

RESEARCH ARTICLE

Under the umbrella: Does management for American woodcock increase reproductive success of a declining songbird?

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Abstract

The umbrella species concept is a popular management approach that assumes conservation efforts for one species confer benefits to others, although most assessments of such benefits to non-target species only measure presence and abundance. We compared the density, territory size, and key metrics of reproductive success for eastern towhee (*Pipilo erythrophthalmus*) between study sites that differed in relative likelihood of selection (RLS), as determined by a resource selection function (RSF), for American woodcock (*Scolopax minor*), a proposed umbrella species for early successional habitat in eastern North America. Higher woodcock RLS sites had higher densities of singing male eastern towhees, which in turn defended smaller territories. Nest survival and provisioning rates of towhees were not related to woodcock RLS, whereas towhee nestlings at higher RLS sites grew to a greater size. Eastern towhees largely benefited from forest management aimed at American woodcock; towhees in higher woodcock RLS sites will likely occur in greater densities and raise chicks with higher fledging masses, potentially increasing recruits to the population.

KEYWORDS

American woodcock, eastern towhee, growth rates, habitat management, male density, *Pipilo erythrophthalmus*, *Scolopax minor*, umbrella species

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The umbrella species concept, where multiple species are indirectly protected by managing one specific species, is intended to enhance conservation efficiency (Simberloff 1998, 1999). While this concept is attractive in part because single-species management is often simpler, managing one umbrella species is often unable to convey protection for all co-occurring species in a community (Roberge and Angelstam 2004, Wang et al. 2021, Carlisle et al. 2023) so understanding which species benefit (or not) is key to evaluating the efficacy of such a conservation focus. Most studies that evaluate the extent to which other species benefit from land management for a given umbrella species simply compare overlap or relative abundance of co-occurring species during the breeding season (Maslo et al. 2016, Fourcade et al. 2017, Rosenblatt et al. 2022). A more meaningful indicator of effective umbrella species management may be the reproductive success of key members of the broader biological community (Callicott and Mumford 1997). Failure to quantify the effects of land management practices on reproductive success of non-target species can lead to unintended negative outcomes, including creation of population sinks, ecological traps, or overall reductions in productivity (Van Horne 1983). No previous studies have compared the abundance, density, and key metrics of seasonal reproductive success of non-target species across a gradient of likelihood of selection as defined for the umbrella species.

Abundance and density, along with demographic and life-history traits, for a wide variety of animals often reliably indicate the quality of a given area (Fretwell and Lucas 1969, Chalfoun and Martin 2007, Perot and Villard 2009, Haché et al. 2013) and therefore are valuable metrics for evaluating whether umbrella species management benefits non-target species (Breckheimer et al. 2014, Bakermans et al. 2015, Barlow et al. 2020, Carlisle et al. 2023). After a selective harvest, for example, ovenbird (*Seiurus aurocapilla*) territory size increased as leaf litter abundance and density of songbirds decreased (Haché et al. 2013). This pattern was consistent with the concept of an ideal free distribution for a territorial songbird where local density is a function of habitat quality (Fretwell and Lucas 1969, Chalfoun and Martin 2007, Haché et al. 2013). In such a case, individuals can achieve the same per capita productivity in different land cover types because of density-dependent variation in habitat quality (Haché et al. 2013). However, estimates of occupancy, abundance, and density of species can be misleading indicators of habitat quality and productive populations (Horne 1983, Vickery et al. 1992).

For birds, demographic parameters such as nest survival, along with key life-history traits such as growth rates and provisioning rates of young, affect population productivity and may be more useful indicators of habitat quality for a given bird species than estimates of abundance alone (Pidgeon et al. 2006, Perot and Villard 2009). For example, female song sparrows (*Melospiza melodia*) that nested in higher quality habitat had earlier laying dates, incubated for longer periods, and had fewer bouts off the nest, which increased embryo development and nestling mass at hatch and thus produced more offspring compared to those nesting in lower quality habitat (Germain et al. 2015). Growth rates of nestlings are influenced by the frequency and efficiency of food provisioning by adults (Ricklefs 1969) and so can indicate differences in food availability and thus habitat quality (Drent and Daan 1980, Pérez et al. 2016, Senécal et al. 2021). In sum, evaluating multiple demographic and life-history traits for species believed to be under the management umbrella is crucial to assess whether management for a designated umbrella species benefits co-occurring songbirds.

Shrubland birds across North America have declined significantly in the last 40 years, with declines attributed to forest regrowth, natural disturbance suppression, and increased anthropogenic pressures (Brawn et al. 2001, Sauer et al. 2013). The decline of early successional vegetation in eastern North America has, in turn, caused a decline in early successional breeding birds (Askins 1993), as habitat loss on the breeding grounds directly and negatively affects songbird populations (Donner et al. 2008, Hallworth et al. 2021). Land management for the American woodcock (*Scolopax minor*) involves producing and maintaining a variety of key early successional land cover types including open fields for singing grounds and roosting, and shrubland and forest (up to 10–15 years old) for nesting and feeding (Kelley et al. 2008, Palmer 2008). These same key land cover types used by American woodcock can also benefit a variety of songbirds that use similar breeding habitat (Roth et al. 2012, Bakermans et al. 2015, Masse et al. 2015, McNeil et al. 2023). Consequently, American woodcock are considered an umbrella species because forest management strategies aimed to create high-quality early successional breeding habitat for

woodcock can benefit co-occurring species in the same ecosystem. Although umbrella species management could apply to all stages of the annual cycle, assessing how spatial variation in reproductive success of non-target species relates to site-specific differences in habitat quality for woodcock, inferred from resource selection functions (RSF), provides a direct way to assess the umbrella species concept. Resource selection functions compare used locations to those available by a suite of spatio-temporal covariates to yield inference on the relative strength of selection of a given location and can thus be used to predict differences in the relative likelihood of selection (RLS) across space or time. In the case of woodcock as an umbrella species, the assumption would be that non-target species of songbirds inhabiting sites with a higher woodcock RLS should have better reproductive success than those inhabiting sites with a lower RLS.

In this study, we evaluated whether American woodcock serve as an effective umbrella species for the eastern towhee (*Pipilo erythrophthalmus*). Eastern towhees are large sparrows that migrate short distances, breed in early successional forest openings and edges, and have declined by about 50% since the mid-1960s (Hagan 1993, Sauer et al. 2013, Greenlaw 2020). Eastern towhee females build nests and lay 3–6 eggs with both parents providing care to nestlings and fledglings until independence, about 30 days from hatching (Greenlaw 2020). We compared male density and territory size, nest survival, provisioning rates, and nestling growth between study sites that differed by woodcock RLS. We predicted that sites with greater woodcock RLS would have higher densities of territorial male eastern towhees that defend smaller territories. We also predicted that male towhees are more likely to adjust their territory size in response to mean local density rather than woodcock RLS alone. We predicted that towhees inhabiting these higher woodcock RLS sites would have higher nest survival and less frequent provisioning rates, producing nestlings in better condition than those at lower RLS sites.

