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WINTER SITE FIDELITY AND BODY CONDITION OF THREE RIPARIAN SONGBIRD SPECIES FOLLOWING A FIRE

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ABSTRACT.—The effects of fire on nonbreeding songbird species in riparian habitat have not been studied. We compared body condition, within-year site fidelity, and between-year site fidelity of 3 songbird species (*Passerella iliaca,* Fox Sparrow; *Catharus guttatus,* Hermit Thrush; and *Regulus calendula,* Ruby-crowned Kinglet) at 2 coastal riparian sites. Wildfire, which is rare in this habitat, had occurred at 1 of the sites before data collection. A significantly larger proportion of *Passerella iliaca* was recaptured in subsequent winters at the unburned site than at the burned site, but little difference was found between sites for *Catharus guttatus* or *Regulus calendula.* Body mass of all 3 species declined during winter at the burned site, but differences between sites were not significant. Similarly, body mass indices of new captures were lower at the burned site than the unburned site for all 3 species, but these differences were not significant. The within-year recapture rate for all 3 species combined declined at the burned site over the course of the study, possibly due to changes in vegetation structure caused by the fire. Overall, our data suggest that wintering songbirds were resilient to this disturbance, but that response to the post-fire environment differed among foraging guilds. Well-replicated studies that include pre-burn data are needed to evaluate the effects of this disturbance in riparian systems.

Key words: riparian, fire, winter songbirds, site fidelity, body condition, Passerella iliaca, Regulus calendula, Catharus guttatus.

Winter site fidelity of Neotropical–Nearctic migrant songbirds is well documented (Holmes and Sherry 1992, Wunderle and Latta 2000, Sandercock and Jaramillo 2002), and variation in winter site fidelity may indicate habitat quality. While the quality of breeding habitats may influence nest success, the quality of nonbreeding habitat during winter also has fitness consequences for migratory birds (Marra et al. 1998, Norris et al. 2004), and large-scale disturbances may play an important role in determining habitat quality (Rotenberry et al. 1995, Brawn et al. 2001).

Fire is one form of disturbance that may influence patterns of winter habitat use by birds. For example, Kreisel and Stein (1999) found that the loss of canopy cover and shrub undergrowth made burned forests more suitable for trunk- and branch-foraging species. Blake (1982) also found certain species restricted to burned or unburned sites in a nonbreeding bird community. However, while fire created suitable habitat for bark-drilling species such as woodpeckers, bark-gleaning species preferred unburned sites. The open canopy of burned sites also supported more aerial insectivores, while foliage-gleaning insectivores declined. A decline in foliage-gleaning insectivores after fire was also noted by Bock and Lynch (1970), but regrowth of brush supported more ground brush–foraging species. In general, woodpeckers, flycatchers, and seedeaters often benefit from the habitats created by large-scale fires (Hutto 1995). The suitability of burned habitat is also likely to vary for different bird species with time since a fire (Raphael et al. 1987). Understanding the development of winter site fidelity by birds in burned plant communities must therefore include knowledge of fire history and avian foraging behavior.

Most studies of songbird response to fire in North America during winter have focused on coniferous forests, whereas study of riparian bird communities is lacking. This bias may be due to the absence of fire as a management tool or as a frequent disturbance event in riparian communities (DeBano and Neary 1996). In contrast, prescribed burning is common in coniferous woodland where fire is often viewed as a natural disturbance. Most studies have also used point-counts or other census methods that prevent analysis of site fidelity and

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demography. Marked populations of birds allow the researcher to identify individuals that return to the same site each season or persist within sites through a specified period of time. If fire has a large impact on riparian habitat, some migratory species may be less likely to return in subsequent seasons or be less likely to persist at a single site through a season. A better understanding of the effects of fire on riparian songbird communities is needed, even if fire disturbance is rare in this habitat.

In this post hoc analysis, we used 6 years of mist-net data from 1 burned and 1 unburned riparian site to investigate the possible effects of wildfire on 3 migratory songbird species during the nonbreeding season. Our objectives were to (1) compare between-year site fidelity in the burned versus unburned sites using recapture data across different winter seasons, (2) compare within-year site fidelity between the 2 sites using within-season recapture data, and (3) determine if body condition differed between sites or changed from early to late winter. To our knowledge, this is the 1st study examining the ecology of nonbreeding songbirds within burned riparian habitat.

