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Research Paper

Conservation value of the umbrella species concept: Prairie Warblers receive few conferred benefits when habitat is managed for American Woodcock in Rhode Island, USA

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ABSTRACT. The umbrella species concept is a popular management approach based on the assumption that conserving one species benefits others, yet assessments beyond abundance often reveal mismatches in benefits to non-target species. We compared the density, territory size, and key metrics of seasonal reproductive success for Prairie Warbler (*Setophaga discolor*, hereafter PRAW) between study sites that differed in relative likelihood of selection (RLS) as determined for American Woodcock (*Scolopax minor*, hereafter AMWO), a proposed umbrella species for early successional habitat in eastern North America. Sites with higher AMWO RLS had higher densities of singing male PRAW, which in turn defended smaller territories. Nest survival of PRAW, and the probability of Brown-headed Cowbird (*Molothrus ater*, hereafter BHCO) parasitism were not related to AMWO RLS, but parasitized nests in high RLS sites fledged smaller nestlings compared to parasitized nests in low RLS sites. If reduced growth rates negatively impact post fledging survival, then PRAW nesting in these high RLS areas would recruit fewer individuals than those nesting in low RLS areas. Even though density of PRAW was greater at sites with high AMWO RLS, PRAW did not fully benefit from forest management aimed at AMWO in Rhode Island, USA in that metrics of reproductive success were lower at sites with high AMWO RLS in part because of BHCO parasitism.

L'intérêt du concept d'espèce parapluie pour la conservation : la Paruline des prés tire peu de bénéfices de la gestion de l'habitat destinée à la Bécasse d'Amérique dans le Rhode Island, aux États-Unis

RÉSUMÉ. Le concept d'espèce parapluie est très répandu dans la gestion des espèces. Cette approche repose sur l'hypothèse selon laquelle la conservation d'une espèce profite à d'autres. Pourtant, les évaluations au-delà de la simple abondance révèlent souvent des lacunes dans les bénéfices pour les espèces non ciblées. Nous avons comparé la densité, la taille des territoires et les principaux indicateurs du succès reproductif saisonnier de la Paruline des prés (*Setophaga discolor*, ci-après PP) entre des sites d'étude présentant des différences en termes de probabilité relative de sélection (PRS), telle que déterminée pour la Bécasse d'Amérique (*Scolopax minor*, ci-après BA), une espèce parapluie proposée pour les habitats en début de succession dans l'est de l'Amérique du Nord. Les sites présentant une PRS plus élevée pour la BA abritaient une plus grande densité de mâles chanteurs de PP, qui, à leur tour, défendaient des territoires plus petits. La survie des nids de PP et la probabilité de parasitisme par le Vacher à tête brune (*Molothrus ater*, ci-après VTB) n'étaient pas liées à la VRS de la BA, mais les nids parasités dans les sites à PRS élevée donnaient naissance à des oisillons plus petits que ceux des nids parasités dans les sites à PRS faible. Si la baisse des taux de croissance a un impact négatif sur la survie après l'envol, alors les populations de PP nichant dans ces zones à taux élevés de survie post-envol recruteraient moins d'individus que celles nichant dans des zones à taux faibles de survie post-envol. Même si la densité de PP était plus élevée sur les sites présentant une PRS élevée pour la BA, la PP n'a pas pleinement bénéficié de la gestion forestière axée sur la BA dans le Rhode Island, aux États-Unis. En effet, les indicateurs de succès reproductif étaient plus faibles sur les sites présentant une PRS élevée pour la BA, en partie à cause du parasitisme du VTB.

Key Words: *American Woodcock; Brown-headed Cowbird; early successional forest; Molothrus ater; Prairie Warbler; Scolopax minor; Setophaga discolor; umbrella species*

INTRODUCTION

The umbrella species concept suggests conserving one key species will provide protection for a broader suite of co-occurring species, improving conservation efficiency by using limited resources to manage multiple species. (Simberloff 1998, Fleishman et al. 2001, Roberge and Angelstam 2004). Land managers that employ umbrella species based strategies often focus on a target species such as charismatic fauna, threatened or endangered species, or game species with well documented habitat requirements, with the expectation that management actions benefiting these focal species will also confer protection to associated non-target species (Pakkala et al. 2003, Masse et al. 2015, Rose et al. 2021). Game birds are often selected as umbrella species because their charisma and popularity generate financial support through hunting revenues, they have well-established management practices, and their management can also provide benefits to nongame species (Suter et al. 2002, Masse et al. 2015). The umbrella species concept is appealing for its simplicity, but it frequently fails to adequately protect all non-target co-occurring species (Seddon and Leech

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2008, Carlisle et al. 2018, Wang et al. 2021). Most studies of umbrella species management focus on abundance of co-occurring species during the breeding season (Pakkala et al. 2003, Masse et al. 2015, Barlow et al. 2020, Rosenblatt et al. 2022) or spatial overlap (Suter et al. 2002, Breckheimer et al. 2014, Maslo et al. 2016). Based on these metrics of relative abundance and spatial overlap, the success of umbrella species conservation efforts varies by spatial scale and by umbrella species (Branton and Richardson 2011, Fourcade et al. 2017, Yang et al. 2023). For example, Barlow et al. (2020) found that the Greater Sage-Grouse (*Centrocercus urophasianus*) umbrella did not adequately protect nesting habitat for the declining Brewer's Sparrow (*Spizella breweri*, hereafter BRSP) as each species selected nest sites based on differing microhabitat preferences. Studies that incorporate reproductive metrics along with abundance estimates demonstrate that management for umbrella species often increases abundance or occupancy of non-target species without improving and in some cases reducing reproductive success (Kramer et al. 2019, Zarri et al. 2024), revealing potential ecological traps or population sinks. Without assessing reproductive outcomes for non-target species, umbrella species management risks creating ecological traps, population sinks, and declines in productivity.

Early successional forest birds like Prairie Warbler (*Setophaga discolor*, hereafter PRAW) have declined significantly because of loss of habitat on breeding and non-breeding grounds (Sauer et al. 2013). PRAW are Nearctic–Neotropical migrants, and their populations have declined by 1.9% annually across their breeding range from 1966 to 2024 (Hostetler et al. 2025). PRAW breed in a variety of shrubby habitats lacking closed canopy (Nolan et al. 2020) and in the northeast frequently breed in early successional forest (Nolan 1978, Akresh 2012), a habitat that has declined in the last 40 years because of forest regrowth, natural disturbance suppression, and increased anthropogenic pressures (Brawn et al. 2001, Sauer et al. 2013). Early successional forest management for wildlife in much of the northeastern United States is designed to improve habitat for several designated umbrella species (Bakermans et al. 2015, McNeil et al. 2023), which may benefit non-target species such as PRAW. American Woodcock (*Scolopax minor*, hereafter AMWO), a popular game bird, and an upland, migratory shorebird that use open fields for breeding display flights, nest in young forest, and feed in mixed woods with moist soils (McAuley et al. 2020). Land management targeted at AMWO involves creating a mosaic of habitats with open fields for singing grounds and roosting, and early successional forest for nesting and feeding (Kelley et al. 2008, Palmer 2008). Management for AMWO, like for other umbrella species, is thought to be successful when non-target species are more abundant and spatially overlap where the umbrella species are also most abundant (Masse et al. 2015, Brenner and McWilliams 2019). These same key habitat types used by AMWO may also benefit a variety of songbirds during the breeding season (King and Byers 2002, Palmer 2008, Bakermans et al. 2015, Masse et al. 2015). If early successional forest management for AMWO benefits nontarget species such as PRAW, then multiple key metrics including abundance and reproductive success of PRAW should be higher at sites managed to increase the relative likelihood of selection for AMWO.

