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Management and Conservation Article

Importance of Montane Riparian Forest and Influence of Wildfire on Nest-Site Selection of Ground-Nesting Birds

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ABSTRACT We studied breeding populations of 2 coexisting ground-nesting birds, the red-faced warbler (*Cardellina rubrifrons*) and yellow-eyed junco (*Junco phaeonotus*), in high-elevation (>2,000 m) forested drainages of the Santa Catalina Mountains, Arizona, USA. From 2004 to 2005, we 1) estimated density and nesting success of breeding populations of red-faced warblers and yellow-eyed juncos, 2) identified nest-site characteristics for each species (i.e., used sites vs. random plots), 3) compared nest-site characteristics between the 2 species, and 4) examined effects of a recent (2003) wildfire on distribution of nests of both species. In addition, we estimated the areal extent of montane riparian forest (the preferred breeding habitat of both species) within high-elevation forests of the Santa Catalina Mountains. We found that red-faced warblers and yellow-eyed juncos were the 2 most common ground-nesting birds within our study area with an average density of 2.4 and 1.4 singing males/ha, respectively, along drainage bottoms. Compared to random plots, most red-faced warbler and yellow-eyed junco nests were located close ($\leq$ 30 m) to drainage bottoms within a strip of montane riparian forest characterized by abundant brush, small woody debris, ferns, and forbs (both species), high number and diversity of saplings and small trees (red-faced warblers), and abundant shrubs and downed logs and less canopy cover (yellow-eyed juncos). Although both species nested in close proximity within montane riparian forest, nest-site characteristics differed between the 2 species, especially at finer spatial scales. For example, most yellow-eyed juncos nested adjacent to grass (principally *Muhlenbergia* spp.), whereas red-faced warblers nested adjacent to a variety of plant species, including grass, bigtooth maple (*Acer grandidentatum*), white fir (*Abies concolor*), and Douglas-fir (*Pseudotsuga menziesii*). Both red-faced warblers and yellow-eyed juncos avoided nesting in areas burned during a recent wildfire. In addition, nesting success was low for red-faced warblers (13%) and yellow-eyed juncos (19%) following the wildfire, suggesting an indirect negative effect of fire on breeding populations in the short-term. Montane riparian forest appears to provide important breeding habitat for red-faced warblers and yellow-eyed juncos. However, little research or conservation planning has been directed toward montane riparian forest in the region, even though this forest type is limited in its areal extent (<11% of high-elevation forest in the Santa Catalina Mountains) and increasingly threatened by disturbance. Results from our study can be used to facilitate the management and conservation of breeding populations of red-faced warblers and yellow-eyed juncos in high-elevation forests of the southwestern United States.

KEY WORDS Arizona, *Cardellina rubrifrons*, fire, ground-nesting birds, habitat associations, *Junco phaeonotus*, montane riparian forest, nest-sites, red-faced warbler, yellow-eyed junco.

Selection of a nest-site has the potential to affect both survival and reproductive success in birds because availability of food, mates, and cover for nest-sites often varies among sites (Cody 1985). Because birds are thought to use proximate environmental cues to select nest-sites (Cody 1985), identification of environmental features associated with nest-sites (i.e., nest-site characteristics) allows managers to predict effects of both management actions and natural disturbances on breeding populations and to develop effective management plans to ensure persistence of species (Martin 1993). This information is particularly important for species of conservation concern and for species that breed in areas that are essential for maintaining regional biodiversity, such as the Sky Island Mountains of the southwestern United States and northern Mexico (Conservation International 2008).

High-elevation (>2,000 m) forests in the Sky Island Mountains provide breeding habitats for a diverse assemblage of bird species, including several ground-nesting passerines. Two of these ground-nesting birds, the red-faced warbler (*Cardellina rubrifrons*) and yellow-eyed junco (*Junco phaeonotus*), breed in close proximity and active nests of both species have been observed as close as 2 m apart (C. Kirkpatrick and C. Conway, University of Arizona, unpublished data). The yellow-eyed junco is locally common (Phillips et al. 1964, Sullivan 1999) but status of the red-faced warbler is less certain (Martin and Barber 1995). Arizona Partners in Flight considers the red-faced warbler a high priority for conservation and ranks the species 34th on a conservation priority list of 234 terrestrial birds in the state (Latta et al. 1999). Despite this conservation concern, basic data on breeding biology and nest-site characteristics of the red-faced warbler are lacking in many parts of the species' range, including the Sky Island Mountains of the southwestern United States (Martin and Barber 1995).

Increasing our knowledge of nest-site characteristics of red-faced warblers and yellow-eyed juncos is important for management and conservation of healthy breeding populations for both species. In addition, understanding how nest-site characteristics differ between the 2 species is important because coexisting, ground-nesting bird species can have profound ecological effects on one another (e.g., displacement from preferred nest-sites; Martin 1993, Martin and Martin 2001). Moreover, populations of red-faced warblers and yellow-eyed juncos within the Sky Island Mountains are vulnerable because the high-elevation forests where they breed encompass only a fraction of the regional landmass.