METHODS

Study Area

We selected 2 riparian study sites, 1 burned and 1 unburned. The burned study site is located at Muddy Hollow (MH) in the Point Reyes National Seashore (PRNS), Marin County, California (38°02′N, 122°48′W). The 30,364-ha PRNS is dominated by a Mediterranean climate with wet winters and moderate, dry summers that receive moisture in the form of coastal fog. Vegetation types occurring in PRNS include mixed evergreen forest, coastal scrub, grassland, and riparian and wetland habitats (Shuford and Timossi 1989). On 3 October 1995 an unintentional human-ignited fire started at the seashore and ultimately burned 5263 ha (17.3%) of the park over a period of 3 days (PRNS 1997). This fire swept through the entire MH study area, including the riparian habitat present at this site. The rapid passing of the fire through MH resulted in a relatively undamaged riparian canopy, while the understory was completely burned. At least 5 km of habitat was burned in all directions surrounding MH. Thus, there was little chance that wintering birds chosen for these analyses foraged in unburned areas during a winter period.

Our unburned study site is at Pine Gulch (PI) near the town of Bolinas, Marin County (37°92′N, 122°69′W). This site lies just outside the PRNS, approximately 20 km south of MH. Both the burned and unburned study sites contain riparian forest dominated by a canopy of red alder (*Alnus rubra*) and arroyo willow (*Salix lasiolepis*). Understory plants common at both sites include red elderberry (*Sambucus recemosa*), California blackberry (*Rubus ursinus*), stinging nettle (*Urtica dioica*), and poison hemlock (*Conium maculatum*). A few plant species were dominant at only one site, e.g., coyote brush (*Baccharis pilularis*) and velvet grass (*Holcus lanatus*) at MH, and gumplant (*Grindelia stricta*) at PI. In addition, PI is partly bordered by a lagoon on one side and mixed evergreen forest on another, while MH is surrounded mostly by coastal scrub. PI was chosen as the unburned riparian study site because data collection had already commenced at this site before the fire at MH.

Study Species

Three wintering bird species were selected for these analyses. Ruby-crowned Kinglet (*Regulus calendula*), Hermit Thrush (*Catharus guttatus*), and Fox Sparrow (*Passerella iliaca*) were selected because of sufficient capture rates; >100 individuals of each species were captured per site, with >200 individual *P. iliaca* and *R. calendula* captured per site. In addition to being common winter residents at both study sites, these 3 species occupy fairly distinct foraging guilds. *Regulus calendula* represents a shrub tree–foraging guild with a winter diet primarily of spiders, insects, and small amounts of vegetative matter (Ingold and Wallace 1994). Populations of *R. calendula* within the study area are female-biased (Humple et al. 2001). *Catharus guttatus* is a terrestrial or bush-gleaning omnivore and thus represents a ground tree–foraging guild (Jones and Donovan 1996). And *Passerella iliaca* occupies a ground-foraging guild where it locates food by scraping dirt and leaf litter (Rogers 1987). Fire may have a differential effect on resource abundance and distribution for different guilds (Raphael et al. 1987). The 3 species chosen for these analyses should therefore provide a stronger overall measure of songbird response to fire at this site.

Data Collection

On 21 October 1995 (18 days after the start of the fire), the Point Reyes Bird Observatory (PRBO) began a constant effort of mist-net capturing birds within riparian vegetation at MH. Fieldwork at PI had begun several months earlier, but only captures within the same date periods as MH were used in these analyses. Ten mist-nets at each site (12 m, 30-mm mesh) were operated once every 10 days for 6 hours, starting 15 minutes after sunrise. We confined our analyses to the winter season (November–February) for winters 1995/96 through 2001/02, except 1997/98. The total period of time nets were open (expressed as net-hours [nh]) was similar between sites (PI = 4032 nh, MH = 3780 nh), thus reducing bias in recapture probability due to variation in effort. Nets were operated at the same locations and in the same orientations throughout the study. Nets were closed early during periods of inclement weather. All birds were banded with a USFWS aluminum band before measurement and release. We recorded mass with an electronic balance to 0.1 g.

