

BLACK-CHINNED HUMMINGBIRD NEST-SITE SELECTION AND NEST SURVIVAL IN RESPONSE TO FUEL REDUCTION IN A SOUTHWESTERN RIPARIAN FOREST

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Abstract. Despite widespread efforts to avert wildfire by reducing the density of flammable vegetation, little is known about the effects of this practice on the reproductive biology of forest birds. We examined nest-site selection and nest survival of the Black-chinned Hummingbird (*Archilochus alexandri*) in New Mexico riparian forests treated or not for fuel reduction. In untreated plots the hummingbirds frequently nested in exotic trees such as saltcedar (*Tamarix* spp.) and Russian olive (*Eleagnus angustifolia*). Following fuel reduction, they increased use of cottonwood (*Populus deltoides* ssp. *wislizenii*) as a nest substrate and nested at greater heights. Though fuel reduction influenced habitat and nest-site selection, it did not immediately affect nest survival. A logistic exposure model containing effects of year and interaction of nest height and substrate explained nest survival better than did other models. Estimates of daily nest-survival rates from this model varied by year from 0.970 (95% CI: 0.949–0.982) to 0.992 (95% CI: 0.983–0.996), corresponding with period survival rates of 31% (95% CI: 13.7%–50.1%) to 73% (95% CI: 52.1%–85.9%). In addition, in all substrates except saltcedar, nest survival decreased with nest height. Our relatively high nest-survival estimates suggest that the riparian forest along the Middle Rio Grande provides high-quality nesting habitat for this species. Fuel reduction, however, reduces nest-site availability and can lower nest survival by removing potential nest sites in the forest understory, forcing hummingbirds to nest at greater heights where predation risk is higher.

Key words: *Archilochus alexandri*, Black-chinned Hummingbird, fuel reduction, nest-site selection, nest survival, riparian.

Selección de Sitios de Anidación y Supervivencia de Nidos de *Archilochus alexandri* en Respuesta a la Reducción del Combustible en un Bosque Ribereño del Sudoeste

Resumen. A pesar de los esfuerzos muy difundidos de evitar los fuegos silvestres mediante la reducción de la densidad de la vegetación inflamable, poco se conoce sobre los efectos de esta práctica sobre la biología reproductiva de las aves de bosque. Examinamos la selección de los sitios de anidación y la supervivencia de los nidos del picaflor *Archilochus alexandri* en los bosques ribereños de Nuevo México, con y sin reducción de combustible. En las parcelas sin tratamiento, los picafloros anidaron frecuentemente en árboles exóticos como *Tamarix* spp. y *Eleagnus angustifolia*. Después de la reducción de combustible, se incrementó el uso de *Populus deltoides* ssp. *wislizenii* como sustrato para los nidos y las aves anidaron a mayores alturas. Aunque la reducción del combustible influyó la selección de hábitat y del sitio de anidación, no afectó inmediatamente la supervivencia de los nidos. Un modelo de exposición logística que incluyó los efectos del año y de la interacción de la altura del nido con el sustrato brindó la mejor explicación de la supervivencia de los nidos. Las tasas de supervivencia diaria de los nidos estimadas con este modelo variaron entre años desde 0.970 (95% IC: 0.949–0.982) a 0.992 (95% IC: 0.983–0.996), correspondiendo a tasas de supervivencia durante el periodo de 31% (95% IC: 13.7%–50.1%) a 73% (95% IC: 52.1%–85.9%). Adicionalmente, en todos los sustratos excepto *Tamarix*, la supervivencia de los nidos disminuyó con la altura del nido. Nuestros estimados de supervivencia de los nidos fueron elevados, lo que sugiere que el bosque ribereño a lo largo de la parte media del Río Grande brinda hábitat de anidación de alta calidad para esta especie. La reducción del combustible, sin embargo, disminuye la disponibilidad de los sitios de anidación y puede bajar la supervivencia del nido mediante la remoción de sitios potenciales de anidación en el sotobosque, forzando a los picafloros a anidar a mayores alturas donde el riesgo de depredación es mayor.

INTRODUCTION

Nest-site availability and nest survival are important components of avian productivity and population growth (Li and Martin 1991, Seather and Bakke 2000, Mattson and Cooper 2007) and are often influenced by the structure and composition of

nesting habitat (Martin and Roper 1988, Martin 1996, 1998, Powell and Steidl 2000). Human management of nesting habitat therefore can affect bird populations. Widespread forest-management practices, such as thinning and harvest, clearly alter the structure and composition of nesting habitat for a variety of bird species (Stephens and Moghaddas 2005). Such changes

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in forest structure have been linked to changes in the abundance of breeding birds (Tomcho et al. 2006), but few studies have related forest management to nest survival (Barber et al. 2001), a demographic which may indicate habitat quality more strongly than does abundance (Van Horne 1983).

As the frequency and intensity of wildfires throughout the U.S. increase, managers have been called upon to reduce fuel loads accumulating from fire suppression and other activities (Agee and Skinner 2005, Youngblood et al. 2005). Treatments involving the mechanical removal of small-diameter trees and shrubs and reduction of litter and debris with controlled low-intensity fires are used to reduce the magnitude and spread of wildfires by increasing crown height and reducing ladder-fuel accumulation (Agee and Skinner 2005). Little is known about the ecological consequences of these activities, however, so there is concern that managers must balance the needs of fire prevention and habitat conservation (Lee and Irwin 2005, Youngblood et al. 2005). Because many forest birds are sensitive to changes in nest-site availability and nest survival, both the positive and negative effects of fuel reduction on breeding birds must be identified.