STUDY AREA

All research was conducted within central and southern Rhode Island, USA, in Washington and Kent counties during April–August 2022 and 2023. The 6 study sites were within 4 state-owned management areas (Great Swamp Management Area [41°27′16.5″N, 71°35′21.6″W], Arcadia Management Area [41°34′40.1″N, 71°43′21.3″W], Big River Management Area [41°38′38.7″N, 71°34′42.1″W], and Tillinghast Pond Management Area [41°38′54.0″N, 71°45′48.1″W]) and 2 non-state properties (Francis Carter Preserve [The Nature Conservancy; 41°26′06.8″N, 71°40′41.8″W] and Marion Eppley Wildlife Refuge [Audubon Society of Rhode Island; 41°31′44.4″N, 71°34′37.0″W]; Figure 1). Sites varied in their vegetation characteristics and composition (see Slezak et al. 2024 for more detail), but all sites commonly had red maple (*Acer rubrum*), oak (*Quercus* spp.), and white pine (*Pinus strobus*) as canopy cover with the understory composed of varying densities of blueberry (*Vaccinium* spp.), mountain laurel (*Kalmia latifolia*), pitch pine (*Pinus rigida*), sweetfern (*Comptonia peregrina*), greenbrier (*Smilax* spp.), and grasses (*Poacea* spp.).

METHODS

Woodcock resource selection data

We selected the focal study sites within each study area (Figure 1) based on 3 criteria: 1) singing male woodcock were regularly observed displaying at the site within the last 5 years (Brenner et al. 2019, Slezak et al. 2024); 2) early successional patches at each site were being actively maintained with brush thinning, mowing or prescribed burning; and 3) sites differed in woodcock RLS value (Masse et al. 2014, Slezak et al. 2024). The RSF serves as the primary tool guiding forest management in our region where land managers use a decision-support application, allowing them to assess how the creation of early successional habitat affects woodcock RLS (Buffum et al. 2021). Using these 3 criteria, we were able to directly evaluate whether sites managed for woodcock, and differing in

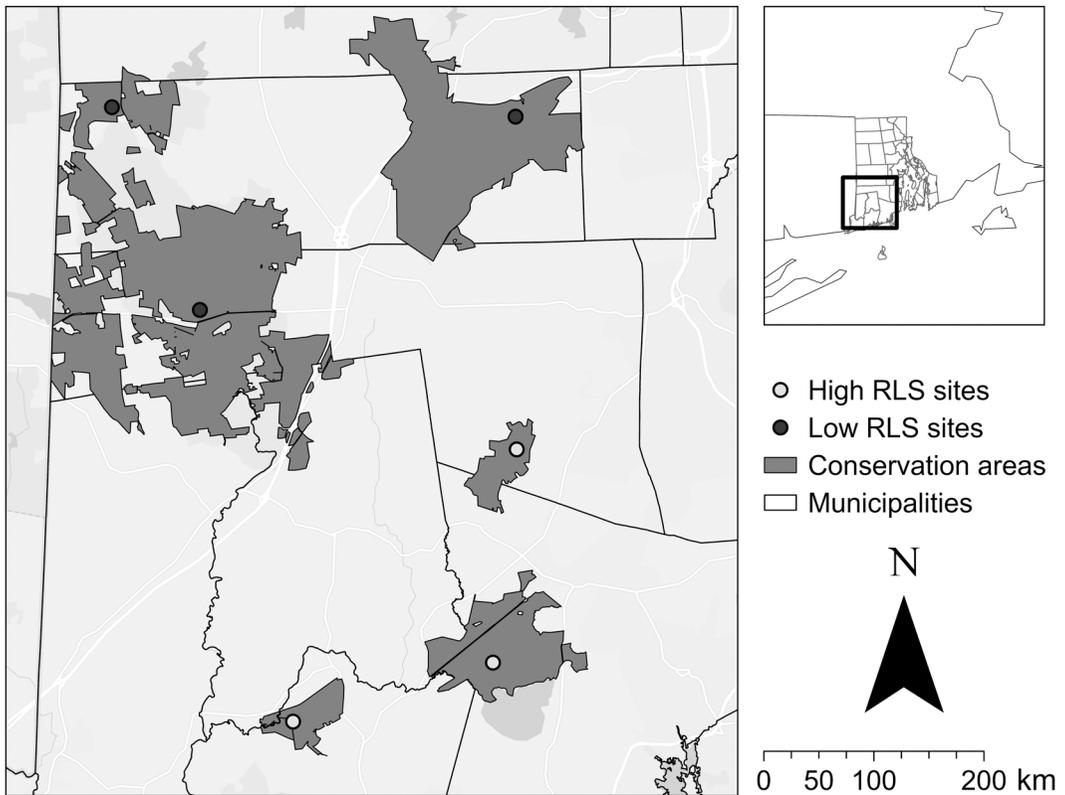


FIGURE 1 Study areas (white and black points) managed for American woodcock within the 4 state management areas and 2 non-state properties (shaded polygons) that we used in our analysis of eastern towhee density, territory size, and nesting ecology in 2022 and 2023 in Rhode Island, USA. Three of the study areas had high relative likelihood of selection (RLS) values for woodcock and 3 of the study areas had low RLS based on a resource selection function developed from tracking radio-marked males from 2010–2021 (RSF; Slezak et al. 2024).

woodcock RLS value, also varied in towhee density, territory size, nest survival, nestling growth, and provisioning rates. Comparing woodcock RLS values with measures of reproductive success provides a critical test of whether management actions intended to benefit a target species, woodcock, also confer benefits to a non-target species, the towhee.

This study used the most recently developed RSF from 2024 (Slezak et al. 2024) to estimate woodcock likelihood of selection for each of our 6 study sites. The RSF is based on daytime tracking locations of radio-marked male ($n = 146$) woodcock during post-breeding (June–August) in Rhode Island over 11 years (2010–2021). Slezak et al. (2024) used these locations to estimate relative selection strength (where estimated values were on a scale of 0 to infinity; Avgar et al. 2017) and produced a spatially explicit state-wide map of low-to-high relative likelihood of selection at a 10-m scale based on top-ranked habitat selection models for males. The model covariates used to produce the state-wide map included elevation, slope, forest cover type, distance to stream, distance to agriculture, distance to upland young forest, and distance to moist soils (for specific details on how the RSF was developed, see Slezak et al. 2024). The RSF model that predicts woodcock habitat selection excluded areas that would not be used by woodcock during the daytime tracking period (non-forested areas including bare land, developed areas, and grassland; Masse et al. 2014, Slezak et al. 2024).

