness outcomes. It is possible, however, that mismatches occur between these preferences and reproductive success when a population experiences sudden changes in its habitat such as through invasion by exotic plants. From 2012 to 2016, we studied breeding habitat use and nesting success of the Veery (*Catharus fuscescens*) in mature forests of northeastern Pennsylvania that had been invaded by exotic shrubs. Our objectives were to document the prevalence of use of exotic shrubs as nesting substrates in this population, determine if use of exotic shrubs reduced nesting success or other measures of productivity, and to evaluate whether habitat or other characteristics of individual nests were useful predictors of nest survival. Although many native substrates were used, almost 60% of 289 nests used exotic substrates, particularly Japanese barberry (*Berberis thunbergii*) and multiflora rose (*Rosa multiflora*). Estimates of nest survival from logistic exposure modeling, mean clutch size, and mean number of young fledged per successful nest did not differ between nests placed in native versus exotic substrates. Annual nest survival rates varied substantially (range = 0.17–0.44). Nest success was also positively related to the age of a nest and decreased when a nest camera was present. However, survival of individual nests showed little relationship with vegetative/habitat variables at three spatial scales. Overall, exotic shrubs did not appear to negatively impact Veery nesting success and instead appeared to be of similar quality as native plants for nesting substrates.

Plantes exotiques et autres caractéristiques de l'habitat n'ont pas d'effets sur le succès de reproduction de la Grive fauve à diverses échelles spatiales dans le nord-est de la Pennsylvanie

RÉSUMÉ. On s'attend à ce que les oiseaux aient des préférences en matière de sites de nidification qui, en moyenne, les conduisent à des résultats positifs en termes de succès de reproduction. Toutefois, il est possible que des décalages se produisent entre ces préférences et le succès de reproduction lorsqu'une population subit des changements soudains dans son habitat, par exemple en raison de l'invasion de plantes exotiques. De 2012 à 2016, nous avons étudié l'utilisation de l'habitat et le succès de nidification de la Grive fauve (*Catharus fuscescens*) dans les forêts matures du nord-est de la Pennsylvanie qui avaient été envahies par des arbustes exotiques. Les objectifs de la présente étude étaient d'examiner la prévalence de l'utilisation d'arbustes exotiques comme substrats de nidification dans cette population, de déterminer si l'utilisation d'arbustes exotiques réduisait le succès de nidification ou d'autres mesures de la productivité, et d'évaluer si l'habitat ou d'autres caractéristiques des nids étaient des variables explicatives utiles de la survie des nids. Bien que de nombreux substrats indigènes aient été utilisés, près de 60 % des 289 nids ont été installés sur des substrats exotiques, en particulier l'épine-vinette du Japon (*Berberis thunbergii*) et le rosier multiflore (*Rosa multiflora*). La survie des nids—calculée à partir de la modélisation logistique de l'exposition—, la taille moyenne de la ponte et le nombre moyen de jeunes à l'envol par nid réussi n'ont pas différé entre les nids placés sur des substrats indigènes ou exotiques. Les taux annuels de survie des nids ont varié considérablement (fourchette = 0,17-0,44). La survie des nids était également liée positivement à l'âge du nid et diminuait en présence d'une caméra. La survie des nids a semblé peu liée aux variables de végétation/d'habitat, et ce, à trois échelles spatiales. Dans l'ensemble, les arbustes exotiques n'ont pas semblé avoir un effet négatif sur le succès de nidification de la Grive fauve et semblent au contraire être d'une qualité similaire à celle des plantes indigènes utilisées comme substrats de nidification.

Key Words: *exotic plants; Japanese barberry; multiflora rose; nest site choice; nest survival; songbird*

INTRODUCTION

The site at which a pair of songbirds choose to place their nest can influence the probability that the nest survives to fledging, as well as other aspects of reproductive productivity (e.g., number of young fledged, fledgling mass), by affecting a suite of factors that have the potential to influence aspects of parental care (e.g., brooding or food provisioning rates) and rates and causes of nest

failure (e.g., predation, brood parasitism, exposure to weather; reviewed in Chalfoun and Schmidt 2012). Much research has focused on understanding how nest-site choice influences songbird reproductive success at many scales, often focusing on its effects on predation risk as predation tends to be the primary cause of nest failure in most open-cup nesting songbirds (Martin 1992). At finer spatial scales, nest-site choice can influence the

probability that a nest is depredated by influencing visual concealment, accessibility of the nest to predators (e.g., nest height or protective characteristics of the nesting substrate, such as thorns), or by influencing predator detection rate by affecting the number of potential sites a predator must search to encounter a nest (Martin 1992, 1993, Schmidt et al. 2005, Chalfoun and Martin 2009). At coarser spatial scales, the broad type of habitat used, size of the habitat patch, or even the positioning of the habitat patch within the landscape (e.g., edge effects; Chalfoun et al. 2002) can all affect predation probability by influencing the types and density of predators. Predation risk can also vary at temporal scales, for example due to changes in habitat structure or complexity across a breeding season (Rodewald et al. 2010) or because of changes in predator species composition or densities among years (Martin 1993, Schmidt et al. 2005). Given the importance of nest-site choice on reproductive success, it is expected that songbirds have evolved preferences that lead to positive fitness outcomes. It is possible, however, that mismatches between evolved habitat preferences and reproductive success may occur particularly when a population is presented with sudden changes in habitat structure, for example, through the actions of humans (Chalfoun and Schmidt 2012).