Statistical Analysis

Individuals initially banded during a winter season and recaptured during any subsequent winter season demonstrated between-year site fidelity. For each species, chi-square tests were used to compare the frequency of banded birds recaptured versus not recaptured between sites. To assess whether burned and unburned sites differed in quality for birds, we first used *t* tests (SPSS, Inc. 2001) to compare changes in body mass of birds that were captured during early winter (November–December) and recaptured during late winter (January–February) with ≥1 month between captures. We also used a body mass index for a larger sample of new captures between November and February to compare body condition between sites. Because body mass of different individuals is confounded with body size, mass was expressed relative to the structural size of an individual (Piersma and Davidson 1991, Brown 1996). Unflattened wing chord was regressed against body mass, and the residual of this analysis (hereafter referred to as the body mass index) was used as the response variable in the following tests. We used *t* tests to compare mean body mass indices between sites for *P. iliaca* and *C. guttatus.* Since *R. calendula* is the only one of the 3 species reliably sexed during winter (Pyle 1997), 2-way ANOVA was used with sex added as a main effect. Comparisons of mass across seasons or between sites can be confounded with diurnal variation in mass, with a gradual gain in mass over the course of a day (Graedel and Loveland 1995). To verify whether this variation biased our analyses of mass, we used *t* tests to compare differences in mean capture times for a randomly selected group of birds from each site during early and late winter.

Birds that were banded and subsequently recaptured ≥2 weeks later were assumed to have spent that winter season within the vicinity of the study site and thus demonstrated within-year site fidelity. The winter season as defined above was extended by 2 weeks on both ends (15 October–15 March) to include birds that arrived during migratory periods but remained within the study areas over the winter as indicated by recapture dates. This improved our sample size for this analysis but was not appropriate for the earlier analyses of body mass because body condition may reflect migratory behavior and resource availability at other sites. Also, recapture rates may be complicated by birds that are faithful to the same migratory paths (Cantos and Tellería 1994, Merom et al. 2000). To compare within-year recapture rates, we used binary logistic regression (PROC GENMOD; SAS Institute, Inc. 1999), which evaluated the impact of year and site on the probability of recapture within a winter season. The model included site as nominal data, year (6 winter seasons) as continuous data, and the interaction term. Because the number of recaptures satisfying the above criteria was low for some species in some seasons, we pooled data for all bird species. This runs the risk of obscuring species-specific responses to predictor variables but provides a more robust measure of overwinter site persistence at each site. We verified that data met parametric assumptions of normality and homogeneity of variance. Means are reported ± $s_{\bar{x}}$, with $\alpha = 0.05$.

RESULTS

A significantly higher frequency of banded *P. iliaca* was recaptured in subsequent winter seasons at PI (27 recaptured of 235 banded)

