

Avian Nest Box Selection and Nest Success in Burned and Unburned Southwestern Riparian Forest

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ABSTRACT Riparian forest communities in the southwestern United States were historically structured by a disturbance regime of annual flooding. In recent decades, however, frequency of flooding has decreased and frequency of wildfires has increased. Riparian forests provide important breeding habitat for a large variety of bird species, and the effects of this altered disturbance regime on birds and their breeding habitat is largely unknown. To evaluate effects of high-intensity spring and summer wildfire on the quality of breeding bird habitat in the Middle Rio Grande valley, we measured vegetation structure and composition, avian nest use, and nest success at 4 unburned plots and 4 wildfire plots over a 3-year period. We measured avian nest use and success at nest boxes located in unburned riparian forest plots and plots recently burned by wildfire. Recent wildfire plots (<7 yr after fire) had a much different vegetation structure than unburned plots; an older (>7 yr after fire) wildfire plot more closely resembled its paired unburned plot than did recently burned plots. Ash-throated flycatchers (*Myiarchus cinerascens*) and Bewick's wrens (*Thryomanes bewickii*; hereafter, flycatchers and wrens, respectively) used nest boxes in most of the plots. A model selection procedure applied to logistic regressions showed that frequency of nest box use by flycatchers was positively associated with wildfire, although flycatchers used boxes in unburned plots as well. Wrens showed a preferential use of nest boxes that were in unburned sites and in close proximity to vegetative cover. Growth rates, feeding rates, and fledging mass of flycatchers were similar in wildfire and unburned plots. Growth rates for wrens were slower in wildfire plots, while feeding rates and fledging mass were similar. Nest predation varied between years, was higher for flycatchers than for wrens, and was not directly influenced by wildfire. Model selection showed that predation increased with grass cover, an indicator of forest openness, and decreased with distance to habitat edge. Recovery of dense vegetation appears important in maintaining populations of Bewick's wrens, whereas ash-throated flycatchers were less sensitive to vegetative structure and composition of postfire succession. Postfire management that maintains nest sites in large forest strips would enhance nesting density and success of these cavity-nesting birds in riparian zones. (JOURNAL OF WILDLIFE MANAGEMENT 71(2):411–421; 2007)

DOI: 10.2193/2005-781

KEY WORDS ash-throated flycatcher, Bewick's wren, Middle Rio Grande, riparian vegetation, secondary cavity-nesting, vegetation structure, wildfire.

Disturbances shape the structure of most terrestrial ecosystems and maintain biodiversity of plants and animals (Brawn et al. 2001). Fire is the most common terrestrial disturbance, and researchers have given much attention to its effects on plants and animals in fire-prone habitats (Whelan 1996, Saab and Powell 2005). Though fire has been shown to benefit organisms in fire-prone habitats, it can be catastrophic in systems where fire intervals were historically long and organisms have not adapted to frequent occurrence of fire (Whelan 1996). Few studies have addressed the effects of wildfire on habitats, such as riparian forests, in which fire was not historically the most frequent type of disturbance (Whelan 1996, Dwire and Kauffman 2003). In some western United States riparian forests, human activities such as flood control, agriculture, and recreation have created a situation in which the natural disturbance process of flooding occurs less frequently, and wildfire disturbance, believed to be historically rare, is increasing in frequency. Short- and long-term ecological effects of this shift are largely unknown (Stromberg et al. 2002, Bock and Block 2005).

The importance of western riparian ecosystems to breeding birds is well documented (e.g., Carothers et al. 1974, Knopf et al. 1988). Because riparian vegetation

supports the highest density and diversity of breeding birds of any southwestern vegetation type, as well as many rare and endangered animal species, these forests have long been recognized as important habitat for a variety of bird and other wildlife species (Carothers et al. 1974, Knopf et al. 1988). In many southwestern regions, riparian forests are more structurally complex than adjacent vegetation types and support higher levels of bird diversity (Carothers et al. 1974, Strong and Bock 1990). Scott et al. (2003) demonstrated that geomorphic processes produced by regular flood disturbances maintain structural complexity of riparian forests. Such disturbances promote the establishment of native vegetation, such as cottonwood (*Populus* sp.), which is associated with very high levels of bird diversity (Carothers et al. 1974, Strong and Bock 1990). Removal of flood disturbance has been linked with decreasing structural complexity of riparian vegetation and quality of breeding bird habitat (Shafroth et al. 2002, Scott et al. 2003).

One factor that can limit bird populations is loss or degradation of breeding habitat that results in reduced reproductive success (Sherry and Holmes 1995). In many bird species, reproductive success is regulated by nest site and food availability (Sherry and Holmes 1995). The diversity of vegetative structure and composition in forested habitats impacts availability of nesting and foraging

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substrates and breeding opportunities for birds (Robinson and Holmes 1984). Vegetation composition can also influence nest success by obscuring nests from predators or attracting nest predators (Martin and Roper 1988, Powell and Steidl 2000). Changes in riparian habitat structure and composition will likely affect bird populations by altering foraging substrates, nest site availability, and nest predation rates.

Human-induced changes in southwestern riparian systems include the introduction and spread of exotic shrub species (Knopf and Olson 1984, Bock and Block 2005) and the construction of dams that have altered hydrological regimes (Shafroth et al. 2002). Natural flood regimes historically maintained native vegetation; changes in this regime and spread of exotic vegetation have resulted in altered forest structure (Howe and Knopf 1991). In southwestern riparian forests, establishment of pyrophilic exotic shrubs, such as saltcedar (*Tamarix ramosissima*), and accumulation of woody debris have created conditions conducive to catastrophic wildfires (Dwire and Kauffman 2003). Due to these changes and increasingly dry conditions, it is conceivable that wildfire may replace flooding as the primary disturbance regime in southwestern riparian forests (Shafroth et al. 2002).