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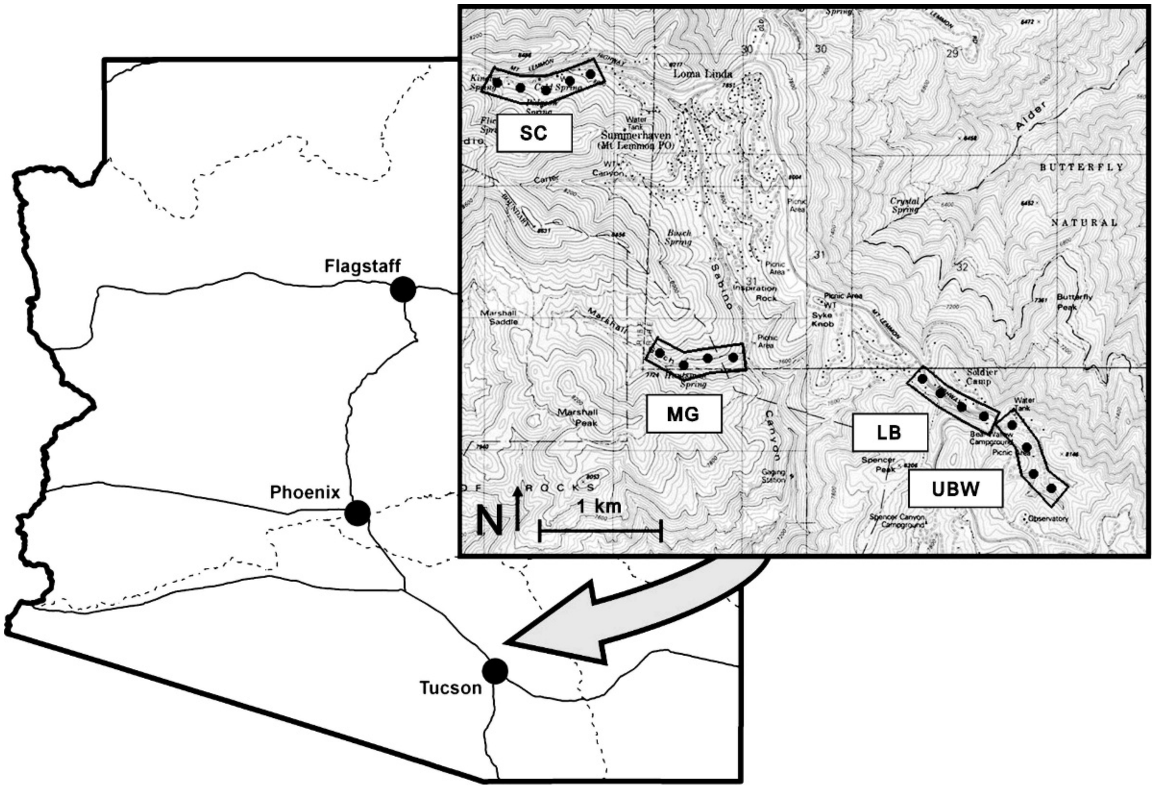

Figure 1. Map of Arizona, USA, showing location of study area in the Santa Catalina Mountains (approx. 30 km NE of the city of Tucson) and specific locations of 4 study sites (LBW = Lower Bear Wallow; MG = Marshall Gulch, SC = Sabino Canyon, UBW = Upper Bear Wallow) where we monitored breeding populations of red-faced warblers and yellow-eyed juncos from 2004 to 2005. Rectangles indicate boundaries of study sites and circles indicate locations of point-count survey stations within each study site.

The potential for disturbance to these important breeding areas appears to be increasing as frequency of wildfires has increased in montane forests of the southwestern United States (Swetnam et al. 1999). Indeed, severe wildfire is considered the greatest conservation concern for breeding populations of red-faced warblers and yellow-eyed juncos (Corman and Wise-Gervais 2005).

We sought to address these issues by studying breeding populations of red-faced warblers and yellow-eyed juncos in high-elevation forests of the Santa Catalina Mountains, Arizona, USA. From 2004 to 2005, we 1) estimated density and nesting success of breeding populations of red-faced warblers and yellow-eyed juncos, 2) identified nest-site characteristics for each species (i.e., used sites vs. random plots), 3) compared nest-site characteristics between the 2 species, and 4) examined effects of a recent (2003) wildfire on distribution of nests of both species. We also estimated the areal extent of montane riparian forest (the preferred breeding habitat of both species) in high-elevation forests of the Santa Catalina Mountains.

STUDY AREA

We conducted our study in high-elevation (>2,000 m) forests of the Santa Catalina Mountains, located approximately 30 km northeast of Tucson, Pima County, Arizona, USA (Fig. 1). The Santa Catalina Mountains are part of the Sky Island ecoregion, a group of approximately 40 isolated mountain ranges in the southwestern United States and northern Mexico. The Sky Island ecoregion has been designated as one of 2 biodiversity hotspots in North America (Conservation International 2008). Climate in the region was arid or semiarid but high-elevation forests were cooler and wetter than surrounding deserts. Mean annual precipitation was 681 mm in the Santa Catalina Mountains with most precipitation falling from localized thunderstorms during summer (Jul–Aug) and widespread frontal storms during winter (Nov–Mar; Brown 1994).

We located (nonrandomly) 4 study sites, upper Bear Wallow Canyon (2,422 m), lower Bear Wallow Canyon (2,367 m), Marshall Gulch (2,319 m), and Sabino Canyon (2,488 m), within 3 large drainages situated in a 20-km^2 area between the 2 highest summits in the Santa Catalina Mountains (Fig. 1). Study sites were 200 m wide and extended 1,000–1,200 m along drainage bottoms. A >34,000-ha wildfire burned most high-elevation forest (much of it severely) in the Santa Catalina Mountains including portions of our study area beginning in late June 2003 (Stephens and Fulé 2005; C. Kirkpatrick, personal observation).

Our study sites contained stands of Madrean montane conifer forest on xeric slopes and Rocky Mountain montane riparian forest along mesic drainage bottoms (Brown 1994). Common overstory trees included Douglas-fir (*Pseudotsuga menziesii*), white fir (*Abies concolor*), ponderosa pine (*Pinus ponderosa*), southwestern white pine (*Pinus strobiformis*), and quaking aspen (*Populus tremuloides*). Understory trees

Table 1. Environmental features measured at 4 spatial scales surrounding red-faced warbler and yellow-eyed junco nests and at 3 spatial scales surrounding random plots within 4 study sites located in high-elevation (>2,000 m) forests of the Santa Catalina Mountains, Arizona, USA, in 2004–2005.

