



Demographic response of a shrubland bird to habitat creation, succession, and disturbance in a dynamic landscape



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ABSTRACT

Shrubland birds have experienced widespread declines in the eastern United States. Habitat for shrubland birds is typically dynamic, in which available habitat changes temporally and spatially in response to disturbance and succession. Despite widespread concerns among conservationists about shrubland birds, much is still poorly understood regarding fundamental demographic processes associated with the persistence of species in dynamic landscapes, such as the age of colonists, their success upon establishment, the fate of birds displaced by disturbance, and the effect of displaced birds on neighboring territories. To address these knowledge gaps, we studied prairie warblers (*Setophaga discolor*) between 2008 and 2012 in a pitch pine-scrub oak (*Pinus rigida*–*Quercus ilicifolia*) barren consisting of newly created, maturing, and disturbed habitat patches. We found that newly created habitat patches were colonized primarily by younger, second-year males, whereas slightly older shrubland habitat was occupied by site-faithful older birds. Second-year males arrived later on the breeding grounds and had slightly lower pairing success compared to older males; however, they had similar reproductive output as older males. Based on mark-resight analyses, we calculated that 72% of adult males and 14% of banded nestlings returned to the study site in a following year. When territories were subject to high-intensity mowing, fire, or selective herbicide during the non-breeding season, only 14% of the males that returned to the study site stayed on their territories the following year. These returning males that acquired a territory within the study area had similar reproductive success to other birds in the study area and did not negatively affect the pairing or reproductive success of birds occupying adjacent areas. Disturbed territories made up a relatively small portion of the suitable habitat in the study area and disturbance affected a low number of territorial males in any given year. Overall, we found that the short-term effects of shrubland management and habitat disturbance on birds are minimal and subsequently allow young birds to colonize and breed. Moreover, the long-term effects of management are beneficial by maintaining ephemeral shrubland habitat for immigrating and site-faithful birds.

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1. Introduction

Disturbance-dependent ecosystems are characterized by spatial and temporal shifts in the age and distribution of habitat patches within the landscape over time. These ecosystems have been considered as having “patch dynamics” (White and Pickett, 1985), or as a “shifting mosaic” equilibrium (Watt, 1947). Whichever conceptual framework one adopts for a dynamic landscape, organisms that depend on early-successional, dynamic habitats are influenced by spatial and temporal shifts in habitat characteristics (Donner

et al., 2010; Fuhlendorf and Engle, 2004; Lent and Capen, 1995). For example, shrubland birds colonize recently disturbed habitat and change in abundance as habitat suitability changes with succession, ultimately becoming locally extirpated as the habitat reverts to older forest (DeGraaf and Yamasaki, 2003; Schlossberg and King, 2009).

Despite the attention that has been directed at understanding the habitat requirements of early-successional species (e.g. Greenberg et al., 2011; Thompson and DeGraaf, 2001), even the most basic demographic processes that influence populations of shrubland species in dynamic habitats remain poorly understood. For example, the sequence in which different bird species colonize shrubland habitats has been understood for decades (Johnston and Odum, 1956); however, whether birds colonizing new habitat

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originate from within the local area or from populations within a larger landscape is largely unknown (Dale et al., 2006; Lehen and Rodewald, 2009). Furthermore, the success of management efforts should include consideration of reproductive success (Sallabanks et al., 2000), but the rate at which newly created habitats become productive after disturbance is not understood. Schlossberg (2009) proposed that newly created habitat would be colonized by young males returning for their first breeding season (“second year” or “SY” males), as SY birds exhibit low natal philopatry (Greenwood and Harvey, 1982; Lehen and Rodewald, 2009) and would be more inclined to disperse and find newly created habitat. Older males (“after second year” or “ASY” males) may exhibit higher site fidelity in existing habitat (Schlossberg, 2009; Donner et al., 2010) and be less likely to colonize new habitat. Given younger birds may be more abundant in newly created habitats, these habitats could have lower productivity because young birds can experience reduced reproductive success (Nol and Smith, 1987; Nolan, 1978). Newly created shrubland habitats also tend to have poorly developed vegetation structure (Chandler et al., 2009; Smetzer et al., 2014), which could negatively affect nest concealment and reproductive success.

In addition, it is important to consider the implications of shrubland habitat management or other natural disturbances on individuals occupying areas prior to disturbance. Birds may disperse to adjacent habitat the breeding season after disturbance (Brotons et al., 2005; Darveau et al., 1995; Schmiegelow et al., 1997), have delayed dispersal, or remain in the habitat after disturbance (Chandler, 2006; Weins and Rotenberry, 1985). Only a few studies have tracked individually marked birds following a disturbance. Betts et al. (2006) observed dispersal of two color-banded mature forest birds that each dispersed over 1 km following timber harvest. Rousseau et al. (2012) observed that 50% of 14 color-banded male white-throated sparrows (*Zonotrichia albicollis*) dispersed over 100 m after most of their forested territories were clear-cut. If individuals disperse after disturbance, this can affect birds in adjacent areas. For example, Hagan et al. (1996) found an increase in forest birds in adjacent, non-disturbed habitat following the disturbance of forest sites by logging, which resulted in decreased pairing success in adjacent habitat, perhaps as a result of crowding. Few studies have examined if this also occurs with shrubland birds, despite disturbance such as mowing, fire, and herbicide treatments being used regularly as part of habitat maintenance for these species.

Understanding the demographic processes underlying patterns of colonization and persistence within dynamic landscapes is important because early-successional habitats and associated species are declining dramatically in the eastern United States and elsewhere (Litvaitis, 1993; Preiss et al., 1997; Trani et al., 2001), representing a critical conservation challenge (Oehler, 2003). To address these knowledge gaps, we studied prairie warblers (*Setophaga discolor*), a Neotropical migratory shrubland bird species, in a managed, inland pitch pine-scrub oak (*Pinus rigida*–*Quercus ilicifolia*) barren consisting of newly created, maturing, and disturbed shrubland habitats. Specifically, we estimated prairie warbler demographic parameters (abundance, age structure, arrival dates, reproductive output, site fidelity, and territory fidelity) as a function of habitat disturbance and succession to determine how shrubland birds respond to the changing habitat conditions that comprised this dynamic landscape. Since the purpose of shrubland habitat management is to support populations of shrubland-dependent species, including birds, detailed knowledge of how these populations are affected by the habitat disturbance and succession associated with management practices is fundamental to understanding the degree to which management activities achieve their intended effects.