There is a substantial literature that relates fire and altered disturbance regimes to habitat quality for birds in habitats such as grasslands and upland forest (Brawn et al. 2001, Saab and Powell 2005). Researchers, however, have not addressed the response of riparian breeding birds to wildfire (Bock and Block 2005). To evaluate effects of wildfire on riparian breeding bird habitat, we measured vegetation structure and composition in unburned and burned riparian forest sites and monitored nests of 2 species of secondary cavity-nesting birds (ash-throated flycatcher [*Myiarchus cinerascens*] and Bewick's wren [*Thryomanes bewickii*]), using nest boxes to determine how changes in vegetative structure and composition affect nest site selection and nest success. If wildfire had a negative effect on the quality of breeding bird habitat, we predicted that fewer birds would nest in wildfire plots, nest success would be lower in wildfire plots than in unburned plots, nestling growth rates would be slower, nestlings would fledge at lower weights, and adults would bring arthropod prey to nestlings at lower rates than in unburned sites. If wildfire has a positive effect on breeding habitat, we predicted that the above trends would reverse in wildfire plots. Finally, if no large effect was present, we predicted that there would be no differences in nest site selection, nest success, feeding rates, and fledging mass in unburned and wildfire sites. These measures of reproductive output are important in determining the suitability of habitat to breeding birds (Van Horne 1983) and they will provide an initial assessment of the quality of burned riparian habitat.

STUDY AREA

Our study area consisted of riparian forests along the Middle Rio Grande in Valencia and Socorro counties, New

Mexico, USA. Along the Middle Rio Grande, riparian vegetation was largely confined between the river channel and levees on either side of the river. Rio Grande cottonwood (*Populus deltoides wislizenii*) was the dominant canopy species, and Gooding's willow (*Salix goodingii*) was also found in the canopy. Native understory shrubs included seepwillow (*Baccharis glutinosa*), coyote willow (*Salix exigua*), New Mexico olive (*Forestiera neomexicana*), false indigo (*Amorpha fruticosa*), screw bean mesquite (*Prosopis pubescens*), and wolfberry (*Lycium torreyi*). Exotic saltcedar and Russian olive (*Elaeagnus angustifolia*) shrubs were found in the understory throughout the forest.

The Middle Rio Grande riparian forest is one of the most extensive cottonwood gallery forests in the southwestern United States (Howe and Knopf 1991) and is considered critical habitat for rare and endangered birds such as the southwestern willow flycatcher (*Empidonax traillii eximius*; United States Fish and Wildlife Service 2005). The forest along the Rio Grande is similar to numerous riparian systems in the arid Southwest in that the natural disturbance regime of regular flooding has been halted and may have been replaced by high-intensity spring and summer wildfires, which are likely occurring with increasing frequency (Stuever et al. 1995, Bock and Block 2005). Historically, flooding occurred annually, varying in extent from year to year (Whitney 1996, Molles et al. 1998). Currently, flooding has not occurred outside the levees for 60 years and rarely occurs within the levees (Molles et al. 1998). Historical occurrence patterns of wildfire are unclear, but it appears that frequency and intensity of wildfire has recently increased due to increased human activity, drought conditions, accumulation of woody debris, and spread of exotic, flammable species (Stuever et al. 1995). There is concern that wildfires will alter the structure and composition of native riparian forests by converting a community composed of Rio Grande cottonwood and willow to one dominated by saltcedar and Russian olive (Busch 1995).

Wildfires within our study area burned in different years, offering no temporal control for analysis of site effects. However, we could examine changes in riparian systems across a range of postburn time because several of the wildfire plots were in close proximity to each other. Recently burned plots, located on land managed by the Middle Rio Grande Conservancy District, were the 20-ha San Francisco wildfire plot that burned in 2003, the 9.4-ha Chavez wildfire plot that burned in 2002, and the 31.4-ha Rio Grande Complex wildfire plot that burned in 2000. The older burn plot was the 22.1-ha San Pedro wildfire plot that burned in 1996 on the Bosque Del Apache National Wildlife Refuge. Distances between wildfire plots ranged from 6 km to 63 km. Wildfires occurred in the spring or summer and burned at high intensities at their cores and lower intensities near their edges. Vegetation was completely consumed or top-killed in high-intensity areas and patchily burned in lower-intensity areas. We focused our study in high- or moderate-intensity areas as defined by Stuever (1997).

Table 1. Percentage of nest boxes used by ash-throated flycatchers and Bewick's wrens and the number installed (*n*) in each plot in 2003 and 2004 along the Middle Rio Grande, New Mexico, USA.

Plot	2003			2004		
	Flycatchers	Wrens	<i>n</i>	Flycatchers	Wrens	<i>n</i>
Rio Grande Complex						
Unburned	0	0.13	8	0	0.10	10
2000 wildfire	0.11	0	9	0.10	0.20	10
San Francisco ^a						
Unburned				0.31	0.08	13
2003 wildfire				0.31	0	13
Chavez						
Unburned	0.10	0.30	10	0.14	0.29	14
2004 wildfire ^b	0.10	0.10	10	0.23	0.15	13
San Pedro						
Unburned ^c	0	0.57	7	0	0.50	10
1996 wildfire ^d	0.22	0.33	9	0.29	0.21	14

^a We did not install nest boxes in the San Francisco plots until 2004.

