Space Use by Prairie Warblers in Regenerating Mixed-oak Forests of Central Pennsylvania

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Abstract - *Setophaga discolor* (Prairie Warbler) is a Nearctic–Neotropical migratory songbird that is experiencing long-term population declines. A potentially important driver behind these decreases is the loss of shrubland and early successional forest communities in the eastern United States. Central to conservation for species like the Prairie Warbler is an understanding of breeding habitat requirements at the scale of the home range. Despite the Prairie Warbler being identified as a species of continental conservation concern, few studies have explicitly quantified habitat conditions within its home ranges. We used radio telemetry to quantify Prairie Warbler use of space during the breeding season as well as associated vegetation data across 3 study sites in north-central Pennsylvania from May to June 2016. We radio-tracked 11 adult male Prairie Warblers. Using the telemetry locations, we estimated kernel densities and classified minimum convex polygons around kernel densities to define males' home ranges and core-use areas. The average home range (95% kernel) was 6.4 ha, and the average core-use area (50% kernel) was 0.73 ha. Prairie Warbler core-use areas contained more shrubs and lower tree count than peripheral portions of home ranges. To this end, management activities that promote a dense shrub layer across early successional communities should benefit Prairie Warblers. Results from this study serve as baseline data that can be used to help direct future studies at the home-range scale of Prairie Warbler breeding-season ecology.

Introduction

Throughout much of the eastern United States, early successional forest and shrubland communities have steadily decreased over the past several decades (King and Schlossberg 2014, Reemts and Cimprich 2014). These losses have been driven by ecological succession coupled with the suppression of natural disturbance regimes like activity of *Castor canadensis* Kuhl (American Beaver) and fires (Askins 2001). The waning of early successional vegetation communities has, in turn, negatively impacted many wildlife populations that require these disturbance-generated habitats (King and Schlossberg 2014, Shake et al. 2012). Indeed, at least 65 species of wildlife that depend on early successional forest and shrublands in the eastern US are considered species of greatest conservation need (Gilbart 2012). These at-risk species span a wide breadth of taxa including reptiles (e.g., *Thamnophis brachystoma* Cope [Shorthead Garter Snake]; Mibroda et al. 2017), mammals (e.g., *Sylvilagus transitionalis* Bangs [New England Cottontail]; Fenderson et al. 2011), game birds (e.g., *Scolopax minor* Gmelin [American

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Woodcock]; Kelley et al. 2008), and a diverse community of songbirds (DeGraaf and Yamasaki 2003, Gilbart 2012). In fact, North American Breeding Bird Survey results suggest that 53% of species belonging to the successional/scrub-breeding guild in eastern North America exhibited population decreases between 1966 and 2015 (Sauer et al. 2017).

Setophaga discolor Vieillot (Prairie Warbler) is a migratory songbird whose abundance on the breeding grounds is strongly linked with the availability of early successional forest and shrubland communities (Nolan 1978, Wilson et al. 2012). This shrubland specialist breeds in eastern North America (Wilson et al. 2012), and has experienced a population drop of 1.85%, annually, across its breeding range from 1966 to 2015 (Sauer et al. 2017). The Prairie Warbler is therefore considered a species of continental conservation concern across much of its breeding range (Rosenberg et al. 2016). Recently, studies focusing on the breeding season ecology and conservation of the Prairie Warbler have improved understanding of this species' broad habitat needs (Akresh et al. 2017b, Margenau et al. 2018, Roach et al. 2018), but limited information regarding the species' within-territory habitat conditions exists to guide conservation of this species' breeding habitat (but see Roberts and King 2017, Shake et al. 2012). This information is especially lacking for Pennsylvania where no studies to date have focused on the breeding and nesting ecology of the Prairie Warbler. Lastly, recent advances in radio technology have allowed even small birds like the Prairie Warbler to be studied with telemetry (Bridge et al. 2011), allowing researchers to examine home ranges with a level of detail previously impossible.