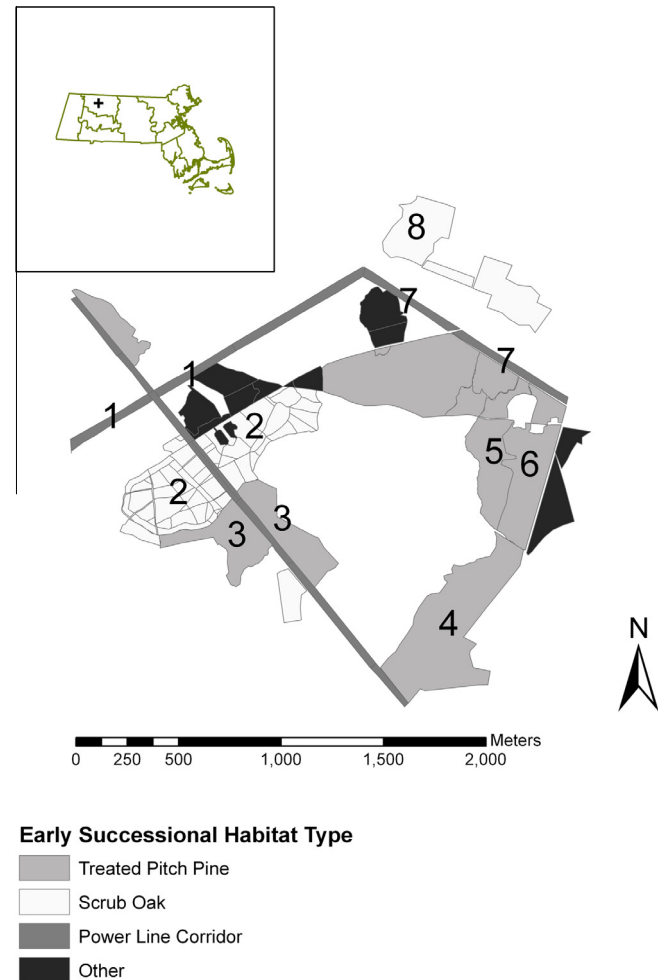


Fig. 1. Map of the MPWMA, located in Montague, MA (inset map of Massachusetts, USA). Numbers indicate plots used in the study. Plot 2 consisted of many smaller treatment patches within the plot. Unmarked, white sections in the study site (i.e., the center area) consist of mostly mature pitch pine and deciduous closed canopy forest. Early-successional habitat types classified as “other” include sand pits or areas with some shrubby understory but with more (>50%) canopy cover.

2. Methods

2.1. Study site

The study took place from 2008 to 2012 on the Montague Plains Wildlife Management Area (MPWMA), a 607 ha, actively managed pitch pine-scrub oak barren located in Western Massachusetts, U.S.A. (N42°34', W72°31'). The MPWMA, like most pitch pine-scrub oak barrens, encompasses plant communities that are highly flammable and naturally adapted to frequent fires (Motzkin et al., 1999). In 2000, the Massachusetts Division of Fisheries and Wildlife started a program of habitat restoration and fuels reduction to reduce wildfire risk and promote biodiversity. This was accomplished by thinning pitch pine stands to 25% residual canopy cover and treating scrub-oak stands with mowing and prescribed fire (King et al., 2011). We sampled birds in scrub oak barrens (2 plots; 28.7 and 6 ha), treated pitch pine (4 plots; 15.1, 22.5, 7.8 and 10.8 ha), and power line corridors (2 plots; 4.2, 5.7 ha), which comprised most of the early-successional area and the principal habitats occupied by prairie warblers within this pitch pine-scrub oak barren (King et al., 2011; Fig. 1). Plots were similar in terms of elevation, topography, and overall vegetation community. Scrub oak

barrens consisted of dense stands of scrub oaks generally <3 m tall with scattered pitch pine and tree oaks, as well as cherry (*Prunus* spp.) saplings, red maple (*Acer rubrum*) saplings, and low blueberry (*Vaccinium angustifolium*). Treated pitch pine consisted of a residual canopy of mature pitch pines and scattered tree oaks, and an understory of oak, pitch pine, red maple, grey birch (*Betula populifolia*), cherry, and other saplings, as well as blueberry, ferns, and sedges. The power line corridor plots were dominated by *Spiraea* spp., pitch pine saplings, and other low shrubs and grasses.

We delineated our plots to help determine the effects of management treatments on birds, however, there were instances where management treatments were conducted in patches smaller than individual plots. The smaller scrub oak plot had not been treated or burned since 1986. The larger of the two scrub oak plots was treated before and throughout the study period, but in patches so small that bird territories often incorporated several different age classes. Thus, it was not always possible to assign a time since treatment to a territory in scrub oak habitat with any confidence, and analyses incorporating time since treatment were confined to plots within treated pitch pine. The treated pitch pine plots were each thinned once before the study period; one plot was thinned in 2004, one in 2006, and two in 2007. Prairie warblers do not occupy untreated pitch pine forest (King et al., 2011), and therefore it was not possible to examine pre- versus post-treatment effects on displaced birds after the initial harvest of pitch pine. However, during the 2011–2012 non-breeding season there were disturbances by high-intensity wildfire and mowing in small areas of two treated pitch pine plots (2.0 ha of plot 3 and 1.7 ha of plot 5, respectively). By 2011 these areas had already been colonized by prairie warblers, and as a result, in 2012 it was possible to examine the effects of displacement on prairie warblers after these disturbances. Furthermore, we examined the effects of displacement on birds in areas of mowing and burning in scrub oak that occurred between 2008 and 2012 (in multiple patches in plot 2, ranging from 0.5 to 4.5 ha), and in areas of herbicide treatments throughout both

power line corridors (before the 2011 and 2012 breeding seasons; Fig. 2).