Invasive, exotic (i.e., non-native) plants are a major, and growing, human-caused global influence because of the novel effects of their presence on native biodiversity and ecosystem functions (Pimental et al. 2000, Levine et al. 2003, Ehrenfeld 2010). Although invasive species have undoubtedly had negative impacts, particularly in highly vulnerable ecosystems like islands (Doherty et al. 2016), recent research has suggested that a more nuanced perspective is needed when assessing the effects of exotic plant invasions as impacts can vary depending on the types of species involved, the intensity of the invasion, the physical structure of the plant species themselves, or even the scale at which the perceived impacts are measured (Davis et al. 2011, Nelson et al. 2017, Peng et al. 2019, McMillan et al. 2023). The impacts of invasive plants on birds have been particularly equivocal. Many songbird species readily use exotic plants for foraging or nesting, some even seeming to prefer exotic plants over native species for certain resources, such as nesting substrates (Heckscher 2004, Schlossberg and King 2010). This ready acceptance of exotic invaders is not necessarily a positive phenomenon, however, if use of exotic plant species results in reduced fitness consequences relative to those gained when using native species. That is especially true if exotic plant species represent “ecological traps”: habitat features that appear to be of high quality, and, thus, are preferentially chosen over native features, but result in negative fitness consequences. Because of the conservation implications of this ecological trap scenario (Battin 2004), and the rapidly growing number of observations of bird species using exotic plants as nesting substrates, numerous studies have attempted to evaluate whether use of exotic plants as nesting substrates influences aspects of nesting success and productivity (reviewed in Nelson et al. 2017). Some studies have found negative impacts on nests placed in exotic substrates supporting the ecological trap hypothesis, such as increased nest predation rates (Schmidt and Whelan 1999, Remeš 2003, Borgmann and Rodewald 2004), increased nest failure rates due to flooding (Nordby et al. 2009), or overall reduced nest survival or productivity (Rodewald et al. 2010, McChesney and Anderson 2015). Many others, however, have found either neutral or even positive effects of exotic

substrate use on nesting success (Stoleson and Finch 2001, Jones and Bock 2005, Maddox and Wiedenmann 2005, Schmidt et al. 2005, Smith et al. 2009, Schlossberg and King 2010, Gleditsch and Carlo 2014).

The Veery (*Catharus fuscescens*) is a declining, area-sensitive, Nearctic-Neotropical migrant songbird that breeds within mesic, deciduous forests across much of the northern United States and southern Canada (Heckscher et al. 2020). This species nests on or near the ground typically in areas of dense, woody understory, but also requires adjacent areas with open understory for foraging (Heckscher 2004, Heckscher et al. 2020). Although recent declines in Veery populations have likely resulted from a variety of causes including degradation and loss of wintering and migratory stopover habitats, potential threats to this species on its breeding grounds have been better studied, particularly in the eastern United States. Particularly prevalent within this research has been the association between the Veery and invasive, exotic shrubs. In many invaded habitats, the Veery appears to readily use exotic shrubs as nesting substrates with current research supporting the idea that exotic substrates may be qualitatively similar to native substrates in at least some locations (Heckscher 2004, Schmidt et al. 2005, Meyer et al. 2015). Further, Heckscher (2004) proposed that range expansion of the Veery in the Mid-Atlantic region since the mid-1900s may have resulted from increased availability of dense, woody understory in forests because of exotic shrub invasions that expanded outward from major metropolitan regions.

We studied the breeding ecology of a Veery population in a mature forest landscape in northeastern Pennsylvania. Exotic shrubs, particularly Japanese barberry (*Berberis thunbergii*) and multiflora rose (*Rosa multiflora*), were patchily-distributed within the understory of this landscape providing potential nesting substrates for the local Veery population. The specific objectives of our study were to (1) document the prevalence of use of exotic shrubs as nesting substrates in this Veery population; (2) determine if use of exotic shrubs reduced nesting success or other measures of productivity in this population, and (3) evaluate the relative importance of ecological variables associated with the nest itself and the broader habitat features in which the nest is located on Veery nest success.

METHODS

Study site

Our study was conducted May–July, 2012–2016 within the 1436 ha Nescopeck State Park, Luzerne County, northeastern Pennsylvania, USA. Nescopeck State Park is a long, narrow tract centered along an ~10 km stretch of Nescopeck Creek. The park is mostly covered by mature forest with dry, deciduous forest dominating at higher elevations (350–450 m) away from the creek, and mesic, mixed deciduous-coniferous forest dominating along the creek at lower elevations (300–350 m). Our main study area was located within 500 m of the creek channel along an approximately 1.5 km stretch of the creek. Habitat in this area consisted largely of mature mesic forest with an overstory dominated by deciduous trees (particularly oaks [*Quercus* spp.], maple [*Acer* spp.], and American beech [*Fagus grandifolia*]), coniferous eastern hemlock (*Tsuga canadensis*), and a well-developed and diverse woody sub-canopy and understory. Common woody components of understory included a diversity

of saplings from overstory trees, numerous native shrub and vine species (e.g., blueberry [*Vaccinium* spp.], roundleaf greenbrier [*Smilax rotundifolia*], spicebush [*Lindera benzoin*], wild grape [*Vitis* spp.], winterberry [*Ilex verticillata*]), and a variety of exotic shrub species (see below). Large areas of floodplain swamp lay along the creek or in depressions within these forests, supporting either an understory of dense shrubs, especially winterberry or buttonbush (*Cephalanthus occidentalis*) or an open, herbaceous understory of skunk cabbage (*Symplocarpus foetidus*) and ferns. This main study area also contained ~25 ha of old field habitats scattered across 10 fields.

Within our study area, five species of invasive, exotic shrubs were present in at least some areas: Japanese barberry, multiflora rose, Morrow's honeysuckle (*Lonicera morrowii*), Russian olive (*Eleagnus angustifolia*), and common privet (*Ligustrum vulgare*). Japanese barberry (hereafter "barberry") was typically present in widely scattered patches within forest understory but was also regularly present along the edges of old fields. Multiflora rose was also widely distributed throughout the study area but was particularly common within the old fields and along the edges of forest openings (e.g., field edges, tree-fall gaps, roadside edges). Morrow's honeysuckle was uncommon in the study area, primarily present in patches associated with old residences that had formerly been present on the site. Russian olive was common within, and along the edges, of old field habitats, but was rare otherwise. Common privet was found almost exclusively in dense patches along the edges of, or in windrows between, some of the old fields. Over the past two decades, park staff and volunteers have engaged in limited mechanical and chemical control efforts targeting these invasive shrubs, particularly along trails and roads and within the old field habitats. However, these efforts have typically occurred outside of the songbird breeding season and have had little long-term impact on the abundance and distribution of these shrubs.