Home-range and core-use area delineations can be used to analyze space use and determine habitat preferences. Home range is the area an animal uses for normal activities including, but not limited to, territory defense (Anich et al. 2009). Core-use area is the portion of the home range with the highest density of telemetry locations (Akresh et al. 2017a, Frantz et al. 2016). The purpose of our study was to examine attributes of Prairie Warbler home ranges and core-use areas in a heavily forested landscape recovering from a wildfire. Herein, we present findings regarding space use and associated vegetation structure of the Prairie Warbler, and discuss our results in the context of the species breeding ecology in central Pennsylvania. Our study provides insight into regional Prairie Warbler breeding-season ecology, a critical component of the full annual cycle (Akresh et al. 2019). Moreover, our results can be used to help guide management actions and future research efforts that seek to inform how the species may respond to increasing use of prescribed fire.

Field-site Description

We conducted this study in the southern portion of Sproul State Forest in central Pennsylvania (41°13' 26.4"N, 77° 50' 45.6"W). Sproul State Forest is ~112,000 ha and includes parts of both Centre and Clinton counties. This region of the Commonwealth is characterized as a rolling plateau north of the Allegheny Front (PA DCNR 2018). Dominant forest types in this region are dry oak and northern hardwoods, and the average forest stand age is 80–110 years old (Bellush et al. 2016). The overstory in Sproul State Forest was dominated by *Quercus* spp. (oaks) and *Carya* spp. (hickories) (Fiss 2018, McCaskill et al. 2013). The understory within our study area was dominated by *Kalmia latifolia* L. (Mountain Laurel), *Hamamelis virginiana* L. (Witch-hazel), *Vaccinium* spp. (blueberries), *Gaylussacia baccata* (Wangenh.) K. Koch (Black Huckleberry), *Comptonia peregrina* (L.) J.M. Coult. (Sweet Fern), and other woody species (Siepielski et al. 2001). We studied Prairie Warblers across 3 sites located at 525–620 m elevation within the footprint of a stand-replacing wildfire that occurred in 1990 (Fig. 1). Although all Prairie Warblers were radio-tagged within early-successional habitats, it is important to remember that these breeding habitats were within the broader context of a heavily forested landscape wherein most territories were within a few hundred meters of a mature forest edge.

Methods

Capture and handling

We used a standard 30-mm, 2.5 m x 6 m, nylon mist net along with Prairie Warbler conspecific playback to capture territorial male Prairie Warblers in May 2016. We banded each captured individual with a USGS metal leg band and 1–2 plastic color bands. Additionally, we attached a very high frequency (VHF) radio-transmitter BD-2N (0.43 g) or LB-2X (0.31 g), (Blackburn Transmitters Inc., Nacogdoches, TX) to males that were larger than 7.5 g. We attached radio transmitters using a figure-eight leg-loop harness method (Rappole and Tipton 1991). Harnesses were