^b One nest box was used twice by Bewick's wrens in 2004.

^c Two nest boxes were used twice by Bewick's wrens in 2003, and one was used twice in 2004.

^d One nest box was used twice by Bewick's wrens in 2003.

METHODS

Avian Nest Monitoring

We used nest boxes to attract 2 secondary cavity-nesting species, ash-throated flycatchers and Bewick's wrens (hereafter, flycatchers and wrens, respectively), to nest in wildfire and unburned sites. We monitored nest boxes and used the data to model nest site selection and nesting success in relation to wildfire. Birds nesting in man-made boxes differ in their exposure to predation and other factors such as parasitism compared to birds nesting in natural sites (Moller 1989, but see Koenig et al. 1992). We therefore designed this study to draw inferences of nest use and success for birds nesting in boxes and not in natural nests, although such results can be used to estimate how wildfire phenomena affect natural populations (Koenig et al. 1992).

Flycatchers and wrens are abundant in the Middle Rio Grande riparian forest and normally nest in cavities previously excavated by woodpeckers (Kennedy and White 1997, Cardiff and Dittmann 2002). Wrens forage in the lower strata of the forest, creeping along substrates that include litter, foliage, and trunks (Kennedy and White 1997, Taylor 2003). In contrast, flycatchers typically forage in all strata of the forest, capturing arthropod prey on the wing by sallying, hover-gleaning, or ground-pouncing (Cardiff and Dittmann 2002). Wrens are yearlong residents in Middle Rio Grande forests, and flycatchers are Neotropical migrants (Kennedy and White 1997, Cardiff and Dittmann 2002).

To examine effects of wildfire on these breeding birds, we measured vegetation and observed nests using a comparative approach with the limited amount of wildfire plots available for study. We collected data in 3 recently burned wildfire plots and one older wildfire plot located along a 106-km stretch of the Rio Grande. We nonrandomly established 4 sites that consisted of a wildfire plot paired with an adjacent unburned plot. We selected unburned plots that were in close proximity to wildfire plots and, when possible, similar

distances from the river. We assumed that vegetation structure and composition in unburned plots resembled that of wildfire plots prior to burning. Distances between paired unburned and wildfire plots was dependent on accessibility of study sites and ranged from 80 m to 630 m.

We placed nest boxes at heights ranging from 2.5 m to 3.5 m and spaced 50–100 m apart at distances from the river ranging from 10 m to 350 m. We installed nest boxes at orientations between 0° and 185° to minimize direct exposure to late-day sun. We installed nest boxes in roughly equal numbers in paired wildfire and unburned plots (Table 1). Although wildfire plots varied in size, the areas within them in which we installed boxes were roughly the same size. Nest box densities were similar between plots because number of nest boxes installed depended on plot size. We systematically chose nest box locations in unburned and wildfire plots by attaching a nest box to the first available tree (large and sturdy enough to hold a nest box) encountered, then walking in the direction of the river for at least 50 m until we saw another available tree, attaching a nest box to that tree, walking 50 m toward the levee until we saw the next available tree, and so on. We first installed nest boxes prior to the 2003 nesting season and added more boxes prior to the 2004 and 2005 seasons. We monitored all flycatcher and wren nests found in boxes during the 2003 and 2004 seasons and all flycatcher nests found in boxes during the 2005 season.

We opened nest boxes throughout the summer to check for occupancy and determine nest success. We classified nest boxes as used by wrens or flycatchers when incubation began. We analyzed nesting success at all used nest boxes in unburned and wildfire plots. In cases where nest boxes were used for multiple nesting attempts, we randomly selected one attempt per box to include in nest success analysis to ensure independence of data points. Nestling duration of both species ranges from 14 days to 16 days (Ehrlich et al. 1988).

We classified nests as successful if we observed nestlings aged ≥ 11 days in the nest before it was empty, or if we observed parents feeding fledglings in the nest area. We classified nests as depredated if nest boxes were empty before nestlings would have been 11 days old. We compared nesting success between unburned and wildfire sites, as well as between species (Mayfield 1961, Hensler and Nichols 1981).

We visited occupied nests at least once every 3 days to determine nesting stage. When nestlings were present, we measured them every 2–3 days to determine growth rates. We measured nestling mass with an electronic balance to the nearest 0.1 g. We used calipers to measure tarsus and wing length of each nestling to 0.1 mm. To measure the effect of wildfire on fledgling mass, we compared the mass of nestlings that we measured at 9–11 days old in unburned and wildfire plots. We could not compare fledgling mass at a single age because we could not visit nests every day and we did not always know the exact age of nestlings.

We videotaped nests during the nestling stage for 4 hours beginning within 1 hour of sunrise to determine prey delivery rates, which we expected to be positively associated with prey availability (Hutto 1990). To control for developmental stages, we filmed nests once during early nestling stage, which we defined as 1–3 days before nestling primary pin feathers broke, which usually occurs around day 8, and once during the later nestling stage, which was 1–3 days after pin feathers broke. We filmed nests with a Sony camcorder placed as close to each nest as possible and concealed to prevent disruption of adult behavior. Cameras placed within 5 m of the nest provided adequate views of adult behavior. We later viewed the videos to calculate mean number of feeding trips to nests per nestling per hour. We were able to identify prey at some nests, and prey size varied throughout the 4-hour period at each nest. Because we were not able to measure prey size at all nests, we assumed that prey size varied within plots and did not vary between plots.