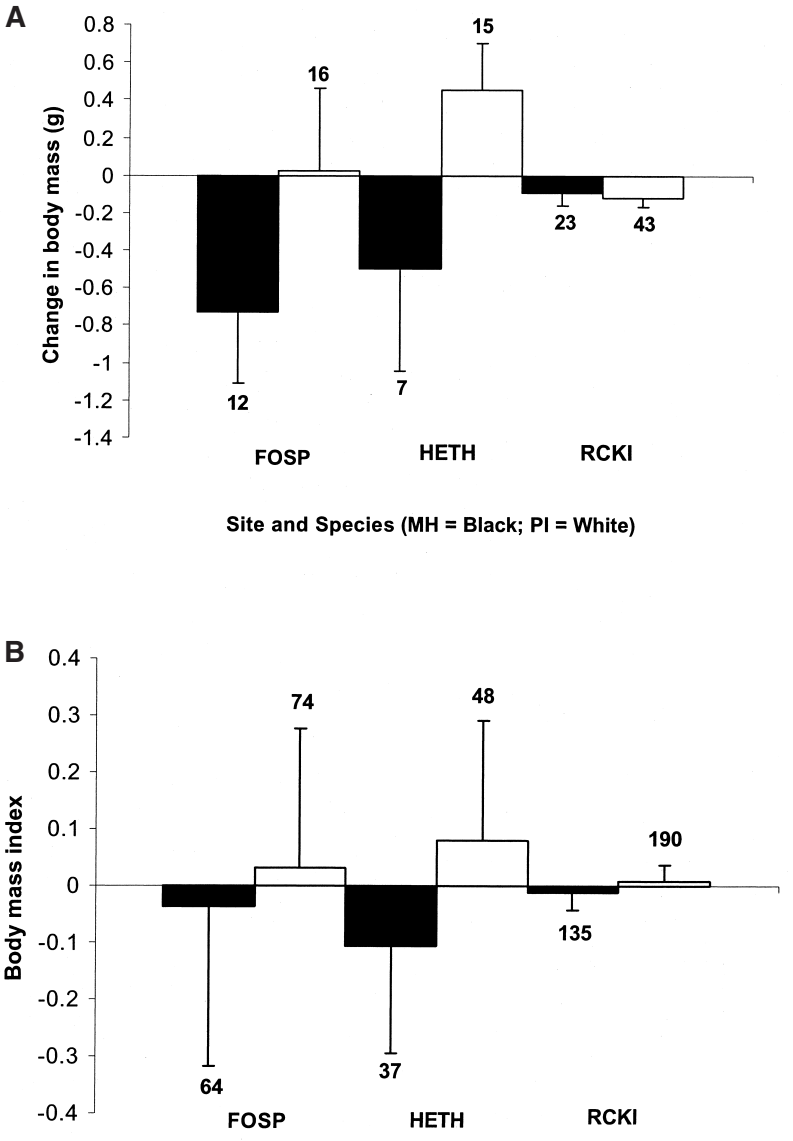

Fig. 1. Mean change in body mass from early (November–December) to late (January–February) winter for 3 species (A), and mean body mass index for new captures during winter (B) at post-fire (MH) and unburned (PI) riparian sites, Marin County, CA. *Passerella iliaca* = FOSP, *Catharus guttatus* = HETH, and *Regulus calendula* = RCKI. Error bars represent $s_{\bar{x}}$, with sample sizes shown above/below bars.

than at MH (7 of 252; $\chi^2_1 = 14.21$, $P < 0.001$). The frequency of *C. guttatus* recaptured at PI (15 of 171) was not significantly different from the proportion recaptured at MH (7 of 110; $\chi^2_1 = 0.54$, $P = 0.46$). Similarly, the between-year recapture rate for *R. calendula* did not differ significantly between PI (30 of 377) and MH (17 of 253; $\chi^2_1 = 0.34$, $P = 0.56$).

Differences in mean capture times (expressed as minutes after sunrise) were similar for the burned (184 ± 14) and unburned (185 ± 13) sites ($t_{120} = -0.05$, $P = 0.96$). Furthermore, differences in mean capture times across the winter season were similar for early (189 ± 12) and late (176 ± 16) winter captures ($t_{95} = 0.69$, $P = 0.49$). Thus, no attempt was made to correct

TABLE 1. Within-year recapture rates for *Passerella iliaca, Catharus guttatus,* and *Regulus calendula* at post-fire (MH) and unburned (PI) riparian sites in Marin County, CA, for winter seasons 1995/96 through 2001/02. N is the number of new captures per 100 net-hours between 15 October and 15 March; R is the number of birds recaptured per 100 net-hours, and %R is the percent of N recaptured.

		Muddy Hollow (MH)			Pine Gulch (PI)		
Species	Year[a]	N	R[b]	%R	N	R[b]	%R
Passerella iliaca	95/96	1.59	0.23	14.5	1.31	0.28	21.4
	96/97	5.93	1.69	28.5	3.74	0.77	20.6
	98/99	3.04	0.23	7.6	6.60	1.97	29.8
	99/00	0.77	0.22	28.6	0.64	0.21	32.8
	00/01	2.13	0.13	6.1	3.39	0.58	17.1
	01/02	2.20	0.14	6.4	1.25	0.25	20.0
Mean ($s_{\bar{x}}$)	95–02	2.61 (0.73)	0.44 (0.25)	15.3 (4.4)	2.82 (0.91)	0.68 (0.27)	23.6 (2.5)
Catharus guttatus	95/96	1.47	0.23	15.6	3.28	1.22	37.2
	96/97	2.18	0.12	5.5	4.40	0.99	22.5
	98/99	1.29	0.47	36.4	2.55	0.69	27.1
	99/00	0.55	0.11	20.0	1.17	0.32	27.4
	00/01	1.59	0.53	33.3	1.40	0.47	33.6
	01/02	2.20	0.82	37.3	1.62	0.50	30.9
Mean ($s_{\bar{x}}$)	95–02	1.55 (0.25)	0.38 (0.11)	24.7 (5.3)	2.40 (0.51)	0.70 (0.14)	29.8 (2.1)
Regulus calendula	95/96	2.72	0.91	33.5	3.57	0.75	21.0
	96/97	9.43	2.66	28.2	6.71	1.65	24.6
	98/99	5.49	1.29	23.5	10.54	2.78	26.4
	99/00	1.54	0.33	21.4	3.30	0.85	25.8
	00/01	2.92	0.13	4.5	4.20	1.40	33.3
	01/02	4.26	0.55	12.9	10.61	3.87	36.5
Mean ($s_{\bar{x}}$)	95–02	4.39 (1.15)	0.98 (0.38)	20.7 (4.3)	6.49 (1.38)	1.88 (0.50)	27.9 (2.4)