Variable	Explanation
Nest scale[a]	
Closest plant to nest	Closest plant (e.g., tree spp., shrub spp., forb, grass) <30 cm from nest. We recorded "in open" if no plant was <30 cm from nest.
Nest-area concealment (overhead)	% of 12.5-cm-radius circle centered on nest that was concealed by vegetation or debris from 1 m above nest
Nest-area concealment (from side)	% of 12.5-cm-radius semicircle centered on nest concealed by vegetation or debris from 1 m to side of nest (average across 4 cardinal directions)
Nest concealment (overhead)	% of nest cup that was concealed by vegetation or debris from 1 m above nest
Nest concealment (from side)	% of nest cup that was concealed by vegetation or debris from 1 m to side of nest (average across 4 cardinal directions)
5-m-radius scale[b]	
Slope	Max. slope (°) measured across plot
Cover (ground)	% cover of bare ground, downed logs, leaf litter, moss, small woody debris, rocks, or water on ground
Cover (0–0.5 m above ground)	% cover of brush, ferns, forbs, grass, saplings, or shrubs 0–0.5 m above ground
Shrubs or saplings	No. shrub or sapling stems (<8 cm in diam) of each species measured at 0.1 m above ground
11.3-m radius scale[c]	
Area burned	% surface area of plot burned
Burn severity[d]	less severe or severe
Canopy cover	% canopy cover from densiometer (average across 4 cardinal directions) measured at plot center
Canopy ht	Average ht of upper canopy (m)
Trees	No. live stems of each tree species in 2 size classes: 1) small (0–23-cm dbh), and 2) large (≥23 cm dbh)
Snags	No. dead stems of each tree species in 2 size classes: 1) small (0–12-cm dbh), and 2) large (>12 cm dbh)
Study-site scale	
Distance to drainage	Distance (m) to closest drainage bottom

[a] Measured at nests only.
[b] Measured within a 5-m radius of nests and random plots.
[c] Measured within an 11.3-m radius of nests and random plots.
[d] See methods and Kirkpatrick et al. (2006) for full description of burn severity index.

included the overstory species listed above as well as New Mexican locust (*Robinia neomexicana*), bigtooth maple (*Acer grandidentatum*), and Gambel oak (*Quercus gambelii*). Common shrubs included mountain snowberry (*Symphoricarpos oreophilus*), fivepetal cliffbush (*Jamesia americana*), New Mexican raspberry (*Rubus neomexicanus*), and orange gooseberry (*Ribes pinetorum*). Grass (principally *Muhlenbergia* spp.), bracken (*Pteridium aquilinum*), and forbs comprised the ground cover.

METHODS

Data Collection

We established bird survey routes bisecting each study site with point-count stations located every 200 m (starting 100 m from the end of each study site) along drainage bottoms (Fig. 1). We conducted 2 bird surveys along each survey route in early May and in late May–early June in 2004 and 2005 to coincide with peak breeding of red-faced warblers, yellow-eyed juncos, and 3 other ground-nesting bird species (i.e., orange-crowned warbler [*Vermivora celata*], Virginia's warbler [*Vermivora virginiae*], and spotted towhee [*Pipilo maculatus*]; Corman and Wise-Gervais 2005). One observer (C. Kirkpatrick) conducted all point-count surveys. Surveys began 15 minutes after sunrise on days without precipitation and with wind speeds <19 km per hour. After arriving at each survey point, the observer waited 1 minute and then recorded species, detection type (i.e., song, call, or visual), minute within the 6-minute survey when the bird was first detected, and distance (m) from the survey point to the bird (measured using an infrared rangefinder whenever possible).

From late April to early July, 8 observers located and monitored nests of ground-nesting birds in 2004 and 2005. We attempted to search the entire area within each study site at least once per week, and we followed standardized nest-monitoring protocols to reduce disturbance to adults and young at nests (Martin and Geupel 1993). At each nest, we collected Universal Transverse Mercator (UTM) coordinates using a handheld Global Positioning System (GPS) receiver. We imported these UTM coordinates into ArcView Geographic Information System (GIS) 3.2 software to measure the distance (m) from each nest-site to the closest drainage bottom. The University of Arizona's Institutional Animal Care and Use Committee approved all protocols (no. 03-123 and no. 06-108).

We sampled a suite of environmental features around each red-faced warbler and yellow-eyed junco nest at 4 spatial scales (Table 1; Martin et al. 1997): 1) the nest scale (i.e., at the nest itself), 2) within a 5-m radius of the nest, 3) within an 11.3-m radius of the nest, and 4) the study-site scale. We derived our sampling protocol from the BBIRD nest-monitoring program, which advocates a standardized field-sampling protocol for estimating nesting success and identifying habitat correlates of breeding birds (Martin et al. 1997). The 5-m and 11.3-m (0.4-ha) radius plots that we used are those recommended by the BBIRD protocol for sampling environmental features at nests (Martin et al. 1997) and likely captured a sizeable portion of territories of both red-faced warblers (territory size in steep canyons in central AZ is 0.3–0.75 ha; Martin and Barber 1995) and yellow-eyed juncos (average territory size in southern AZ is 0.7 ha; Sullivan 1999) within our study area.

We also sampled environmental features using the same methods at each spatial scale (except the nest scale) at 70 plots distributed randomly within our 4 study sites in 2004 (henceforth, random plots). Because we sampled environmental features at nests after all nesting attempts were completed (Jul–Aug, primarily), we also sampled environmental features at random plots during the same time period to prevent bias in the timing of our sampling. We used a handheld GPS receiver to record UTM coordinates at each random plot. We imported these UTM coordinates into ArcView GIS to measure distance (m) from each random plot to the closest drainage bottom.

We measured fire metrics at 3 spatial scales. At the nest scale, we recorded whether each nest was located inside or outside the perimeter of the 2003 wildfire. At the 11.3-m-radius scale, we estimated percent surface area burned and the dominant burn-severity class (e.g., less-severe or severe; Kirkpatrick et al. 2006) surrounding each nest or random plot. At the study-site scale, we mapped the extent of the burn within each study site by walking along the edge of the burn while recording UTM coordinates using a GPS receiver. We imported these UTM coordinates into ArcView GIS to map the perimeter of the burn and calculate the percent area burned within each study site.