Nest searching and monitoring

Starting in mid-May each year, we used adult behaviors to locate Veery territories and then located nests by either observing adult activities or by systematically searching the understory vegetation. Upon locating a nest, we typically used a short extendable mirror to check nest contents and recorded a detailed description of the nest site to allow for re-location. Nests were revisited every 2–4 days to monitor fate. On most visits, we checked nests from a distance to simply confirm that the nest remained active. However, on at least some visits, particularly when no adults were present, we approached nests to check contents to allow estimation of expected hatching and fledging dates, and to determine clutch sizes and number of young fledged. On our study site, Veery nestlings fledge between 9 and 12 days post-hatch (Goguen 2019). We concluded that a nest had failed if it contained cold eggs with no adult activity on at least two consecutive checks, or if all young died or disappeared from the nest prior to 9 days post-hatch. For nests that survived beyond 8 days post-hatch, we attempted to confirm that a nest had fledged by locating fledglings or adults with food in the vicinity of the nest on the final nest check. In rare cases in which fledglings or adults could not be detected, we assumed that the nest was successful unless there was physical evidence of predation (e.g., nest disturbed, fledgling pin feathers or body parts below the nest).

Habitat sampling

As soon as possible after a nest fledged or failed, we measured a suite of microhabitat and landscape characteristics associated with each nest. Focusing initially on characteristics of the nest, at each nest we recorded all substrates providing substantial support to the nest, by species, and measured nest height from the ground to the bottom of the nest cup, to the nearest cm. We also measured nest concealment by visually estimating the percentage of the nest concealed by vegetation from 1 m away at the height of the nest from the four cardinal directions (side cover), and from 1 m above the nest (above cover).

To describe characteristics of the habitat in the broader area around the nest, we performed plot-based sampling within two concentric, circular areas centered around the nest. Within a 5 m radius (0.008 ha) of the nest (i.e., the nest area), we measured the following variables: (1) an ocular estimate of the percentage of ground covered below 25 cm for the following categories: live woody plants (recorded for all species, and for exotic species only), live grass, live forb, live fern, dead organic litter, bare ground/rock, dead log (> 8 cm diameter), and water; (2) percent horizontal cover, by height: an estimate of the percentage of vegetation cover around the nest, from 0 to 1 m, and 1 to 2 m in height. These variables were estimated using a profile board set as close to the nest as possible, with cover assessed from 5 m away in the four cardinal directions; and (3) sapling density: a count of all woody stems > 2 cm but < 8 cm diameter at breast height (1.4 m high; DBH).

Within an 11.3 m radius (0.04 ha) of the nest (i.e., the nest patch), we estimated live tree density by counting stems > 8 cm DBH, by species. We measured the distance of each nest to the nearest significant (> 0.5 ha) opening in the forest canopy created by either large ponds or old fields, or by continuous linear openings, such as road clearings or rivers. Nests that were located within an open habitat that lacked a forest canopy were assigned a distance of 0 m. Finally, we categorized the broad habitat type associated with each nest into one of the following five types: mature mesic forest: moist forest with a closed canopy dominated by species adapted to moist conditions (e.g., red maple [*Acer rubrum*], American beech, white oak [*Quercus alba*], eastern hemlock); forest opening: upland shrub and sapling dominated habitats within any natural (e.g., tree-fall gap) or artificial (e.g., road or powerline clearing) opening in the forest canopy; shrub-dominated swamp: moist, wetland habitats lacking a closed canopy, and dominated by either dense winterberry and spicebush, or dense common buttonbush; forest-field edge: habitats within 3 m of the boundary between forest and old field habitats. We chose this distance because on our site this was the approximate range across which differences in light availability (e.g., greater light penetration into the forest) or other edge effects appeared to have influenced the density and diversity of vegetation present relative to the more distant field or forest regions; old field: open grass- or forb-dominated habitats > 3 m from a forest edge, but invaded, to varying degrees, by woody shrubs.

Statistical analyses

Initially, nests were categorized based on their supporting nesting substrate(s) as either supported entirely by native substrates or supported, entirely or partially, by exotic substrates. Because of the prominence of barberry and multiflora rose as nesting

substrates, we also decided to categorize nests supported by exotic shrubs into three groups for some analyses: those supported by barberry, multiflora rose, or by other exotic species. For analyses involving these categories, we omitted four nests that were supported by both barberry and multiflora rose because they could not be placed into only one of these categories.

We used logistic-exposure analyses (Shaffer 2004) in the statistical package R 3.6.1 (R Core Team 2019) based on success within each nest-check interval (mean = 3.2 days, SD = 1.5 days, range: 1–10 days) to initially estimate nesting success, evaluating the importance of nesting substrate category (native, barberry, multiflora rose, and other exotic substrate) and year relative to the null model. To evaluate if other measures of reproductive success differed between nests supported by native versus exotic substrates, or between nests supported by the four most common substrates (American beech, barberry, eastern hemlock, multiflora rose) we compared mean clutch sizes and mean number of young fledged per successful nest among the groups using generalized linear models and analysis of deviance in R with a Poisson distribution to determine if substrate type improved model fit compared to the null model. To calculate mean clutch size, we used only nests whose contents were checked at least once during the incubation stage to ensure that clutches were complete.

We then performed additional analyses to investigate the relationship between nesting success and 15 potentially important nest variables by performing logistic-exposure analyses for all nests using a mixed model with year as a random variable. Correlation between predictor variables was < 0.7 for all combinations of variables and thus collinearity was not expected to significantly impact model estimation (Dormann et al. 2013). To reduce the number of potential models, we performed these analyses in two stages. First, we compared models in groups based on three spatial scales that might impact adult behavior or predation risk (nest, nest area, and patch-level scales) using Akaike's Information Criterion corrected for small sample size (AIC_c).