The riparian forests of the Middle Rio Grande in central New Mexico (Whitney 1996) constitute the most extensive cottonwood gallery in the southwestern U.S. (Howe and Knopf 1991), providing important habitat for a variety of breeding, migrating, and wintering birds (Farley et al. 1994, Smith et al. 2006). The Middle Rio Grande forests are also notable for catastrophic wildfires that have increased in frequency and intensity, in part because of accumulation of woody debris and exotic vegetation in the understory (Stuever et al. 1995, Finch et al. 2006). These fires drastically alter vegetation structure and composition, promote the spread of exotic species, and threaten property in rural and urban areas (Busch 1995, Smith et al. 2006, 2007, 2009). Throughout the region various fuel-reduction programs have been proposed and implemented to prevent ecological and economic consequences (Finch et al. 2006, Middle Rio Grande Bosque Community Wildfire Protection Plan 2007).

Hummingbirds are abundant in the southwestern U.S. (Wethington and Russell 2003, Wethington et al. 2005). The Black-chinned Hummingbird (*Archilochus alexandri*) nests primarily in riparian forests, where, for centuries, humans have altered the structure and composition of habitat (Scurlock 1998, Periman and Kelly 2000). Despite the importance of riparian forests to southwestern hummingbirds, hummingbirds' nest survival has been little studied in these areas (Baltosser 1986). In addition, the few studies have been limited in scale and have not addressed effects of habitat change. In the heavily managed forests of the Middle Rio Grande the Black-chinned Hummingbird is found in high densities (Finch et al. 2006) and is therefore ideal for evaluating the effects of habitat restoration on the breeding biology of riparian birds.

As part of a multi-agency large-scale fuel-reduction experiment, we examined the response of Black-chinned

Hummingbirds to habitat alterations caused by fuel reduction. On treated and untreated plots, we compared nest-site selection and nest survival, measured vegetation structure and composition, and related these variables to nest survival. We used model selection to determine if variation in nest survival was best explained by (1) temporal effects that are independent of fuel reduction, (2) changes in nest-site selection that result from fuel reduction, or (3) plot-scale changes in forest structure and composition. Our goal was to provide guidelines for managers seeking to reduce wildfire risk while protecting habitat important to breeding birds.

METHODS

STUDY AREA

We conducted our study in riparian forest along the Middle Rio Grande in central New Mexico. Our study area borders Albuquerque on the north and extends approximately 140 km south to Bosque del Apache National Wildlife Refuge. The Middle Rio Grande flows south through several basins within the Rio Grande Rift Valley (Whitney 1996). This valley includes a metropolitan area, several Native American pueblos, numerous farms and ranches, and state and federal wildlife refuges. The forests along both banks of the river are bordered by a variety of land-cover types including agricultural fields, desert scrub, residential areas, and managed wetlands.

Following European colonization, the spatial characteristics of the riparian forest throughout the Middle Rio Grande valley were heavily altered. Historically, the river meandered across the floodplain, supporting a dynamic mosaic of wetlands and riparian vegetation in multi-aged stands. In the late 19th century widespread livestock grazing and upland logging increased the magnitude and frequency of floods. By the end of the 20th century, several dams had been constructed along the Middle Rio Grande and the active river channel was confined between levees to reduce flooding. Numerous conveyance canals were constructed throughout the valley to aid transport of water for irrigation. These structures disconnected the river from much of the floodplain (Scurlock 1998). As a result, most riparian vegetation in the valley is now located between the levees and the active river channel. What was once a naturally fragmented multi-aged forest is now a continuous canopy of large and decadent cottonwood trees undergoing little recruitment (Howe and Knopf 1991, Whitney 1996, Molles et al. 1998).

The riparian forests at our study sites consisted of Rio Grande cottonwood (*Populus deltoides* ssp. *wislizenii*) canopy with some Goodding's willow (*Salix gooddingii*) and boxelder (*Acer negundo*). Saltcedar (*Tamarix* spp) and Russian olive (*Eleagnus angustifolia*) are among several exotic species established throughout the forest understory, with saltcedar more prevalent in the southern reaches and Russian olive more common in the north (Knopf and Olson 1984). Native

understory shrubs include coyote willow (*Salix exigua*), New Mexico olive (*Foresteria neomexicana*), and seepwillows (*Baccharis* spp.).

We established three blocks in the northern, middle, and southern reaches of our study area. U.S. Forest Service staff and management agencies selected study blocks that met the following criteria: high fuel loads, access by levee roads, and minimal disturbances such as grazing. Each block was divided into four plots for a total of 12 experimental plots. The U.S. Fish and Wildlife Service owns and manages two of the southern plots, located on Bosque del Apache National Wildlife Refuge. The remaining southern plots and all middle plots are owned and managed by the Middle Rio Grande Conservancy District. The northern plots are on land owned by this agency but managed by the city of Albuquerque and New Mexico State Parks.

We used a randomized block design to assign the four experimental treatments (Finch et al. 2006). In each block, we randomly selected one of the four plots as a control where no fuel reduction took place, and we assigned three treatment types to the remaining plots. These treatments, which took place during the nonbreeding season, were initiated in 2002 and completed in 2004 (Table 1). Land managers were responsible for carrying out treatments in each block. Under the first treatment (CHH), exotic shrubs and woody debris

were cut and mechanically chipped and herbicide was applied twice to the root crowns of exotic species. The second treatment (CHPH) was similar to the first, but native shrubs were planted following removal of exotic species. Under the third treatment (PHFH), exotic shrubs and woody debris were cut, piled, and burned, and herbicide was applied twice to the root crowns of exotic species. The middle and southern blocks received all three treatments, but the northern block did not receive the PHFH treatment. Instead, two plots there received the CHH treatment (Table 1).

HABITAT MEASUREMENTS

We measured vegetation structure and composition at each plot before and after fuel reduction. We measured live vegetation at eight preestablished sampling points within each experimental plot (Finch et al. 2006). At each sampling point we established a 4-m-diameter plot placed in a randomly assigned direction from the sampling point. We identified and counted all shrubs and trees within the sampling plots and measured their diameter at breast height (DBH). We classified all plants with a DBH <5 cm as shrubs or saplings and all plants with a DBH ≥5 cm as trees. For each treatment type, we calculated the mean number of individuals per sampling plot in each size class and extrapolated this value to number of individuals per hectare.