2.2. Habitat sampling and analyses

We used point-intercept vegetation surveys within mapped male prairie warbler territories to quantify the vertical structure and composition of the vegetation (King and DeGraaf, 2000). To survey vegetation throughout each territory, we took measurements at 20 survey points within each territory using a novel method of stratified random sampling. We first selected 20 equally spaced locations along a transect spanning the length of a male territory. From these locations, we selected a random direction, right or left, from the transect and paced out a random distance between 0 and the width of a given territory, to get to our final survey points. We measured overstory vegetation and height, understory substrate and height, and vegetation structure at these survey points. At each point location, we vertically placed a 3-m density pole, and vegetation structure was measured by recording the number of times vegetation contacted the pole at 0.5-m intervals. Overstory vegetation and its height were defined as the tallest vegetation species over 3-m and its corresponding height at the point, and understory substrate and height were the tallest vegetation species less than 3-m and its corresponding height at the point (the highest contact on the 3-m pole).

Point-level vegetation survey data were combined for each territory. Overstory height, understory height, and vegetation structure were computed by calculating the per-territory average. We tallied the number of times overstory vegetation was recorded at the 20 surveyed points on each territory to estimate canopy cover. We grouped vegetation substrate into six categories: ground (includes bare ground, leaf litter, dirt roads, moss, and brush piles), low woody 'berry' vegetation (blueberry and dewberry), forbs and ferns, graminoids (grasses and sedges), conifers, and woody-stemmed, deciduous vegetation. As with canopy cover, we



Fig. 2. Pictures of habitat and disturbance in the study site. (a) Scrub oak, (b) scrub oak after mowing disturbance, (c) treated pitch pine after wildfire and (d) power line corridor (plot 1) after herbicide application.

computed the proportion of the 20 points that each vegetation category occurred on each territory.

Statistical analyses were carried out using the program R, version 3.01, and the lme4 package (Bates et al., 2013; R Development Core Team, 2013). Unless otherwise noted, we conducted analyses using generalized linear mixed models with plot as a random effect to account for the temporal interdependence of sampling the same plots over multiple years, consistent with a repeated-measures design. Moreover, when individual or territory was the sampling unit (for all analyses except when examining bird density and male age structure with years since treatment), the random effect of plot accounted for the spatial interdependence of individuals or territories within plots. When noted, we also examined models with an additional random effect of individual to account for the temporal interdependence of individual birds or territories sampled over multiple years. We could not determine if unbanded birds were sampled over multiple years; therefore, we subset the data to only include banded birds when conducting analyses with an additional random effect of individual.

For vegetation data in treated pitch pine, we ran separate models with each vegetation measure as the response variable, and time since treatment as the predictor variable. We fit the overstory and understory height data to normal distributions in separate general linear mixed models. We examined the effect of time since treatment on vegetation structure separately for the following height intervals: 0–0.5 m, 0.5–1 m, 1–1.5 m, 1.5–2 m, and 2–3 m. For each height interval, we rounded the per-territory averages of vegetation structure (the number of vegetation hits) to whole numbers, and fit the data to Poisson distributions. For canopy cover and vegetation composition, we fit the proportional data to binomial distributions (Crawley, 2007). For the entire set of vegetation analyses, to reduce experiment-wise error rates, we adjusted *P*-values by using the Bonferroni–Holm method (Holm, 1979). Although some males were surveyed for vegetation in their territories during multiple years (20% of the males), each territory was treated as a separate sample in the analysis because the vegetation changed rapidly over time, males moved or shifted territories, and different point locations within an area were surveyed in different years. We found similar results for analyses where we subset the data for banded birds and included a random effect of individual male, but given the similar results we did not present these additional analyses.

2.3. Bird sampling and analyses

To facilitate many aspects of the study, we captured birds using targeted mist-netting with prairie warbler songs and a decoy. All captured birds were banded with a United States Geological Survey aluminum band and a unique color combination of 2–3 plastic color bands. Birds were classified upon capture by age class and sex using plumage, breeding condition, feather wear, and molt limits (Pyle, 1997).

We determined male prairie warbler territoriality, pairing success, and nesting success by visiting each territory for 30–60 min between 5:30 and 14:00 approximately once per week in 2008 and every 2–4 days in 2009–2012 between late April and the end of July. Territories were visited at different times of the day throughout a season. We estimated male prairie warbler territory density and location by mapping male territories. We recorded locations of singing males using handheld global positioning system (GPS) units, and we also plotted the singing locations relative to landmarks on treatment maps and aerial photographs. Territories for males that we were unable to color band were determined by a singing bird's consistent presence in a given area and the presence of neighboring color-banded males. During visits to a territory, we followed males and took 1–10 GPS points at male

singing locations, taking points until the bird completed a circle around his territory or until the bird was lost. During each visit, GPS points were taken only when a male moved at least 5 m from his previous location, and GPS accuracy was always equal to or less than 5 m. Using the adehabitat package in R, we created 95% minimum convex polygons in order to examine territory size for color-banded males in which we obtained a minimum of 30 GPS points (mean number of GPS points for these males = 43, SD = 12).

Males were considered territorial if they bred within the site or if they were observed twice in a given territory over a period greater than 10 days (Bibby et al., 1992). Some males were 'non-territorial' as well, including previously unbanded birds that were banded early in the season in May, but were observed in the study site for less than 10 days. Pairing success was determined by whether males were observed (1) exhibiting mated behavior with a female (e.g. mate-guarding or copulation) or (2) attending a nest within the territory. The earliest date during each season that we first observed an individual was considered the arrival date. Males are conspicuous and sing on arrival to the study site. In addition, plots were covered extensively every 2–3 days early in the season with re-sighting as the primary focus. We therefore believe we detected most arriving males within a day or two of arrival.