We estimated areal extent of montane riparian forest in high-elevation (>2,000 m) forests of the Santa Catalina Mountains by first estimating the width of montane riparian forests along the entire length of our 4 study sites. Because bigtooth maple is a signature riparian tree of montane riparian forests in southern Arizona (Szaro 1989), we estimated the width of montane riparian forest by using an infrared rangefinder to measure distance (m) across the drainage encompassing bigtooth maple growth at each bird survey point in each study site. In ArcView GIS, we used average width of the montane riparian forest strips calculated across our 4 study sites to buffer all stream channels within Madrean montane conifer forest (i.e., high-elevation forest; Arizona GeoData Portal 2009) in the Santa Catalina Mountains. We then calculated percentage of montane riparian forest contained within Madrean montane conifer forest. We did not select our 4 study sites randomly so this percentage likely represents an overestimate because we purposefully selected study sites in large drainages that contained montane riparian forest.

Statistical Analysis

For our bird survey data, we selected the survey in each year (early May or late May–early Jun) with the maximum number of detections for each ground-nesting bird species. We then calculated relative abundances across our 4 study sites for each year by averaging the number of singing males within 50 m of the observer across all point-count stations at each study site. We limited our data to singing males within 50 m because we were interested in relative abundance (and ultimately density) of territorial males and because we found that detection functions, derived using Program DISTANCE (Version 5.0, <www.ruwpa.st-and.ac.uk/distance/>, accessed 15 Jul 2009), decreased steadily beyond 50 m for most species. We averaged relative abundance values from 2004 and 2005 because we were unable to find a difference ($P > 0.250$) in relative abundances between years for any species except orange-crowned warbler.

For red-faced warblers and yellow-eyed juncos, we generated detection histories, which summarized when we first detected each singing bird during the 6-minute survey. We used these detection histories to estimate P_{sings} (i.e., probability that a bird within the survey area sings; see Kirkpatrick et al. 2007) using a removal model in Program CAPTURE (Version 1, <www.mbr-pwrc.usgs.gov/software.html>, accessed 15 Dec 2008; sensu Farnsworth et al. 2002). We used estimates of P_{sings} to adjust our estimates of relative abundance into density estimates of singing males/ha for red-faced warblers and yellow-eyed juncos (the 2 ground-nesting bird species for which we had sufficient data to estimate P_{sings}).

For our nest-monitoring data, we estimated daily nest survival and overall nesting success (incubation through nestling periods; Mayfield 1961, 1975) for red-faced warblers and yellow-eyed juncos using nests with known fates during 2004 and 2005 and compared daily nest survival for red-faced warblers and yellow-eyed juncos using a Z-test (Hensler and Nichols 1981). We had an insufficient number of nests with known fates to compare nest-site characteristics at successful versus unsuccessful nests.

For our nest-site characteristics data, we screened data and eliminated variables for which >90% of observations were equal to zero. We eliminated highly correlated variables by combining pairs of correlated variables into one (e.g., we combined small and large ponderosa pine saplings into ponderosa pine saplings). We tested data for multivariate outliers by calculating Mahalanobis distances and applied transformations (e.g., sq root + 1, log10 + 1, logit, rank) to variables to control outliers where necessary (Morrison et al. 1998, Meyers et al. 2006). We used exploratory factor analysis to reduce our large sets of continuous explanatory variables to smaller sets of uncorrelated factors for use in subsequent logistic regression analyses (Meyers et al. 2006). We retained factors with eigenvalues ≥ 1 and used a varimax rotation to facilitate interpretation of factor weights (Meyers et al. 2006).

We identified 13 factors (from 38 continuous variables) for the red-faced warbler versus random plot analysis, 10 factors (from 34 continuous variables) for the yellow-eyed junco versus random plot analysis, and 14 factors (from 45 continuous variables) for the red-faced warbler versus yellow-eyed junco nest-site analysis. These 3 sets of factors retained 71%, 68%, and 70% of variability within our data sets, respectively. The Kaiser–Meyer–Olkin measures of sampling adequacy were >0.70 for all 3 factor analyses, indicating that our data were suitable for factor analysis (Meyers et al. 2006). We named each factor based on the variables that had factor weights ≥ 0.55 (indicating that

Table 2. Relative abundance, P_{sings}, density, and total number of nests of 5 ground-nesting bird species found breeding within 4 study sites in high-elevation (>2,000 m) forests of the Santa Catalina Mountains, Arizona, USA in 2004–2005.

Species	Relative abundance[a]		P_{sings}[b]	Density[c]		Nests[d]
	$\bar{x}$	SE		$\bar{x}$	SE	
Red-faced warbler	1.88	0.204	0.986	2.43	0.262	151
Yellow-eyed junco	0.74	0.136	0.548	1.36	0.251	78
Orange-crowned warbler	0.29	0.164				9
Spotted towhee	0.12	0.051				1
Virginia's warbler	0.06	0.033				0[e]

[a] We calculated relative abundance by averaging no. of singing M within 50 m of surveyor (2004–2005 survey data combined).
[b] P_{sings} = probability of M singing during a 6-min point-count survey (2004–2005 survey data combined; birds within 50 m of surveyor).
[c] Density of singing M/ha after accounting for vocalization probability = 10,000 × {relative abundance + [relative abundance × (1 − P_{sings})]}/π × (50)^2.
[d] Total no. of nests found in 2004–2005.
[e] We confirmed breeding by Virginia's warblers in our study area in 2007 (C. Kirkpatrick and C. Conway, University of Arizona, unpublished data).

≥30% of variance in the variable was accounted for in the factor).

We ran 3 logistic regressions using PROC NOMEG (SPSS Version 16.0; SPSS Inc., Chicago, IL) with the binary response variable being either 1) used sites versus random plots for red-faced warblers, 2) used sites versus random plots for yellow-eyed juncos, or 3) red-faced warbler versus yellow-eyed junco nest-sites. The red-faced warbler versus yellow-eyed junco nest-site analysis allowed us to compare environmental features at the nest scale (e.g., nest-area concealment, closest plant to nest) that were not applicable to (and hence not measured at) random plots (Table 1). For our explanatory variables, we used factor scores generated from factor analyses and dummy variables for our one nominal variable (i.e., closest plant to nest). In addition to these explanatory variables, we controlled for the potentially confounding influence of nuisance variables such as study site, year, nest initiation date, and lag-time in vegetation sampling (i.e., days between nest initiation and vegetation sampling) by including these variables in our multivariate analyses.