In this study, we evaluated whether AMWO serve as an effective umbrella species for PRAW. We compared the density and territory size of breeding male PRAW, as well as nest survival and nestling growth at six study sites that differed in AMWO relative likelihood of selection (RLS). PRAW are hosts for Brown-headed Cowbird (*Molothrus ater*, hereafter BHCO), so we also compared rate of BHCO parasitism between high and low RLS sites. If AMWO are an effective umbrella species, then we predicted that sites with higher RLS by AMWO would have higher densities of territorial male PRAW that defend smaller territories. We also predicted that PRAW inhabiting these higher RLS sites would have higher nest success despite BHCO parasitism and produce nestlings in better condition compared to lower RLS sites. If the above predictions are confirmed, then habitat management to improve areas for AMWO should also benefit PRAW.

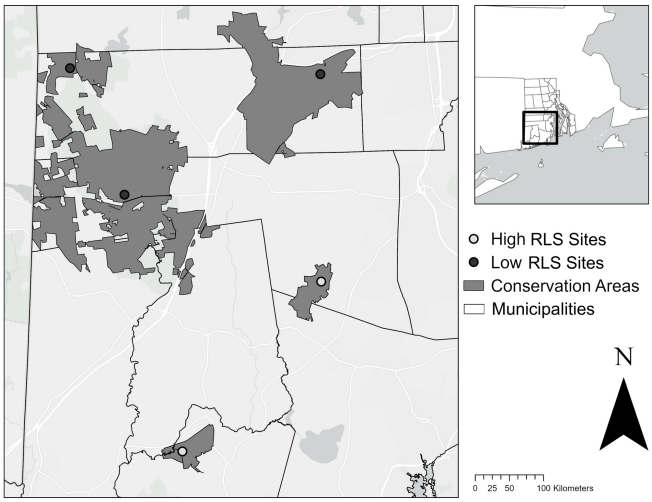
METHODS

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 six study sites were within four 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 two non-state properties: Francis Carter Preserve (The Nature Conservancy, [41°26′06.8″N, 71°40′ 41.8″W]) and Marion Eppley Preserve (Audubon Society of Rhode Island, [41°31′44.4′N, 71°34′37.0″W]; Fig. 1). No PRAW defended territories or nested at the study site within Great Swamp Management Area during 2022 or 2023, and thus this site was excluded from further analysis. For each study area, we distinguished between (1) a standardized 4-km^2 spatial extent used to summarize AMWO RLS values, and (2) the area of early successional forest managed for AMWO within which PRAW were surveyed and territories were mapped. Sites differed in vegetation characteristics and composition (see Slezak et al. 2024 for more detail), but all sites commonly had red maple (*Acer rubrum*), oaks (*Quercus* spp.), pitch pine (*Pinus rigida*) and white pine (*Pinus strobus*) as canopy and understory while the rest of the understory was composed of varying densities of blueberry (*Vaccinium* spp.), mountain laurel (*Kalmia latifolia*), sweet fern (*Comptonia peregrina*), greenbrier (*Smilax* spp.), and grasses (*Poacea* spp.).

The focal study sites within each study area (Fig. 1) were selected based on three criteria: (1) singing male AMWO were regularly observed displaying at the site within the last 5+ years (Brenner et al. 2019, Slezak et al. 2024), (2) early successional forest patches were actively maintained with management (i.e., brush thinning, mowing, or prescribed burning), and (3) sites differed from each other in predicted RLS by AMWO based on a resource selection function (RSF; Masse et al. 2014, Slezak et al. 2024). The RSF is the primary tool guiding forest management in our region. Land managers utilize a decision-support application that allows them to assess how the creation of early successional habitat affects the RSF value and, by extension, the predicted likelihood of AMWO selection (Buffum et al. 2021) to create early successional forest in areas with the greatest benefit. The use of these three criteria

Fig. 1. Five study sites (circles, representing general locations of study sites) within three state management areas and two non-state properties (dark gray polygons) used in our analysis of Prairie Warbler (*Setophaga discolor*, hereafter PRAW) density, territory size, and nesting ecology in 2022 and 2023 between May to August in areas managed for American Woodcock (*Scolopax minor*, hereafter AMWO) in Rhode Island, USA. Two of the study areas were high (white circles) relative likelihood of selection (RLS) and three of the study areas were low AMWO RLS (dark circles) based on a Resource Selection Function (RSF; Slezak et al. 2024). Great Swamp, a fourth state management area that was considered high RLS was the sixth study site, is not shown because we found no breeding PRAW at this site.



enabled us to more directly assess whether sites actively managed for AMWO that differed in predicted likelihood of selection (i.e., RLS value) also differed in PRAW density, territory size, nest survival, nestling growth, and rate of parasitism. Comparing AMWO likelihood of selection with measures of reproductive success of a non-target species provides a critical test of whether management intended to benefit a target species also confers benefits to PRAW.

Development of the RSF and relative likelihood of selection values

Resource selection functions (RSFs) quantify animals' selection or avoidance for different components of their environment (Manly et al. 2002). Specifically, RSF models estimate a relative probability of use for each pixel in a rasterized study area by combining spatially explicit values of habitat covariates using a fitted RSF equation (Fieberg et al. 2021). This study used the most recently updated 2024 RSF (Slezak et al. 2024), which quantifies relative probability of use by AMWO across our five study sites. The RSF is based on daytime tracking locations of radio-marked male (n = 146) AMWO during post-breeding (June–August) in Rhode Island over 11 years (2010–2021). These locations were used to produce a spatially explicit state-wide map of low-to-high-likelihood of selection (i.e., relative probability of use) areas at a 10-m scale based on top-ranked habitat selection models for males with areas of high RLS assumed to confer greater benefits to AMWO than areas of lower RLS (Slezak et al. 2024). The model covariates used to produce the state-wide likelihood of selection 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 AMWO habitat selection excluded areas that would not be used by AMWO during the daytime tracking period (non-forested areas including bare land, developed areas, and grassland. For more details, see Masse et al. 2014 and Slezak et al. 2024). To adequately test AMWO as an umbrella species we selected the area of 4-km² as past research has shown that this encompasses AMWO breeding, roosting, and daytime feeding areas (Kelley et al. 2008, Palmer 2008) and current management practices for AMWO are recommended at this scale (Williamson 2010, Brenner et al. 2019, Masse et al. 2019). We averaged RLS values at the 10-m scale estimated by the 2024 AMWO RSF across 4-km² buffers around each study site (Esri 2021, see Brenner et al. 2019 for more details) to obtain site-level RLS values at the ecological scale at which AMWO management is recommended. Throughout the remainder of the manuscript, "relative likelihood of selection" refers to these site-level RLS values rather than raw 2024 RSF outputs for individual 10-m pixels. The site-specific values used in this study where high-likelihood of selection values were > 1.60 and low-likelihood of selection values were < 1.45 (Table 1). Following the initial development of the RSF (Masse et al. 2014) the RSF was validated using a reciprocal transplant experiment (Brenner et al. 2019). In that study, most male AMWO translocated from high to low RLS sites quickly returned to their original high RLS sites. Conversely, most male AMWO moved to high RLS sites remained there, suggesting that males assess habitat quality in ways consistent with RLS as predicted by the RSF.