Nests were found by observing parent behavior and conducting systematic searches (Martin and Geupel, 1993). Nests were marked with flagging placed 10–15 m from the nest and monitored at intervals of 2–4 days until the nestlings fledged or the contents of the nest had disappeared (Martin and Geupel, 1993). We color banded nestlings from found nests when they were approximately 8 days old. We determined whether adults fledged young by monitoring nests (including additional nesting attempts after nest failures), systematically searching for fledglings in territories where nests were found empty and young could have fledged based on their stage of development in the previous nest check, and by searching territories for adults feeding fledglings in territories where we did not locate a successful nest. In these latter territories where we just found adults feeding fledglings, we did not know the exact number of fledglings and assumed that the territory produced the mean number of fledglings for successful nests found during that year. This accounted for 10% of the territories in our reproductive success analyses. Despite extensive search effort in our study plots, we never observed polygamous males or double-broods. Moreover, 72% of adult males and 40% of females were banded, fledglings were relatively loud and conspicuous, and territories were visited 20–30 times each season. We are therefore confident we were aware of the majority of reproductive efforts within the study area.

We surveyed the entire study site in all five years to estimate male territory density, age structure, and site fidelity. However, we did not measure vegetation structure and composition, male arrival dates, pairing success, or reproductive success in 2008, and did not obtain reproductive data over the entire site in 2010, 2011 and 2012. In these cases, the portions of the study area not surveyed were omitted from the analyses.

We computed territorial male bird density by calculating the number of mapped territories per ha within each plot. Study plots were adjacent to each other, and male territories occasionally overlapped plots. When this happened, we assigned the bird in the plot where most of his territory was located. This occurred for ~5% of the territories. We analyzed bird density as a function of time since treatment using linear mixed models, with territorial male birds per ha as the response variable. We included a quadratic effect for year since treatment as the predictor variable because shrubland birds often show modal responses to time since treatment (Schlossberg and King, 2009). We excluded the small disturbed portions (2.0 and 1.7 ha) of the treated pitch pine study plots in 2012 from our density analyses because the habitat was no longer

suitable in the last year of the study; the few returning, displaced males ($n = 4$) did not have any discernable effects on density in adjacent areas in the following year.

We analyzed territorial male prairie warbler age structure in treated pitch pine plots as a function of a quadratic effect for year since treatment with proportion data fit to a binomial distribution (Crawley, 2007). We excluded unbanded birds in this analysis and we acknowledge that male age proportions per plot could be biased by returning ASY males captured in a previous year. A higher percentage of territorial males were banded in the later years of this study: 50% in 2008, 63% in 2009, 70% in 2010, 77% in 2011, and 94% in 2012. To circumvent this possible bias and to more accurately determine the age of colonizing birds, we also examined the age structure for territorial males captured for the first time in treated pitch pine plots 1–2 years since treatment.

We examined the relationship between male arrival date (ordinal day of arrival) and age class using a linear mixed model. Arrival dates after June 1 were omitted (<3% of the males), as these late arrivals could have been birds immigrating into the study site from the surrounding area (Nolan, 1978). We tested if male age structure differed between territorial and non-territorial males using a mixed model fit to a binomial distribution. In this analysis we only included non-territorial males that were unbanded before being captured in May.

To analyze reproductive success we constructed separate models of fledging success per territory as a function of male age class, year since treatment (for treated pitch pine plots), or year. Fledging success (whether or not a territory fledged at least one prairie warbler young) was fitted to a binomial distribution. Each model was based on a different subset of the data. For example, only the banded males could be used in the bird age model. We also ran additional analyses, (1) with an additional random effect of individual bird, (2) with the number of fledglings per territory as the response variable, fitting the data to a Poisson distribution, and (3) examining nest survival rates in relation to year since treatment, year, and other covariates (Akresh, 2012). However, we obtained similar results as the analyses using fledging success as the response and did not present these additional analyses. In particular, there was no difference in nest survival rates between male age classes ($\beta = 0.34$, $SE = 0.28$, one-covariate model using Program MARK) (Dinsmore et al., 2002). Most territories (90%) fledged 0, 3, or 4 young; this data produced a bi-modal distribution of the number of fledglings with little variation in the number of fledglings produced for successful nests, and therefore we believed the reproductive success data was best modeled as fledging success. We excluded territories for which we were unable to determine fledging success with certainty (approximately 10% of territories) as well as unpaired birds from analyses of fledging success. We examined pairing success separately with the same predictor variables, but with pairing success as the response variable.

We ran separate models for “site fidelity” (whether or not a male bird returned to the study site) and “territory fidelity” (whether or not the male’s territory overlapped with the previous years’ territory; Payne and Payne, 1993) with a binomial distribution. We ran models with the dependent variable as site or territory fidelity, and an independent variable of male age class. We then screened the data to include only birds originally territorial in treated pitch pine habitat, and ran models with the independent variable of year since treatment. When conducting these analyses, we only included undisturbed, territorial birds. Each year a bird returned to the study site was treated as a separate sample in the analysis, as the same individual could act differently in different years based on whether it was an SY or an older bird. We ran additional analyses with an additional random effect of individual, but found similar results and therefore did not present these analyses.

We searched for color-banded birds whose territories were mowed, burned, or had herbicide applied the previous year to determine whether they dispersed from their former territory or the study site. We searched for birds within study plots, and in other early-successional habitats within the study site (Fig. 1). We deemed a territory as disturbed if the majority of the territorial area was affected by disturbance; most territories were completely disturbed. We compared site and territory fidelity of undisturbed versus disturbed territorial males using mixed models fit to binomial distributions. We also conducted mixed models fit to binomial distributions to determine whether disturbed birds had similar reproductive success in the following year as birds whose territories were not disturbed. We monitored the surrounding territories to determine whether there was evidence of crowding by dispersing birds in the following year. Lastly, we examined pairing and reproductive success in territories within 300 m of disturbed areas, a distance in which the majority of disturbed birds dispersed, compared with other territories throughout the study site, fitting the data to a binomial distribution. For this last analysis we also tried adding random effects of year and individual, but we obtained similar results and did not present these additional analyses.