TABLE 1. Fuel-reduction status of study plots and number of Black-chinned Hummingbird nests monitored along the Middle Rio Grande, New Mexico, 2000–2007.

Plot	Land manager(s) ^a	Plot type	Treatment year	Fuel reduction ^b	Number of hummingbird nests	
					Pre-treatment	Post-treatment
North 1	MRGCD, COA, NMSP	Control	—	None	140	—
Middle 4– Middle 7 ^c	MRGCD	Control	—	None	88	—
South 1	MRGCD	Control	—	None	25	—
North 3	MRGCD, COA, NMSP	Treatment	2003	CHH	33	21
North 4	MRGCD, COA, NMSP	Treatment	2002	CHH	41	81
Middle 1	MRGCD	Treatment	2003	CHH	47	31
South 4	USFWS	Treatment	2002	CHH	3	1
North 2	MRGCD, COA, NMSP	Treatment	2002	CHPH	30	46
Middle 3	MRGDC	Treatment	2003	CHPH	36	9
South 2	MRGCD	Treatment	2002	CHPH	9	26
Middle 2	MRGCD	Treatment	2004	PHFH	35	11
South 3	USFWS	Treatment	2002	PHFH	7	5

^aCOA, city of Albuquerque; MRGCD, Middle Rio Grande Conservancy District; NMSP, New Mexico State Parks; USFWS, U.S. Fish and Wildlife Service.

^bCHH, removal of exotic shrubs and woody debris followed by two applications of herbicide; CHPH, removal of exotic shrubs and woody debris followed by herbicide and planting of native shrubs; PHFH, removal of exotic shrubs and woody debris followed by herbicide and fire.

^cPlot MI4 was burned in a wildfire prior to the 2002 season and was replaced by MI7.

NEST MONITORING

From 2000 to 2007, field crews searched for nests of Black-chinned Hummingbirds in all plots. Nest-searching periods differed from year to year but generally began during the first week of May and ended by the third week of August. Nests were located by flushing birds or by following them to their nests. We marked the location of each nest with flagging tape several meters away. We recorded the location of the nest with a hand-held GPS receiver and wrote the direction to the nest on the tape to allow revisits every 3 to 5 days until the nesting attempt was complete. The stage of some nests was difficult to observe because of height or visual obstructions; however, each nest was visited by multiple observers, including some with many years of experience at these study sites. Nest fates were interpreted by one individual to maximize accuracy and consistency in determination of nest survival. We assumed that empty nests were successful if nestlings within 4 days of fledging age had been observed in the nest during the last nest check, if fledglings were seen or heard in the area, or if we observed fecal material inside the nest. We assumed that empty nests were not successful if they were empty >4 days prior to fledging, if the nest was greatly disturbed, or if fragments of egg or nestlings were seen in or near the nest. We omitted nests from our survival analyses if they were abandoned during nest building or failed because of human interference. Upon completion of each nesting attempt, we measured nest height and identified the species and condition (live or dead) of the nest plant.

STATISTICAL ANALYSES

We used one-way analysis of variance (ANOVA) in SAS PROC GLM (SAS Institute 2004) to test for differences in habitat variables between control and treatment plots. We used Tukey's studentized range tests to make pairwise comparisons of variables measured in control, pre-treatment, and post-treatment sites, setting $P < 0.05$ for significance. We first compared habitat variables that were measured prior to fuel reduction to test for pre-treatment differences between control and fuel-reduction plots, which could confound post-treatment comparisons. We then tested for differences between control and fuel-reduction plots measured post-treatment to describe effects of fuel reduction on habitat structure and composition. We used ANOVA to test for effects of fuel reduction on the hummingbirds' nest-site use. We compared nest height and percent use of each substrate (nest-plant species) in control, pre-treatment, and post-treatment plots.

To describe the difference in structure and composition of woody vegetation, we used principal-component analysis (PCA) in SAS PROC FACTOR to collapse 14 variables describing the density of native and exotic vegetation in two size classes into a smaller set of noncorrelated components that describe variation in plots before and after fuel reduction. We

interpreted the biological meaning of the principal components, which explain the greatest amount of combined variation within the vegetation data, by examining the component loadings of each variable (McGarigal et al. 2000). We calculated the mean scores of each retained component at control and fuel-reduction plots before and after treatments. We incorporated these scores into nest-survival models, described below, to evaluate the effects of vegetation structure and composition while reducing the number of intercorrelated variables in the model set.

We used a multi-stage approach (Dinsmore and Dinsmore 2007) to test for effects of fuel reduction on nest survival and to determine the relative importance of plot- and nest-scale habitat variables. We first used information-theoretic model selection (Burnham and Anderson 2002) to identify the temporal structure of nest survival. We then tested for an effect of fuel reduction by comparing estimates of nest survival at control and treatment plots. We incorporated measurements of vegetation and nest-site use into a final model set to select the best model relating habitat variables to nest survival. Finally, we estimated nest-survival rates across the ranges of variables found in the best-supported temporal and habitat models.

We used the logistic exposure method developed by Shaffer (2004) to determine which temporal variables best explained variation in daily survival rate. In some areas, time-specific variables have been shown to have greater importance to nest survival than variation in habitat (Grant et al. 2005, Davis 2005) and can account for variables such as climate and predator trends that are not modeled with habitat data. We therefore included "year" as a categorical variable and "date" as a continuous variable in our model sets. For "date," we assigned each day of the nesting season a number, beginning with 1 for 30 April, the earliest date that we observed nesting behavior. We assigned each nest-check interval a date by averaging dates across the interval (Shaffer 2004). As trends in nest survival are often nonlinear (Grant et al. 2005), we included quadratic and cubic effects of date, as well as interactions between year and date effects. Because some nests were at heights that made it difficult to determine nest age or stage, we did not include these variables in temporal models. Omission of these variables can bias nest-survival estimates (Shaffer and Thompson 2007), but we assumed that these biases were the same in treated and untreated forest because the ranges of nest heights in treated and untreated sites were similar. For this analysis we included all observation intervals that began with at least one egg laid in the nest. When an interval ended with the completion of a nesting attempt, we used the midpoint between checks as the termination date of that interval (Mayfield 1975).