Surveys to determine density of singing male PRAW

Surveys for singing male PRAW 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 on fair-weather days (low wind, Beaufort scale < 5) with little to no precipitation (Robbins 1981). Surveys at each site involved observers counting all PRAW males that were present along a walking route that covered all the available early successional habitat managed for AMWO and where PRAW were detected. All surveys were conducted from 30 minutes before sunrise to six hours after sunrise. Survey duration varied by site depending on density of males and the acreage of the site but was on average 192 minutes (SD ± 18.2) in 2022 and 225 minutes (SD ± 17.6) in 2023. In 2022, a single observer conducted surveys by visiting three sites one day and the other three sites on the following day. On the third day the first three sites were visited 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 minimum 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 observers were rotated through sites to avoid being influenced by past observation. Surveys were submitted using the Survey123 app (Version 5.1.80, ESRI 2021).

Table 1. Male density (birds per hectare) of Prairie Warbler (*Setophaga discolor*, hereafter PRAW) at each of the five study sites in 2022 and 2023 between May to August. Three of the study areas were designated low American Woodcock (*Scolopax minor*, hereafter AMWO) relative likelihood of selection (RLS) and two sites were designated high AMWO RLS, the presumed umbrella species, based on a resource selection function (RSF; Slezak et al. 2024). Number of surveys conducted in 2022 and 2023, and male density (mean ± SD) estimated from the surveys for each year and across both years during the peak of singing (May 5 to June 30) for each of the five sites surveyed in Rhode Island, USA.

Likelihood of selection (RLS value)	Site	Surveys	2022 male density (birds/ha)	2023 male density (birds/ha)	Mean male density (birds/ ha)
Low RLS (1.39)	Arcadia	4	0.1	0.1	0.1
Low RLS (1.29)	Big River	6	0.11 ± 0.03	0.12 ± 0.02	0.12 ± 0.02
Low RLS (1.42)	Tillinghast[†]	11	0.74 ± 0.05	0.46 ± 0.16	0.56 ± 0.19
High RLS (1.61)	Francis Carter	9	0.68 ± 0.14	0.58 ± 0.18	0.64 ± 0.15
High RLS (1.62)	Eppley	5	0.69 ± 0.09	0.48 ± 0.04	0.56 ± 0.19

[†] Density of males at Tillinghast was the only site with significant differences in density between the two years ($t = 4.40$, $p = 0.0026$).

Density

We observed the peak density of singing male PRAW (birds per hectare) occurring at all sites between 5 May and 30 June in 2022 and 2023, which coincided with when most males had established territories and territorial disputes between adjacent males had resolved. Density of singing male PRAW at each site was calculated as the number of males detected divided by the total area in hectares of early successional forest managed for AMWO within that site. We measured the area (ha) of early successional forest managed for AMWO at each site using ArcGISPro (Version 3.2.2) 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 PRAW (e.g., large fields or tracts of sandy, bare land) that we excluded from our estimate of the area at each site occupied by singing, territory-holding male PRAW. These excluded areas did not influence the RLS values used to designate each site as high or low AMWO RLS because the RSF was developed using daytime locations of AMWO and excluded non-forested land cover types not used by AMWO (see Slezak et al. 2024 for more details).

Territory size of PRAW

Our goal was to map territories of all or most individual males per site per year depending on the density of PRAW males at the site. We captured and color-banded males beginning in May, soon after territory establishment in spring, and then continued to capture breeding males until the end of June. Not all individuals were captured at a given site and year, so territories were mapped for both marked and un-marked males. Across all sites we marked 78% of all male PRAW. We observed all color-marked males maintaining exclusive territories, so we assumed un-marked males did also. Males were captured using conspecific audio playback in 30-millimeter mist nets. After capture, birds were aged, sexed, and weighed to the nearest 0.1 gram and wing chord measured to the nearest 0.1 millimeter (Pyle 2022). Each bird ($n = 39$) received a unique plastic color-band combination along with the standard USGS aluminum band (BBL permit # 22923). In 2023 as part of a separate study on movement ecology, a subset of adult breeding males ($n = 19$) were also outfitted with a CTT PowerTag transmitter (weight = 0.35 g, < 5% body mass) attached with either an elastic modified leg-loop harness (Rappole and Tipton 1991) or glued on (Loctite Super Glue, Gel Control). When returning color-marked males from 2022 were recaught, we removed their color bands to reduce the weight of auxiliary markers ($n = 10$).

We used spot mapping (Falls 1981) to delineate territory boundaries and estimate territory size of individual males during May to July for each of the two years of the study (except Big River in 2023 for logistical reasons). Observers would target a single bird on a given day, with or without auxiliary markers, that had been resident in a certain area within a site for at least six days. The observer used audio playback of PRAW songs to define the bird's territory boundaries at 20-meter intervals along the territory perimeter and corners. Territory boundaries for each male were delineated when a male stopped following playback, or an adjacent territorial male came to playback (Falls 1981). A minimum of five GPS points were taken 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 longer, in which case observers would stop delineating territory boundaries to avoid prolonged disturbance to the bird and then return within five days to complete the spot mapping. GPS points taken at territory boundaries were then mapped using adehabitatHR (Calenge 2023) to create minimum convex polygons. Only territories with a minimum of five GPS points were included in the analysis. We measured the polygons in hectares, and the mean territory size was generated for each site.

Estimating nest survival and nestling growth

To assign nests to a given female or females to a male defending a territory, in 2022 we opportunistically marked four females with color bands and the USGS aluminum band while target netting for males; in 2023, as part of a separate study on movement ecology, we marked 13 females with the USGS aluminum band and equipped them with either glue-on or harness transmitters (CTT PowerTag [$n = 11$)] VHF tag [$n = 2$]) allowing us to track them back to their nests. We captured females beginning in May and until the end of July. If a nest with an unmarked female was located, we attempted to capture the female to track successive nesting attempts. If we could not capture the female within 30 minutes, we either abandoned the attempt or attempted capture a following day to limit potential predation of the nest by increased activity. We experienced no abandonment of nests from catching actively nesting females. Overall, nests were found in three ways: (1) watching females that were displaying breeding behavior until they returned to the nest (carrying nesting material, food, or fecal sacs), (2) incidentally flushing an incubating female while territory mapping, or (3) tracking a transmitter-tagged female back to the nest.

The nesting period of PRAW starts with nest building (variable 2–10 days) and for the next 26 days (± 2) includes four stages: laying (one egg a day) and incubation of the eggs (~12 days), and provisioning and caring for nestlings before fledging (~10 days; Nolan 1978, Nolan et al. 2020). Female PRAW typically have a single brood and will attempt to renest until late June and early July. We commonly found PRAW nests 0.5 to 2 meters off the ground in a thickly vegetated bush (Nolan 1978). When nests were found, observers took GPS points both at the nest location and the flagging location that was approximately 5–10 meters 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) as well as the number of BHCO eggs. For nests with an unknown hatch day, we estimated day of hatch based on a combination of mass and tarsus length measurements along with general nestling appearance (downy feathers, presence of pin feathers, begging, and eyes open or closed) as well as comparing against Nolan's (1978) measurements.