3. Results

3.1. Habitat change over time

As treated pitch pine matured, canopy cover, understory height, vegetation structure (number of vegetation contacts) between 1.0 and 3.0 m, and the cover of deciduous woody vegetation increased, while overstory height and the cover of bare ground, forbs, ferns, and graminoids decreased (Table 1). As vegetation height increased over time since treatment, some saplings grew over 3-m, making the average overstory (over 3-m) vegetation height decline over time since treatment due to our sampling method.

3.2. Bird abundance, demography, and territoriality

We mapped 404 prairie warbler territories within the plots during the five years of the study: 63 territories in 2008, 71 in 2009, 86 in 2010, 101 in 2011, and 83 in 2012. Average territory size was 0.97 ha ($SD = 0.45$ ha, $n = 51$). Newly created treated pitch pine habitat initially had low bird densities that peaked at 4–5 years of age for most plots and then began to decline (linear $\beta = 0.403$, $SE = 0.073$, $t = 5.5$; quadratic $\beta = -0.036$, $SE = 0.009$, $t = -4.2$; Fig. 3). The majority of territorial males in newly treated pitch pine habitat were SY birds (Fig. 4). Specifically in treated pitch pine plots 1–2 years of age, 81% of territorial males captured for the first time ($n = 16$) were SY males. As treated pitch pine matured, the proportion of ASY males increased, and then either reached a plateau or began to decline (linear $\beta = 1.363$, $SE = 0.481$, $z = 2.8$, $P = 0.005$; quadratic $\beta = -0.119$, $SE = 0.053$, $z = -2.2$, $P = 0.03$).

For all years combined, ASY males arrived significantly earlier (mean = May 6, $SE = 0.3$ days) than SY males (mean = May 11, $SE = 0.7$ days, $n = 248$, $t = 7.3$, $P < 0.001$). Between 2009 and 2012, we captured 18 previously unbanded, non-territorial males in May that we did not re-sight after 10 days of capture; 56% of these non-territorial males were SY birds. In comparison, a significantly lower percentage of captured, territorial males were SY birds (21%, $z = -3.1$, $P = 0.002$).

We recorded reproductive success for 204 territories during the study. Average seasonal fecundity was 1.79 fledglings per territory, with 57% of territories fledging at least one prairie warbler over all years combined. Fledging success did not differ significantly with time since treatment in treated pitch pine ($n = 127$, $z = -1.3$,

Table 1

Mean vegetation characteristics in prairie warbler territories by years since treatment in treated pitch pine habitat, MPWMA, Montague, MA between 2009 and 2012 ($n = 66$). Standard errors are presented in parentheses. Z values are for analyses using Poisson or binomial distributions; t values are for analyses using normal distributions (overstory and understory height). P -value is the adjusted P -value using the Bonferroni–Holm method.

	Years since treatment							z/t	Adj. P
	2 ($n = 19$)	3 ($n = 15$)	4 ($n = 6$)	5 ($n = 10$)	6 ($n = 7$)	7 ($n = 5$)	8 ($n = 4$)		
OVER ^a	17.8 (1.3)	13.3 (1)	11 (1.8)	13 (1.1)	11.1 (0.9)	11.2 (1)	12.6 (2.2)	−3.2	0.003
CANOPY	15.5 (2.8)	20.1 (2.1)	11.7 (1.1)	22.5 (1.9)	25 (3.8)	32 (7.2)	31.2 (6.9)	4.4	<0.001
UNDER	66.2 (4.4)	83.2 (7.1)	107.1 (3.6)	106.5 (12.3)	107.3 (8.6)	136.8 (7.4)	137.2 (19.6)	7.4	<0.001
STR 0–0.5 m	4.4 (0.5)	3.3 (0.3)	3.8 (0.2)	3.2 (0.2)	3.6 (0.5)	2.9 (0.5)	4.2 (0.6)	−0.8	0.864
STR 0.5–1 m	1.6 (0.2)	1.5 (0.2)	1.9 (0.3)	1.6 (0.4)	1.7 (0.3)	1.2 (0.2)	1.6 (0.4)	0.5	0.864
STR 1–1.5 m	0.5 (0.1)	0.6 (0.1)	1 (0.1)	1.3 (0.3)	0.8 (0.2)	1 (0.2)	0.9 (0.2)	3.0	0.017
STR 1.5–2 m	0.3 (0.1)	0.3 (0)	0.6 (0.1)	0.8 (0.2)	0.7 (0.1)	1 (0.3)	0.6 (0.1)	3.6	0.002
STR 2–3 m	0.1 (0.1)	0.1 (0)	0.3 (0.1)	0.4 (0.1)	0.3 (0.1)	0.7 (0.2)	1.0 (0.2)	3.7	0.002
GROUND	18.2 (3.1)	15 (2.7)	5 (2.2)	11.5 (4.1)	9.3 (3)	13 (4.9)	11.2 (4.3)	−3.7	0.002
BERRY	10.3 (2.1)	14.3 (3.2)	12.5 (3.8)	14 (3.8)	19.3 (4.3)	18 (4.4)	13.8 (5.9)	−1.3	0.676
CONIFER	7.1 (1.6)	4.7 (1.8)	6.7 (1.7)	3 (1.1)	2.1 (1)	3 (2)	8.8 (3.1)	−1.4	0.676
FORBFERN	6.3 (1.5)	4 (1.5)	4.2 (1.5)	5 (3)	4.3 (2)	0 (0)	1.2 (1.2)	−2.6	0.051
GRASS	13.4 (1.6)	8.3 (2.7)	4.2 (2)	7 (2)	5 (1.1)	3 (2)	3.8 (2.4)	−3.9	0.001
WOODY	45 (3.5)	53.3 (5.6)	67.5 (5.9)	59.5 (8.3)	60 (7)	63 (6.4)	61.3 (10.1)	6.7	<0.001

^a OVER = Overstory Height (m); CANOPY = Canopy Cover (%); UNDER = Understory Height (cm); STR 0–0.5 = Structure 0–0.5 m; STR 0.5–1.0 = Structure 0.5–1 m; STR 1–1.5 = Structure 1–1.5 m; STR 1.5–2 = Structure 1.5–2 m; STR 2–3 = Structure 2–3 m; GROUND = Ground (%); BERRY = Blueberry/Dewberry (%); CONIFER = Conifer (%); FORBFERN = Forb/Fern (%); GRASS = Graminoid (%); WOODY = Deciduous woody (besides berry) (%).