At the “nest” scale we evaluated the following variables that were associated closely with the nest itself: (1) HEIGHT = nest height measured in cm; (2) CONCEALMENT = estimate of overall percent concealment of the nest at 1 m calculated as an average of the four side- and one above-cover measures; (3) AGE = mean nest age during the nest check interval calculated as the days since the first egg was laid; (4) SUBSTRATE = nest substrate classified as either native or exotic; and (5) CAMERA = whether or not a video camera was present at the nest during the nest check interval. We included these vegetation variables (HEIGHT, CONCEALMENT, and SUBSTRATE) because, in some species, vegetative characteristics of the nest or nesting substrate have been found to influence success, particularly by influencing predator detection or accessibility (Martin 1993, Chalfoun and Martin 2009, Rodewald et al. 2010). We included AGE because changes in the behavior of the adults and young that occur as a nest progresses from initiation to fledging can impact its probability of survival by influencing activity, noise, and odors at the nest, all of which may affect a nest's detectability to predators (reviewed in Weiser 2021). CAMERA was included as a variable because during 2014–2016 we placed video cameras at a subset of nests to study nest predators (see Goguen and Murray

2021). We felt it important to include this variable in this current analysis because the presence of a camera at a nest can potentially affect nest survival by altering adult behaviors or by influencing predator detection (reviewed in Richardson et al. 2009). Although our camera study was not designed to compare predators or predation rates based on nesting substrates, the total number of exposure days with a camera at a nest were nearly identical for nests in native (342 days) and exotic substrates (339 days). Because of the greater percentage of nests placed in exotic substrates at our site, however, those camera exposure days represented a slightly greater percentage of the total exposure days for nests in native (24%) versus exotic substrates (16%).

At the “nest area” scale we evaluated the following variables that described aspects of vegetation density in the area near the nest (i.e., within 5 m) and within the lower vegetation levels (< 2 m) in which Veeries typically nest: (1) TOTAL WOODY GC = percentage of ground covered by native and exotic woody plants; (2) EXOTIC WOODY GC = percentage of ground covered by exotic woody plants only; (3) LIVE GC = percentage of ground covered by living woody plants, grasses, forbs, and ferns; (4) SAPLINGS = number of saplings; (5) HC 0-1 = the mean horizontal cover estimate from 0 to 1 m above ground; and (6) HC 1-2 = the mean horizontal cover estimate from 1 to 2 m above ground. We included these variables because vegetation density around a nest has been found, in some cases, to impact nest success, particularly by affecting predator detection probabilities (Bowman and Harris 1980, Martin 1992, 1993, Chalfoun and Martin 2009).

At the “patch-level” scale we evaluated the following variables that related to the broader features of the habitat and timing of the nest initiation: (1) TREES = number of trees within an 11.3 m radius of the nest; (2) DISTANCE = distance from the nest to a forest opening; (3) DATE = timing within the nesting season calculated as the number of days since 1 January to the midpoint of the nest check interval; and (4) HABITAT = broad habitat type the nest was in from among the five types described previously. We included these broader-scale habitat variables (TREES, DISTANCE, and HABITAT) because these characteristics have been shown to influence nest success by potentially influencing insect food availability, competitive interactions, or the types and density of predators present (Chalfoun et al. 2002, Chalfoun and Martin 2007, Vasseur and Leberg 2015, Akresh et al. 2024). We included DATE because seasonal variation in nest success has been observed in many bird species due to variation in such factors as food availability, vegetation density, adult condition or behavior, or changes in predator species composition or search effectiveness (Pogue and Carter 1995, Arnold et al. 2004, Gilg et al. 2006, Shustack and Rodewald 2011, Keever et al. 2023). At each scale, we determined which variables were present in models within two AIC_c units of the best model and used only those variables in our subsequent analyses.

As the second stage of our analyses, we used the reduced variable set in an all-possible additive models analysis (i.e., interaction terms were not included in any models) with all variables included in an equal number of models, including the null model. To compare the relative contribution of variables in explaining nesting success, we calculated relative variable importance weights

by summing the weight of evidences for all models including a given variable within two units of the best overall model (Burnham and Anderson 2002). Variable importance weights range from 0 to 1 with larger values indicating greater importance of the given variable relative to the other variables examined. Model-averaged coefficients were used to indicate the direction of the relationship between nest success and explanatory variables (Burnham and Anderson 2002). All continuous variables were scaled by subtracting the mean and dividing by the standard deviation to help with model convergence and comparison of coefficients.

The average probability of a nest surviving a day (daily survival rate) was calculated for a given model based on the model-averaged estimates and holding all variables constant at their respective means. Nesting success for the entire nesting period (nest survival) was estimated by raising daily nest survival to the typical number of days in the nesting cycle (egg-laying, incubation, and nestling stages) observed on our study site (23.5 days).

Model fit cannot be assessed with usual goodness-of-fit tests for logistic-exposure models of nest success (Shaffer and Thompson 2007). We used an ad-hoc graphical method to assess model fit to observed nest survival rates (Shaffer and Thompson 2007). Daily nest survival for nests within two-day age categories (i.e., greater than or equal to 0 and less than 2 days, greater than or equal to 2 and less than 4 days, ...) based on the average age during a nest observation interval were calculated using a logistic-exposure model with no additional explanatory variables. Calculated daily survival rates were plotted with the predicted daily survival from the average model to allow for visual estimate of data fit to the model.

RESULTS

Over five years, we located and monitored 289 Veery nests. Only two nests were built on the ground, with the remainder built an average of 50.8 ± 1.6 cm above the ground on either live or dead vegetation. Most nests (92.7%) were supported by a single substrate, with 118 (40.8%) supported by only native substrates, 168 (58.1%) supported by only exotic substrates, and 3 (1.0%) supported by both native and exotic substrates. Native substrates included the ground, dead branches from native trees on the ground, three taxa of live, herbaceous plants, and 21 taxa of live, woody plants (Table 1). Six species of exotic substrates were used, with barberry and multiflora rose the most used substrates overall, supporting 31.1% and 22.5% of nests, respectively (Table 1).

Of 284 Veery nests with a known final fate, 106 successfully fledged at least one young. Predation was the dominant cause of nest failure, responsible for 89.9% of the 178 nest failures. Brown-headed Cowbird (*Molothrus ater*) parasitism was unimportant: only three nests experienced cowbird parasitism, and all three failed because of predation during the incubation stage.