Because we considered up to 29 explanatory variables and were not testing among explicit mechanistic hypotheses, we used a backward stepwise procedure to fit candidate models (Stephens et al. 2005; Steidl 2006, 2007). We used liberal criteria for variable inclusion ($P \leq 0.250$) and retention ($P \leq 0.300$) due to the exploratory nature of our analyses (Hosmer and Lemeshow 2000). We considered resulting odds ratios of <0.66 (i.e., approx. 50% decrease) or >1.50 (i.e., approx. 50% increase) as indicative of biologically significant effects. Because we presumed that nest-scale environmental features were important to ground-nesting birds in Arizona (Martin 1998), we conducted univariate analyses on the 5 nest-scale variables recorded at nests of red-faced warblers and yellow-eyed juncos (Table 1). We used independent samples t-tests for continuous variables and contingency table analyses for the nominal variable (i.e., closest plant to nest). We used a Bonferonni adjustment to keep the experiment-wise error rate at $\alpha < 0.05$.

RESULTS

Red-faced warblers and yellow-eyed juncos were the 2 most common ground-nesting birds within our study area based on relative abundance of singing males detected during bird surveys and total number of nests located during the study (Table 2). Number of singing males/ha was 79% greater ($t = 3.0$, $P = 0.026$) for red-faced warblers than yellow-eyed juncos and we found 94% more red-faced warbler than yellow-eyed junco nests, in part, because red-faced warbler nests were easier to find (93% located via parental behavior cues vs. 1% via flushing birds) compared to yellow-eyed junco nests (33% located via parental behavior cues vs. 53% via flushing birds).

Yellow-eyed juncos initiated nests as early as 11 April and as late as 1 July ($n = 78$ nests), and red-faced warblers initiated nests as early as 4 May and as late as 19 June ($n = 151$ nests). Nest depredation accounted for 92% of all nest failures: 89% for red-faced warblers and 98% for yellow-eyed juncos. Estimates of daily nest survival and nest success were 0.922 (95% CI = 0.904–0.940) and 13%, respectively, for red-faced warblers, and 0.936 (95% CI = 0.919–0.953) and 19%, respectively, for yellow-eyed juncos. We were unable to detect a difference in daily nest survival between the 2 species ($Z = 1.1$, $P = 0.282$).

Most (≥70%) nests of both species were located ≤30 m from drainage bottoms: red-faced warbler averaged 26.2 m (SD = 23 m; median = 20 m) and yellow-eyed junco averaged 21 m (SD = 17 m; median = 18 m). All nests were situated on the ground except for 2 yellow-eyed junco nests located 10 m and 6 m, respectively, above the ground in large white fir trees (yellow-eyed juncos have previously been reported to occasionally nest in trees; Moore 1972, Sullivan 1999).

For comparison of red-faced warbler used sites versus random plots, the logistic regression analysis produced a model (Table 3) that was a significant improvement over the intercept-only model ($\chi^2 = 131$, df = 10, $P < 0.001$). Overall predictive success was high (85%) with 92% of red-faced warbler nest-sites classified correctly and 71% of random plots classified correctly. Ten factors were predictors ($P \leq 0.300$) of red-faced warbler nest-sites (Table 3). We found strong (odds ratios > 1.50) positive associations for 6 of the 10 factors: 1) brush cover, Gambel oak saplings and trees (small), small woody debris cover; 2) fern cover, forb cover; 3) bigtooth maple saplings and trees (small); 4) New Mexican locust saplings and trees (small); 5) southwestern white pine

Table 3. Habitat variables and factors (generated from factor analyses that created independent multivariate habitat parameters) associated with nest-sites of red-faced warblers and yellow-eyed juncos based on 3 stepwise logistic regression analyses: 1) red-faced warbler nest-sites (n = 149) versus random plots (n = 70); 2) yellow-eyed junco nest-sites (n = 78) versus random plots (n = 70); and 3) red-faced warbler versus yellow-eyed junco nest-sites. We collected data from 4 study sites in high-elevation (>2,000 m) forests of the Santa Catalina Mountains, Arizona, USA in 2004–2005. We ordered habitat variables and factors by strength of odds ratios.