To obtain RLS values for specific 4-km² sites within each of our study areas, we averaged the finer-scale RLS values in ArcGIS (Esri, Redlands, CA, USA; see Brenner et al. 2019 for more details) from the output of the RSF

(Slezak et al. 2024). For this study, we considered high RLS values as those >1.60 and low RLS values as those <1.45 (Table 1). We selected site areas of 4 km^2 because past research has shown that this encompasses woodcock breeding, roosting, and daytime feeding areas (Kelley et al. 2008, Palmer 2008), and current management practices for woodcock are recommended at this scale (Williamson 2010, Masse et al. 2019). Following the initial development of the RSF (Masse et al. 2014), Brenner et al. (2019) validated the RSF using a reciprocal transplant experiment. In that study, most male woodcock translocated from high- to low-RLS sites quickly returned to their original high-RLS sites. Conversely, most male woodcock moved to high-RLS sites remained there, suggesting that males assess habitat quality in ways consistent with likelihood of selection as predicted by the RSF.

Arrival date and density of male towhees

Surveys for singing male towhees began on 25 April 2022 and 11 April 2023 and continued until 15 July to encompass arrival and the peak of singing. The goal of each survey was to determine how many individuals at each site were singing during the morning ($\sim 0500\text{--}1200$) on fair-weather days (low wind Beaufort scale <5) with little to no precipitation (Robbins 1981). Surveys were a complete survey of the area with observers counting all towhee males that were present along a walking route that covered all available early successional habitat managed for woodcock (Figure S1). Survey duration varied by site depending on density of males and the area of the site but was on average 192 minutes (± 18.2) in 2022 and 225 minutes (± 17.6) in 2023. In 2022, a single observer surveyed 3 sites from dawn until noon one day and the other 3 sites on the following day. On the third day, the observer visited the first 3 sites again but in different sequences so that over time all sites were surveyed at the dawn chorus period. In 2023, multiple observers were available so that each site was surveyed at dawn at least every other day except for Arcadia and Big River, which were surveyed at least once per week because there were consistently fewer breeding males. Experienced observers conducted the surveys and rotated through sites to avoid being influenced by past observations. Observers submitted surveys using the Survey123 app (version 5.1.80; Esri 2021).

We determined arrival date of towhees in 2023 at each of 5 sites as the first survey date when at least one singing male was detected. We excluded Big River from this estimate of arrival date because towhees had already arrived at the time of the first survey in 2023. At all sites, once males were first observed singing, they subsequently established a territory; thus, these first-arriving, singing males were resident and marked the beginning of the local breeding period. We did not determine arrival date of towhees in 2022 because surveys started 2 weeks later than in 2023, and in 2022 singing males were already detected at many of the first survey dates.

We estimated density of singing male towhees at each site for each survey conducted at each of the 6 study sites. The peak density of singing male towhees (number per unit area) occurred at all sites between 1 May and 15 June in 2022 and 2023, which coincided with when most males had established territories and territorial disputes between adjacent males had resolved. We measured area of each site (ha) using ArcGISPro (version 3.2.2; Esri) mapping tools and Rhode Island satellite imagery (RIGIS 2022). At Francis Carter Preserve, Big River, and Eppley Preserve, there were areas within each site that were not inhabited by towhees (e.g., large fields or tracts of sandy, bare land) that we excluded from our estimate of area at each site occupied by singing, territory-holding male towhees (Figure S1). These excluded areas did not influence the RLS values because the RSF was developed using daytime locations of woodcock and excluded non-forested land cover types that were not used by woodcock (Slezak et al. 2024).

Depending on density of males at the site, our goal was to map territories of all or most individual males per site per year. We captured and color-banded males beginning in April, soon after territory establishment in spring, and then continued to capture breeding males until the end of June. We did not capture all individuals at a given site and year, so we mapped territories for both color-marked and un-marked males. On average, at least 27% of males were marked and all color-marked males maintained exclusive territories, so we assume un-marked males did also. We captured males using conspecific audio playback in either 38-mm or 60-mm mist nets. After capture, we aged

TABLE 1 First arrival date of eastern towhees in 2023 at each of 5 study sites that differed in relative likelihood of selection (RLS) by woodcock as determined by a resource selection function based on tracking radio-marked male American woodcock from 2010–2021 (RSF; Slezak et al. 2024). We also present the number of surveys conducted in 2022 and 2023 combined, and male density (mean \pm SD) during the period of peak singing (1 May to 15 June) for each year and across both years for each of the 6 sites surveyed in Rhode Island, USA, during the breeding seasons 2022 and 2023.

Likelihood of selection	Site name	Site size (ha)	First arrival 2023 ^a	Surveys	2022 male density (birds/ha)	2023 male density (birds/ha)	Male density (birds/ha)
Low-likelihood (RLS = 1.39)	Arcadia	9.73	125	5	0.45 \pm 0.12	0.26 \pm 0.07	0.37 \pm 0.14
Low-likelihood (RLS = 1.29)	Big River	35.08	NA ^b	8	0.14 \pm 0.05	0.18 \pm 0.10	0.15 \pm 0.07
Low-likelihood (RLS = 1.42)	Tillinghast ^c	20.62	111	14	0.64 \pm 0.09	1.02 \pm 0.21	0.88 \pm 0.26
High-likelihood (RLS = 1.61)	Francis Carter	21.02	101	13	0.54 \pm 0.13	0.42 \pm 0.14	0.48 \pm 0.14
High-likelihood (RLS = 1.62)	Eppley	15.87	111	7	0.82 \pm 0.11	0.77 \pm 0.11	0.79 \pm 0.10
High-likelihood (RLS = 2.21)	Great Swamp	17.66	111	8	0.68 \pm 0.08	0.81 \pm 0.10	0.74 \pm 0.11

^aOrdinal day 100 is 10 April; first arrival of towhees in 2022 is not presented because surveys started 2 weeks later than in 2023, and singing males were already detected at many of the first survey dates in 2022.

^bIn 2023, surveys at Big River began after birds had arrived, and so first arrival date was unknown.

^cDensity of males at Tillinghast was the only site with evidence of differences in density between the 2 years ($t_{11,45} = -4.68, P \leq 0.001$).

and sexed birds, weighed them to the nearest 0.1 g, and measured wing chord to the nearest 0.1 mm (Pyle 2022). Each male (2022, $n = 13$, 2023, $n = 28$) received a unique combination of 3 colored plastic leg bands along with the standard United States Geological Survey aluminum band. In 2023, as part of a separate study on movement ecology, we outfitted all but one of these color-banded males with an elastic modified leg-loop harness (Rappole and Tipton 1991) affixed to a transmitter (weight = 1.5 g, <5% body mass; LifeTag, Cellular Tracking Technologies [CTT], Rio Grande, NJ, USA).