Nests were monitored following the methods outlined in Martin and Geupel (1993). Every 1–3 days and until nestlings were 8 days old, we measured mass to the nearest 0.1 gram and tarsus length to the nearest 0.1 millimeters using vernier calipers following the definition in the Pyle Guide (Pyle 2022). Individuals were differentiated by coloring the tarsus with different colored non-toxic felt tipped marker that was not permanent and had to be reapplied on subsequent visits. Most nestlings were directly aged by hatch day (day 1 = hatching day). On the last day of measuring, we banded nestlings with the USGS aluminum band. Because PRAW nests are commonly parasitized by BHCO (Nolan 1978, Nolan et al. 2020), when BHCO nestlings were present in a nest, we measured all nestlings including the BHCO. To determine nest fate after 8 days old and until fledging (usually 10 days old), we continued to monitor nests from a distance to listen for nestlings begging, or adults feeding nearby. If no activity was seen in the vicinity, observers would slowly walk by the nest location to determine if the female was brooding or if the nest was depredated. We determined nest fate as either successful (i.e., at least one PRAW nestling fledged), depredated (i.e., eggs or nestlings gone), abandoned (eggs cold), or infertile. PRAW abandoned nests that were partially depredated, or heavily parasitized by BHCO. We detected no nest abandonment that we attributed to our own research activities.

Statistical analysis

Our continuous variable of RLS was scaled and centered (mean = 0 and SD = 1) prior to conducting analysis. We used a path analysis (Wootton 1994, Shipley 1997, 2004) with the blavaan package (Merkle et al. 2021) to evaluate the hypothesis that individuals are more likely to adjust their territory size in response to local density than RLS value alone. We assigned a single 4-km² RLS value to each study site, and all PRAW density and territories within a site were associated with this value; although PRAW territories are smaller than 4-km², using the site-level RLS reflects the landscape-scale habitat that AMWO select and is consistent with recommended management practices (Williamson 2010, Brenner et al. 2019 Masse et al. 2019). To account for non-independence of territories mapped within the same site, we clustered observations by site in a two-level Bayesian structural equation model. Consistent with path analysis terminology we estimated the direct effect of RLS on territory size and density as well as the indirect effect of RLS mediated through local density.

We calculated daily survival rates (DSR) and cumulative nest success using the Mayfield method (Mayfield 1961, 1975) with exposure days defined as the number of days from nest initiation to the last nest check. For nests with unknown initiation dates, we used half of the observed interval between first detection and last check as an approximation of exposure days (Hensler and Nichols 1981), allowing inclusion of nests that would otherwise be excluded. We also used a binomial generalized linear model with logit link and the log of exposure days as an offset, equivalent to the logistic-exposure method (Hazler 2004, Shaffer 2004). Because of the small sample size, statistical power to detect differences was limited, so Mayfield estimates are presented descriptively alongside GLM predictions. We used Fisher's Exact Test to compare the proportion of nests parasitized by BHCO in high and low RLS sites. We used a Bayesian Poisson regression model to test whether initial or final brood size varied with parasitism, RLS, or their interaction. The model included categorical effects of nest type (parasitized or unparasitized), RLS (high or low), and their interaction as fixed effects, assuming a Poisson distribution for count data. We used weakly informative priors (normal distribution with mean = 0 and SD = 5) for both the fixed effects and the intercept. We ran four parallel Markov Chain Monte Carlo (MCMC) chains with 4000 iterations each, including 1000 warmup iterations.

We calculated PRAW growth rates by fitting a Gompertz growth model in a Bayesian framework using the brms package (Bürkner 2017). 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 and is commonly used to describe songbird patterns of growth (Ricklefs 1969, Garrido-Bautista 2023). BHCO nestlings (n = 7) were measured inconsistently, and we were unable to model growth effectively. We had no PRAW nests monitored for growth without BHCO nestlings at high RLS sites, so we modeled growth for PRAW nestlings in three groups (high RLS, parasitized; low RLS, unparasitized; and low RLS, parasitized). We restricted our analysis to PRAW nestlings with three or more measurements and accounted for the shared nest environment by including a hierarchical random effect structure, with nestling ID nested within nest ID. Because of our small sample size, we applied weakly informative priors (normal distribution with mean = 0 and SD = 20) to all model parameters based on previous studies of asymptotic mass and tarsus (Nolan 1978, Pyle 2022) to provide modest regularization (Lemoine 2019). We ran four parallel MCMC chains with 10,000 iterations each, including 5000 warmup iterations. Posterior estimates for parameters a, b, and c from the Gompertz growth model were extracted to calculate growth trajectories from hatching to fledging, 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.

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

Separate, linear Bayesian models with an effect of group (high RLS, parasitized; low RLS, parasitized; and low RLS, unparasitized) were used to compare these three a, b, and c parameters between the three groups. We ran four parallel MCMC chains with 4000 iterations each, including 1000 warmup

Table 2. Number of Prairie Warbler (*Setophaga discolor*, hereafter PRAW) males (mean ± SD), total number of territories mapped, and territory size (mean ± SD, hectares) for each year for each of the five sites in Rhode Island, USA during breeding, May to August, 2022 and 2023. Three of the study areas were designated low American Woodcock (*Scolopax minor*, hereafter AMWO) relative likelihood of selection (RLS) and two sites were designated high AMWO RLS, the presumed umbrella species, based on a resource selection function (Slezak et al. 2024).

Likelihood of selection (RLS value)	Site	Number of males 2022	Territories mapped 2022	Territory size (ha) 2022	Number of males 2023[†]	Territories mapped 2023	Territory size (ha) 2023
Low RLS (1.39)	Arcadia	1.0 ± 0	1	0.495	1.0	1	0.83
Low RLS (1.29)	Big River	4.0 ± 1	5	2.74 ± 1.72	4 ± 0.6	NA[‡]	NA[‡]
Low RLS (1.42)	Tillinghast	15 ± 0.9	11	0.61 ± 0.46	9 ± 3.3	8	0.99 ± 1.02
High RLS (1.61)	Francis Carter	14 ± 2.9	11	0.43 ± 0.22	12 ± 3.7	12	0.33 ± 0.39
High RLS (1.62)	Eppley[§]	11 ± 1.4	10	0.87 ± 0.51	8 ± 0.6	6	0.42 ± 0.22

[†] Of 41 males marked with auxiliary markers in 2022, 18 males returned in 2023 (Arcadia = 1, Big River = 1, Tillinghast = 4, Francis Carter = 7, Eppley = 5). Of 4 females marked in 2022, one returned to Eppley in 2022.
[‡] Male PRAW territories were mapped at Big River in only one of the two years (2022).
[§] Territory size of males at Eppley was the only site with significant differences in area between the two years (t = 2.53, p = 0.02).

iterations. Each model provided estimates of the mean parameter value and 95% credible intervals for that specific group, allowing direct comparisons between the three groups.