We used SAS PROC GENMOD to determine which temporal model received the most support from the data (Burnham and Anderson 2002, Shaffer 2004). For each model, we calculated Akaike's information criterion adjusted for sample

size (AIC_c) to quantify the level of support. We identified the model with the lowest AIC_c value as the best-supported model in the set. We ranked all models with ΔAIC_c and Akaike weights (w_i), which represent the relative degree of support for each model in the set (Burnham and Anderson 2002).

To test for effects of fuel reduction on nest survival, we estimated survival rate in plots pooled into four categories: control plots before onset of fuel reduction at treatment plots, treatment plots before fuel reduction, control plots after fuel reduction at treatment plots, and treatment plots after fuel reduction. We chose this method in lieu of incorporating treatment status into logistic exposure models or null-hypothesis tests because the individual nest was the sampling unit and treatments were applied to plot-level replicates, limiting our ability to infer effects of fuel reduction on the population of hummingbirds. To ensure that nest survival was adequately modeled in each plot type, we incorporated temporal variables from the best-supported model in the above analysis into these estimations. We used the ESTIMATE function in SAS to estimate daily survival rates in treated and untreated forests, accounting for temporal variation as recommended by Shaffer and Thompson (2007). We adjusted daily survival rates to period survival, the predicted survival rate of all nests per year or across years, by raising daily survival rate to the power of number of days in the hummingbirds' nesting cycle, which we estimated as 38 on the basis of our observations and other studies summarized by Ehrlich et al. (1988). We calculated 95% confidence intervals for daily and period survival estimates. We determined that survival of nests in treated and untreated forests differed if confidence intervals did not overlap. We did not test for differences in nest survival among the three treatment types because numbers of nests found in some post-treatment plots were low (Table 1).

Because in an examination of nest survival multiple scales should be considered (Chalfoun et al. 2002, Stephens et al. 2003), we constructed habitat models with variables measured at the scale of the nest or plot. Nest-scale variables were measures of nest-site use, and their values were unique to each nest. Plot-scale variables had values shared by all nests within a plot and described vegetative composition and structure. Below, we describe our justification for constructing each model.

Nest-scale habitat models described the effect of riparian vegetation use on nest survival. The three most commonly used substrates across all sites were cottonwood, Russian olive, and saltcedar (Finch et al. 2006). We predicted that if birds choose a substrate safer than another (Martin and Roper 1988), there would be support for models containing nest substrate. The categorical variable "substrate" had four values: cottonwood, Russian olive, saltcedar, or other. "Nest height" was a continuous variable reflecting nest placement. If accessibility of nests to predators affects nest survival, we predicted nest survival would increase or decrease with nest height. We also

constructed models containing interactions between nest height and nest substrate to determine if effects of height differ by nest-plant species. To ensure that nest-scale habitat models accurately described nest survival, in addition to habitat variables we constructed additional models containing the variable(s) from the best temporal model. These methods resulted in four nest-scale habitat models: one containing effects of nest site, one containing the interaction of nest substrate and nest height, and two containing nest-site and temporal variables.

We constructed a plot-scale habitat model containing measurements of variation in vegetation structure and composition, which are often associated with variation in nest survival (Martin and Roper 1988, Martin 1996, 1998, Powell and Steidl 2000). This model contained mean principal-component scores for each plot. We predicted support for models containing PCA scores if the composition and structure of the riparian forest, altered by fuel reduction, influences nest survival. We also added a model containing principal-component scores and the best-supported temporal variable(s).

Our procedure resulted in a final set of eight habitat models: six containing plot- and nest-scale habitat variables, a global model with all variables, and the best-supported temporal model, which we included as a null model. We tested fit of the global model with Hosmer and Lemeshow (1989) goodness-of-fit tests and again calculated ΔAIC_c to select the model best supported across scales and variable types.

To determine the strength and direction of their effects on nest survival, we calculated odds ratios and their confidence intervals for continuous variables found in models within two ΔAIC_c units of the best-supported temporal and habitat models (Burnham and Anderson 2002). In cases where several models were supported by the data, indicating high model uncertainty, we used model-averaged parameter estimates and unconditional standard errors to calculate odds ratios and their confidence intervals (Burnham and Anderson 2002). When categorical variables or their interaction were found in supported models, we evaluated their effects by estimating nest-survival rate and 95% confidence intervals at each of their levels.

RESULTS

HABITAT VARIABLES

All three fuel-reduction treatments decreased density of exotic vegetation (Fig. 1). Russian olive shrubs were rare at all plots, but Russian olive trees were present at all plots before treatment, and their density was significantly reduced after treatment ($F_{3,175} = 19.98, P < 0.0001$). Saltcedar was the most abundant shrub before treatment, and its density was also reduced following fuel reduction ($F_{3,176} = 10.08, P < 0.0001$). Before treatment, saltcedar trees were less abundant than saltcedar shrubs; their density was reduced after treatment as well ($F_{3,175} = 21.5, P < 0.0001$). Cottonwood saplings were