We used spot mapping (Falls 1981) to delineate territory boundaries and estimate territory size of individual males during the May to July breeding season for each of the 2 years of the study (except Big River in 2023 for logistical reasons). Observers targeted a single bird on a given day, with or without auxiliary markers, which had been resident in a certain area within a site for at least 6 days. The observer used audio playback of towhee songs to define the bird's territory boundaries at approximately 20-m intervals along the territory perimeter. We delineated territory boundaries for each male when a male stopped following playback or an adjacent territorial male came to playback (Falls 1981). We took a minimum of 5 global positioning system (GPS) points along each delineated territory boundary. In most cases, spot mapping each male took no more than 45 minutes to complete. Occasionally spot mapping a given male took more than 45 minutes, in which case observers would stop delineating territory boundaries to avoid prolonged disturbance to the bird and then return within 5 days to complete the spot mapping. We then mapped GPS points taken at territory boundaries using the *adehabitatHR* package (Calenge 2023) to create minimum convex polygons. We included only territories with ≥ 5 GPS points in the analysis. We measured the polygons in hectares, and generated the mean territory size for each site.

Nest survival, nestling growth, and provisioning rates

To assign nests to a given female or females to a male defending a territory, in 2022 we opportunistically marked 3 females with color bands and a United States Geological Survey (USGS) aluminum band while target netting for males; in 2023, as part of a separate study on movement ecology, we marked 14 females with color bands and a USGS aluminum band and 13 of these females also received transmitters (CTT LifeTag, $n = 8$; CTT PowerTag, $n = 4$; ATS series A1000, very high frequency [VHF] tag, $n = 1$) allowing us to track them back to their nests. We captured these females beginning in April until the end of June. If we located a nest with an unmarked female, we attempted to capture the female to track successive nesting attempts. If we could not capture the female within 30 minutes, then we either abandoned the attempt or tried a different day to limit potential predation of the nest by increased activity. Of the 18 actively nesting females that were captured and marked in 2022 and 2023, we concluded only one abandoned her nest. Overall, we found nests in 3 ways: watching females that were displaying breeding behavior until they returned to the nest (carrying nesting material, food, or fecal sacs), incidentally flushing an incubating female while territory mapping, or tracking a transmitter-tagged female back to the nest.

The breeding period of towhees is 28 days (± 2) with 4 stages: nest building (4 days), laying and incubation of the eggs (12 days), and provisioning and caring for nestlings before fledgling (12 days; Greenlaw 2020). However, we often found nestlings would leave the nest around 9 days, while others would stay for 12 days. Female towhees typically have 1–2 broods and will attempt to renest until late July (Greenlaw 2020; M. E. Gray, University of Rhode Island, personal observation). They build their nests on the ground under thick vegetation or in bushes and trees 1–10 m in height (Greenlaw 2020). When we found nests, we took GPS points both at the nest location and the flagging location, which was approximately 5–10 m in a certain direction from the nest. We recorded nest initiation date (i.e., the date the first egg was laid), clutch size, and hatch date (i.e., date the first egg hatched). For nests with an unknown hatch day, we estimated day of hatch based on a combination of mass and tarsus length measurements of nestlings along with general nestling appearance (downy feathers, presence of pin feathers, begging and eyes open or closed), all of which we collected on known-age nestlings, and verified estimations against Barbour (1950).

We monitored nests following the methods outlined in Martin and Geupel (1993). Every 1–3 days and until nestlings were 9 days old, we measured mass to the nearest 0.1 g by using a digital scale and tarsus length to the nearest 0.01 mm using vernier calipers (Pyle 2022). We differentiated individual nestlings by coloring the tarsus with different colored non-toxic felt-tip markers that were not permanent and reapplied color on subsequent visits. Most nestlings were directly aged by hatch day (day 1 = hatching day). We found a single towhee nest that had been parasitized by a brown-headed cowbird (*Molothrus ater*), but the nest was depredated before hatch. On the last day of measuring, we banded nestlings with the USGS aluminum band. To determine nest fate after 9 days old and until fledging (usually 10–12 days old), we continued to monitor nests from a distance to listen for nestlings begging, or adults feeding nearby. If we did not see activity in the vicinity, we would slowly walk by the nest location to determine if the female was brooding or the fate of the nestlings. We determined nest fate as either successful (i.e., at least one nestling fledged), depredated (i.e., eggs or nestlings gone), abandoned, or infertile. Abandoned nests ($n = 8$) were associated with poor weather and partial egg predation. Research activities contributed to one known nest abandonment. We monitored infertile nests past the likely hatch date or candled them to confirm lack of development ($n = 2$).

We used trail camera photos at nests ($n = 45$) to estimate provisioning rates and hatch date and to monitor predation events. We used camouflaged cameras (Strike Force Extreme, Browning Trail Cameras, Morgan, UT, USA; Command Ops Elite, Bushnell, Overland Park, KS, USA) zip-tied to a length of rebar within 5 m of the nest. Using the camera trapping software Camelot (version 1.6.16; Hendry and Mann 2018), we tagged photos with the activity (provisioning, incubating, at nest) and the sex of the parent when it could be discerned (male, female, or unknown). We calculated camera active hours by using the earliest time a provisioning visit took place over all nests (0440) to the latest (2130), as songbirds only provision during the daylight hours. However, if the nest was depredated during the day, we truncated the end time for that day at the predation event. We excluded a day from the provisioning rate dataset if the provisioning rate was 0 for a day where a nest had hatched or if the estimated provisioning rate for a given day deviated significantly from the mean provisioning rate calculated across all chick ages. Based on these criteria, we excluded 10 days of data from 6 nests. We were able to quantify provisioning rates of male and female towhees at 25 nests. We restricted the data to only include provisioning rates up to nest age 8, as only a few nests had data beyond this point, and some nests had fledged on day 9.

Statistical analysis

We used linear regression to evaluate the predicted relationship between the woodcock RLS value and both density and territory size of singing towhee males across the 6 study sites. We used R^2 and visual inspection of residual plots to assess model fit. We scaled and centered (mean = 0 and SD = 1) our continuous variable of woodcock RLS value prior to conducting the linear regressions. We used a path analysis (Wootton 1994; Shipley 1997, 2004) with the lavaan package (Rosseel 2012) to evaluate the hypothesis that individuals are more likely to adjust their territory size in response to mean local density than the RLS value alone.

We estimated the daily survival rate (DSR; the probability that a nest survives 1 day) from the known-fate records for all nesting attempts with the following information: 1) known or backdated initiation date, 2) the last day the nest was active, 3) the last day the nest was checked, and 4) known nest fate (i.e., successful or depredated; Mayfield 1961, Dinsmore et al. 2002). We then determined the extent to which DSR of towhees was related to woodcock RLS. We estimated DSR using the RMark package, which estimates DSR using a maximum likelihood estimate with the logit-link function and our included variable of interest, woodcock RLS (Laake et al. 2013). This model assumes that DSR was the same for all nests on all days and for all nest ages, and nest fates are independent and identically distributed (Rotella 2006). We estimated DSR from the log-odds of survival, and calculated the probability of surviving the full nesting period by raising DSR to the power of the number of nesting days, 28 days for towhees (Rotella et al. 2004). To interpret the effect size of woodcock RLS on nest survival, we calculated the

odds ratio (OR) by exponentiating the model coefficient (Allison 2001). Our continuous predictor variable, RLS, was scaled and centered (mean = 0 and SD = 1).