Analysis	Habitat variables and factors selected in final models[a]	Coeff.		Wald		Odds ratio	
		b	SE	χ^2	P	Exp b	95% CI
Red-faced warbler nest-sites vs. random plots	Brush cover, Gambel oak saplings and trees (small), small woody debris cover	1.56	0.28	30.0	<0.001	4.8	2.7–8.3
	Fern cover, forb cover	1.41	0.28	25.1	<0.001	4.1	2.4–7.1
	Bigtooth maple saplings and trees (small)	1.27	0.29	19.0	<0.001	3.6	2.0–6.3
	New Mexican locust saplings and trees (small)	0.88	0.26	11.7	0.001	2.4	1.4–4.0
	Area burned, snags	−0.63	0.22	8.0	0.005	0.5	0.3–0.8
	Southwestern white pine trees (large)	0.56	0.21	6.9	0.009	1.8	1.2–2.6
	Douglas-fir saplings and trees (small), white fir saplings and trees (small)	0.56	0.21	6.8	0.009	1.8	1.2–2.6
	White fir large trees (large)	−0.49	0.22	4.9	0.027	0.6	0.4–1.0
	Slope, absence of mountain snowberry shrubs	0.37	0.23	2.6	0.107	1.4	0.9–2.2
	Downed log cover	−0.32	0.20	2.6	0.110	0.7	0.5–1.1
	Intercept	1.48	0.26	31.8	<0.001		
Yellow-eyed junco nest-sites vs. random plots	Small woody debris cover, brush cover, mountain snowberry shrubs	1.64	0.33	25.1	<0.001	5.2	2.7–10.0
	Forb cover, fern cover, close to drainage bottom	1.38	0.28	24.0	<0.001	4.0	2.3–6.9
	Canopy cover, white fir trees (large)	−0.81	0.26	9.8	0.002	0.4	0.3–0.7
	Snags, area burned	−0.79	0.26	9.2	0.002	0.4	0.3–0.8
	Downed log cover	0.39	0.25	2.3	0.126	1.5	0.9–2.4
	Leaf-litter cover, absence of bare ground cover, absence of rock cover	−0.32	0.22	2.1	0.148	0.7	0.5–1.1
	Douglas-fir saplings and trees (small), white fir saplings and trees (small)	0.29	0.23	1.6	0.211	1.3	0.8–2.0
	Intercept	0.25	0.25	1.0	0.315		
Yellow-eyed junco vs. red-faced warbler nest-sites	Closest plant to nest (Douglas-fir or white fir)	−2.20	1.17	3.5	0.060	0.1	0.0–1.1
	Closest plant to nest (other tree spp.)	−1.15	0.96	1.4	0.230	0.3	0.0–2.1
	Closest plant to nest (bigtooth maple)	−0.72	0.91	0.7	0.424	0.5	0.1–2.9
	Closest plant to nest (grass)	0.38	0.57	0.4	0.505	1.5	0.5–4.5
	Closest plant to nest (forb or fern)	−0.82	0.70	1.4	0.241	0.4	0.1–1.7
	Closest plant to nest (shrub)	−0.44	0.86	0.3	0.610	0.6	0.1–3.5
	Closest plant to nest (in open)[b]	0					
	White fir saplings and trees (small)	−0.62	0.23	7.2	0.007	0.5	0.3–0.8
	Southwestern white pine trees (large)	−0.58	0.20	8.6	0.003	0.6	0.4–0.8
	Fern cover, downed log cover	0.50	0.22	5.4	0.020	1.7	1.1–2.5
	Ponderosa pine trees, southwestern white pine saplings	−0.39	0.20	3.8	0.052	0.7	0.5–1.0
	Snags	−0.29	0.20	2.2	0.134	0.8	0.5–1.1
	Leaf-litter cover, absence of bare ground cover, absence of rock cover	−0.28	0.19	2.1	0.146	0.8	0.5–1.1
	Shrub cover	0.28	0.19	2.0	0.154	1.3	0.9–1.9
	White fir trees (large)	−0.20	0.19	1.1	0.288	0.8	0.6–1.2
	Nest initiation date	−0.08	0.02	16.6	<0.001	0.9	0.9–1.0
	Lag time	−0.02	0.01	2.5	0.111	1.0	1.0–1.0
	Intercept	11.01	3.09	12.7	<0.001		

[a] Variables include nest initiation date, lag time, and closest plant to nest (all others are factors).
[b] Reference category for variable closest plant to nest.

trees (large); and 6) Douglas-fir saplings and trees (small), white fir saplings and trees (small). We found strong (odds ratios < 0.66) negative associations for 2 of the 10 factors: 1) area burned, snags; and 2) white fir trees (large).

For comparison of yellow-eyed junco used sites versus random plots, the logistic regression analysis produced a model (Table 3) that was a significant improvement over the intercept-only model (χ^2 = 91, df = 7, P < 0.001). Overall predictive success was high (82%) with 79% of yellow-eyed junco nest-sites classified correctly and 84% of random plots classified correctly. Seven factors were predictors of yellow-eyed junco nest-sites (Table 3). We found strong positive associations for 3 of the 7 factors: 1) small woody debris cover, brush cover, mountain snowberry shrubs; 2) forb cover, fern cover, close to drainage bottom; and 3) downed log cover. We found strong negative associations for 2 of the 7 factors: 1) canopy cover, white fir trees (large); and 2) snags, area burned.

Comparison of red-faced warbler and yellow-eyed junco nest-sites produced a model (Table 3) that was a significant improvement over the intercept-only model (χ^2 = 82, df = 16, P < 0.001). Overall predictive success was high (82%) with 93% of red-faced warbler nest-sites classified correctly and 57% of yellow-eyed junco nest-sites classified correctly. Eight factors and 3 variables (1 nominal and 2 nuisance) differentiated yellow-eyed junco nest-sites from red-faced warbler nest-sites (Table 3). We found strong positive associations for fern cover, downed log cover, and strong negative associations for 1) closest plant to nest (Douglas-fir or white fir), 2) white fir saplings and trees (small), and 3) southwestern white pine trees (large).

At the nest scale, univariate analyses revealed that yellow-eyed junco nests had greater nest-area concealment from the side (56%) than did red-faced warbler nests (46%; t = 2.9, df = 214, P = 0.004). The closest plant to most red-faced warbler and yellow-eyed junco nests was grass (Fig. 2).

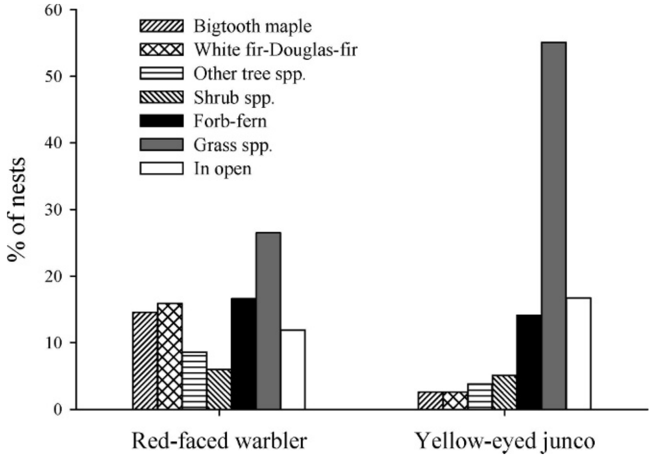

Figure 2. Percentage of red-faced warbler and yellow-eyed junco nests found in 2004–2005 that were associated with each of 7 nesting substrates within 4 study sites in high-elevation (>2,000 m) forests of the Santa Catalina Mountains, Arizona, USA. We recorded the plant that was closest to each nest but recorded "in open" if no plant was <30 cm from the nest (as per BBIRD protocols; Martin et al. 1997).