Vegetation Measurement

We measured the vegetative structure at all nest boxes in 2003 and 2004. We established circular vegetation sampling plots with an 11.3-m radius with the nest box as the center of each plot. Following adjusted BBIRD protocol (Martin et al. 1997), we identified all trees and shrubs and counted the number of each species in various size classes within each plot. In addition, we counted number of cottonwood snags (standing dead trees) in various size classes within each plot. We measured litter depth (cm) at 12 locations in each vegetation plot. To quantify nest concealment, we estimated distance from each side of the nest box to live, obscuring vegetation, such as leaves, branches, or vines. We measured ground cover by estimating the number of forb and grass stems in vegetation plot quadrants. For each quadrant, we assigned a class designating density of forb and grass stems (stems/quadrant; 1 = 0–10, 2 = 10–50, 3 = 50–100, 4 = 100+) and calculated mean class number for each vegetation plot. To estimate the density of understory vegetation, we placed a 4-m-tall aluminum pole 5–10 m (randomly assigned) from the nest in each cardinal direction and

counted the number of times vegetation contacted the pole. We estimated canopy coverage, which we defined as live vegetation >4 m tall, at each nest site using a spherical densiometer at 4 locations facing each direction.

To evaluate changes in vegetation structure following wildfires, we compared vegetation variables in unburned and wildfire plots. We compared unburned and wildfire data at 2 spatial scales. First, we compared means between all unburned and wildfire plots. Second, we compared the means from individual wildfire plots with their paired unburned plots.

Data Analysis

We calculated means and standard errors or confidence intervals of vegetation and nest-use variables measured in unburned and wildfire plots. To test for wildfire effects on nestling growth rates, we plotted measurements of mass, tarsus length, and wing length against nestling age and fit them to logistic growth curves for flycatchers and wrens. We used these logistic curves to calculate residuals for nests in unburned and wildfire plots. To ensure independence of data points plotted in growth curves, we only included the median values from each measurement day at each nest instead of the measurements of all individuals, which were likely confounded by brood-specific effects. These growth curves were based only on nestlings for which the exact age was known. We compared mean residuals of nests in wildfire and unburned plots for flycatchers and wrens to determine if wildfire affected growth rates (Ricklefs 1983).

Due to recent concern about the validity of null hypothesis tests and associated *P*-values in comparative studies (Johnson 1999), we estimated effect sizes to evaluate the strength of the effect of wildfire on growth rate using the following equation:

$$\text{Effect size} = \frac{U - W}{UCI},$$

where *U* is the mean residual of nestlings measured in unburned plots, *W* is the mean residual for nestlings in wildfire plots, and *UCI* is the difference between upper and lower limits of the 95% confidence interval for measurements of nestlings in unburned plots. With this formula, an absolute value of effect size ≥ 1 indicates that means are separated by the confidence interval and therefore deserve attention. We also used this effect size estimation to evaluate differences in vegetation in unburned and wildfire plots.

We constructed multiple logistic regression models to determine which variables best explained nest box use in wildfire and unburned plots during the summer of 2004. Individual nest boxes were the sampling unit. We constructed a set of 12 models and applied them separately to data for flycatcher and wren nest box use. We performed separate analyses for nest box use to test for differences in each species' preferences in nest sites. We constructed models to evaluate variables we expected to be important components of nest use based on our experience in the field and previous research (Carothers et al. 1974, Taylor 2003). The selection of variables was subjective; therefore, our

Table 2. Means, standard errors, and effect size estimates (*E*) of vegetation variables measured at 94 nest boxes in pooled unburned and wildfire plots along the Middle Rio Grande, New Mexico, USA, 2004.

Variable	Unburned		Wildfire		<i>E</i> ^a
	\bar{x}	SE	\bar{x}	SE	
Understory density (hits/nest plot)	11.4	1.2	13.4	1.1	0.38
Distance to nest cover (cm)	450.8	33.1	387.7	44.9	0.47
Litter depth (mm)	12.1	1.6	5.7	1.1	0.97
Forb cover class (1–4) ^b	2.2	0.2	3.1	0.2	1.29
Grass cover class (1–4) ^b	2.4	0.2	2.0	0.2	.57
% canopy coverage	69.9	4.2	5.5	2.1	3.79
Cottonwood snags (individuals/nest plot)	1.0	0.3	6.1	1.2	4.73
Russian olive (individuals/nest plot)	4.3	1	2.8	0.6	0.38
Saltcedar (individuals/nest plot)	40.4	4.6	29.9	3.4	0.56
Cottonwood (individuals/nest plot)	13.2	1.6	10.3	1.4	0.47
Small cottonwood ^c (individuals/nest plot)	1.8	0.6	7.7	1.0	2.46
Medium cottonwood ^d (individuals/nest plot)	7.2	1.1	2.2	0.8	1.09
Large cottonwood ^e (individuals/nest plot)	4.3	0.5	0.4	0.1	2.05

^a Effect size estimates ≥ 1 indicate separation of CIs.

^b Cover class (stems/quadrat): 1 = 0–10, 2 = 10–50, 3 = 50–100, 4 = 100+.

^c ≤ 10 cm dbh.

^d 10–25 cm dbh.

^e 25–60 cm dbh.

model selection determined effect of variables in relation to each other and did not seek to explain underlying phenomena (Johnson and Omland 2004, Stephens et al. 2005). Models were relatively simple, which is appropriate for smaller sample sizes (Burnham and Anderson 2002). For each model, the binary response variable was nest use (1 = used, 0 = unused). We constructed models with one or more

explanatory variables that we measured during the 2004 nesting season, which included nest-site vegetation variables (described above) and spatial variables (height, distance to levee). We included wildfire status of plot (burned or unburned) as a single explanatory variable and incorporated it into the spatial and vegetation models. We restricted the variables entered in the models to 7 measures that were not

Table 3. Means and standard errors of vegetation variables at sites where variables differed between paired unburned and wildfire plots (effect size ≥ 1) along the Middle Rio Grande, New Mexico, USA, 2004.