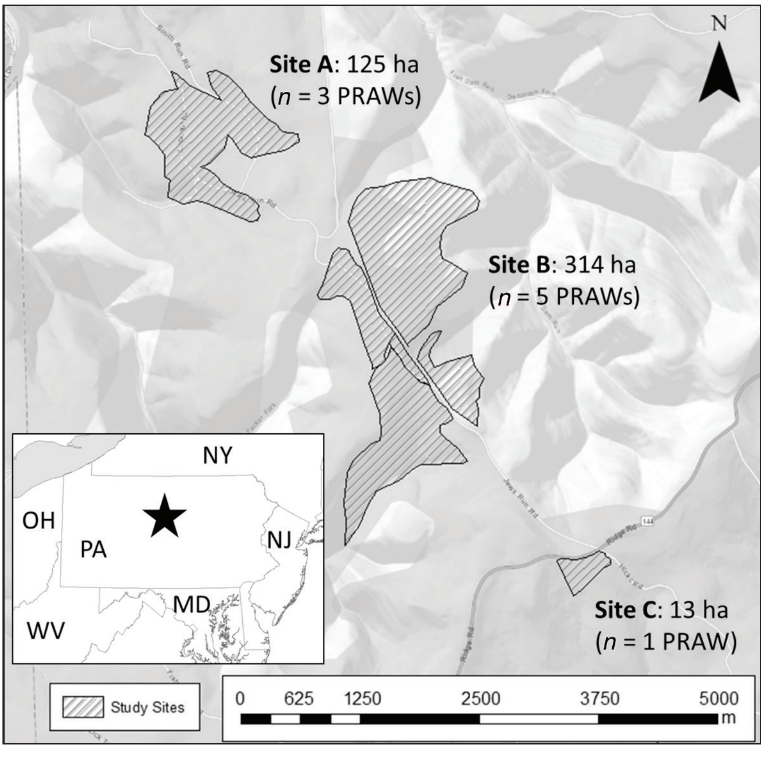

Figure 1. Location and size of, as well as number of Prairie Warblers (PRAW) tracked at, the 3 study sites (represented by the diagonally striped areas located in Sproul State Forest, PA, shown as a star on the inset state-wide map.

constructed from <1 mm elastic thread. Transmitters with harnesses weighed <5% of the body mass of each Prairie Warbler to which they were attached (Fair et al. 2010). Total handling time for each bird was ~5 min, and we released birds at the location of capture.

Radio-tracking

We monitored each radio-tagged Prairie Warbler daily using the homing method (White and Garrott 1990). We tracked individuals until their location was visually confirmed. Locations of individuals were obtained while remaining distant enough so that each bird's behavior was not perceptibly affected (Vitz and Rodewald 2010). All radio-tracking was conducted between 5:30 and 16:00 EST. To reduce time-of-day bias on individual radio-marked birds, we varied the order in which individuals were monitored daily (Shields 1977). We allowed at least 5 min to pass between successive relocations to ensure telemetry locations were biologically independent (Barg et al. 2005, Lair 1987). We recorded the location of each radio-marked Prairie Warbler using a hand-held GPS unit (Garmin eTrex20).

Delineation and analysis of core-use areas and home ranges

We defined home range as area used by the Prairie Warbler during all activities, excluding 5% of telemetry locations. Core-use area was defined as the area within the home range that the Prairie Warbler used the most, and included only 50% of the telemetry locations. To assess the size of home ranges and core-use areas, we incorporated all telemetry locations into a geographic information system (ArcGIS v10.3; ESRI, Redlands, CA). We used the "kernel density" tool in ArcGIS to estimate kernel density, which fitted a smooth curve over each telemetry location (ESRI 2011). Bandwidth was automatically determined by ArcGIS, using the number of telemetry locations and spatial configuration (ESRI 2011). We then extracted the density values for each telemetry location and made a minimum convex polygon (MCP) around the lowest 50% of locations (a polygon containing 50% of telemetry locations with the highest probability), and created another MCP around the lowest 95% of locations (a polygon containing 95% of telemetry locations with the highest probability). We considered the MCP of the 50% of locations to be the core-use area and the MCP around the 95% telemetry locations to be the home range (Fig. 2; Venables and Ripley 2002). We excluded males with fewer than 9 days of location data from our analyses (n = 2). The minimum number of locations for a single bird was 43 radio locations, which surpasses the recommended minimum sample size when using kernel-based methods (Seaman et al. 1999). We used ArcGIS to calculate areas of each home range and core-use area. We used Pearson's correlation coefficient to test for correlation between (1) number of telemetry locations and size of core-use area and home range and (2) number of days an individual was tracked and size of core-use area and home range.

Vegetation sampling

We used the "create random points" tool in ArcGIS to plot locations for vegetation sampling within each core-use area and home range. We generated

10–15 random points within each core-use area (depending on size) and 15 random points within each home range but outside of the core-use area. All random points were spaced at least 10 m apart. At each point, we sampled vegetation within nested-design sampling plots. Within a 1-m^2 plot at point center, we visually estimated percent cover of (i) short woody vegetation (saplings and shrubs under 0.5 m tall); (ii) ferns; (iii) herbaceous plants (grasses, forbs, etc.); (iv) non-vegetation (bare ground, leaf litter, etc.); and (v) *Rubus* spp. (blackberry). Within a 5-m radius (78.5-m^2) plot around point center, we counted and identified all shrubs and saplings >0.5 m tall. Lastly, at each vegetation sampling point, we measured tree count with a 10x prism.