However, relative to yellow-eyed junco nests, red-faced warbler nests were situated less frequently adjacent to grass (26% vs. 55%) and more frequently adjacent to bigtooth maple (15% vs. 3%) or white fir-Douglas-fir (16% vs. 3%) saplings and trees ($\chi^2 = 29.5$, df = 6, $P < 0.001$).

At the nest scale, we found no red-faced warbler or yellow-eyed junco nests located inside the perimeter of the 2003 wildfire. At the 11.3-m-radius scale, both red-faced warbler and yellow-eyed junco nest-sites were negatively associated with percent surface area burned compared to random plots (see above). Most (84%) nest-sites and random plots that were burned to some extent were affected by low-severity surface fires. At the study-site scale, the wildfire burned 0% of the upper Bear Wallow Canyon, 10% of the lower Bear Wallow Canyon, 26% of the Sabino Canyon, and 70% of the Marshall Gulch study sites. We found that the typical burn pattern within each of the 3 study sites affected by fire was that forests burned more extensively on slopes above drainages (rather than in the drainage bottoms). We considered the possibility that the spatial pattern of the wildfire may have biased nest-site characteristics of red-faced warblers and yellow-eyed juncos by forcing birds to nest lower in drainages in areas of unburned montane riparian forest. However, our models were similar when we reran analyses after removing data from the extensively burned Marshall Gulch study site.

Geographic Information System coverage of the biotic communities of Arizona (Arizona GeoData Portal 2009) indicated 5,825 ha of Madrean conifer forest in the Santa Catalina Mountains. Based on an average width of montane riparian forest within our 4 study sites of 57 m (SE = 12.2 m), we estimated that approximately 620 ha (SE = 132 ha) or 10.6% of this high-elevation forest contained montane riparian forests. This is likely an overestimate because our 4 study sites were located within 3 of the largest drainages in the Santa Catalina Mountains.

DISCUSSION

Red-faced warblers and yellow-eyed juncos were the most common ground-nesting birds breeding within high-elevation, forested drainages of the Santa Catalina Mountains, Arizona, USA. Three other ground-nesting birds (orange-crowned warblers, Virginia's warblers, and spotted towhees) nested within our study area but were uncommon. These species tend to breed in greater numbers at lower elevations (e.g., spotted towhee, Virginia's warblers; Corman and Wise-Gervais 2005) or at higher latitudes (e.g., orange-crowned warbler, Virginia's warbler; Sogge et al. 1994, Olson and Martin 1999). In fact, our records of nesting orange-crowned warblers represent the most southerly breeding population of this species in Arizona. Given the paucity of other ground-nesting birds, red-faced warblers and yellow-eyed juncos are the 2 species most likely to compete for critical resources such as nest-sites within our study area (Martin and Martin 2001).

Red-faced warbler nest-sites were associated with a greater number and diversity of saplings and small trees, which may enhance foraging opportunities because red-faced warblers forage close to the ground in bigtooth maples, white firs, and occasionally Douglas-firs within our study area (K. Decker, University of Arizona, unpublished data). Elsewhere in Arizona, red-faced warblers forage close to the ground in deciduous trees (Marshall 1957), bigtooth maples and firs (Martin and Barber 1995), and medium to large southwestern white pines (Franzreb and Franzreb 1983) among other species. Similar to previous studies, we found that red-faced warbler and yellow-eyed junco nest-sites were associated with more ground cover (especially ferns and forbs) and more small woody debris compared to random plots (Moore 1972, Martin 1998, Sullivan 1999, Short 2003). Yellow-eyed juncos are known to favor nest-sites with coarse woody debris that they use to conceal nests (Short 2003). In addition, we found that yellow-eyed junco nest-sites were associated with more mountain snowberry shrubs and less canopy cover compared to random plots (yellow-eyed juncos are known to select territories with some open areas; Sullivan 1999).

Red-faced warblers and yellow-eyed juncos nested across the moisture gradient within our study area, from mesic drainage bottoms to xeric slopes and ridge tops. However, most (>70%) nests of both species were close ($\leq$30 m) to drainage bottoms. Many of the environmental features that we found positively associated with nest-sites of red-faced warblers and yellow-eyed juncos are typical of montane riparian forests located in drainage bottoms in the southwestern United States. For example, southwestern montane riparian forests support a compositionally and structurally diverse mix of shorter deciduous and taller coniferous trees, with the dominant aspect of this forest type being one of shrubbery (i.e., an increased presence and extent of saplings and shrubs [including mountain snowberry] in the understory; Whittaker and Niering 1975, Fitzhugh et al. 1987, Brown 1994). Montane riparian forests in the region also support a rich herb layer of grass, ferns, and forbs

(Whittaker and Niering 1975, Fitzhugh et al. 1987, Szaro 1989). In contrast, adjacent mixed-conifer forest typically contains large trees with a dense canopy, a trait that tends to restrict growth of shrubs, saplings, and forbs in the understory (Whittaker and Niering 1975, Brown 1994). Similarly, adjacent ponderosa pine forest typically lacks an extensive understory of shrubs and saplings (Brown 1994).

Our results suggest that red-faced warblers and yellow-eyed juncos prefer nesting in montane riparian forest because surrounding forest types lack many of the proximate structural (e.g., presence of shrubs and saplings) and compositional (e.g., diversity of tree species and ground cover) cues that promote settlement and nest-site selection by breeding birds. Ultimately, food availability may drive selection of nest-sites in montane riparian forest. Indeed, montane riparian forests in the Santa Catalina Mountains have one of the highest rates of net primary productivity ($1,123 g/m^2/yr$ aboveground) of any forest type within this mountain range (Whittaker and Niering 1975). Conversely, nest depredation may ultimately drive selection of nest-sites by red-faced warblers and yellow-eyed juncos within our study area. We found that nest depredation was the leading cause of nest failure for both red-faced warblers and yellow-eyed juncos (a pattern that has been reported for red-faced warblers and other ground-nesting bird species elsewhere in the southwestern United States; Martin 1992, Martin and Martin 2001). Moreover, nest depredation affects nest-site selection in red-faced warblers and other ground-nesting birds (Martin 1998).