The logistic-exposure model with nest substrate as an explanatory variable did not improve the data fit compared with the null model, with high uncertainty in the estimates (Table 2). Other measures of nesting productivity also showed no effect of nest substrate category. Models of mean clutch size including substrates as explanatory variables did not improve model fit compared to the null model for comparisons between native and

Table 1. Prevalence of native (n = 132) and exotic (n = 177) substrates supporting 289 Veery (*Catharus fuscescens*) nests in northeastern Pennsylvania, 2012–2016.

Substrate	Number of nests [†]
Native	
Eastern hemlock (<i>Tsuga canadensis</i>)	27
American beech (<i>Fagus grandifolia</i>)	19
Fallen dead branch of a native tree	13
Meadowsweet (<i>Spirea</i> spp.)	12
Roundleaf greenbrier (<i>Smilax rotundifolia</i>)	10
Blueberry (<i>Vaccinium</i> spp.), spicebush (<i>Lindera benzoin</i>)	5
Eastern white oak (<i>Quercus alba</i>), winterberry (<i>Ilex verticillata</i>)	4
Black cherry (<i>Prunus serotina</i>), common buttonbush (<i>Cephalanthus occidentalis</i>), swamp white oak (<i>Quercus bicolor</i>), wild grape (<i>Vitis</i> spp.)	3
American hornbeam (<i>Carpinus caroliniana</i>), blackberry (<i>Rubus</i> spp.), dogwood (<i>Cornus</i> spp.), elderberry (<i>Sambucus</i> spp.), fern, on the ground, red pine (<i>Pinus resinosa</i>), Sedge (<i>Carex</i> spp.)	2
Common witch-hazel (<i>Hamamelis virginiana</i>), eastern skunk cabbage (<i>Symplocarpus foetidus</i>), hobblebush (<i>Viburnum lantanoides</i>), red maple (<i>Acer rubrum</i>), sugar maple (<i>Acer saccharum</i>)	1
Exotic	
Japanese barberry (<i>Berberis thunbergii</i>)	90
Multiflora rose (<i>Rosa multiflora</i>)	65
Morrow's honeysuckle (<i>Lonicera morrowii</i>)	12
Russian olive (<i>Eleagnus angustifolia</i>)	8
<i>Forsythia</i> spp., Norway spruce (<i>Picea abies</i>)	1

[†] Some nests were supported by > 1 plant species.

Table 2. Estimates of daily nest survival rate and nest survival for a 23.5 day nesting cycle with lower (LCI) and upper (UCI) 95% confidence limits from a logistic exposure model with only nest substrate category (AIC_c = 922.89, AIC_c for null model = 922.70).

Substrate	Daily survival rate			Nest survival		
	Estimate	LCI	UCI	Estimate	LCI	UCI
Native	0.943	0.662	0.993	0.25	0.00	0.85
Japanese barberry	0.954	0.711	0.994	0.33	0.00	0.88
Multiflora rose	0.953	0.698	0.994	0.32	0.00	0.87
Other exotic species	0.921	0.556	0.991	0.14	0.00	0.81

exotic substrates (234 df, $\chi^2 = 233.3 = 84.4$, $P = 0.4986$), or among the four most common substrates (157 df, $\chi^2 = 183.1$, $P = 0.9246$; Table 3). Model fit for mean number of young fledged per successful nest also did not improve compared with an intercept only model when native substrates and exotic substrates (104 df, $\chi^2 = 128.4$, $P = 0.9472$), or the four most common substrates (74 df, $\chi^2 = 84.4$, $P = 0.8091$), were used as explanatory variables (Table 3).

The logistic-exposure model with a year effect better fit the data than the null model suggesting a year effect on nest success (Table 4). Daily survival rate and nest survival were highest in 2014 and 2015 and lowest in 2013 and 2016 (Table 4).

At the nest scale, the model with AGE and CAMERA was the best model with two other models within two AIC_c units. The variables AGE and CAMERA were in all three of these top models with CONCEALMENT and SUBSTRATE also in one

Table 3. Comparison of mean (+SE) clutch size and number of young fledged per successful nest based on nesting substrate category for a Veery (*Catharus fuscescens*) population in northeastern Pennsylvania, 2012–2016.

	Native	Exotic	American beech	Barberry	Eastern hemlock	Multiflora rose
Clutch size	3.34+0.07 (94)	3.51+0.06 (142)	3.76+0.14 (17)	3.54+0.07 (74)	3.47+0.14 (19)	3.41+0.10 (51)
Number fledged	3.05+0.12 (39)	3.07+0.10 (67)	3.56+0.24 (9)	3.06+0.15 (36)	2.71+0.18 (7)	3.04+0.16 (26)

Number of nests per category is given in parentheses.

Table 4. Estimates of Veery (*Catharus fuscescens*) daily survival rate and nest survival for a 23.5 day nesting cycle with lower (LCI) and upper (UCI) 95% confidence intervals from a logistic exposure model with only year effect ($AIC_c = 915.58$, AIC_c for null model = 922.70).

Year	Daily survival rate			Nest survival		
	Estimate	LCI	UCI	Estimate	LCI	UCI
2012	0.948	0.923	0.965	0.28	0.15	0.43
2013	0.936	0.854	0.973	0.21	0.02	0.53
2014	0.965	0.907	0.988	0.44	0.10	0.75
2015	0.963	0.907	0.986	0.42	0.10	0.72
2016	0.927	0.832	0.970	0.17	0.01	0.49

model each (Table 5). At the nest-area scale, the null model was the best model with five other models including four variables within 2 AIC_c units (Table 5). The variables EXOTIC WOODY GC and HC 1-2 were included in two competing models. LIVE GC and SAPLINGS were each in a single competing model. At the patch-level scale, a model including DATE as the only explanatory variable was the best model with the null model second and three other models within 2 AIC_c units (Table 5). DATE was included in three competing models, TREES was in two models, and DISTANCE was in a single model.