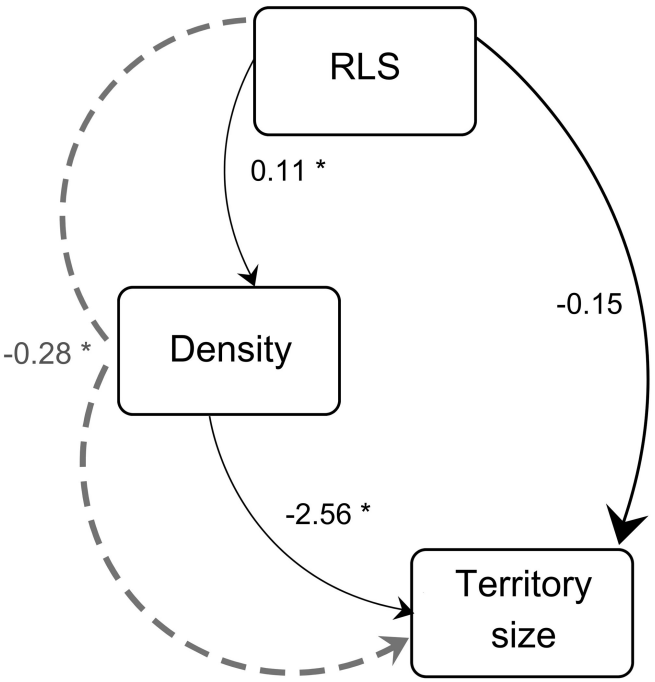
For all Bayesian analysis we assessed model convergence visually using trace plots and the Gelman-Rubin diagnostic, where R-hat values < 1.05 indicated adequate mixing and convergence (Gelman 2004). We also ensured sufficient sampling by examining effective sample sizes (ESS), with all parameters exceeding 1000, suggesting low autocorrelation and adequate exploration of posterior distributions. Parameters estimated from frequentist models are presented ± their 95% confidence intervals and empirical Bayesian parameter estimates are presented ± their 95% credible intervals; CI is used to denote confidence intervals and CRI is used to denote credible intervals. All data manipulation and statistical analyses were done in R version 4.4.2 (R Core Team 2024).

RESULTS

Density and territory size of PRAW

During 2022 and 2023, we conducted a total of 35 surveys across all five sites during the peak of singing over two years (Table 1), and we mapped a total of 65 male territories at these same five sites (Table 2). Both density and territory size of male PRAW was similar across the two years (t-test p > 0.05) for all study sites except density at Tillinghast was lower in 2023 (t = 4.40, p = 0.0026; Table 1) and territory size at Eppley was smaller in 2023 (t = 2.53, p = 0.025; Table 2). Based on the unstandardized beta coefficients from the Bayesian path analysis (Fig. 2), we found that RLS value did not influence territory size of PRAW directly (β = -0.15, 95% CRI: -0.42, 0.13) but when mediated through density, territories were smaller (β = -0.28, 95% CRI: -0.49, -0.07). As RLS value increased by one unit, the density of territorial males increased by 0.11 birds per hectare (β = 0.11, 95% CRI: 0.08, 0.14), and for every one-unit increase in birds per hectare, territory size decreased by 2.56 hectares (β = -2.56, 95% CRI: -4.30, -0.78). Thus, RLS is positively associated with density of PRAW, which in turn is a key factor in territory size determination.

Fig. 2. Sites that were high American Woodcock (*Scolopax minor*) relative likelihood of selection (RLS) as determined by a resource selection function (RSF; Slezak et al. 2024) had higher densities of singing male Prairie Warbler (*Setophaga discolor*; β = +0.11) and these sites with higher male density had smaller territories (β = -2.56) whereas RLS had no significant direct effect (β = -0.15) but did have an indirect (dotted gray line, β = -0.28) influence on territory size. Sites were surveyed for singing males and territory mapped during the breeding season, between May to August. Asterisks next to unstandardized beta coefficients indicate statistically significant relationships in the path analysis where the credible intervals do not overlap 0.



Nest success and BHCO brood parasitism

We found a total of 28 nests (15 in 2022, 13 in 2023), of which 26 were used to evaluate daily survival rate. The two nests not used were found during a predation event and thus had unknown exposure days. For eight of the 26 nests we did not know the initiation date and so we used the midpoint of exposure days. Of these, 16 nests were successful (57%) and 12 failed from predation (25%) or abandonment (18%). Across all nests, the Mayfield daily survival rate was 0.97 (95% CI: 0.96-0.99), corresponding to a cumulative nest success of 45% (95% CI: 33–63%) over the 26-day nesting period. Nests in high RLS sites had a DSR of 0.97 (95% CI: 0.95–0.99) and cumulative nest success of 45% (95% CI: 27–63%), while nests in low RLS sites had a DSR of 0.98 (95% CI: 0.96–1.00) and cumulative nest success of 59% (95% CI: 31–100%). Logistic-exposure modeling produced similar estimates of daily survival and we did not find an effect of high or low RLS on daily nest survival (β = -0.05 ± 0.92 SE, p = 0.96).

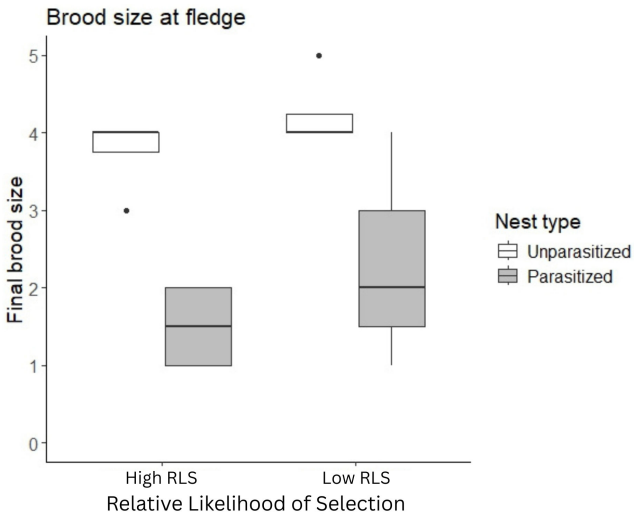
We assessed the rate of BHCO parasitism at high and low RLS sites for a subset of PRAW nests. Given that five of the 28 total nests found were abandoned or depredated before the full clutch was completed and so could still have been parasitized, we were able to assess rate of BHCO parasitism for 23 nests across the two years. Of the 13 nests in high RLS sites, five were parasitized and eight were unparasitized. Of the 10 nests in low RLS sites, three were parasitized and seven were unparasitized. Although the rate of parasitized nests was slightly higher in high RLS sites (38%) compared to low RLS (30%), Fisher's Exact Test indicated no significant difference in parasitism between high and low RLS sites (odds ratio = 0.70, CI: 0.08, 5.28, p = 1.0).

We analyzed differences in brood size for 15 nests that fledged at least one PRAW, including eight nests in high RLS sites (4 unparasitized, 4 parasitized) and seven in low RLS (4 unparasitized, 3 parasitized). Six unparasitized nests were found only later during chick growth (4 in high RLS, 2 in low RLS), and so to estimate initial brood size we assumed no nestling loss in these unparasitized nests (Nolan 1978). All MCMC trace plots and R-hat values indicated that models converged. Initial brood size did not differ between parasitized (n = 7) and unparasitized nests (n = 8; -0.07, CRI: -0.85, 0.71) or between habitat qualities (0.12, CRI: -0.56, 0.84) and was on average 3.9 (SD ± 0.5). Final brood size was significantly lower in parasitized nests compared to unparasitized nests (-0.95, CRI: -1.97, -0.01) but was not affected by high or low RLS (0.14, CRI: -0.56, 0.89). The effect of parasitism on brood size did not differ between high or low RLS (0.30, CRI: -1.01, 1.61), indicating that parasitism consistently reduced brood size regardless of AMWO RLS (Fig. 3).