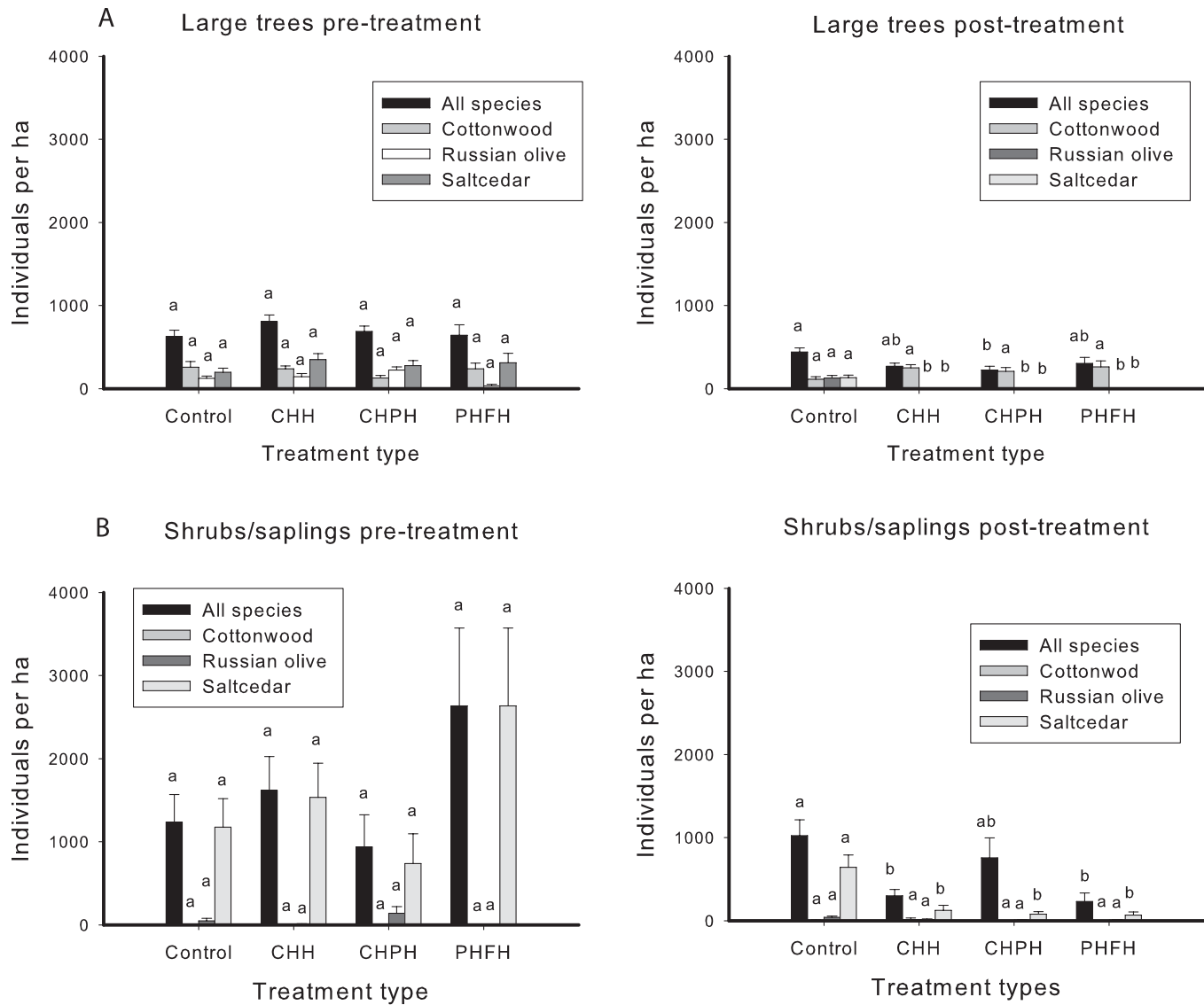


FIGURE 1. Comparisons of vegetation variables describing control and fuel-reduction plots along the Middle Rio Grande, New Mexico, measured from 2000 to 2007. Values are the number of individuals per circular plot of adjusted to number of individuals per hectare. Bars represent means and 95% confidence intervals. For each species of woody vegetation, differing letters indicate significant ($P < 0.05$) differences between treatment types. Treatment types: CHH, removal of exotic shrubs and woody debris followed by two applications of herbicide; CHPH, removal of exotic shrubs and woody debris followed by herbicide, then planting of native shrubs; PPHH, removal of exotic shrubs and woody debris followed by herbicide and fire. Values have been changed from the number of individuals per plot to the number of individuals per hectare.

present only in post-treatment sites, and numbers of cottonwood trees in control and post-treatment plots did not differ ($F_{3,175} = 2.29, P = 0.08$). Before fuel reduction, overall tree abundance in control and treatment plots did not differ ($F_{3,175} = 1.02, P = 0.39$), but after fuel reduction it did ($F_{3,175} = 3.66, P = 0.01$). Overall shrub and sapling abundance at control and post-treatment sites also differed ($F_{3,176} = 5.58, P = 0.001$), with shrub and sapling density greater in control plots than in all post-treatment plots except for those receiving the CHPH treatment (Fig. 1b).

We retained the first three principal components that explained 63% of the variation in woody vegetation. On the basis of component loading, we interpreted component one (PCA1) as representing a gradient in shrub cover from native to exotic. Component two (PCA2) represented a gradient from seepwillow, cottonwood, and native trees to exotic trees. Component three (PCA3) represented a gradient in cover of New Mexico olive, driven primarily by fuel-reduction plot 2 in the southern block, where the cover of this species was much higher than at other sites. We added the component scores from the first two

TABLE 2. Percent use of nesting substrates by Black-chinned Hummingbirds at control plots, fuel-reduction plots before treatment, and fuel-reduction plots after treatment along the Middle Rio Grande, New Mexico, 2000–2007. Values within a row that do not share letters are significantly ($P < 0.05$) different.

Substrate	Control	Fuel reduction		P
		Pre-treatment	Post-treatment	
Russian olive, <i>Eleagnus angustifolia</i>	0.35 A	0.32 B	0 B	<0.001
Cottonwood, <i>Populus deltoides</i> ssp. <i>wislizenii</i>	0.35 A	0.23 B	0.87 C	<0.001
Saltcedar, <i>Tamarix</i> spp.	0.15 A	0.31 B	0.0 C	<0.001
White mulberry, <i>Morus alba</i>	0.04	0.05	0.01	0.11
Siberian elm, <i>Ulmus pumila</i>	0.02	0.01	0.01	0.25
Tree of heaven, <i>Ailanthus altissima</i>	0.02	0.03	0.01	0.26
Boxelder, <i>Acer negundo</i>	0.02 A	0 B	0 B	0.004
Goodding’s willow, <i>Salix gooddingii</i>	0.004	0.01	0.004	0.78
Shrub snag	0.02 AB	0.03 A	0 B	0.04
Tree snag	0.02 AB	0 A	0.04 B	0.005
New Mexico olive, <i>Foresteria neomexicana</i>	0 A	0.01 A	0.05 B	0.001
Honey locust, <i>Gleditsia triacanthos</i>	0	0.01	0	0.14

principal components to logistic exposure models of habitat at the plot scale. We did not add the third component because its effects could be correlated with other variables specific to south plot 2.