Vegetation analysis

We used generalized linear mixed models to compare vegetation between Prairie Warbler core-use areas and the remainder of the home range (peripheral home range). Specifically, we assessed the ability of core-use area vs. peripheral home-range locations to explain variation among 11 vegetation variables (Table 1). We fit models separately for each vegetation variable. Variables based on counts (i.e., saplings, shrubs, and trees) were fit using a Poisson distribution, and those based on percent cover estimates were logit transformed and then fit using a normal distribution. All models included a random effect for bird ID to control for variation among individual territories. We ran models using the 'rjags' package (Plummer 2018) in Program R v.3.2.2 (R Core Team 2015). We considered vegetation differences to be significant if beta coefficients and associated 95% credible intervals did

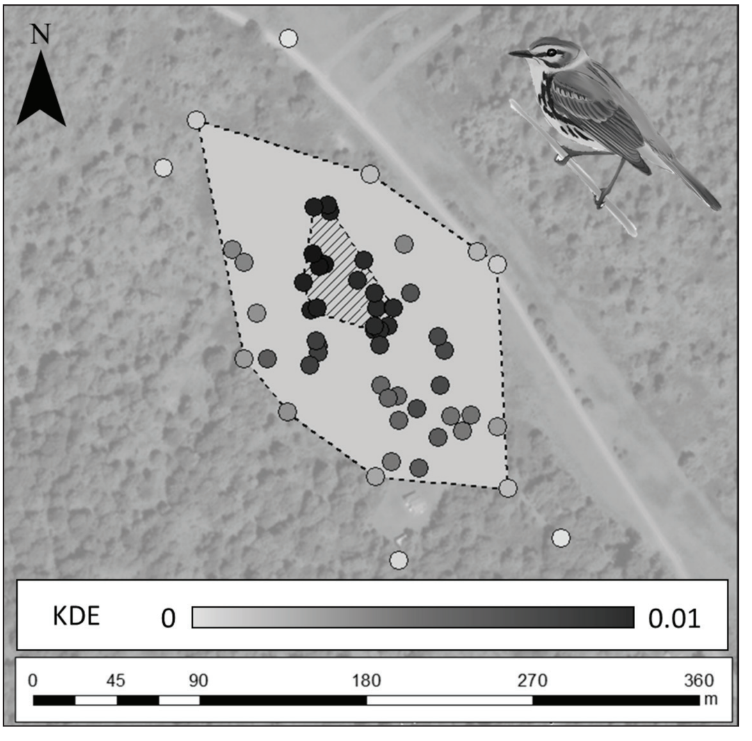

Figure 2. Schematic diagram that illustrates telemetry locations (circles) within a Prairie Warbler core-use area (diagonally striped area) and peripheral portion of a home range (solid area), in Sproul State Forest, PA, during June 2016. Lighter colored circles have a lower kernel density estimation (KDE) and darker colored circles have a higher KDE.

not overlap zero (Kéry 2010). We ensured all models reached convergence based on *R*-hat values < 1.1 (Gelman and Rubin 1992) and assessed model fit using Bayesian *P*-values (Gelman et al. 1996).