Nestling growth

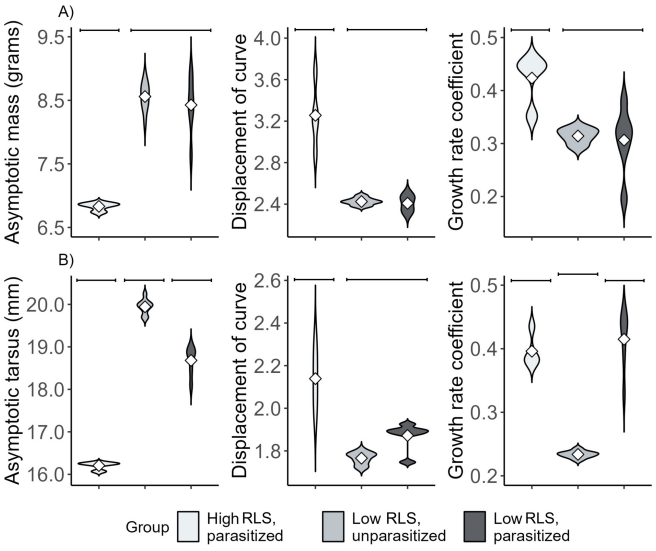
We monitored nestling growth in seven nests in which we were able to measure all PRAW nestlings at least three times throughout growth. We estimated growth rates for nestling mass and tarsus length from these seven nests (low RLS n = 5, high RLS n = 2) for 19 total individuals (low RLS, unparasitized n = 9; low RLS, parasitized n = 6; high RLS, parasitized n = 4) over the two years of the study. All MCMC trace plots and R-hat values indicated that models converged. The eight unparasitized nests in high RLS sites were depredated (n = 3) or found too close to the fledging date to obtain three measurements (n = 5) and so we did not measure these nestlings to avoid premature fledging.

Fig. 3. Comparison of brood sizes at fledging for Prairie Warbler (*Setophaga discolor*) nests that were parasitized by Brown-headed Cowbird (*Molothrus ater*, hereafter BHCO) or unparasitized at two high American Woodcock (*Scolopax minor*, hereafter AMWO) relative likelihood of selection (RLS) and two low AMWO RLS sites in 2022 and 2023 in Rhode Island, USA, during the breeding season, May to August. Brood size at hatch (not represented here) was similar for parasitized and unparasitized nests at both high and low RLS sites and was on average 3.9 ± 0.5. Brood size did not change between hatching and fledging in unparasitized nests at either high or low RLS sites. BHCO parasitism significantly reduced brood size at fledging in parasitized nests at both high and low RLS sites, but RLS did not affect brood size. The RLS values are based on a resource selection function for AMWO (Slezak et al. 2024). Boxes represent the middle 50% of the data with the line splitting the box being the median, the whiskers extending to the minimum and maximum values and points representing outliers that fall outside the whiskers.



Nestlings in parasitized nests at high RLS sites reached lower asymptotic mass compared to nestlings in parasitized nests at low RLS sites (a, mean difference = -1.60 grams, CRI: -2.02, -1.18) and nestlings in unparasitized nests at low RLS sites (a, mean difference = -1.73 grams, CRI: -2.12, -1.34; Fig. 4A). Nestlings in parasitized nests at high RLS sites had a higher curve displacement shifting growth later compared to nestlings in parasitized nests at low RLS sites (b, mean difference = 0.85, CRI: 0.64, 1.06) and compared to nestlings in unparasitized nests at low RLS sites (b, mean difference = 0.83, CRI: 0.64, 1.03; Fig. 4A). Nestlings in parasitized nests at high RLS sites had a higher growth rate coefficient reaching their predicted smaller asymptotic mass faster than those in parasitized nests at low RLS sites (c, mean difference = 0.12, CRI: 0.06, 0.18) and nestlings in unparasitized nests at low RLS sites (c, mean difference = 0.11, CRI: 0.05, 0.16). Nestlings in parasitized nests at low RLS sites grew similarly to nestlings in unparasitized nests at low RLS sites (Fig. 4A). Mean predicted asymptotic mass was 7.21 (SD ± 0.72) grams for nestlings in

Fig. 4. Posterior distribution estimates for the three growth parameters (asymptote, displacement of curve, growth rate coefficient) for mass (A) and tarsus (B) from Prairie Warbler (*Setophaga discolor*, hereafter PRAW) nestlings at four sites in 2022 and 2023 in Rhode Island, USA during the breeding season, May to August. Brown-headed Cowbird (*Molothrus ater*) parasitized all PRAW nests monitored for growth at sites with high American Woodcock (*Scolopax minor*, hereafter AMWO) relative likelihood of selection (RLS); thus, nests were grouped into three groups: high RLS parasitized, low RLS unparasitized, and low RLS parasitized. RLS values are from a resource selection function for AMWO (Slezak et al. 2024). Horizontal lines above each panel that are not shared across groups denote significant differences between the group(s). Horizontal lines on different planes represent differences between that group and the two other groups.



parasitized nests at high RLS sites compared to 8.17 (SD ± 0.85) grams for nestlings in parasitized nests at low RLS sites and 8.58 (SD ± 0.22) grams for nestlings in unparasitized nests at low RLS sites.

Nestlings in parasitized nests at high RLS sites reached a smaller asymptotic tarsus length compared to nestlings in parasitized nests at low RLS sites (*a*, mean difference = -2.48 mm, CRI: -2.79, -2.15) and unparasitized nests at low RLS sites (*a*, mean difference = -3.74 mm, CRI: -4.04, -3.44; Fig. 4B). Nestlings in parasitized nests at high RLS sites had a higher curve displacement shifting growth later compared to nestlings in parasitized nests at low RLS sites (*b*, mean difference = 0.27, CRI: 0.16, 0.37) and compared to unparasitized nests at low RLS sites (*b*, mean difference = 0.37, CRI: 0.27, 0.47; Fig. 4B). Nestlings in parasitized nests at high RLS sites had a higher growth rate coefficient, reaching their predicted smaller asymptotic tarsus faster than those nestlings in unparasitized nests at low RLS sites (*c*, mean difference = 0.16, CRI: 0.12, 0.20). Nestlings in parasitized nests at low RLS sites followed this delayed growth pattern as compared to nestlings in unparasitized nests in low RLS, reaching a smaller final asymptotic tarsus length (*a*, mean difference = -1.26 mm, CRI: -1.52, -1.00) because of a later curve displacement (*b*, mean difference = 0.11, CRI: 0.02, 0.19) and a higher growth rate coefficient (*c*, mean difference = 0.18, CRI: 0.15, 0.22). Mean predicted asymptotic tarsus was 16.9 mm (SD ± 1.3) for nestlings in parasitized nests at high RLS sites compared to 18.2 mm (SD ± 1.0) and 20.0 mm (SD ± 0.2) for nestlings in parasitized nests and unparasitized nests, respectively, at low RLS sites.