NEST-SITE USE

Patterns of the Black-chinned Hummingbird’s nest-site selection changed in response to fuel reduction. The birds built a higher percentage of nests in cottonwoods in the post-treatment plots than in control or pre-treatment plots (Table 2). A larger percentage used Russian olive and saltcedar as substrates in control and pre-treatment plots than in post-treatment plots (Table 2). New Mexico olive was the only native shrub used as substrate following fuel reduction, and all nests constructed in this species were located in south plot 2. Mean nest height was greater in post-treatment plots (8.28 m, $n = 217$) than in control (4.85 m, $n = 244$) or pre-treatment (3.92 m, $n = 235$) plots ($F_{2, 693} = 86.8, P < 0.0001$).

NEST SURVIVAL

From 2000 to 2007, we observed 635 hummingbird nests over intervals sufficient for logistic exposure analysis. Overall apparent nest survival was 61.1%. Of the 237 nests known to have failed, 62% failed because of an undetermined cause, 21.5% failed because of predation, 8.4% failed because of weather, 2.9% were abandoned at a late stage or failed because of the female’s mortality, 2.1% were consumed by fire, 1.7% contained unviable eggs, and 0.8% failed because of starvation.

The best-supported temporal nest-survival model represented an effect of year on survival (Table 3). Model-derived estimations of daily survival rates varied from a low of 0.970 in 2006 to a high of 0.992 in 2004, corresponding to a period survival rate of 31% in 2006 and 73% in 2004 (Fig. 2). Confidence intervals of some annual estimates did not overlap others,

indicating a considerable effect of year on nest survival. The model containing effects of year and date received some support as well, while the constant-survival model received very little support (Table 3). Odds ratios calculated from model-averaged parameter estimates of date indicated that nest survival increased as the season progressed, but confidence intervals overlapped 1, indicating a weak effect on nest survival. We therefore included only the variable “year” to represent temporal effects in the habitat-model set.

Nest-survival estimates in control plots before and after fuel reduction were similar. Survival estimates in fuel-reduction plots were lower after treatment than before treatment, but confidence intervals of fuel-reduction plots overlapped those of control plots both before and after treatment (Fig. 3).

TABLE 3. Selection results for models describing temporal trends in nest survival of Black-chinned Hummingbirds along the Middle Rio Grande, New Mexico, 2000–2007.

Model ^a	K ^b	ΔAIC_c ^c	w_i
S(year)	8	0.0	0.46
S(year, date)	9	1.23	0.25
S(year × date)	16	2.52	0.13
S(year, date ²)	10	3.20	0.09
S(year, date ³)	11	4.90	0.04
S(year × date ²)	17	6.31	0.02
S(year × date ³)	18	9.38	0.004
S(.)	1	14.55	0.003

^aModel terms: S, survival; year, year of nesting attempt; date, average date of observation interval; date², quadratic effect of date; date³, cubic effect of date; (.), constant survival.

^bNumber of parameters.

^cAIC_c of the top model was 1806.06.

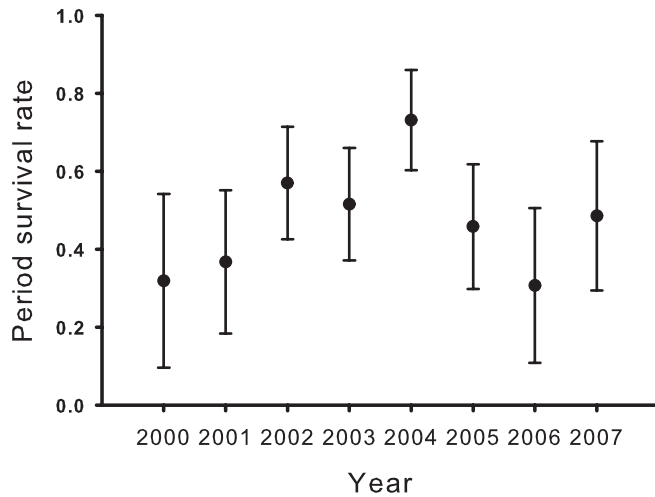


FIGURE 2. Model-based estimates of annual survival of Black-chinned Hummingbird nests along the Middle Rio Grande, New Mexico, 2000–2007. Bars represent means and 95% confidence intervals.

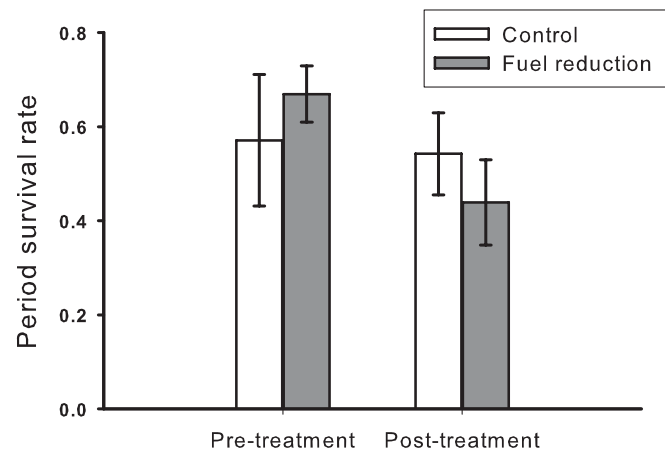


FIGURE 3. Model-based estimates of period survival rate of Black-chinned Hummingbird nests in control and fuel-reduction plots before and after treatments along the Middle Rio Grande, New Mexico, 2000–2007. Bars represent means and 95% confidence intervals.