Variable	Site ^a	Unburned		Wildfire	
		\bar{x}	SE	\bar{x}	SE
Understory density	Rio Grande Complex	7.9	1.3	16.1	1.4
Distance to nest cover	Rio Grande Complex	447.7	77.9	102.4	30.3
Litter depth	San Francisco	6.8	1.3	1.5	0.4
	Chavez	14.9	2.6	3.5	1.2
	San Pedro	1.3	0.5	6.3	2.2
Forb cover class	Chavez	1.8	0.3	3.9	0.04
	Rio Grande Complex	1.5	0.3	3.4	0.3
Grass cover class	San Francisco	3.4	0.2	2.6	0.4
Canopy	San Francisco	62.9	6.1	0	0
	Chavez	80.0	5.6	0	0
	Rio Grande Complex	62.0	13.0	0	0
	San Pedro	74.1	9.70	19.1	6.1
Cottonwood snags	San Francisco	0.6	0.3	13.8	2.9
	Chavez	1.2	0.4	1.3	2.1
	Rio Grande Complex	0.3	0.3	1.5	0.5
Saltcedar	San Pedro	12.7	2.9	28.1	3.7
Cottonwoods	San Francisco	13.2	3	8.1	2
	Chavez	14.4	3.2	8.8	2.3
	Rio Grande Complex	10.8	2.3	8.4	2.9
	San Francisco	3.9	0.6	0.4	0.3
Large cottonwoods	Chavez	3.0	0.7	0.2	0.2
	Rio Grande Complex	5.3	1.1	0	0
	Chavez	10.5	2.6	0	0
Medium cottonwoods	San Francisco	1.5	0.6	7.7	2.2
Small cottonwoods	Chavez	0.8	0.6	8.6	2.3
	Rio Grande Complex	2.1	1	7.1	2.2

^a We did not include sites where individual variables did not differ.

Table 4. Explanatory variables, number of parameters (K), relative Akaike's Information Criterion adjusted for small sample size (ΔAIC_c), and Akaike weights (w_i) for the models predicting nest selection for ash-throated flycatchers and Bewick's wrens in 2004 along the Middle Rio Grande, New Mexico, USA.

Species	Model ^a	K^b	ΔAIC_c	w_i
Ash-throated flycatcher	BURNED	2	0	0.21
	DIST.LEVEE	2	0.50	0.16
	SALTCEDAR	2	1.30	0.11
	GRASS	2	1.40	0.10
	HEIGHT	2	1.50	0.10
	COVER	2	1.70	0.09
	COTTONWOOD	2	1.90	0.08
	DIST.LEVEE + HEIGHT	3	2.03	0.08
Bewick's wren	COVER	3	0	0.21
	GRASS	3	0.58	0.16
	HEIGHT	3	0.89	0.14
	BURNED	3	1.37	0.11
	COTTONWOOD	3	1.53	0.10
	DIST.LEVEE	3	1.63	0.09
	SALTCEDAR	3	1.89	0.08

^a Variables: BURNED = nest plot wildfire status (burned or unburned in last 10 yr); COTTONWOOD = cottonwood density around nest box; COVER = mean distance from sides of nest box to obscuring vegetative cover; DIST.LEVEE = distance to levee road (habitat edge); GRASS = grass cover class (1–4) near nest box; HEIGHT = ht of nest box; SALTCEDAR = saltcedar density around nest box.

^b Quasi-Akaike's Information Criterion was used in wren models to correct for over-dispersed data, increasing K by 1 for each model.

intercorrelated, that logically explained variation in nest selection, and were realistic management targets.

To determine which variables best explained variation in nest success, we constructed 12 multiple logistic regression models that incorporated the same explanatory variables used to explain nest use. Models contained the binary response variable of nest success (1 = successful, 0 = depredated) and ≥ 1 explanatory variables. For this analysis, we included wren nests that were monitored in 2003 and 2004, as well as flycatcher nests that we monitored in 2003, 2004, and 2005. We did not include abandoned nests in this analysis.

To evaluate models explaining nest use and success, we used information-theoretic methods to determine which logistic regression models, constructed a priori, were best supported by the data (Burnham and Anderson 2002). We used information-theoretic model selection, as opposed to

frequentist methods such as stepwise regression, to avoid using P -values that are not appropriate for a comparative study that is exploratory in nature. We used Akaike's Information Criterion corrected for small sample size (AIC_c) and, when necessary, over-dispersed data ($QAIC_c$) to determine which models were best supported by the data (Burnham and Anderson 2002). We calculated AIC_c values using $-2\log$ likelihood output in PROC LOGISTIC (SAS Institute, Cary, NC). We compared models using relative AIC_c values (ΔAIC_c), with the lowest values belonging to the best-fit models (Burnham and Anderson 2002). We examined all models with ΔAIC_c values ≤ 2.0 , which Burnham and Anderson (2002) identify as the cutoff for models that are likely to be well supported by the data. We used ΔAIC_c to calculate Akaike weights, which estimate the probability of each model in the set being the best

Table 5. Model-averaged parameter estimates, model-averaged standard errors, and means at used and unused nests for variables selected to predict nest box use by ash-throated flycatchers and Bewick's wrens in 2004 along the Middle Rio Grande, New Mexico, USA.