$P = 0.19$), or between male age classes (SY: 49% fledged young, 1.49 fledglings per territory, ASY: 58% fledged young, 1.80 fledglings per territory, $n = 158$, $z = -0.87$, $P = 0.38$). Reproductive success differed among years: 2012 had the lowest fledging success (38%) and number of fledglings produced per territory (1.26), which was significantly lower compared to 2009 (64% fledged young, 1.97 fledglings per territory, $z = 2.4$, $P = 0.018$) and 2010 (68% fledged young, 2.05 fledglings per territory, $z = 2.7$, $P = 0.007$), but was not significantly different from 2011 (55% fledged young, 1.60 fledglings per territory, $z = 0.6$, $P = 0.53$).

Approximately 97% of 311 territorial males were paired. Pairing success was significantly lower for SY males (92%, $n = 49$) compared to ASY males (99%, $n = 198$) ($z = -2.5$, $P = 0.01$), and did not vary significantly with time since treatment in treated pitch pine, or among years ($P > 0.05$).

Of 174 cases of banded males on undisturbed territories in 2008–2011, 72% (126) returned to the study site the following year, and 71% (90) of the returning birds remained on their previous territory. For males that moved their territory within the study site, the median distance between territory centers was 253 m

(range = 60–2760 m). There was no significant change in site fidelity ($n = 116$, $z = 0.48$, $P = 0.63$) or territory fidelity ($n = 79$, $z = 1.29$, $P = 0.20$) over time since treatment. Younger males had similar site fidelity compared to older males (65% and 75%, SY and ASY birds, respectively; $z = -1.2$, $P = 0.23$), although they had significantly lower territory fidelity (54% and 76%, SY and ASY birds, respectively; $z = -2.2$, $P = 0.03$).

We banded 336 nestlings, of which 47 (14%) male and female birds returned to the study site. On average between 2010 and 2012 (only 12 nestlings were banded in 2008), 4.5% of males observed in the study site consisted of male natal returns that we banded as nestlings in the previous year in our study area.

We mapped 50 territorial males in scrub oak, treated pitch pine, and power line corridor habitats that were subsequently mowed to the ground, extensively burned, or treated with herbicides during the non-breeding season. Thirty-eight of these males were color-banded, with 19 of these in power line corridors that were applied with herbicide, 11 males in mowed scrub oak, 2 in burned scrub oak, 2 in mowed treated pitch pine, and 4 in burned treated pitch pine. Out of all 38 males, 17 (45%) returned and set up a territory in

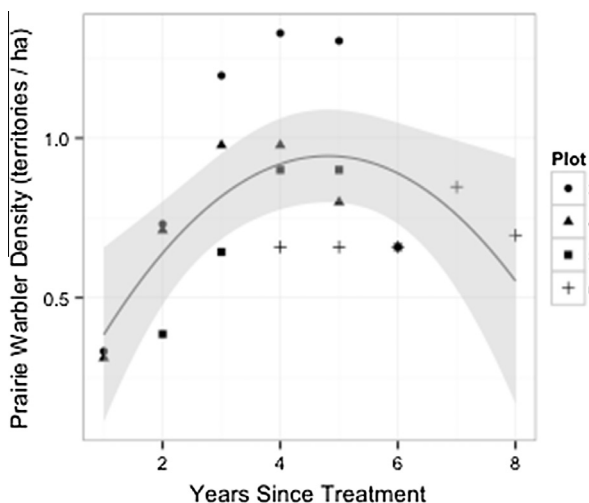


Fig. 3. Prairie warbler density in newly created and maturing treated pitch pine in the MPWMA by year since treatment. Grey line and shading represents regression curve and 95% confidence interval.

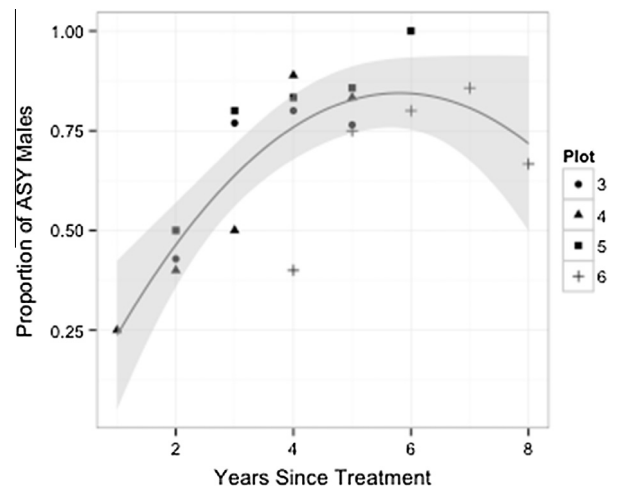


Fig. 4. Proportion of ASY prairie warbler males in treated pitch pine by year since treatment. Grey line and shading represents regression curve and 95% confidence interval.