We calculated growth rates by fitting separate models using the Gompertz growth model for all nestlings raised in high-RLS and low-RLS areas (Figure 1); too few nestlings were measured at each site for a site-level analysis of nestling growth. The Gompertz model assumes a sigmoidal growth pattern, where growth is slow at the start, increases in the middle, and then slows again as maximum size is approached. It is commonly used to describe songbird patterns of growth (Ricklefs 1967, Garrido-Bautista et al. 2023). We restricted our analysis to nestlings with ≥ 3 measurements and incorporated the shared nest environment by including nestling IDs within nest IDs as random effects. We modeled the Gompertz growth equation in a Bayesian framework using the brms package (Bürkner 2017). We applied wide non-informative priors (normal distribution with mean = 0 and SD = 100) to all model parameters. We ran 4 parallel Markov chain Monte Carlo (MCMC) chains with 10,000 iterations each, including 5,000 warmup iterations. We extracted posterior estimates for parameters a , b , and c from the Gompertz growth model (Equation 1) to compare growth parameters, where a is the upper asymptote, b sets the displacement of the curve along the x -axis, c is the growth rate coefficient, t is time in days and $y(t)$ is the value of each variable (mass or tarsus) at time t .

$$y(t) = a \times \exp(-\exp(b - c \times t)) \quad (1)$$

We used Bayesian linear models to assess how woodcock RLS influences the towhee growth parameters (a , b , and c) by fitting separate models for each growth parameter with RLS as a categorical predictor (high or low). From each model, we extracted the estimated effect of woodcock RLS on the growth parameter and its 95% credible interval to estimate the mean difference between groups. To compare mass and tarsus at the minimum observed fledging age (day 9), we used the derivative of the Gompertz growth model (Equation 2) to calculate growth rates (dM/dt) and derive mass and tarsus length for each chick on the given day, followed by a Bayesian analysis to compare potential fledging mass between habitat qualities using the median posterior estimates and 95% highest posterior density (HPD) intervals. The derivative of the Gompertz growth model defines the growth rate at any time t :

$$dM/dt = a \times c \times b \times \exp(-c \times t) \times \exp(-b \times \exp(-c \times t)). \quad (2)$$

Growth of songbird nestlings is related to provisioning rate and potentially food availability (Goodbred and Holmes 1996, Pérez et al. 2016, Grames et al. 2023), which may differ among sites, so we compared provisioning rates between sites that differed in woodcock RLS. We used a paired t -test to detect differences in provisioning rates between parents, using a single provisioning rate for each chick age day (1–9) calculated across all observation periods for each parent at each nest. To detect the effect of RLS on provisioning rates, we grouped chick age into 4 groups of 2-day intervals (1–2, 3–4, 5–6, 7–8). We modeled the effect of chick age group (categorical) and RLS (continuous) on the number of provisioning visits using a negative binomial model to account for overdispersion and right-skewed data in a Bayesian framework using the brms package (Bürkner 2017) for accommodating our small sample size. The model included chick age group and RLS as fixed effects with an interaction term, a random intercept for each nest to account for individual variation (25 levels), and an offset for total hours the camera was active. Our continuous variable of RLS value was scaled and centered (mean = 0 and SD = 1). We applied wide non-informative priors (normal distribution with mean = 0 and SD = 100) to the intercept and regression coefficients. For the random effect standard deviation at the nest level, we used an exponential prior with a rate of 1, which imposes a weakly regularizing constraint. Additionally, we placed an exponential prior (rate = 1) on the shape parameter to provide weak regularization while allowing flexibility in the distributional shape of the response (Lemoine 2019). We ran 4 parallel MCMC chains with 10,000 iterations each, including 5,000 warmup iterations. We extracted posterior estimates for the effects of age group and RLS, along with 95% credible intervals, to evaluate the impact of these factors on provisioning rates.

For all Bayesian analysis, we assessed model convergence visually using trace plots and the Gelman-Rubin diagnostic, where R -hat values < 1.05 indicated adequate mixing and convergence (Gelman 2004). We also ensured sufficient sampling by examining effective sample sizes (ESS), with all parameters exceeding 1,000, suggesting low autocorrelation and adequate exploration of posterior distributions. Results are presented with either 95% confidence intervals (CI), 95% credible intervals (CRI), or 95% highest posterior density (HPD) intervals. We conducted all data manipulation and statistical analyses in R version 4.4.2 (R Core Team 2024).

RESULTS

Density and territory size

During 2022 and 2023, we performed 55 surveys across all 6 sites during the peak of singing (Table 1) and mapped 91 male territories at these same 6 sites (Table 2). Density of singing male towhees across the 6 sites modestly increased with woodcock RLS value (slope = 0.09; $F_{1,53} = 4.58$, $P = 0.04$). Both density and territory size of male towhees were similar across the 2 years (t -test, $P > 0.05$) for all study sites except density at Tillinghast, which was higher in 2023 ($t_{11.45} = -4.68$, $P \leq 0.001$; Table 1). As predicted, territory size of male towhees across the 6 study sites decreased considerably with an increase in RLS value (slope = -0.22 ; $F_{1,89} = 7.52$, $P = 0.007$). Based on the unstandardized beta coefficients from the path analysis (Figure 2), we found that RLS did not influence territory size in towhees either indirectly through density ($\beta = -0.005$, 95% CI = -0.01 , 0.00 ; $P = 0.21$) or directly ($\beta = -0.09$, 95% CI = -0.21 , 0.03 ; $P = 0.15$). As RLS increased by 1 unit, the density of territorial males increased by 0.05 birds/ha ($\beta = 0.05$, 95% CI = 0.01 , 0.10 ; $P = 0.01$). For every 1-unit increase in birds/ha, territory size decreased by 2.36 ha ($\beta = -2.36$, 95% CI = -2.94 , -1.79 ; $P \leq 0.001$), highlighting the importance of density in determining territory size.

Nest survival

We found 73 nests over the 2 breeding seasons ($n = 25$ in 2022, $n = 48$ in 2023), of which 59 nests met our inclusion criteria and were used to estimate nest survival ($n = 22$ in 2022, $n = 37$ in 2023). The 14 nests excluded from this analysis included 2 nests with infertile eggs and 12 nests that failed (abandoned, partial predation or weather event such as heavy rain or cold snap) or were depredated during the incubation stage and had an

TABLE 2 Average number of territorial male eastern towhees (mean \pm SD), total number of territories mapped, and average territory size (mean \pm SD, ha) at each of the 6 sites in Rhode Island, USA, during May to early July in 2022 and 2023. Relative likelihood of selection (RLS) values were determined by a resource selection function based on tracking radio-marked male American woodcock from 2010–2021 (RSF; Slezak et al. 2024).