Species	Variable	Estimate	SE	Used		Unused	
				\bar{x}	SE	\bar{x}	SE
Ash-throated flycatcher	Burned (% nests in wildfire plot)	0.73	0.02	0.67	0.1	0.49	0.1
	Cottonwood density	0.01	0.0	12.2	2.8	11.6	1.1
	Distance to cover (cm)	0.0004	0.0	446.6	59.3	410.6	32.2
	Distance to levee (m)	-0.01	0.0	71.7	10.6	88.4	6.6
	Grass (cover class 1–4)	0.16	0.001	2.3	0.3	2.1	1.4
	Ht (cm)	0.20	0.004	292.6	6.1	286.5	3.1
	Saltcedar density	0.01	0.0	39.6	5.7	33.8	3.3
Bewick's wren	Burned (% nests in wildfire plot)	-0.60	0.001	0.41	0.1	0.55	0.1
	Cottonwood density	0.02	0.0	13.5	2.2	11.3	1.2
	Distance to cover (cm)	-0.002	0.0	306.5	54.9	442.0	31.9
	Distance to levee (m)	0.003	0.0	93.5	13.4	83.4	6.3
	Grass (cover class 1 to 4)	-0.39	0.003	1.7	0.3	2.2	0.1
	Ht (cm)	-0.38	0.004	277.4	6.1	289.6	3.1
	Saltcedar density	0.003	0.0	34.9	8.2	34.9	3.0

Table 6. Explanatory variables, number of parameters (K), relative Akaike's Information Criterion adjusted for small sample size and over-dispersed data (ΔQAIC_c), Akaike weights (w_i), parameter estimates for variables in each model, and model-averaged standard errors for variables in models predicting nest success in boxes occupied by ash-throated flycatchers or Bewick's wrens from 2003–2005 in the Middle Rio Grande, New Mexico, USA.

Model ^a	K	ΔQAIC_c	w_i	Estimate	SE
Grass	3	0	0.29	−0.63	0.01
Distance to levee	3	0.22	0.26	0.02	0.0

^a Only models with $\Delta\text{QAIC}_c \leq 2$ are included.

explanation of the nest selection or success (Burnham and Anderson 2002).

To reduce bias in parameter estimation and incorporate model selection uncertainty, we calculated model-averaged parameter estimates that reflect the effect of a variable on nest site selection or nest success. We calculated parameter estimates on variables found in well-supported models ($\Delta\text{AIC}_c \leq 2.0$). These estimates incorporated Akaike weights across all the models in which we used the estimated parameters (Burnham and Anderson 2002). We used Akaike weights to calculate unconditional variances of the parameter estimates, which were used to calculate standard errors (Burnham and Anderson 2002).

RESULTS

Vegetation in Unburned and Wildfire Plots

Seven vegetation variables differed between wildfire and unburned plots overall (effect size ≥ 1), and 12 variables differed within ≥ 1 pair of wildfire and unburned plots (Tables 2, 3).

Nest Box Use

Flycatchers used nest boxes more frequently in wildfire plots than in unburned plots, while wrens used nest boxes more frequently in unburned plots (Table 1). In 2005, we monitored 18 flycatcher nests at the Bernardo and Chavez sites to increase the number of samples for this species. We used data from these nests in nest-success analyses but not in nest-use analyses. There was high model selection uncertainty for nest box use models because most models were well supported by the data ($\Delta\text{AIC}_c \leq 2$; Table 4). For flycatchers, the model containing wildfire status was best supported by the data, but 7 other models were also well supported (Table 4). Model-averaged parameter estimates showed that wildfire, distance to cover, cottonwood density, saltcedar density, grass cover, and height had positive effects on nest box use by flycatchers. Distance to levee had a negative effect on their nest box use (Table 5).

The logistic regression model that best explained nest

selection by wrens had one explanatory variable, distance to obscuring vegetation. Seven other models were well supported by the data (Table 4). Model-averaged parameter estimates showed that cottonwood density, saltcedar density, and distance to levee had positive effects on nest selection. Distance to obscuring vegetation, nest box height, and wildfire had negative effects on nest selection (Table 5).

Nest Success

During the combined summers of 2003, 2004, and 2005, flycatcher nests were less successful (67%; 95% CI: 48–86%, $n = 27$) than those of wrens (91%; 95% CI: 78–100%, $n = 22$) monitored in 2003 and 2004. Combined nest success for both species was similar between unburned (82%; 95% CI: 64–98%, $n = 22$) and wildfire (74%; 95% CI: 57–91%, $n = 27$) plots. One hundred percent of nests of both species were successful in 2003 ($n = 11$), 75% of all nests were successful in 2004 (95% CI: 57–93%, $n = 24$), and 64% of flycatcher nests were successful in 2005 (95% CI: 37–91%, $n = 14$). Two logistic regression nest success models, each with only one explanatory variable, had AIC_c values of ≤ 2 , indicating that they were well supported by nest success data (Table 6). The logistic regression model containing grass cover as the explanatory variable was the best explanation of variation in nest success. The model containing distance to levee had a similar Akaike weight and therefore received nearly equal support (Table 6). Grass cover negatively affected nest success, while distance from levee had a positive effect (Table 6).

Feeding Rates

Feeding rates were similar between early and late nestling stages for flycatchers and wrens, so we combined data from both stages when comparing between wildfire and unburned plots. We also combined data from 2003, 2004, and 2005 for flycatchers and data from 2003 and 2004 for Bewick's wrens because rates were similar between years. The number of feeding trips per nestling per hour did not differ between nests in unburned or wildfire plots for flycatchers (unburned $\bar{x} = 2.5$ trips, 95% CI: 1.9–3.0, $n = 11$; wildfire $\bar{x} = 2.4$ trips,

Table 7. Growth curve R^2 values, mean residuals for mass, wing, and tarsi, and estimates of effect size (E) for ash-throated flycatcher and Bewick's wren nestlings measured in unburned and wildfire plots from 2003 to 2004 along the Middle Rio Grande, central New Mexico, USA.