Results

Delineation of core-use area and home range

We captured and processed 19 Prairie Warblers. Eight of them were too small (i.e., <7.5 g) to be fitted with a radio transmitter and were thus not included in our study. We deployed radio transmitters on the remaining 11 Prairie Warblers across our 3 study sites. We visually confirmed that 2 transmitters failed shortly after deployment (<9 days), and the remaining 9 individuals were tracked for a minimum of 9 days after transmitter attachment. Three of these Prairie Warblers were radio tracked in Site A, which spanned 125 ha, 5 Prairie Warblers were radio tracked in Site B, which was 314 ha in size, and 1 Prairie Warbler was radio tracked in Site C, which had an area of 13 ha (Fig. 1). These 9 birds were tracked from 17 May to 28 June 2016. Tracking included at least some portion of the post-fledging period, as a male Prairie Warbler was observed feeding a fledgling on 16 June 2016 . The average tracking span for these 9 birds was 23 days (SD = 9.71, min–max = 9–33 days). An average of 4 telemetry locations (SD = 1.6, min–max = 1–9 locations) were taken per bird each day they were tracked. We recorded a total of 661 telemetry locations, with an average of 73 (SD = 24.43) radio-locations per bird. The mean home-range size (95% Kernel) was 6.4 ha (SE = 2.58, min–max = 0.97–20.87 ha)

Table 1. Description of 11 vegetation variables sampled in the core-use areas and peripheral home ranges of 9 radio-tagged Prairie Warblers in managed forests of north-central Pennsylvania during May–June 2016.

Variable	Description
1-m^2 plot	
Short woody	Estimated percentage of short woody vegetation (saplings and shrubs <0.5 m tall) ground cover
Fern	Estimated percentage of fern ground cover
Herbaceous	Estimated percentage of herbaceous (forbs and grasses) plant ground cover
Bare	Estimated percentage of non-vegetated (bare ground, leaf litter, etc.) ground cover
Rubus	Estimated percentage of Blackberry ground cover
5-m radius (78.5-m^2) plot	
Sapling count	Number of saplings >0.5 m tall counted
Sapling richness	Number of sapling species >0.5 m tall
Shrub count	Total number of shrubs >0.5 m tall
Shrub richness	Number of shrub species 0.5 m tall
10x prism	
Tree count	Number of in-trees
Tree richness	Number of in-tree species

and the mean core-use area size (50% Kernel) was 0.73 ha (SE = 0.24, min–max = 0.19–2.54 ha). Total number of telemetry locations per bird was not significantly correlated with size of core-use area (ρ = 0.23, *P* = 0.55) or home range (ρ = 0.5, *P* = 0.18). Total number of days tracked per bird was not significantly correlated with size of core-use area (ρ = 0.49, *P* = 0.18), but was significantly correlated with size of home range (ρ = 0.69, *P* = 0.038).

Vegetation differences between core-use area and home range

We sampled vegetation from 9 to 15 July 2016. We evaluated a total of 10 vegetation models. Shrub count (density) was significantly different between core-use areas and peripheral home ranges (*β* = 0.41, 95% CI: 0.02–0.80; Table 2). Core-use areas contained more shrubs (93.2 shrubs per 5-m radius [78.5-m^2] plot, SE = 7.6) than peripheral home ranges (74.6 shrubs per 5-m radius [78.5-m^2] plot, SE = 6.8). We also found that core-use areas trended towards lower tree count (1.01 m^2/ha, SE = 0.15) compared to peripheral home ranges (1.49 m^2/ha, SE = 0.22; *β* = -0.41, min–max = -0.84–0.02), though not quite to a statistically significant degree. No other vegetation models indicated a significant difference between core-use areas and peripheral home ranges. The most common shrubs over 0.5 m in height were Blueberries, followed by Mountain Laurel in both the core-use areas and peripheral portions of home ranges. Additionally, *Acer rubrum* L. (Red Maple) and *Sassafras albidum* (Nutt.) Nees (Sassafras) were the most typical saplings over 0.5 m in height in both the core-use areas and peripheral portions of home ranges. However, in the core-use area, Red Maple was more common than Sassafras, while in the peripheral portions of the home range, Red Maple was less typical than Sassafras. Lastly, in both core-use areas and peripheral home ranges, the most common ground cover in each 1-m^2 plot on average were, in order: (1) non-vegetated, (2) ferns (typically *Dennstaedtia punctilobula* [Michx.] T. Moore [Hay-scented Fern]), and (3) herbaceous.

Table 2. List of 11 vegetation variables used in our analysis and their associated beta coefficients (*β*) and 95% credible intervals.