[a]No capture data are available for winter 1997/98.
[b]Recaptured no less than 2 weeks after being banded, and within the date period 15 October–15 March.

for diurnal changes in body mass. Mean change in body mass from early to late winter was negative for all 3 species at MH and slightly positive for *P. iliaca* and *C. guttatus* at PI (Fig. 1A). However, differences between sites were not significant for any species (*P. iliaca*: $t_{26} = -1.26$, $P = 0.22$; *C. guttatus*: $t_{20} = -1.84$, $P = 0.08$; *R. calendula*: $t_{64} = 0.30$, $P = 0.76$). Mean body mass indices were slightly negative for all 3 species at MH and slightly positive for all 3 species at PI (Fig. 1B). However, these differences between sites were also not significant (*P. iliaca*: $t_{136} = -0.19$, $P = 0.85$; *C. guttatus*: $t_{83} = -0.63$, $P = 0.53$; *R. calendula*: $F_{1,321} = 0.55$, $P = 0.46$). For *R. calendula,* there was a significant effect of sex ($F_{1,321} = 21.95$, $P < 0.001$), with males having a larger mean body mass index than females. This difference between sexes was consistent between sites.

The mean percent of birds recaptured ≥2 weeks after initial capture but within the same winter season was lower at MH for all 3 species (Table 1). During the course of the study, the rate of recapture within a winter season for all species combined declined at MH, while at PI the rate remained relatively constant, increasing slightly by the end of the study (Fig. 2). This interaction between site and year was significant (Table 2).

DISCUSSION

The significantly smaller proportion of *P. iliaca* recaptured in subsequent winter seasons at MH may reflect the effect of fire on guilds of birds that forage exclusively on open ground. *Catharus guttatus* also utilizes terrestrial food sources but readily occupies dense understory regrowth. As the understory began to recover after the fire, there was a rapid loss of open ground where *P. iliaca* prefers to feed. It is likely this species lost suitable foraging habitat as dense vegetation began to grow over riparian areas that had burned. Since the winter diet of *P. iliaca* includes many kinds of seeds (Rising 1996), a loss of preferred seed type might also result in a smaller number of birds returning to this site in subsequent winters.

Although we found little evidence the fire adversely impacted body condition of birds

TABLE 2. Logistic regression model estimating the impacts of site and year on within-year recapture rate for 3 species during 6 winter seasons at Muddy Hollow (MH) and Pine Gulch (PI), Marin County, CA, 1995–2002.

Variables	df	β	$s_{\bar{x}}$	χ^2	P
Intercept	1	–1.15	0.16	50.40	<0.0001
Site	1	0.12	0.25	0.24	0.62
Year	1	0.06	0.04	2.09	0.15
Site × Year	1	–0.17	0.07	5.43	0.02

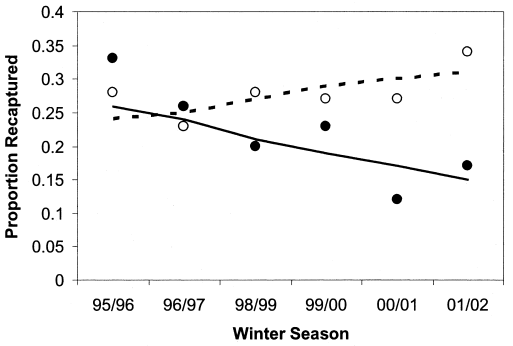

Fig. 2. Proportion of birds recaptured during winter for 3 species combined (*Passerella iliaca, Catharus guttatus,* and *Regulus calendula*) as predicted from the logistic model (logit[$\pi(x)$] = –1.0305 – 0.1123x) for burned (MH = solid line) and (logit[$\pi(x)$] = –1.1526 + 0.060x) for unburned (PI = dashed line) riparian sites, Marin County, CA, 1995/96 through 2001/02. The actual proportions of birds recaptured ≥2 weeks after initial capture during a winter season are shown as solid circles for MH and open circles for PI. No capture data are available for 1997/98.