Measurement	Ash-throated flycatcher				Bewick's wren			
	R^2	Residual unburned	Residual wildfire	E	R^2	Residual unburned	Residual wildfire	E
Mass	0.96	−0.12	0.10	0.20	0.97	0.21	−0.27	0.91
Wing	0.97	−0.10	0.09	0.14	0.96	0.01	−0.16	0.05
Tarsus	0.97	−0.02	0.01	0.08	0.95	0.18	−0.26	0.31

CI: 2.1–2.8, $n = 13$) or for wrens (unburned $\bar{x} = 2.4$ trips, CI: 1.8–3.0, $n = 10$; wildfire $\bar{x} = 2.6$ trips, CI: 1.9–3.3, $n = 9$).

Nestling Growth Rates and Fledging Mass

Measurements of mass, tarsus length, and wing length were well described by logistic growth curves for both species (Table 7). We did not observe any correlations between brood size and median nestling measurement values of wrens or flycatchers. Brood size, therefore, was not a confounding factor in comparisons of growth rate between unburned and wildfire plots. The mean residuals from growth curves for flycatchers were positive in wildfire sites and negative in unburned sites, suggesting that growth was faster in wildfire sites, but the effect size was small. Mean residuals from growth curves for wrens were positive in unburned sites and negative in wildfire sites, suggesting that growth was faster in unburned sites. There was a large effect of wildfire on wren nestling mass gain. Effect size of wildfire on other measurements on wrens was smaller (Table 7).

Estimates of fledging mass were similar at nests in combined unburned and wildfire plots for flycatchers (unburned $\bar{x} = 23.2$ g, 95% CI: 21.7–24.7, $n = 12$; wildfire $\bar{x} = 23.1$ g, 95% CI: 22.0–24.2, $n = 16$) and for wrens (unburned $\bar{x} = 9.1$ g, 95% CI: 8.3–9.8, $n = 12$; wildfire $\bar{x} = 9.3$ g, 95% CI: 8.7–10.0, $n = 10$).

DISCUSSION

Our results provide initial evidence that, like burned pine (*Pinus* spp.) forests (Hutto 1995, Dwyer and Block 2000), burned riparian forests can be viewed as productive wildlife habitat for certain species. Secondary cavity-nesting birds are an important component of southwestern riparian breeding bird assemblages (Sedgwick and Knopf 1990), and our results showed that at least one of these species (ash-throated flycatcher) responded positively to wildfire. By installing nest boxes, we provided an important nesting resource (nest sites) and determined how variation in other resources, such as vegetation, influences both use of nest sites and nesting success.

The presence of natural cavities in nest box plots may confound nest-use data, but we assume that densities of cavities do not differ greatly between unburned and wildfire plots. Natural cavities are abundant in unburned sites because stressed cottonwoods have large dead branches that are frequently used by woodpeckers. Many of these cavities remain following wildfire, and additional cavities are subsequently excavated. As large trees fall in wildfire sites, woodpeckers add additional cavities in remaining trees, keeping cavity densities somewhat constant. Although we did not quantify natural cavities, we assume that their presence had similar influence on nest box use in unburned and wildfire plots.

Model selection showed that wildfire, vegetation, and spatial variables influenced nest use. Wildfire status was important in explaining nest site use by both species but in different ways. Flycatcher nest use was positively associated with wildfire, whereas wren nest use was negatively associated with wildfire. These results are in accord with

the predicted responses of these 2 species to fire in oak woodlands (Purcell and Stephens 2005). Kirkpatrick et al. (2002) found similar abundances of flycatchers in burned and unburned mesquite–grasslands. The results of these studies show that flycatchers therefore are more likely to use habitats recently altered by wildfire than are wrens. Though we did not quantify densities of flycatchers and wrens at our plots, previous counts have found them in similar densities to each other in unburned plots (Smith et al. 2006a). Differences in nest use following wildfire were likely a result of altered forest structure and not differences in density prior to wildfire.

There was some evidence for competition between species at some nest sites because flycatchers usurped 2 wren nests in 2004. Overall, however, wrens most often used nest boxes that were closer to the ground in areas with high shrub density while flycatchers most often used boxes higher from the ground in open areas. Flycatchers and wrens therefore had little effect on each other's use of nest sites.

The pattern of higher nest use in recent wildfire plots by flycatchers than wrens may be explained by the differential impact of wildfire on nest sites and food used by these 2 species. At our study sites, flycatchers nesting within burned riparian forests took advantage of multiple foraging opportunities by feeding in the forest and in adjacent habitats. Annual cicadas (*Tibicen dealbatus*), which are a large portion of flycatcher diets (Rosenberg et al. 1982), conspicuously emerge in recently burned sites, thus providing an important resource in burned riparian habitat (Smith et al. 2006b). Flycatchers may be capable of nesting in recently burned plots because they are tolerant of high temperatures (Cardiff and Dittmann 2002) and are better able than wrens to nest in burns where surface temperatures averaged up to 6° C higher in wildfire plots than in unburned plots (Smith et al. 2006b). Model selection showed that the variable that best explained nest box use by wrens was distance to vegetative cover. The negative relationship of distance to cover and wren selection suggests that wrens chose nest boxes that were better concealed or shaded and thus safer and cooler than nest boxes with greater distance to cover. Time since fire can positively influence postfire habitat use by certain species (Smucker et al. 2005). This appears to be the case for wrens because they frequently used nest boxes in the plot that burned in 1996 but rarely used boxes in burns that had occurred more recently (Table 1). Flycatcher use of nest boxes did not vary as much between wildfire plots, suggesting that time since fire is not as important for this species. From model selection results and these observations, we conclude that 1) wildfire does not negatively effect flycatcher nest box use because it does not negatively affect foraging habitat and flycatchers can tolerate high temperatures, and 2) wildfire negatively affects wren nest box use, at least in the short-term because it reduces shading nest cover as well as dense brush and litter near the nest site in which wrens forage.