The final set of models combined across the three scales included all 11 variables present in models within 2 AIC_c units of the best model at each scale. These 11 variables were: AGE, CAMERA, CONCEALMENT, DATE, DISTANCE, EXOTIC WOODY GC, HC 1-2, LIVE GC, SAPLINGS, SUBSTRATE, and TREES. From the 2048 possible models built from the 11 variables, the model with AGE and CAMERA as explanatory variables was the best model with 16 other models within 2 AIC_c units (Table 6). AGE and CAMERA were included in all 17 competing models. DISTANCE was the only variable not included in at least one competing model. Variable weights supported the importance of AGE and CAMERA to explain nest success with CONCEALMENT the only other variable with a weight greater than 0.5 (Table 7). Daily survival rate increased approximately linearly with nest age (AGE; Table 7, Fig. 1). Observed daily survival rate for two-day age categories fit the predicted daily survival rates from the average model well with 10 of 12 observed daily survival rate values falling with the 95% confidence limits of the model (Fig. 1).

Table 5. Logistic exposure models for Veery (*Catharus fuscescens*) nests within 2 AIC_c units of the best model for each ecological scale: nest (32 models), nest area (64 models), and patch-level (16 models) scales. Model weights (w) were calculated based on all models at each level.

Variables in model	k	AIC_c	ΔAIC_c	w
Nest scale				
AGE + CAMERA	4	903.39	0.00	0.21
AGE + CAMERA + CONCEALMENT	5	903.83	0.44	0.17
AGE + CAMERA + SUBSTRATE	5	904.02	1.53	0.10
Nest area scale				
NULL	2	920.06	0.00	0.10
HC 1-2	3	920.85	0.78	0.07
EXOTIC WOODY GC	3	921.29	1.23	0.05
EXOTIC WOODY GC + HC 1-2	4	921.79	1.73	0.04
LIVE GC	3	922.05	1.99	0.04
SAPLINGS	3	922.05	1.99	0.04
Patch-level scale				
DATE	3	919.72	0.00	0.19
NULL	2	920.06	0.34	0.16
TREES + DATE	4	920.68	0.96	0.12
TREES	3	921.11	1.39	0.09
DISTANCE + DATE	4	921.59	1.87	0.07

Table 6. Logistic exposure models for Veery (*Catharus fuscescens*) nests within 2 AIC_c units of the best model from 2048 final models. Model weights (w) are based on the final 17 competing models.

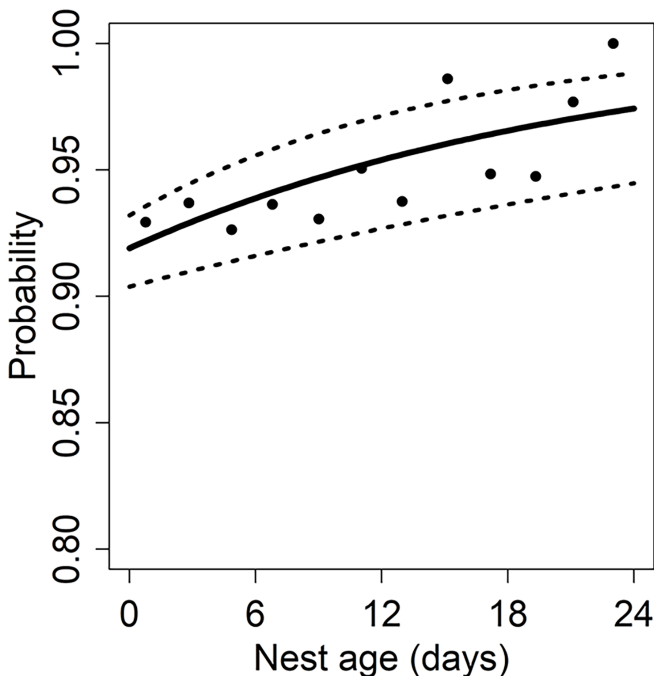
Variables in model	k	AIC_c	ΔAIC_c	w
AGE + CAMERA	4	903.39	0.00	0.11
AGE + CAMERA + CONCEALMENT + TREES	6	903.58	0.19	0.10
AGE + CAMERA + CONCEALMENT	5	903.83	0.44	0.09
AGE + CAMERA + TREES	5	904.37	0.98	0.07
AGE + CAMERA + EXOTIC WOODY GC	5	904.71	1.32	0.06
AGE + CAMERA + HC 1-2	5	904.77	1.38	0.06
AGE + CAMERA + CONCEALMENT + HC 1-2	6	904.80	1.41	0.05
AGE + CAMERA + SUBSTRATE	5	904.92	1.53	0.05
AGE + CAMERA + CONCEALMENT + SAPLINGS + TREES	7	904.94	1.56	0.05
AGE + CAMERA + CONCEALMENT + HC 1-2 + TREES	7	904.96	1.57	0.05
AGE + CAMERA + CONCEALMENT + SAPLINGS	6	904.99	1.60	0.05
AGE + CAMERA + CONCEALMENT + LIVE GC	6	905.06	1.67	0.05
AGE + CAMERA + SAPLINGS	5	905.19	1.80	0.05
AGE + CAMERA + DATE	5	905.30	1.92	0.04
AGE + CAMERA + CONCEALMENT + HC 1-2 + SAPLINGS	7	905.30	1.92	0.04
AGE + CAMERA + CONCEALMENT + LIVE GC + TREES	7	905.33	1.94	0.04
AGE + CAMERA + LIVE GC	5	905.38	1.99	0.04

The presence of a camera near a nest (CAMERA) decreased nest success (Table 7; Fig. 2; Daily survival rate: Camera present = 0.933 [95% CI: 0.867,0.968], No camera = 0.956 [0.939,0.968]; Nest survival: Camera present = 0.20 [0.03,0.47], No camera = 0.35 [0.23,0.47]). Model coefficients were near zero for the other nine variables examined (Table 7).

Table 7. Model-averaged coefficient estimates (SE) and variable weights (w_i) for the 11 variables considered in the final set of models based on models within 2 AIC_c units of the best model.