Likelihood of selection	Site	Number of males	Total territories mapped	Territory size (ha)
Low-likelihood (RLS = 1.39)	Arcadia	4 \pm 1.34	6	1.98 \pm 0.83
Low-likelihood (RLS = 1.29)	Big River ^a	5 \pm 2.39	6	2.72 \pm 0.33
Low-likelihood (RLS = 1.42)	Tillinghast	18 \pm 5.28	19	0.42 \pm 0.23
High-likelihood (RLS = 1.61)	Francis Carter	10 \pm 3.00	19	0.65 \pm 0.53
High-likelihood (RLS = 1.62)	Eppley	13 \pm 1.62	20	0.47 \pm 0.32
High-likelihood (RLS = 2.21)	Great Swamp	13 \pm 1.89	21	0.61 \pm 0.60

^aMale territories were mapped at Big River in only 1 of the 2 years (2022).

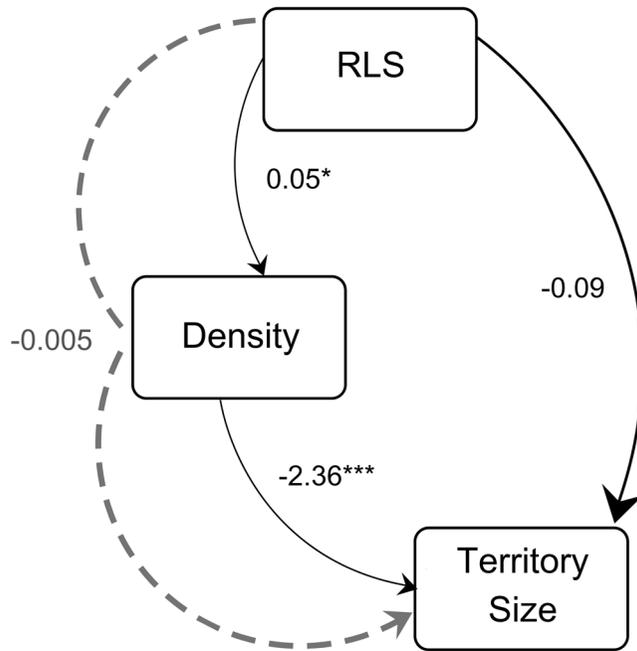


FIGURE 2 Path analysis indicated that sites that with a higher relative likelihood of selection (RLS) for American woodcock as determined by a resource selection function (RSF; Slezak et al. 2024) had higher densities (birds/ha) of singing male eastern towhees ($\beta = 0.05$) and these sites with higher male density had smaller territories (ha; $\beta = -2.36$), whereas RLS had no direct ($\beta = -0.09$) or indirect (dashed line) influence on territory size ($\beta = -0.005$) in Rhode Island, USA, 2022–2023. Lines designate the paths and stars mark significance between paths (*: $P < 0.05$; ***: $P \leq 0.001$).

unknown initiation date. Of these 59 nests used to estimate nest survival, 36 were successful (61%) and 23 nests failed (39%) either due to nest predation (78%) or abandonment (22%). The unadjusted daily survival probability mean for towhees across the 2-year study was 0.96 (95% CI = 0.94, 0.97). The total probability of surviving the nesting period of 28 days based on constant DSR (daily survival rate) was 0.29 (95% CI = 0.16, 0.43). We did not find an effect of woodcock RLS on towhee DSR with an odds ratio of 1.11 (95% CI = 0.64, 1.93), indicating no clear relationship between RLS and nest survival.

Growth rates

We estimated nestling growth rates for body mass ($n = 51$ individuals) and tarsus length ($n = 43$ individuals) over the 2 years of the study. All MCMC trace plots and R -hat values indicated that models converged. Nestlings in low-RLS sites reached a lower asymptotic mass (a -parameter, mean difference = -6.52 g, 95% CRI = $-6.94, -6.11$) compared to those in high-RLS sites (Figure 3A). Although nestlings in low-RLS sites exhibited a higher growth rate compared to high-RLS (c -parameter, mean difference = 0.04 , 95% CRI = $0.03, 0.06$), they started growing later, ultimately reaching a smaller final mass. Similarly, for tarsus length (Figure 3B), nestlings in low-RLS sites reached a lower asymptotic length (a -parameter, mean difference = -1.54 mm, 95% CRI = $-1.78, -1.30$ mm). The growth curve was shifted later in low-RLS sites (b -parameter, mean difference = -0.13 , 95% CRI = $-0.16, -0.10$), and with a higher growth rate (c -parameter, mean difference = 0.03 , 95% CRI = $0.01, 0.04$) indicating that nestlings grew rapidly later, reaching a smaller final tarsus length. Predicted mass of nestlings at fledging (day 9) in low-RLS sites was