Our results indicate differing effects of wildfire on habitat quality for the 2 species studied. If wildfire had a negative

effect on bird habitat, we predicted lower nest use in wildfire plots, as well as fewer food deliveries to the nest, slower nestling growth, and decreased fledging mass than in unburned plots. None of these predictions held true for flycatchers, suggesting that wildfire did not decrease their nesting habitat quality in any way. Wrens, on the other hand, selected fewer nests in wildfire sites and had slower nestling growth rates, evidence that wildfire had a negative effect on their habitat quality. Differences in effects of wildfire on these 2 species are likely a result of different foraging strategies or thermal tolerances, characteristics that researchers should consider when examining wildfire effects of other riparian bird species.

Nest predation is one of the most significant forms of mortality in birds and is often the primary cause of reproductive failure (Martin 1993, 1995). Identifying the environmental factors associated with variation in nest predation is therefore essential to evaluating the quality of breeding habitat. Nest predation was high for flycatchers nesting in boxes in 2004 and 2005 but much lower for wrens. Although no vegetation or spatial variables were better than the other variables at explaining nest selection, grass cover and distance from levees were strongly associated with variation in nest success.

Habitat fragmentation and edge has been linked with high nest predation rates in studies of midwestern riparian forests (Paton 1994, Chalfoun et al. 2002) but has been negatively associated with predation rates in some western riparian forests (Tewksbury et al. 1998, Saab and Vierling 2001). In this study, distance to habitat edge (measured as distance from levee) and patch size appeared to be positively associated with predation rates at nest boxes, consistent with patterns observed in midwestern forests. Prior to intensive human development of the Middle Rio Grande valley, the riparian forest existed as a mosaic of different-aged forest patches and wetlands, resembling a fragmented landscape (Whitney 1996). Under current conditions, however, the riparian forest forms a continuous linear strip that borders agricultural habitats that may contain high densities of nest predators (Saab and Vierling 2001). In this altered landscape, birds nesting in small patches or near edges are likely to incur increased nest predation rates (Saab and Vierling 2001, Peak et al. 2004). Further study of nest success across a variety of bird species in different patch sizes and shapes is necessary to test whether patch size and edge influence reproductive success in this system.

Model selection showed that wildfire did not have a direct effect on nest predation; however, wildfire may influence predation indirectly. Grass cover was positively associated with predation. If grass cover provides habitat for nest predators, wildfire may increase nest predation risk by clearing litter and opening up the canopy to enhance grass growth. We did not observe nest predation events and therefore did not identify nest predators. At most depredated nests, the linings of the nests were undisturbed and we did not find fragments of eggs or nestlings in the nest, indicating snakes as the likely predators. We often observed

gopher snakes (*Pituophis melanoleucus*) and coachwhips (*Masticophis flagellum*) in the nest box areas, both of which have been observed climbing trees and consuming contents of nest boxes (Finch 1989, Degenhardt et al. 1996). Additional research on vegetation associations of these or other predator species is necessary to examine their connections with grass cover and habitat edge to determine if increased predator activity is the mechanism through which these variables influence nest success.

MANAGEMENT IMPLICATIONS

Our results show that certain bird species will successfully breed in burned riparian forests if nest sites are available. Following wildfire, cottonwood recovery should be aided by managed flooding or planting to prevent dominance of exotic shrubs, such as saltcedar and Russian olive, which provide fewer natural nest sites. Managers should preserve large snags and surviving trees in a variety of size classes to maintain primary and secondary cavity-nesting bird diversity. Recovering forests should remain intact to prevent establishment of forest fragments with high edge-to-volume ratios. Such patches may become ecological traps where nest density is high but recruitment is low due to high rates of nest predation. Because we studied 2 bird species in one riparian forest, full generalization of our results to birds in other nesting guilds or in other riparian systems should be made with caution. To fully understand effects of wildfire on riparian breeding bird communities, managers should institute longer-term projects monitoring abundance and reproductive success of additional bird species in a variety of wildfire sites.

ACKNOWLEDGMENTS

We thank C. Crowder, E. Greenlee, and J. Johnson for valuable assistance in the field. G. Carpenter aided us with many aspects of the work in New Mexico, and W. Porter helped us construct many nest boxes in a very short time. S. Swanson provided valuable comments on early manuscripts and assisted us through various stages of this project. Reviews from K. Hobson, W. Gram, K. Greenberg, C. Vaughn, and 2 anonymous reviewers greatly improved this manuscript. Y. Najmi of the Middle Rio Grande Conservancy District and J. Taylor of Bosque Del Apache National Wildlife refuge graciously provided access to the field sites. The United States Department of Agriculture Forest Service Rocky Mountain Research Station's Albuquerque Laboratory, the George Miksch Sutton Scholarship in Ornithology, and the University of Oklahoma Student Association Graduate Student Senate Research and Creative Activity Grant funded this research.

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Associate Editor: Greenberg.