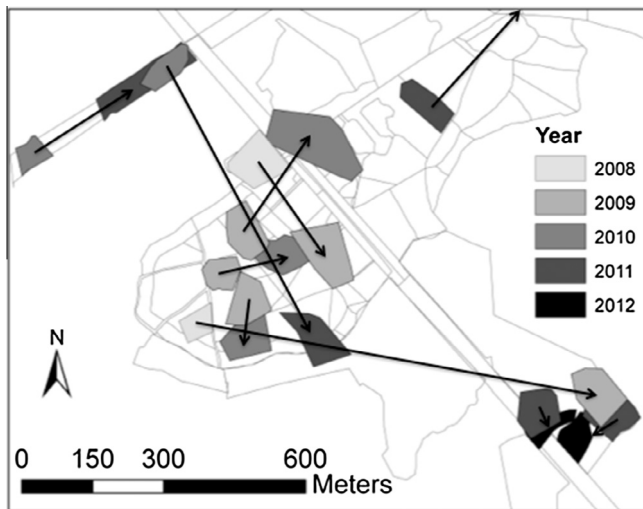


Fig. 5. Map of the western section of the study site showing 10 male territories that were then disturbed after a given breeding season, and these males' subsequent territories in the following year. Arrows indicate the males' dispersal. The arrow in the northeast corner does not connect 2 territories on this map; when this male's territory was mowed after the 2011 breeding season, the bird dispersed to plot 8 in 2012 (see Fig. 1).

the study site the breeding season immediately after the disturbance, a significantly lower rate than the 72% of males in undisturbed territories ($z = -3.0$, $P = 0.003$). We also observed an additional 5 (13%) color-banded males from disturbed territories that were observed in the study plots the following year early in the breeding season, but did not set up a territory throughout the season. Almost all of the returning males moved away from their disturbed territories (14% territory fidelity), a significant contrast to the 71% territory fidelity observed for birds in undisturbed territories ($z = -4.1$, $P < 0.001$). The three birds that remained on their disturbed territory were in power line corridors that had some shrubby vegetation still present within the territory.

Examining all disturbed males who returned the following year, dispersed, and set up a territory within the study site, the median distance moved between their previous territory center to their new territory center was 183 m (range = 50–1230 m, $n = 14$). Of these 14 males, 71% dispersed to a new territory that was in the same habitat type as their old territory (Fig. 5). Moreover, despite being displaced, disturbed males that acquired a territory within the study site all paired successfully the year following disturbance, and had similar reproductive success to undisturbed males (disturbed males: 55% fledged young, 1.67 fledglings per territory, undisturbed males: 57% fledged young, 1.79 fledglings per territory, $z = -0.3$, $P = 0.75$). Finally, pairing success and fledging success did not differ between males located in areas within 300 m of disturbance (in the year following disturbance) and males located in the rest of the study site (pairing success: $z = 0.7$, $P = 0.48$, fledging success: $z = 0.4$, $P = 0.72$).

4. Discussion

Our study is the first to illustrate the demographic processes associated with the colonization and dispersal of a shrubland bird species within a dynamic landscape—processes that are fundamental characteristics of populations occupying disturbance-dependent systems. We found the pattern of post-disturbance colonization similar to past studies, with prairie warblers colonizing at low densities after initial logging and increasing up to 4–5 years after treatment (King et al., 2011; Schlossberg and King,

2009). As treated pitch pine matured, we also witnessed a decline in bird density as found in other studies (Schlossberg and King, 2009). Given that a large portion of the study site consisted of treated pitch pine, the increase in mapped territories in the entire study site between 2008 and 2011, and the drop in territories in 2012, probably reflected the function of bird density and time since treatment. The increase in bird densities as sites recovered from logging appeared to correspond to prairie warblers' habitat requirements, principally dense woody shrubs suitable for nesting (Nolan, 1978; Slay, 2010). Average shrub height in the first year or two after harvesting was typically lower than the height range of most selected prairie warbler nest sites in our study (Akresh, 2012; King et al., 2011), potentially accounting for the relatively low densities of birds in the years directly following logging.

Although the pattern of colonization of newly created habitat has been documented, the nature and origin of these new arrivals is poorly understood, despite the fact that the arrival of birds in newly created habitat is the objective of these management practices. Furthermore, comprehensive evaluation of habitat management projects requires inclusion of metrics of reproductive success (Sallabanks et al., 2000). Our findings indicate newly created habitat was mostly colonized by SY males, which arrived later than ASY males on the breeding grounds. Past studies have also found ASY males arrive earlier and outcompete younger males for territories in preferred habitats; consequently, SY males obtain non-preferred habitat or exhibit delayed breeding due to unavailability of high-quality breeding sites (e.g., Lanyon and Thompson, 1986; Lozano et al., 1996; Petit and Petit, 1996). We found slightly lower pairing success for SY males. In addition, more 'non-territorial' males were SY males, although these 'non-territorial' males may have found territories elsewhere after leaving the study site. Nevertheless, most SY males in our study, including birds in newly created habitat, were still able to acquire mates and breed. Moreover, although SY male reproductive success was slightly lower than ASY males, this difference was not statistically significant, a finding comparable to the observations of King et al. (2001) and Joos et al. (2014) in studies on chestnut-sided warblers (*Setophaga pensylvanica*) and Bell's vireos (*Vireo bellii bellii*), respectively.

These results contrast with studies reporting reproductive success to be significantly lower for SY birds due to later arrival and egg-laying dates (Nolan, 1978; Nol and Smith, 1987). One explanation for our findings is that despite arriving later, most SY males still arrived before the majority of nesting began (Akresh, 2012). Additionally, in some years in our study area, the first nests of the season had low survival rates before vegetation fully leafed out (Akresh, 2012); as a result, birds that arrived and started nesting earlier usually did not have a reproductive advantage. Although we hypothesized that the vegetation structure in newly created habitats may lead to decreased reproductive success for SY birds, we found that once vegetation grew enough to provide nest sites, the shorter vegetation structure did not appear to negatively affect reproductive output. Chandler et al. (2009), in a study of shrubland birds in wildlife openings, also found that nest survival did not differ with time since treatment. Since reproductive output was the same between new and older habitat in our study, we suggest that territory fidelity and territory preemption by established males is more likely the cause of differences in age structure than actual habitat quality (i.e., food or nesting opportunities; Donner et al., 2010).