wintering at MH, there was a significant decrease over time in within-year recapture rates at MH. During the 1st winter after the fire, very little vegetation had grown back within the burned area of the park, even within the riparian habitat at MH. Since all 3 bird species breed elsewhere, site-faithful individuals returning to nonbreeding areas as well as immature birds arriving for the first time in fall would have found a landscape dramatically altered and structurally much simpler than comparable unburned habitat. Yet the small difference between sites in within-year recapture rate this 1st winter suggests that, contrary to expectations, sufficient resources were available for birds to remain within the study area through the winter. The decline over time in within-year recapture rates at MH was somewhat surprising, since this site witnessed a net increase in understory vegetation over the study period (Gardali et al. 2003). *Passerella iliaca* contributed to this decline, however, further suggesting a decrease in appropriate foraging habitat for this species as the understory became dense in the years after the fire. In contrast, the canopy tree *Alnus rubra* initially survived the fire but then began to die after 3–4 years. Widespread mortality of this dominant tree species might have reduced the number of birds that initially fixed on this site after fall arrival and remained there through a winter season. Site fixation by sparrows was found to occur primarily in late winter by Ralph and Mewaldt (1975), although evidence is lacking for a distinct sensitive period when site fixation occurs (Ketterson and Nolan 1990). During later seasons of the study, birds initially caught in early winter may have moved out of the MH study area by late winter. Alternatively, birds may have started foraging over a wider area within the burned zone.

The fire burned fast and hot, scorching the riparian understory but leaving the canopy intact. This may explain why foliage-gleaning species such as *R. calendula* were present almost immediately after the fire here, while Blake (1982) observed this species in coniferous woodland during winter only in unburned sites following fire. The higher abundance of foliage-gleaning species in unburned coniferous forests has also been reported during the breeding season (Bock and Lynch 1970, Apfelbaum and Haney 1981, Raphael et al. 1987). As *Alnus rubra* gradually began to fall down at MH, suitability of this site for foliage-gleaning insectivores likely declined, and *R. calendula* may have switched to foraging in nonriparian habitats.

Our study was limited in several important ways that deserve further discussion. First, we were unable to establish long-term field sites in a well-replicated study design, partially because of the limited number of riparian systems that burned in the fire. Our conclusions

are therefore based on single burned and unburned sites, which makes it difficult to attribute the changes we observed to the fire rather than to other site-specific differences. Attempts to generalize these results to other riparian systems should be made with caution and should address the potentially different effects of natural and human-ignited fires. Second, it is important to consider the habitat that borders riparian sites when examining the effects of fire. Riparian surrounded by coniferous woodland, for example, might contain a heavier fuel load in the form of woody debris, and the accumulation of leaf litter and woody debris may affect fire severity and the fate of riparian trees (Ellis 2001). The riparian at MH is surrounded by a mosaic of habitats classified as coastal scrub and mixed evergreen forest (Shuford and Timossi 1989). This habitat also burned, and the intact riparian canopy at MH was the only green vegetation present immediately afterward. This may have contributed to the abundance of all 3 bird species at the MH site soon after the fire. Passage of a fire through the riparian at PI would be different, since this site is bordered by a lagoon on one side. Thus, the effects of fire are confounded by landscape structure. Finally, the unintentional nature of this fire prevented us from obtaining valuable pre-fire data. Researchers interested in the effects of fire on avian ecology should consider prescribed burns as experimental treatments, backed by at least 5 years of pre-fire data to help interpret population fluctuations. Even without pre-fire data, however, small-scale studies such as this can be used in meta-analyses that combine results of many individual studies.

The PRNS has recently conducted research to determine how prescribed burns will play a role in future ecosystem management within the park. While human-ignited fires historically occurred at mean intervals of 7.7 to 8.5 years in the Douglas-fir (*Pseudotsuga menziesii*) forests of PRNS during the 18th and 19th centuries, there is little evidence of fire in recent decades (Brown et al. 1999). The historical pattern of fire within riparian communities at this site is unknown, but recovery of vegetation at MH has been rapid; young *Alnus rubra* are now abundant and a thick understory of shrubs and herbs is present. Our data, together with breeding season data from these sites (Gardali et al. 2003), suggest that the effects of fire on songbirds are complex and will differ among species. In general, however, songbirds at this riparian site appear to be resilient to fire during the breeding season (Gardali et al. 2003) and the nonbreeding season.

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