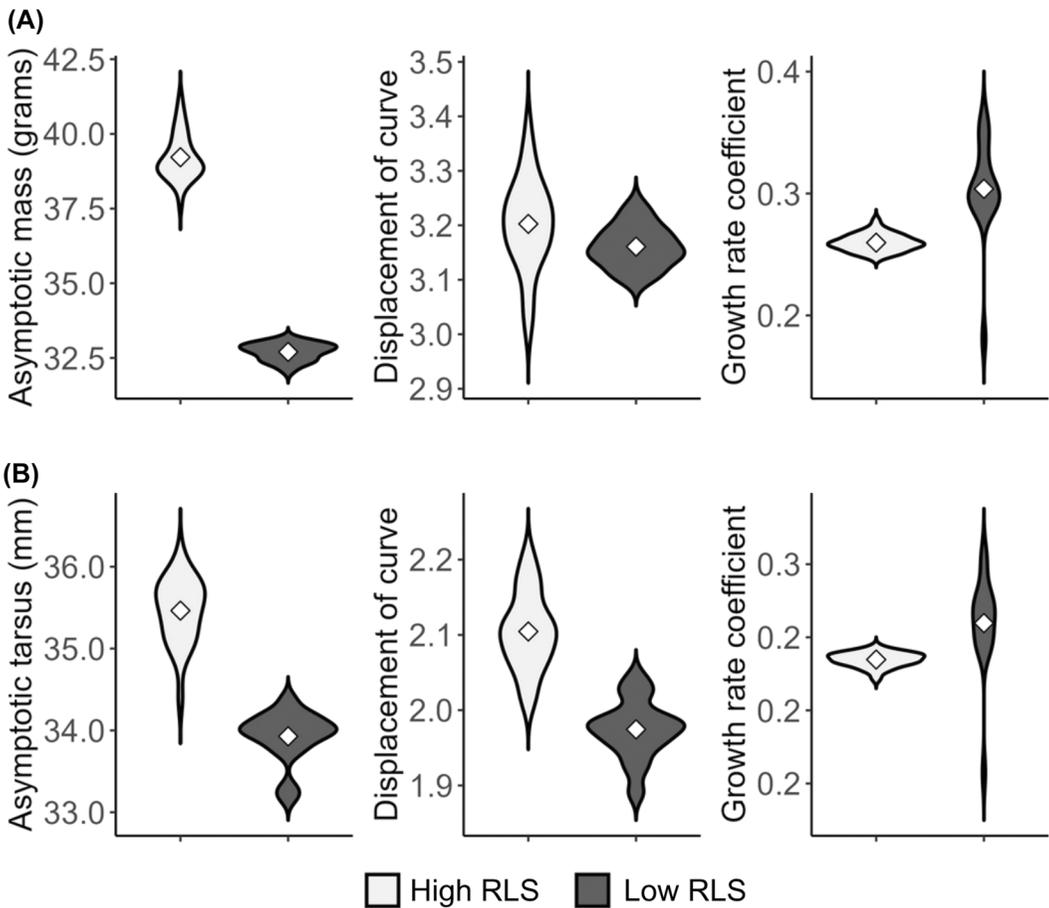


FIGURE 3 Posterior distributions of the 3 growth parameters (where a is the upper asymptote, b sets the displacement of the curve along the x -axis, c is the growth rate coefficient) for mass (A) and tarsus (B) of eastern towhee nestlings at 3 sites with high woodcock relative likelihood of selection (RLS) ($n = 34$) and 2 low-RLS sites ($n = 16$) in 2022 and 2023 in Rhode Island, USA, during May to August. Nestlings in low-RLS sites reached a lower asymptotic mass compared to those in high-RLS sites (A) and, similarly, for tarsus length (B), nestlings in low-RLS sites reached a lower asymptotic length and achieved this length later. High- versus low- RLS sites for woodcock, the designated umbrella species, was determined by a resource selection function based on tracking radio-marked males from 2010–2021 (RSF; Slezak et al. 2024).

approximately 2.43 g lighter (95% HPD interval = $-3.54, -1.37$ g) than those at high-RLS sites. Predicted tarsus length of nestlings at fledging was similar in high-and low-RLS sites (-0.34 mm, 95% HPD interval = $-1.32, 0.58$ mm).

Provisioning rates

We used photos from 25 nests to assess provisioning rates. These nests were monitored for 1,600 active camera hours and recorded 4,608 provisioning visits with 2,447 male visits, 2,097 female visits, and 64 visits from unknown-sex parents where lighting was too dark or the angle was too poor for sex identification. Mean provisioning rate for all chick ages was 2.63 ± 1.78 (SD) visits per hour, with mean rates of 1.54 ± 1.06 (SD)

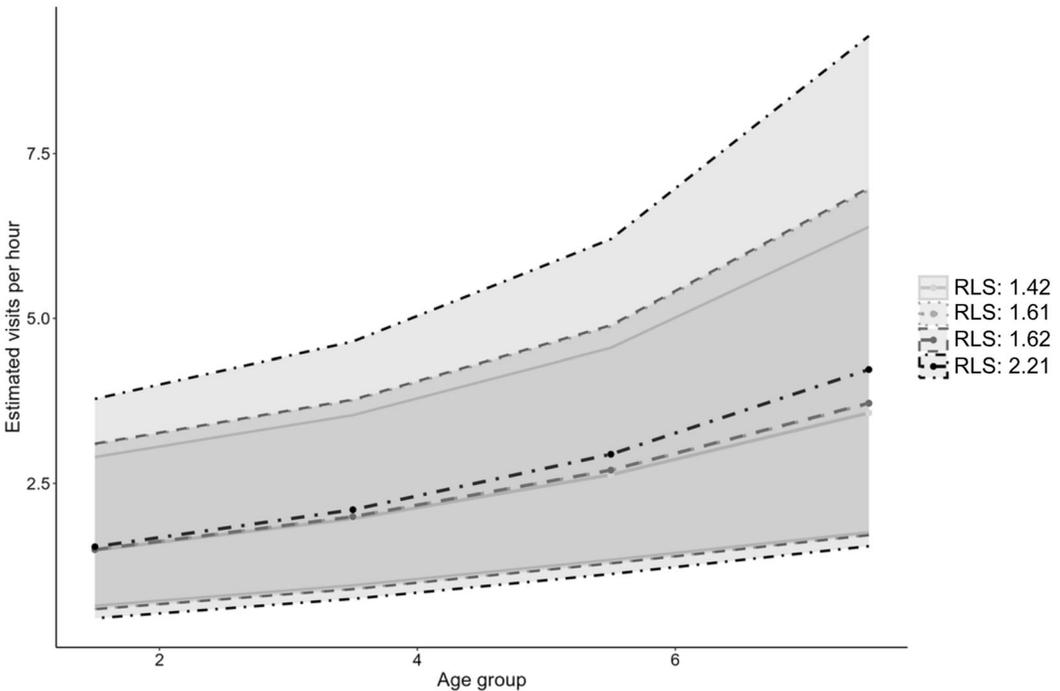


FIGURE 4 Predicted age-specific provisioning rates from camera-monitored eastern towhee nests ($n = 25$) in Rhode Island, USA, during May to August 2022–2023, at 4 sites that differed in woodcock relative likelihood of selection (RLS = 1.42, $n = 8$; RLS = 1.61, $n = 10$; RLS = 1.62, $n = 5$; RLS = 2.21, $n = 2$). The age group of nestlings had a positive effect on the number of visits to nests, whereas woodcock RLS showed no effect on visits. Shaded areas represent 95% credible intervals. Woodcock, the designated umbrella species, RLS values were based on a resource selection function from tracking radio-marked males from 2010–2021 (RSF; Slezak et al. 2024). Lines for RLS values 1.61 and 1.62 are overlaid on each other because of their closeness in values.

per hour for males and 1.09 ± 0.95 (SD) for females. All MCMC trace plots and R -hat values indicated that models converged. Provisioning rates of males and females did not differ for any chick age (paired t -test, $P > 0.05$ for all ages). The age group of nestlings had a positive effect on the total number of visits to nests (0.10, 95% CRI = 0.05, 0.16), whereas woodcock RLS showed no effect on total visits (-0.10 , 95% CRI = -0.60 , 0.40; Figure 4).

DISCUSSION

Higher RLS sites for woodcock had higher densities of singing male towhees as predicted, although path analysis revealed that territory size of towhees was related more directly to the density of towhees rather than woodcock RLS. In general, songbirds are known to adjust their territory sizes based on population density (Haché et al. 2013), although high-quality environments may be necessary to support smaller territories (Fretwell and Lucas 1969, Haché et al. 2013). For example, experimental reduction in density of male great tits (*Parus major*) increased territory size among remaining birds, supporting a density-dependent effect on territory size (Both and Visser 2000). Canada warbler (*Cardellina canadensis*) territory size was smaller, and density was higher in higher quality habitats, where resources like dense shrubs were abundant (Flockhart et al. 2016). Although we did not assess habitat characteristics within each towhee territory, management aimed at creating high-RLS habitat for

woodcock establishes young forest patches with dense shrubs that support high densities of territorial towhees during the breeding season.