DISCUSSION

Density and territory size

We found support for the prediction that sites with higher AMWO RLS had higher densities of male PRAW, which defended smaller territories, although one of our highest RLS sites (Great Swamp [GSMA], RLS value: 2.21) had no breeding PRAW during either year of the study. The exact reasons for this discrepancy are unknown but likely reflect site level differences in vegetation composition and soil moisture. The area managed for AMWO at GSMA was markedly different from the other five study sites, with wetter soils, denser understory including greenbrier (*Smilax* spp.) and American holly (*Ilex opaca*), greater stem density, and vegetation height. In contrast, the other sites were dominated by pine (*Pinus* spp.), blueberry (*Vaccinium* spp.), and oak (*Quercus* spp.) in drier, more open, early-successional landscapes, which PRAW prefer (Nolan 1978). Two other early-successional forest species, Chestnut-sided Warbler (*Setophaga pensylvanica*) and Blue-winged Warbler (*Vermivora cyanoptera*), breed at GSMA (Clarkson et al. 2023) and will nest in moister and denser deciduous growth (Byers et al. 2020, Gill et al. 2020), supporting the interpretation that habitat composition, rather than AMWO RLS, explains the absence of PRAW at this site. The lack of breeding PRAW at GSMA demonstrates that sole reliance on AMWO RLS for predicting suitability for PRAW is naïve because PRAW occurrence also depends on other aspects of vegetation structure and composition. Nevertheless, PRAW densities were higher at the other two sites with higher AMWO RLS compared to those with lower AMWO RLS, suggesting that AMWO management can support PRAW occupancy under appropriate conditions.

Because AMWO RLS is not expected to directly govern songbird space use, we evaluated its effects within a broader framework linking habitat quality, density, and territory size. Our path analysis indicated that RLS by AMWO was positively associated with PRAW density, which subsequently affected territory size, rather than RLS having a direct effect on territory size. Management efforts to create high quality AMWO habitat that includes early successional forest patches with dense shrubs also supported high densities of territorial PRAW during the breeding season. Songbirds often adjust their territory sizes in response to population density (Haché et al. 2013), with smaller territories requiring the availability of high-quality environments (Fretwell and Lucas 1969, Haché et al. 2013) with denser foliage and greater available food resources (Marshall and Cooper 2004). However, caution is warranted when interpreting density as an indicator of habitat quality, as this relationship can be misleading (Van Horne 1983, Vickery et al. 1992, Mortelliti et al. 2010) and can negatively impact reproductive success. For example, experimental reductions in male density have been shown to increase territory

sizes among the remaining birds, demonstrating density-dependent effects on territory size (Both and Visser 2000, Sillett et al. 2004), whereas increased density resulted in reduced breeding productivity in Black-throated Blue Warbler (*Setophaga caerulescens*; Sillett et al. 2004). Such negative relationships between male density, recruitment, and population growth can occur because of increased direct competition (Sillett et al. 2004) or the pre-emptive occupancy of the highest-quality territories (Rodenhouse et al. 2003). However, higher adult density does not always equal higher nest density as observed in BRSP (Brewer's Sparrow) where fewer nests were initiated at sites with higher adult pair density (Ruth et al. 2023). Thus, the relationship between breeding density and reproductive success varies and seems context specific. Although we did not assess territory characteristics such as food availability or habitat composition, our finding that density of PRAW was greater at sites with higher RLS by AMWO suggests that if only density is considered as done in other studies (Bakermans et al. 2015, Masse et al. 2015, Rose et al. 2021), AMWO are an effective umbrella species for PRAW.

Nest survival

Contrary to our predictions, RLS had little effect on nest survival of PRAW. Ideally, a larger sample size would be used to assess how nest survival of PRAW is influenced by AMWO RLS. Like other songbirds, PRAW nest success is influenced by predator assemblage cycles (Schmidt and Whelan 1999, Hollander et al. 2013, Flockhart et al. 2016) and fine-scale nest site selection (Martin 1993, Colombelli-Négrel and Kleindorfer 2009, Borgmann et al. 2013) rather than by broader site quality metrics. A similar pattern was observed in BRSP, which settled in high densities within preferred nesting habitats but did not achieve higher nest success because of high predation (Chalfoun and Martin 2007). Several studies have shown that PRAW select nest sites with dense vegetation (Nolan 1978, Akresh 2012), which may reduce nest depredation and improve nest success (Martin and Roper 1988, Martin 1993, Rangel-Salazar et al. 2008). However, other studies have found no relationship between nest site selection and nest survival as predator pressure was so high that vegetation offered little protection (Filliater et al. 1994, Braden 1999, Davis 2005, Bulluck and Buehler 2008). BHCO frequently parasitize PRAW nests (Nolan 1978) often reducing nest success through clutch destruction, which forces hosts to renest (Granfors et al. 2001). Additionally, parasitized nests can face a higher risk of predation during the nestling stage (Dearborn 1999) because of increased begging of the BHCO and the host nestlings (Parker et al. 2002). We observed multiple instances of partial or complete clutch loss attributed to BHCO in the incubation and nestling phases, including egg ejection, nest abandonment with multiple BHCO eggs, premature nestling removal, and nestlings crushed in the nest cup. Overall, site level variation in predation and parasitism had a stronger influence on PRAW nest survival than broad site quality differences like those associated with AMWO habitat management.

Growth rates

Nestling growth rates were influenced by both BHCO parasitism and AMWO RLS, but parasitism had a stronger effect on the growth of PRAW nestlings. Nestlings in parasitized nests, whether in low or high RLS sites, reached smaller asymptotic tarsus length and attained this later than nestlings in unparasitized nests at low RLS sites. However, nestlings in parasitized and unparasitized nests at low RLS sites had similar asymptotic mass and attained these at similar times. BHCO parasitism is known to affect the reproductive success of host species by not only damaging or removing eggs, but also by reducing nestling growth and survival (Marvil and Cruz 1989, Hoover and Reetz 2006, Rasmussen and Sealy 2006, Rock et al. 2013, Scharf et al. 2021). In general, food shortages during the nestling period limit growth and lead to a reduction in body condition of songbird nestlings (Anders et al. 1997, Ausprey and Rodewald 2011, Vitz and Rodewald 2011). Songbirds parasitized by BHCO frequently have reduced brood condition, rates of mass gain, and suffer delayed fledging (Dearborn et al. 1998, Hoover 2003, Rock et al. 2013, Scharf et al. 2022) with nestlings in poor condition at fledging less likely to survive to adulthood (Naef-Daenzer et al. 2001, Vitz and Rodewald 2011, Evans et al. 2020). Thus, the negative effects of BHCO parasitism on nestling growth in high RLS sites may have lasting consequences for survival and recruitment, further contributing to PRAW declines by reducing reproductive output.