The final habitat-model set contained eight models with effects of year, nest-scale variables, plot-scale variables, combinations of year and nest-scale effects, and combinations of year and plot-scale effects (Table 4). The goodness-of-fit test showed that the global model fit the data ($\chi^2 = 8.33$, $df = 8$, $P = 0.401$). The best-supported habitat model contained nest-scale and temporal variables, which were effects of year and the interaction between nest height and nest substrate (Table 4). Estimates of daily survival rate derived from this model indicate that nest survival was negatively associated with nest

height in all substrates except saltcedar, but the effects of this interaction were somewhat weak, as judged by high overlap of confidence intervals (Fig. 4). Model-averaged parameter estimates indicated that overall nest survival decreased with height, but confidence intervals of the odds ratios overlapped 1. Estimations of period survival rate for nests constructed at mean heights in the three most commonly selected substrates indicated that nest survival was lower in cottonwood than in Russian olive or saltcedar, though there was some overlap of confidence intervals (Fig. 5).

TABLE 4. Selection results for the final set of habitat models describing survival of Black-chinned Hummingbird nests along the Middle Rio Grande, New Mexico, 2000–2007.

Model	Variables ^a	<i>K</i>	ΔAIC_c^b	w_i
Nest-scale habitat use with interaction and temporal variables	Nest height × substrate, year	15	0.0	0.79
Global	Nest height, substrate, nest height × substrate, PCA1, PCA2, year	17	3.16	0.16
Nest-scale habitat use with temporal variables	Nest height, substrate, year	12	6.45	0.03
Nest-scale habitat use with interaction	Nest height × substrate	8	8.59	0.01
Nest-scale habitat use	Nest height, substrate	5	13.56	0.001
Null	Year	8	14.82	0.001
Plot-scale habitat and temporal variables	PCA1, PCA2, year	13	18.35	0.0
Plot-scale habitat variables	PCA1, PCA2	3	30.52	0.0

^a Terms: year, year of nesting attempt; PCA1, score of the first principal component of woody vegetation structure and composition; PCA2, score of the second principal component of woody vegetation structure and composition; nest height, height, in meters, of hummingbird nests; substrate, species of plant supporting nest.

^b AIC_c of the top model was 1645.17.

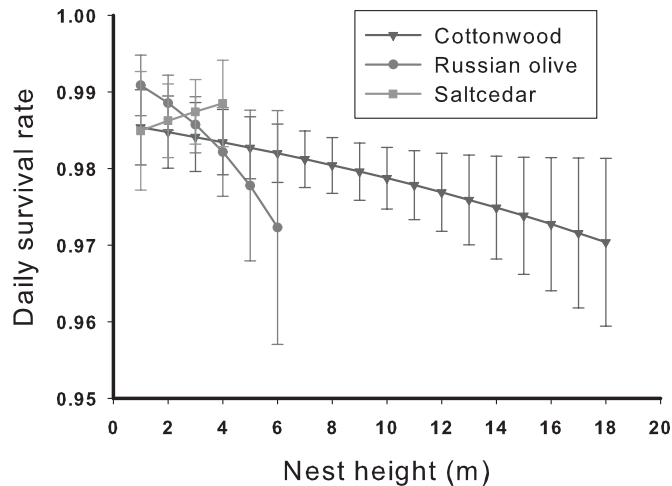


FIGURE 4. Model-based predicted relationship of height and daily survival rate of Black-chinned Hummingbirds nests in the three substrates most commonly used along the Middle Rio Grande, New Mexico, 2000–2007. Bars represent 95% confidence intervals.

DISCUSSION

Fuel reduction altered the structure and composition of our riparian forest study sites, and these changes were reflected in the Black-chinned Hummingbird's patterns of nest-site selection. Prior to fuel reduction, riparian forest plots consisted of a dense understory below a continuous cottonwood canopy. Following treatment, fuel-reduction plots resembled open woodlands with low densities of native shrubs. The removal of exotic vegetation resulted in hummingbirds shifting from nesting in both understory and canopy to nesting primarily in the cottonwood canopy.

Nest survival is an important demographic variable that could be altered by habitat management. Our estimates of the hummingbird's annual nest survival ranged from 31% to 73%. Most of these estimates are greater than apparent survival rates measured in other riparian habitats in New Mexico and Arizona, which ranged from 17% to 46% by year and study site (Baltosser 1986, Greeney and Wethington 2009). Nest survival is only one component of population dynamics, but an understanding of its variation is needed for evaluation of habitat quality for relatively short-lived species such as hummingbirds, whose populations are sensitive to variation in productivity (Sæther and Bakke 2000). Conservation of southwestern hummingbirds requires the identification of suitable breeding habitat (Wethington et al. 2005). In terms of nest survival, the riparian forest of the Middle Rio Grande appears to provide such habitat for the Black-chinned Hummingbird, as nest-survival rates in control and fuel-reduction plots after treatment were similar. We therefore did not find evidence that fuel reduction strongly affected this component of habitat quality.