Variable	Coefficient	SE	w_i
Intercept	3.07	0.17	--
AGE	0.35	0.09	1.00
CAMERA	-0.44	0.21	1.00
CONCEALMENT	0.07	0.09	0.53
TREES	0.04	0.06	0.31
HC 1-2	-0.02	0.03	0.20
SAPLINGS	0.01	0.03	0.19
LIVE GC	-0.01	0.02	0.13
EXOTIC WOODY GC	0.00	0.01	0.06
SUBSTRATE	0.01	0.02	0.05
DATE	0.00	0.01	0.04
DISTANCE	0.00	0.00	0.00

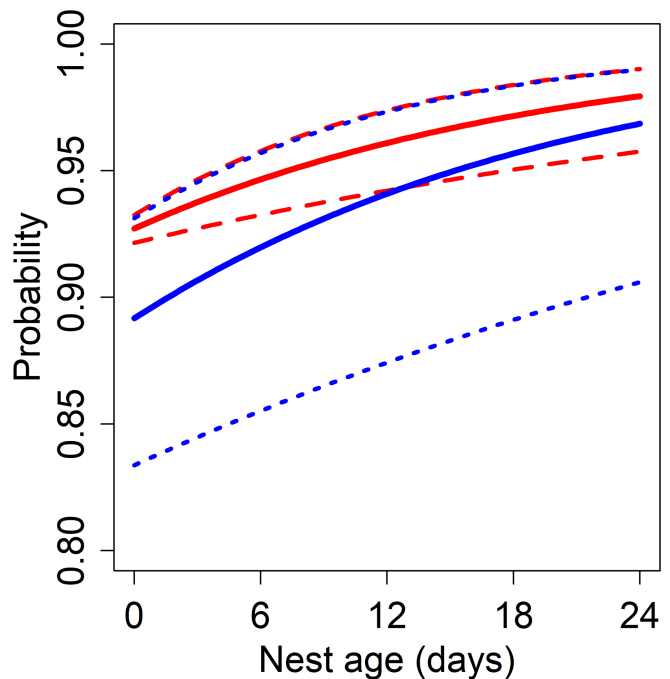
Fig. 1. Predicted relationship between nest age and daily survival rate, with 95% confidence intervals, for Veery (*Catharus fuscescens*) nests in northeastern Pennsylvania, 2012–2016 (n = 287). Solid circles represent observed daily survival of nests in two-day age categories.



DISCUSSION

In northeastern Pennsylvania, Veeries nested almost exclusively above the ground in the understory layer using a wide variety of native and non-native plant species as substrates suggesting that many plant species provide structural cues, and grow in the broad habitat context that the Veery seeks in choosing its nest site. Native substrates were particularly diverse with no native plant species supporting greater than 10% of nests. Exotic substrates, although less diverse, dominated in terms of use with nearly 60% of nests

Fig. 2. Relationship between nest age and daily survival rate for nests with cameras (blue) and without cameras (red), with 95% confidence intervals (dashed lines), for Veery (*Catharus fuscescens*) nests in northeastern Pennsylvania, 2012–2016 (n = 287).



supported entirely by exotic shrubs, particularly Japanese barberry and multiflora rose. The Veery's apparent preference for exotic shrubs as nesting substrates has been well documented in other regions of the northeastern United States. For example, in Delaware, 83% of nests were supported by multiflora rose, with exotic shrubs representing a significantly greater percentage of total shrub density within 5 m of nests compared to similar-sized, randomly located unused plots (Heckscher 2004). In New York, 55% of nests were supported by exotic shrubs, in this case barberry, multiflora rose, and Amur honeysuckle (*Lonicera maackii*); based on use relative to availability at this site, barberry and rose were preferred over native species as nesting substrates (Meyer et al. 2015). We did not quantify use relative to availability of exotic shrubs in our study and, thus, cannot evaluate preference. However, the high percentage of nests built in exotic substrates on our site at least supports the conclusion that exotic shrubs are not avoided.

Do exotic shrubs act as ecological traps?

Within our Veery population, we found no evidence that use of exotic substrates reduced reproductive success. Nesting success, mean clutch size, and mean number of young fledged from successful nests did not differ between nests placed in native substrates versus those in barberry, multiflora rose, or in all exotic substrates combined. In fact, the only reproductive variable that approached significance was clutch size, with mean clutch size tending to be larger in nests placed in exotic substrates, especially barberry, compared to native substrates. This result could reflect

seasonal patterns in both nest substrate selection and clutch sizes in Veeries. In the northeastern United States, exotic shrubs, including barberry, honeysuckle, and multiflora rose, tend to leaf out earlier in the spring compared to native species (Trisel and Gorchov 1994, Xu et al. 2007, Shustack et al. 2009, Rodewald et al. 2010) making them potentially more desirable as nesting cover very early in the season. Given that clutch size of Veery nests, like many songbirds, tends to be largest in initial clutches and decline as the season progresses (Heckscher et al. 2020), greater use of exotic shrubs early in the season could potentially result in a greater mean clutch size estimate for nests in exotic shrubs relative to nests in native substrates. Seasonal patterns of substrate use on our study site support this possible explanation: across all years of our study, 67% of nests initiated in the first week of the breeding season (15–21 May, $n = 29$ nests) were placed in exotic substrates compared to only 43% of nests initiated near the end of the season (≥ 24 June; $n = 28$ nests; Goguen and Murray, *unpublished data*). Concentrating nests in a small number of exotic shrub species early in the spring could lead to greater predation rates if predators are able to cue in on the reduced nest-site diversity at this time (Rodewald et al. 2010). We found only limited evidence of a temporal pattern in daily survival rates across the breeding season and, ultimately, the mean number of young fledged per successful nest was nearly identical regardless of nesting substrate.

Our failure to detect an ecological trap is consistent with observations at other sites in the northeastern United States that have similarly found exotic substrates to be equally suitable as native substrates for Veery reproduction. For example, in New York at a site where Veeries regularly nested both on and above the ground, researchers found that nests placed in barberry had lower predation rates than ground nests, and that barberry was particularly beneficial as a nesting substrate during years with high densities of rodents (Schmidt et al. 2005). Schmidt et al. (2005) hypothesized that physical characteristics of barberry, particularly its height and spine-covered stems, may deter small, ground-dwelling rodents, such as deer mice (*Peromyscus* spp.) or eastern chipmunks (*Tamias striatus*), species that were the dominant nest predators for Veeries in their region. In this same region, additional research found that there was no difference in daily survival probability of Veery nests placed in native versus exotic substrates, or for nests in patches dominated by native versus exotic vegetation (Meyer et al. 2015). In Delaware, where 84% of nests were supported by exotic plants, the low number of Veery nests in native substrates prevented a comparison of survival rates (Heckscher 2004). However, nesting success was high overall (70%) suggesting that exotic shrubs represented high quality substrates.