Nestling growth rates were possibly influenced by AMWO RLS although this was only apparent when comparing asymptotic mass and tarsus length of nestlings in parasitized nests given that BHCO parasitized all PRAW nests monitored for growth at high RLS sites. Although our small sample size of nests limits the strength of our conclusions, PRAW nestlings in parasitized nests at low RLS sites reached a greater asymptotic mass and tarsus length than those at high RLS sites (Fig. 4A, 4B, left panels). Nestlings in poor condition at fledging, such as those from high RLS parasitized nests in our study, are less likely to survive the post-fledging period (Naef-Daenzer et al. 2001, Vitz and Rodewald 2011, Evans et al. 2020). However, our conclusions are based on relatively few nests ($n = 7$) and given that the effects of BHCO parasitism on nestling growth can vary between years (e.g., Indigo Bunting [*Passerina cyanea*]; Burhans et al. 2000), further study is needed to confirm this effect of AMWO RLS on growth of PRAW nestlings in parasitized nests. Differences in nestling growth in our study were likely driven primarily by parasitism, although other factors including brood size (Hegner and Wingfield 1987, Sanz 1997), adult competition for resources (Sillett et al. 2004), food availability (Germain et al. 2015, Stantial et al. 2021, Grames et al. 2023) and food quality (Martin 1987, Wilkin et al. 2009, Razeng and Watson 2015, Piel et al. 2021) may also affect nestling growth of PRAW and deserve further study. Future studies that document nutritional content of prey, provisioning rates for hosts versus BHCO, as well as prey availability would be especially enlightening.

Umbrella species, brood parasitism, and the ecological sink

AMWO require a mosaic of habitat, including open fields and early successional forest (Palmer 2008, Masse et al. 2019). These wood-field ecotones may also create ideal conditions for BHCO, potentially increasing brood parasitism on songbird hosts and possibly contributing to an ecological sink. BHCO avoid contiguous forest stands, favoring wood-field ecotones such as early successional forest (Gates and Gysel 1978, Brittingham and Temple 1983, Johnson and Temple 1990), where they can access breeding hosts for egg deposition in the morning (Neudorf and Sealy 1994) and open foraging habitats in the afternoon (Rothstein and Peer 2005). BHCO abundance in eastern North America is limited by the availability of hosts in fragmented landscapes that provide

feeding areas (Morrison and Hahn 2002). Because BHCO rely on host availability, their abundance is often highest in fragmented landscapes where suitable hosts and foraging areas overlap. In fact, sites managed for AMWO in Rhode Island were found to have higher species richness and greater abundance of songbirds (Masse et al. 2015), many of which are potential hosts for BHCO (Friedmann et al. 1977, Lowther 2020) such as Common Yellowthroat (*Geothlypis trichas*), Chipping Sparrow (*Spizella passerina*), Field Sparrow (*Spizella pusilla*), and Indigo Bunting (Masse 2014). The high songbird diversity at sites managed for AMWO may increase brood parasitism and create an ecological sink where host density may be high but reproductive success for hosts is low (Rogers et al. 1997, Ward and Smith 2000, Hannon et al. 2009, Walker et al. 2016). Thus, management efforts to create habitat for AMWO may not only attract diverse songbird communities but also may provide ideal conditions for BHCO, potentially increasing parasitism and reducing reproductive success for vulnerable host species such as PRAW.

PRAW may perceive sites with high AMWO RLS as suitable habitat, leading to increased density, however, the reduced growth rates of nestling PRAW at these high AMWO RLS sites resulted in decreased size at fledgling and likely overall reproductive success for PRAW in that fewer young are added to the population. If the pattern that we found with our limited sample size is replicable across areas managed for AMWO in the state, then it is possible that reproductive output across the state is low for the declining PRAW. In contrast, other songbirds, like Eastern Towhee (*Pipilo erythrophthalmus*, hereafter EATO), largely avoid BHCO parasitism and thus benefit from habitat management for AMWO. At these same study areas in the same years, EATO were seldom parasitized by BHCO and EATO had increased reproductive success in sites that were high RLS by AMWO (Gray et al. 2025). In general, smaller species like PRAW experience greater costs from brood parasitism than species closer in size to BHCO (≥ 20 g), such as EATO (Lorenzana and Sealy 1997). These costs may extend beyond nest failure, as increased parental effort can reduce adult return rates, as seen in Prothonotary Warbler (*Protonotaria citrea*; Hoover and Reetz 2006). We found PRAW territories occupied in 2022 that were not reoccupied in 2023, and one site, Tillinghast, had several territories not reoccupied and so had lower PRAW density the following year. At a Massachusetts, USA study site, Akresh et al. (2015) found that 72% of adult PRAW returned the following year, with 71% of these males reoccupying their previous territories. In contrast, we observed a lower overall return rate of 42% (19 of 45 banded individuals of both sexes; site specific details on returning birds provided in Table 2[†]) and a higher overall BHCO parasitism rate (34%), more than double the 16% reported by Akresh (2012). Our lower return rate may be from effects of parasitism but it may also be due to negative carry over effects from poor non-breeding habitat quality (Rockwell et al. 2012, Akresh et al. 2019, Cooper et al. 2024). Although sites with high AMWO RLS may seem suitable for PRAW and other songbirds like EATO, the high parasitism costs incurred by PRAW in Rhode Island, USA may reduce their reproductive success, but further research is needed on reproductive output per territory to determine population level declines.

Management under the umbrella species

Although PRAW density was greater at high AMWO RLS sites, brood parasitism slowed nestling growth and reduced fledglings' size, possibly lowering reproductive success by reducing recruits to the population. Although AMWO habitat management could benefit PRAW, the high prevalence of BHCO parasitism negates these potential advantages. Similarly, studies have shown management for a single designated umbrella species often fails to confer benefits to non-target species when nesting success, productivity, and fledging success are considered (Carlisle et al. 2018, 2024, Kramer et al. 2019, Zarri et al. 2024). A clearer understanding of which species benefit, or fail to benefit, from AMWO umbrella species management can help guide more targeted conservation efforts. The negative effects of parasitism we found at our sites is likely due to the surrounding landscape. Our study areas in southern New England lie within a highly urbanized and fragmented landscape (Novak and Wang 2004, Zhou and Wang 2007) an environment where BHCO can thrive (Petit and Petit 2000, Cavitt and Martin 2002, Barnagaud et al. 2015) and PRAW may not (Schlossberg et al. 2011). At the landscape scale, AMWO selected areas closer to agriculture (Masse et al. 2014), whereas distance to agriculture was not an important predictor at the home-range scale in Rhode Island (Slezak et al. 2024), a distinction that is especially relevant in the highly urbanized and fragmented landscape of southern New England. Reproductive outcomes for PRAW in our study areas may remain limited even where AMWO habitat quality is high because BHCO parasitism occurs throughout this fragmented landscape. Other areas of early successional forest managed for AMWO throughout the northeast may provide adequate habitat for PRAW with fewer risks of BHCO parasitism. As seen in Kirtland's Warbler (*Setophaga kirtlandii*) conservation, BHCO culling may provide short-term benefits for PRAW (Kelly and Decapita 1982). However, without concurrent habitat expansion, it is neither a sustainable nor cost-effective long-term solution (Rothstein and Peer 2005, Peer et al. 2020). Early successional forest at least 10 km from agricultural areas forces BHCO to extend their commuting flights and subsequently lowers parasitism rates by lowering fecundity (Chace et al. 2005). Effective habitat management for PRAW should create tracts of early successional forest far from BHCO feeding areas to reduce parasitism and mimic natural openings that can support multiple pairs of breeding birds.

Author Contributions:

M. Gray designed the study; M. Gray, L. Corcoran, and field crews collected the data; M. Gray and L. Corcoran supervised research; M. Gray analyzed the data; M. Gray wrote the paper; L. Corcoran and S. McWilliams edited the paper. S. McWilliams contributed materials, resources, and funding.

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