Predation has been identified as the leading cause of failure of hummingbird nests in southwestern riparian forests (Baltosser 1986). The best-supported habitat model showed that

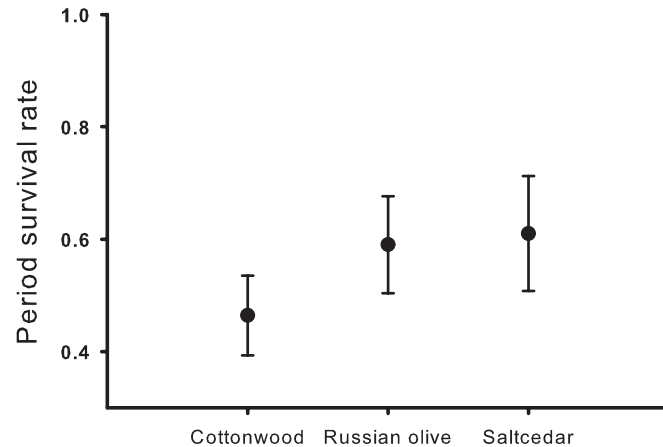


FIGURE 5. Model-based estimates of period nest survival at mean nest heights in each of the three substrates most commonly used by Black-chinned Hummingbirds along the Middle Rio Grande, New Mexico, 2000–2007. Bars represent 95% confidence intervals.

on most substrates hummingbirds' nest survival decreased as nest height increased, indicating that nests built in the forest canopy are at greater risk of predation than those built in the understory. Though confidence intervals suggest that the effects of substrate and height are weak, the high level of support for this model over the null or global models shows that these effects warrant attention. Baltosser (1983) also found an inverse relationship between nest height and nest survival of the Black-chinned Hummingbird in riparian habitat and attributed this pattern to avian nest predators. Hummingbird nests located high in cottonwood trees are at risk of predation by birds of various sizes, including passerines (Baltosser 1986). Along the Middle Rio Grande, hummingbird eggs and nestlings could be consumed by a diversity of birds that we observed in the forest, such as the Cooper's Hawk (*Accipiter cooperii*), American Kestrel (*Falco sparverius*), Yellow-billed Cuckoo (*Coccyzus americanus*), Western Screech-Owl (*Megascops kennicottii*), Greater Roadrunner (*Geococcyx californianus*), Ash-throated Flycatcher (*Myiarchus cinerascens*), Western Kingbird (*Tyrannus verticalis*), Summer Tanager (*Piranga rubra*), Black-headed Grosbeak (*Pheucticus melanocephalus*), and Bullock's Oriole (*Icterus bullockii*). Most of these birds forage in the cottonwood canopy, which could explain the lower nest-survival estimates in that stratum.

The negative relationship we observed between nest height and survival contradicts studies of other species in western riparian forests. Along the upper Gila River, the productivity of the Willow Flycatcher (*Empidonax trailii extimus*) increases with nest height, a pattern likely driven by cowbird parasitism (Brodhead et al. 2007). Flycatchers selected substrates that allowed nesting at greater heights, suggesting that predation and parasitism decrease with nest height (Stoleson and Finch 2003). In riparian forests in Montana, nest survival of the Dusky Flycatcher (*Empidonax oberholseri*) also increased with nest

height (Carle 2006). The difference in nest height and survival patterns between our site and others may be explained by differences in the habitat quality provided by the dominant tree species (i.e., healthy boxelder along the Gila River, decadent cottonwood along the Rio Grande), differences in predation risk, ability of adults to deter predation, or hummingbirds' not risking parasitism. Additional studies incorporating data from multiple river systems are needed to elucidate factors limiting nest survival of riparian birds (Tewksbury et al. 2006).

Although we did not find that fuel reduction affects hummingbirds' nest survival directly, we did find evidence that it could reduce nest survival indirectly. The best-supported habitat model contained nest-scale variables, suggesting that the nest-scale variables we considered affected nest survival more strongly than did plot-scale variables. In this study we did not quantify visual obstruction of nests, but we have observed that nests in dense, multi-stemmed shrubs are often more difficult to locate than nests built high in cottonwoods. Many cottonwoods along the Middle Rio Grande have canopies that have died back because of advanced age and occasional drought stress (Molles et al. 1998). This continuing canopy loss could decrease the visual obstruction of nests. By removing dense shrubs such as saltcedar and Russian olive, fuel reduction has the potential to decrease this species' nest survival by forcing the birds to nest in canopies of cottonwoods where they may be increasingly visible to predators as the trees continue to senesce. Estimates from the best-supported habitat model suggest that nest survival decreased with nest height in Russian olive but increased with nest height in saltcedar. These patterns may result from differing growth forms of these exotic species in the forest understory. Saltcedars, which tolerate less shade than do Russian olives (Shafroth et al. 1995, Sher et al. 2002), grow with small sapling-like forms under a cottonwood canopy, while Russian olives resemble wide, multi-stemmed shrubs (D. M. Smith, personal observation). Nests located low in saltcedar may therefore be less obscured than nests at similar heights in Russian olive. Alternatively, the positive association of nest height and nest survival in saltcedar could be an artifact of the smaller range of nest heights in this substrate. Additional observations or experiments are necessary for interactions between substrate, nest height, and nest survival to be understood fully.

We found evidence that nest survival was greater in the exotic understory than in the cottonwood canopy. This finding suggests that, following fuel reduction, exotic shrubs should be replaced with native shrubs and saplings to provide nest sites for hummingbirds. Native shrubs planted as part of the treatment at some plots, could have increased nest survival following fuel reduction. Hummingbirds used one species of native understory shrub at only one of these fuel-reduction sites, however, so we could not determine if plantings actually influenced nest survival. Hummingbirds may not have responded to plantings because shrubs had not grown to a size necessary for nest

use during our study. Over a longer period, differences in nest height and nest survival among treatment types may develop, but additional monitoring is needed to detect such a trend.

CONCLUSIONS

The relatively high estimates of nest survival at our study sites suggest that forests along the Middle Rio Grande provide high-quality nesting habitat for the Black-chinned Hummingbird. The quality of this habitat likely results from the dense understory, which provides abundant and relatively safe nest sites. Because this understory also contributes to risk of wildfire, managers must reduce understory density while limiting loss of habitat quality. We found a negative relationship of nest height and survival in cottonwood, the substrate most commonly used after fuel reduction. Exotic vegetation, therefore, should be replaced with native vegetation of low stature, such as New Mexico olive, to prevent decreases in nest survival. As understories recover from fuel reduction, managers should determine if additional native species are selected as nest plants. In addition, studies of other riparian birds and their nest predators are needed to determine if removal of exotic understory affects predation rates, which could offset the gains of planting native shrubs. Fuel-reduction sites should be monitored over a longer term to test for differences in productivity of nesting birds.

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