Variable	*β*	95% credible interval
Short woody	0.08	-0.27–0.42
Fern	0.21	-0.25–0.65
Herbaceous	0.13	-0.27–0.55
Bare	-0.15	-0.54–0.24
Rubus	0.10	-0.29–0.48
Sapling count	-0.02	-0.26–0.23
Sapling richness	0.11	-0.09–0.31
Shrub count	0.41	0.02–0.80
Shrub richness	0.15	-0.01–0.31
Tree count	-0.41	-0.84–0.02
Tree richness	-0.11	-0.45–0.20

Discussion

This study is the first to use radio-telemetry to delineate core-use areas and home ranges of the Prairie Warbler. Our results are limited by a small sample size of radio-tracked birds (n = 9) and the use of sites created by a single disturbance event. Future studies that explore Prairie Warbler space use and associated vegetation should monitor more individuals and include a variety of shrubland types (i.e., timber harvests, prescribed fire, old fields). Despite our limitations, this study produced results comparable to those of other studies.

Our analyses revealed a notable size difference between core-use areas and home ranges whereby the latter were larger by a factor of 8. Such differences are in part due to the analytical methods we used to find home-range and core-use area sizes, as home ranges used 95% of locations and core-use areas used 50% of locations. Other studies have compared songbird home ranges to breeding territories, in which the home ranges are derived from all songbird activities and breeding territories are created using only locations where the bird sang to defend its territory (Anich et al. 2009, Frantz et al. 2016, Leonard et al. 2008). These studies have demonstrated that songbird home ranges can be 1.4–8 times larger than defended breeding territories (Anich et al. 2009, Frantz et al. 2016, Leonard et al. 2008). For example, a previous study of *Vermivora chrysoptera* L. (Golden-winged Warbler) within our study area found average telemetry use area was 6.3 ± 1.7 ha and defended breeding territory was 0.50 ± 0.08 ha (Frantz et al. 2016). These values are similar to those we found for average size of Prairie Warbler home ranges and core-use areas, suggesting that these 2 declining shrubland-dependent species have similar space requirements.

Previous researchers have characterized the Prairie Warbler as an area-sensitive species (Roberts and King 2017, Shake et al. 2012). The average home-range size of male Prairie Warblers monitored in our study (6.4 ha) is consistent with findings from a previous study that concluded 5.5 ha was the optimum minimum area of shrubland for the species, whereby optimum was defined as >0.90 probability of occupancy for an individual patch (Shake et al. 2012). Our average home-range size is larger than some other average territory sizes reported elsewhere such as 1.56 ha (Nolan 1978), 0.36 ha (Morimoto and Wasserman 1991a), and 0.97 ha (Akresh et al. 2015). It is possible that including post-fledging movements in our analysis inflated home-range sizes. Additionally, peripheral areas of the home ranges may have also been defended as Prairie Warbler were singing in them, which could have also increased home-range sizes. Indeed, 7 of the 9 Prairie Warbler home ranges did have overlap with adjacent home ranges. However, the size of our average core-use area (0.73 ha) is similar to the 1.1-ha estimate thought to be the minimum amount of early successional habitat required by Prairie Warblers to establish a breeding territory (Roberts and King 2017, Shake et al. 2012). These results highlight the importance of considering spatial scales and associated habitat features outside territories defended by male Prairie Warblers.