The patterns of age structure as a function of time since treatment may be driven by the high territory fidelity of ASY males because (1) this keeps territories in more mature shrubland occupied and thus unavailable to presumably competitively inferior SY birds, and (2) this also reduces the number of ASY males available to colonize newly created habitat. In contrast, newly created habitats are unoccupied at first, so SY males are not at a disadvantage competing against ASY males in these areas. In older treated pitch

pine, many of the territorial ASY males had originally colonized the plots as SY individuals, although the exact proportion of ASY males that were SY colonizers is unknown because some colonizing SY birds were not captured. Our finding that site and territory fidelity of male prairie warblers is high relative to mature forest birds is consistent with the review by Schlossberg (2009), as well as with observations of the shrubland-dependent chestnut-sided warbler (King and Byers, 2002; King in Schlossberg, 2009) and Kirtland's warbler (*Setophaga kirtlandii*; Donner et al., 2010), but contradicts the earlier view that shrubland species occur as "fugitive species" with low site fidelity and high dispersal (Thompson and Nolan, 1973; Lent and Capen, 1995). This suggests that the decline in bird density over time for shrubland birds in older habitat is possibly due to a function of attrition of site-faithful ASY males and low recruitment of SY males.

Given the standard caricature of shrubland birds as fugitive species (Askins, 2000), it is understandable that managers appear to assume that if shrubland is created, shrubland birds will colonize it. Also, given the centrality of this assumption to the success of management efforts for these species, it is therefore important to understand the origin of the individuals colonizing the site. Contrary to the expectation based on this paradigm that immigration and emigration would be high, we observed high male site fidelity and the majority of the males present either had nested previously or had been born at the site. High site fidelity for adult shrubland birds has been shown to occur even in landscapes where suitable habitat is less clustered than it is in our site (Holmes and Sherry, 1992; Lehnen and Rodewald, 2009). One reason for our relatively high natal return rates could be because of the large number of locally suitable territories for prairie warblers in our compact study area in relation to the surrounding landscape, allowing us to detect birds that survived and returned at a local scale (Fajardo et al., 2009; McKim-Louder et al., 2013). Nevertheless, the study site was not completely isolated; multiple power line corridors and other early-successional habitats within 5 km of the study site provided suitable prairie warbler habitat that held territorial singing males. We conducted some surveys to resight male prairie warblers in these periphery areas in later years of the study, but this yielded few sightings of dispersing color-banded birds (Akresh unpublished data).

This is one of the few studies to document and track color-banded shrubland birds dispersing from occupied territories following disturbance of their breeding habitat (Rousseau et al., 2012). Dispersal from disturbed territories was expected given the lack of suitable nesting substrate in most disturbed territories, especially those extensively mowed or burned. Our finding that disturbed birds were relatively successful in pairing and breeding in the following year was also not surprising, given these were birds able to acquire suitable territories within the study site and were returning as ASY males.

Site fidelity of male prairie warblers in disturbed territories was significantly lower than the site fidelity of undisturbed birds. This contrasts with Rousseau et al.'s (2012) finding that male white-throated sparrows in territories that were subject to timber harvesting had similar return rates as birds in non-harvested areas. Since management treatments were conducted during the non-breeding season, one would expect return rates to be similar for birds on disturbed territories because they would have no knowledge of disturbance until arrival on the breeding grounds (Rousseau et al., 2012). There were an additional 5 returning, but non-territorial, disturbed males within our study site the year after disturbance that we did not classify as having site fidelity. After observing these birds in early May, we do not know what happened to these birds later in the season; they could have dispersed and set up a territory somewhere outside the study area, or could have become undetected 'floater' males within the study site (Zack

and Stutchbury, 1992). Interestingly, 4 out of 5 of these birds returned and set up a territory in the study site two years after disturbance, and 1 additional disturbed male was not seen after disturbance until he set up a territory in the study site three years later. These 6 males, and similar males that could have gone undetected, could account for the difference between disturbed versus undisturbed males' site fidelity in our study.

Most of the disturbed males dispersed short distances within the study site, similar to previous studies that have tracked color-banded birds after disturbance (Betts et al., 2006; Rousseau et al., 2012). This highlights the importance of having suitable habitat near the disturbed habitat. The majority of disturbed males dispersed into the same habitat type as they held before dispersal, but this could have been a function of dispersal distance and territory availability rather than specific habitat selection per se. Further research is needed at larger landscape scales to examine how size and proximity of disturbed and available habitats affects dispersal (Donner et al., 2010).

In our study, there appeared to be no crowding effect of displaced birds or decreased pairing success adjacent to disturbed areas. Displaced birds often found vacant, suitable habitat, sometimes dispersing to an area that had previously been occupied by a male who did not return from the non-breeding season. This contrasts with past studies that report increased densities of forest birds when adjacent forest is destroyed (Darveau et al., 1995; Hagan et al., 1996; Schmiegelow et al., 1997). Results from previous studies may contrast with our results because the patches of disturbed habitat in our study were smaller, disturbance was conducted over multiple years, and the adjacent habitat was extensive relative to the size of disturbance. As a result, fewer birds in our study were displaced into the adjacent habitat, which was large and thus able to absorb more dispersing birds. There are alternative hypotheses to explain our results; for instance, different bird species, or guilds, may respond differently to disturbance (Schmiegelow et al., 1997). Shrubland birds could exhibit different responses to disturbance compared to the forest bird species that were examined by most other researchers. Given that many previous studies have made inferences without tracking individually banded birds, more intensive studies with color-banded individuals of various species are needed.

5. Conclusions

Because disturbance-dependent habitats are ephemeral, species that depend on them require continuous habitat management (DeGraaf and Yamasaki, 2003; King et al., 2009). Although management is clearly necessary to ensure the long-term persistence of these habitats (Oehler, 2003; Thompson and DeGraaf, 2001), conservationists and managers may be concerned about the short-term effects of habitat treatments. We found newly treated areas are not "sink" habitats. Instead, young birds are colonizing these areas and exhibiting similar reproductive output to established birds in mature habitat; as a result, they are likely bolstering the population growth rate. Although management practices eliminate breeding habitat immediately after treatment, most individuals occupying the treated areas are able to shift to adjacent habitats and breed successfully without decreasing the breeding success of the other occupants. Thus, we believe that managers can proceed with relatively small mowing, burning and herbicide treatments (5–10% of the shrubland area) directed at setting back succession without concerns about the welfare of existing shrubland bird populations.

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