Do nest characteristics predict Veery nest survival?

Substrate was not the only nest characteristic to show little relationship with Veery nesting success. In fact, overall, vegetative and other habitat characteristics of Veery nests appeared to have little relationship with nest survival. This finding is not entirely unusual, and could reflect methodological shortcomings (e.g., failure to measure vegetative or habitat characteristics that were actually important in this system) or the effects of spatiotemporal variation in the ecosystem (Chalfoun and Schmidt 2012). Instead, the main characteristics that we found to influence nest survival

were either factors extrinsic to the nest site (year or camera presence) or intrinsic to the nest itself (nest age during the nesting cycle). Annual nest survival at our site varied significantly among years (range = 0.17–0.44), with this variability driven by variation in the dominant nest mortality source, predation. Both the range of annual nest survival rates observed and the dominance of predation as the primary source of nest mortality are consistent with observations from other Veery populations across its range (e.g., Schmidt and Ostfeld 2003, Dellinger et al. 2007, Falk et al. 2011, Kelly et al. 2017). For example, in New York, Kelly et al. (2017) documented considerable variation in annual nest survival (ranging from 0.15 to 0.58 over 12 years) and demonstrated that annual nest survival was strongly and negatively correlated to the abundance of two terrestrial rodent predators, deer mice and eastern chipmunks. We did not measure rodent density at our site. However, based on the video camera study we conducted over three breeding seasons (2014–2016), chipmunks were only minor predators at our site and deer mice were not detected as nest predators at all (Goguen and Murray 2021). Instead, long-tailed weasel (*Mustela frenata*) predation events fluctuated greatly with no weasel predation events recorded in 2014 or 2015 (two years with higher annual nesting survival rates), and many recorded (~30% of predation events) in 2016, the year with lowest annual nest survival rate. Long-tailed weasel populations are known to fluctuate greatly at a local scale presumably in response to variation in prey abundance (Sheffield and Thomas 1997). Perhaps our results indirectly reflect variation in terrestrial rodent abundance as well, particularly if the annual abundance of these small mammals drives the abundance of weasels.

In our final multi-scale analyses evaluating the importance of nest characteristics on nest survival, variable weights and model coefficients supported only the importance of nest age (AGE) and camera presence (CAMERA). AGE reflects how far through the nesting cycle a given nest was and was positively related to daily survival rate; basically, daily survival rate increased from nest initiation through fledging. The relationship between nest age and daily survival rate appears to be complex and variable, at least among open-cup nesting, altricial birds. Typically, negative age effects have been expected because of the increase in visual, auditory, and olfactory cues that occur at a nest after hatching (e.g., nestling begging calls, increased parental visits with food; Dinsmore et al. 2002, Weiser 2021). This expected pattern has been observed in many studies of altricial songbirds. However, almost as many other studies have observed positive age effects, similar to ours, or even more complex patterns, suggesting that these effects may be species or site specific (reviewed by Weiser 2021). A positive age effect may arise during the incubation stage simply because the most vulnerable, exposed nests tend to be found early in incubation (Dinsmore et al. 2002). During the nestling stage, daily survival rate may increase with nestling age because as nestlings age they become less vulnerable to inclement weather, they become more vigilant and capable of responding appropriately to a threat, and, in the case of nestlings near fledging, they become capable of fleeing a potential threat (Grant et al. 2005, Franzeb and Zarnoch 2011, Segura and Reborada 2012). Parents may also contribute to this pattern if the intensity of their nest defense efforts increases as young get nearer to fledging (Grant et al. 2005). Why the combination of factors that influence daily survival rate result in positive patterns in some altricial species but negative patterns in others remains unclear.

The presence of a video camera near the nest (CAMERA) decreased nest survival. This result was unexpected because most past studies involving video cameras at nests have typically found no effect or a slight increase in nest survival when cameras were present (reviewed in Richardson et al. 2009). We have hypothesized elsewhere that this result may have at least partially arisen from a shortened nest check interval at nests with cameras compared to those without in our study (Goguen and Murray 2021). Camera placement near an already active nest is obviously a human effect and is unrelated to nest-site selection for a songbird. Regardless, an implication of this result is that our estimates of annual nest survival in 2014–2016 may have been artificially reduced because of the presence of cameras at a portion of nests studied in those years.

Conservation implications

In northeastern Pennsylvania, the Veery appears to be flexible in nest site choice using many plant species that provide the appropriate structural cues, including frequent use of exotic shrubs. Nest success, however, showed little relationship with vegetative or habitat variables at multiple spatial scales, including those related to use or presence of exotic shrubs; exotic shrubs appeared to be of similar quality as native plants for nesting substrate, and, overall, the prevalence of exotic shrubs in the understory did not affect nesting success. Although these findings limit our ability to suggest management actions that could be used to enhance Veery breeding habitat, they also represent a positive finding for Veery conservation simply because, given the physical and economic challenges associated with the removal of invasive plants (Davis et al. 2011, Kettenring and Adams 2011), the reality is that in most invaded regions exotic plants have become a permanent component of the modern landscape. Based on results from our site and others in the northeastern United States (Meyer et al. 2015, Hecksher et al. 2020) the Veery appears to be a species that is broadly able to identify and use features of habitats invaded by exotic shrubs in a way that does not lower its reproductive success.

Acknowledgments:

We thank K. Dolecki and R. Pouffary for assistance with fieldwork. Access and logistical support for this research was provided by the Pennsylvania Department of Conservation and Natural Resources and the staff of Nescopeck State Park. Funding for this research was provided by Faculty Research Development Grants to CBG from Pennsylvania State University, Hazleton, and to LDM from the Pennsylvania State University, Abington. All methods described in the study were carried out with the approval of the Pennsylvania State University Institutional Animal Care and Use Committee, protocol #39918.

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