Our study is also the first to quantify habitat features within entire, radio-tracked home ranges of the Prairie Warbler. Our results support the conclusions of previous studies that reported positive associations between Prairie Warbler and shrub cover at other spatial scales (Akresh et al. 2015, Askins et al. 2012, Schlossberg et al. 2010). Additionally, the species is considered a shrubland indicator (Gifford et al. 2010) and shrubland specialist (Askins et al. 2007). With these designations in mind, it is not surprising that we found shrub densities (predominantly Mountain Laurel and Blueberries) to be greater within core-use areas than within peripheral portions of home ranges. In further support of the species' strong association with shrub cover, almost all Prairie Warbler nests found during this study were constructed in shrubs, similar to previous studies (Morimoto and Wasserman 1991b). Five nests were placed in Mountain Laurel and 1 was placed in Blackberry stems. Akresh (2012) found that Prairie Warbler nested in Blackberry stems as well. Prairie Warbler nests have also been documented in conifers (Nolan et al. 2014), *Ulmus americana* L. (American Elm; Nolan 1978), and *Spiraea* spp. (meadowsweet) shrubs and oak shrubs or saplings (Akresh et al. 2017b). Akresh (2012) noted that leaf-out dates or frost tolerance of different plant species may also affect nest substrate selection, as Prairie Warblers predominately place their nests in leafed-out vegetation. Therefore, it is suggested that fast-growing saplings, or early-leafing shrubs, such as Mountain Laurel, be retained in efforts to manage for warbler habitat (Akresh 2012). Similarly, Nolan (1978) noted that the Prairie Warbler prefers to nest in trees and shrubs with many leaves distributed throughout the plant.

Aside from shrub density and area differences, vegetation structure in peripheral home-ranges was not unlike core-use areas in our study. While home ranges tended to have slightly higher tree counts, they remained completely within the post-fire shrubland communities characterized by our study sites. This result aligns with past studies indicating that territorial Prairie Warblers avoided mature forest edges (Rodewald and Vitz 2005), and placed nests more than 20 m away from this habitat feature (Woodward et al. 2001). Nests placed at this distance from forest edges were found to be on average more successful (Slay 2010). Akresh (2012) found that Prairie Warblers nested near roads or fire breaks, but still in dense vegetation. Similarly, dependent fledgling Prairie Warblers are understood to prefer dense thickets of vegetation and have also been found to remain within adult male's nesting territories (Nolan 1978). As such, home ranges similar in vegetation structure (i.e., shrub cover) to core breeding territories likely provide habitat for dispersing young. Nonetheless, post-fledging habitat requirements are an important element of Prairie Warbler breeding-season ecology that remains poorly understood. As such, future studies that use telemetry to examine habitat selection and space use of fledging Prairie Warblers would further inform conservation efforts for this species.

Our findings combined with those of others suggest that land managers seeking to conserve or create Prairie Warbler breeding habitat should consider shrub cover at scales beyond the defended core territory. The shrubland in our study sites was created by wildfire, which adds to a growing body of literature suggesting that Prairie Warblers can respond positively to fire disturbances that regenerate with a strong shrub component (Akresh et al. 2015, Comer et al. 2011, Wilson et al. 1995). In fact, fire rotations as short as 2–3 y were found to maximize Prairie Warbler abundance in pine–hardwood communities of Mississippi and Arkansas (Burger et al. 1998, Wilson et al. 1995). Similarly, Prairie Warblers in Missouri were detected in burned glades, but never in unburned glades or forests (Comer et al. 2011). Collectively, the literature demonstrates that breeding Prairie Warblers nest in a variety of shrubby natural and managed habitats without closed canopies, including abandoned farmland with a shrub layer and Christmas tree farms (Nolan et al. 2014); burned/mowed *Quercus ilicifolia* Wangenh (Bear Oak), herbicide-treated *Pinus rigida* Mill. (Pitch Pine), and power line corridors (Akresh et al. 2015, King et al. 2011); and clearcuts (Slay 2010). Albeit, time since treatment is worth consideration for certain management types, as Prairie Warblers may not occupy a treated habitat until shrubs have regenerated (Akresh 2012). In fact, Prairie Warbler abundance tends to peak 4–8 years after major disturbance, and 4–9 years post harvest (Perry and Thill 2013). To create stable Prairie Warbler habitat, more active management, such as rotational mowing and ongoing selective tree and invasive species removal has also proven effective (Slay 2010). To this end, land managers wishing to benefit this species of conservation concern appear to have a variety of options at their disposal. Our results, combined with those of several past studies, indicate that Prairie Warblers will colonize fire-generated early successional communities as long as a shrub component regenerates.

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