Daily survival rates of nests were not influenced by woodcock RLS, likely due to differences in nesting needs of woodcock and towhees. Nest survival is influenced by factors such as stem density, concealment, and phenology, although the strength of these influences is often species-specific (Colombelli-Négrel and Kleindorfer 2009, Schill and Yahner 2009, Borgmann et al. 2013). Kramer et al (2019) compared the productivity of breeding woodcock and golden-winged warblers (*Vermivora chrysoptera*) across a shared landscape. They found that golden-winged warbler productivity decreased in areas with high woodcock productivity in part because of differences in landscape composition and configuration (Kramer et al. 2019). This is not the only study to document mismatches between nesting ecology and the umbrella species concept, where managing habitats for one species may inadvertently affect others with differing ecological requirements. Habitat management under the greater sage-grouse (*Centrocercus urophasianus*) umbrella program increased nest success for species with similar sagebrush habitat associations but provided minimal benefits to songbirds reliant on forested conifer ecosystems (Zarri et al. 2024). Moreover, areas managed for conifer removal negatively affected the green-tailed towhee (*Pipilo chlorurus*), often considered a near-obligate sagebrush songbird (Zarri et al. 2024), emphasizing the importance of considering species-specific habitat needs within umbrella species management.

Given their contrasting nesting strategies and types of young, towhees and woodcock are likely exposed to different predator communities and thus predation risk. Woodcock begin breeding nearly 2 months earlier in the spring (February–March), before towhees have established their breeding territories. Woodcock have precocial young with females attending but not feeding chicks until independence (McAuley et al. 2020), whereas towhees have altricial young and biparental care (Greenlaw 2020). This staggered timing and differences in parental care likely expose each species' nests and young to differing risks from predators. Woodcock in Rhode Island have low nest and brood success (10% and 16%, respectively) primarily because of predation (Slezak 2024) from crows and ravens (*Corvus* spp.), long-tailed weasels (*Mustela frenata*), American mink (*Neogale vison*), and other predators (McAuley et al. 2005, Masse et al. 2013). Predation is also typically the primary factor limiting survival rate of songbird nests (Martin 1993), and towhees in our study had a high rate of nest predation (78% of nest failures). We did not quantify predator presence at our study sites, but nest cameras allowed us to identify red squirrel (*Tamiasciurus hudsonicus*), eastern chipmunk (*Tamias striatus*), broad-winged hawk (*Buteo platypterus*), and eastern rat snake (*Pantherophis alleghaniensis*) as common predators at towhee nests. Similarly to other species, towhee nesting success appears to be more influenced by predator assemblage cycles (Flockhart et al. 2016, Hallworth et al. 2024) and fine-scale nest site selection (Martin 1993, Colombelli-Négrel and Kleindorfer 2009, Borgmann et al. 2013) than by broader site RLS metrics. While each site might contain features conducive to successful nesting (e.g., abundant cover or resources), our findings suggest that site-level metrics do not predict nest survival as strongly as localized, fine-scale factors like shrub density or proximity to predators. Even in low-RLS sites, towhees can likely have successful nests by selecting optimal nest sites at a microhabitat scale, potentially mitigating risks from predation and other pressures. Our results suggest that woodcock RLS has less influence on towhee nest survival compared to predator assemblages, nesting strategies, and site selection at the microhabitat scale.

Towhee nestlings in high-RLS woodcock habitat grew to greater asymptotic mass and tarsus length compared to those in low-RLS sites. The predicted mass of nestlings at fledging (day 9) in low-RLS sites was 2.4 g lighter than those in high-RLS sites. In contrast, we observed no effect of RLS on nestling provisioning rates. Our initial hypothesis was that towhee provisioning rates would be lower in high-RLS sites, where food may be more abundant and accessible. Yet similar provisioning rates across the RLS gradient suggest that food quality, rather than abundance, may better explain the habitat-related nestling growth differences that we observed. Songbirds are known to adjust foraging efforts based on prey quality (Senécal et al. 2021), as prey types like caterpillars that are nutritionally valuable are preferentially selected by songbirds (Eeva et al. 2010, Piel et al. 2021). For example, great tit nestlings in boxes nearer oak trees, where caterpillars were abundant, received diets richer in caterpillars and required less provisioning by parents (Wilkin et al. 2009). Food shortage during the nestling period can limit growth

and lead to a reduction in body condition of nestlings (Naef-Daenzer et al. 2000, Searcy et al. 2004, Pérez et al. 2016, Grames et al. 2023), and nestlings in better condition at fledging have an increased likelihood of surviving this perilous post-fledging period, along with potential carry-over effects in surviving other parts of the annual cycle (Naef-Daenzer et al. 2001, Sánchez et al. 2007, Vitz and Rodewald 2011, Evans et al. 2020). These changes in post-fledgling survival have been shown to influence population growth rates (Anders et al. 1997, Versluijs et al. 2016). These same habitats used by woodcock can also benefit a variety of songbirds that use similar habitat during the breeding season (King et al. 2001, Masse et al. 2015, Brenner and McWilliams 2019, McNeil et al. 2023) or move to early successional forests during the post-fledging stage (Rappole et al. 1998, Vitz and Rodewald 2010, Chandler et al. 2012). In sum, higher predicted asymptotic mass and size of towhee nestlings in higher RLS woodcock habitat may improve post-fledging survival, and this implies that forest management for woodcock also benefits towhees.

MANAGEMENT IMPLICATIONS

Umbrella species habitat management holds broad ecological value by incorporating multi-species benefits into conservation strategies, but it must be carefully evaluated to avoid unintended negative effects on non-target species. We demonstrate that assessing nest survival, growth rates, and provisioning rates of nesting non-target songbird species offers a more comprehensive assessment when managing for an umbrella species. We found similar towhee nest survival and adult provisioning rates across all sites with varying woodcock RLS. Towhee nestlings' higher predicted asymptotic size combined with the presence of more breeding males at high RLS sites for woodcock suggest that forest management for woodcock enhances early nestling development and leads to more towhee fledglings in better condition, potentially improving post-fledging survival and increasing recruits to the population. Further understanding how landscape management influences all species of concern helps prevent unintended consequences where some but not all species benefit, particularly as some species are known to prefer areas that appear suitable but reduce survival or reproduction. Future research should focus on how management for woodcock affects other songbirds with more specialized habitat requirements, and how these management activities affect early successional species in different regions.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

ETHICS STATEMENT

All bird trapping, handling, and tagging activities were conducted in accordance with the University of Rhode Island Animal Care and Use Guidelines under Animal Care and Use Protocol AN#10-02-017 and Bird Banding Lab Permit #22923.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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