Compared to red-faced warblers, most yellow-eyed juncos nested adjacent to grass, whereas red-faced warblers nested adjacent to a variety of plant species, including grass, bigtooth maples, white firs, and Douglas-firs. Previous studies have reported selection of these plant species at the nest scale by yellow-eyed juncos in montane forests of southeastern Arizona (Moore 1972, Short 2003) and by red-faced warblers in montane forests on the Mogollon Rim, Arizona (Martin 1993, 1998). Moreover, selection of herbaceous cover by yellow-eyed juncos (Short 2003), firs by red-faced warblers (Martin 1998), and bigtooth maples by other ground-nesting birds (e.g., orange-crowned warblers; Martin and Martin 2001) has been associated with reduced nest depredation. Thus, red-faced warblers and yellow-eyed juncos may reduce nest-site overlap (and thereby reduce nest depredation; Martin and Martin 2001) and coexist in our study area by selecting nest-sites with different environmental features, especially at the nest scale.

However, we observed one instance of a yellow-eyed junco building a nest in the exact site where a red-faced warbler had been observed building a nest several days prior (C. Kirkpatrick, personal observation). In addition, yellow-eyed juncos often chase and fight with red-faced warblers early in the breeding season, suggesting some degree of competition between red-faced warblers and yellow-eyed juncos (Sullivan 1999; C. Kirkpatrick, personal observation). If these 2 species compete for nest-sites, yellow-eyed juncos may dominate physically and behaviorally because of their larger size ($\bar{x}$ = 20 g vs. $\bar{x}$ = 10 g; Martin and Barber 1995, Sullivan 1999) and their ability to arrive on the breeding grounds, establish territories, and initiate nesting attempts earlier (by approx. 3 weeks) in the breeding season than do red-faced warblers. Indeed, yellow-eyed juncos placed nests lower in drainages, had an average of 23% more vegetation concealing nests from the side, and had slightly higher nesting success (although the difference was not statistically significant) than did red-faced warblers.

Red-faced warblers and yellow-eyed juncos avoided nesting in portions of our study area that were burned by a predominantly low-severity surface fire in 2003. Low-severity surface fires in forests can temporarily reduce abundance of herbs, brush, small woody debris, downed logs, shrubs, and saplings (Artman et al. 2001, Short 2003), environmental features that we found positively associated with nest-sites of red-faced warblers and yellow-eyed juncos. Although red-faced warblers and yellow-eyed juncos avoided burned areas in the short term, low-severity surface fires may improve long-term habitat quality for both species by encouraging regrowth of understory vegetation including grass, forbs, ferns, shrubs, and saplings (Short 2003). Indeed, nesting success of yellow-eyed juncos declined substantially 1 year after a low-severity surface fire in southern Arizona but increased in the second year postfire when understory cover from grass and ferns increased (Short 2003).

Besides limiting availability of nest-sites within our study area, the 2003 wildfire may have reduced nesting success of red-faced warblers and yellow-eyed juncos indirectly by increasing nest depredation. Nesting success for both red-faced warblers and yellow-eyed juncos was low (13% and 19%, respectively) during the 2-year postfire period in 2004–2005. In contrast, nesting success of these species was higher (50% and 68%, respectively) in our study area in 2002–2003 (C. Kirkpatrick and C. Conway, unpublished data) and during subsequent nest monitoring of yellow-eyed juncos in our study area in 2007 (41%) and red-faced warblers in our study area in 2008 (42%; K. Decker, University of Arizona, unpublished data; C. Kirkpatrick and C. Conway, unpublished data), suggesting that reduced nesting success observed for both species in 2004–2005 was not typical. Ground-nesting birds that nest in recently burned forests often place their nests in remaining unburned vegetation and may be more susceptible to nest depredation if predators have to search fewer potential nest locations before finding a nest (Best 1979, Aquilani et al. 2000). Thus, nests placed in unburned vegetation surrounded by large areas of burned vegetation (as in our study during the first 2 yr postfire) may be temporarily more susceptible to nest depredation following fire (Short 2003).

Our results provide some of the first quantitative data to support observations that breeding densities of red-faced warblers and yellow-eyed juncos are greatest in stands of montane riparian forests within high-elevation forests of southern Arizona (Bulmer 1966, Corman and Wise-Gervais 2005). Moreover, our estimate of red-faced warbler breeding density (2.4 M/ha along drainage bottoms) was noticeably higher than in other high-elevation forests in the southwestern United States (e.g., the Mogollon Rim of central

AZ; C. Conway, personal observation; K. Decker, personal communication). Although we need additional research to identify specific nest-site characteristics associated with fitness parameters (Martin 1993, Morrison et al. 1998), persistence of healthy breeding populations of red-faced warblers, yellow-eyed juncos, and other ground-nesting birds (e.g., orange-crowned warblers; Sogge et al. 1994) likely depends on conserving montane riparian forest in the region. Yet, little research or conservation planning has been directed toward montane riparian forest, even though this forest type is limited in its areal extent (e.g., <11% of high-elevation forest in the Santa Catalina Mountains) and increasingly threatened by disturbances such as extensive, stand-replacement wildfire.

MANAGEMENT IMPLICATIONS

Our study represents a first attempt at developing nest-site models for red-faced warblers and yellow-eyed juncos in high-elevation forests of southern Arizona and future studies should test our models against alternative nest-site models. In the meantime, we recommend that managers maintain breeding populations of red-faced warblers and yellow-eyed juncos in montane riparian forest by promoting the environmental features that we found associated with nest-sites of these 2 ground-nesting birds, especially 1) abundant brush, small woody debris, ferns, and forbs (both species), 2) high number and diversity of saplings and small trees (red-faced warblers), and 3) abundant shrubs and downed logs and less canopy cover (yellow-eyed juncos). In addition, managers should consider management options that maintain native grasses that appear to be an important nesting substrate for both red-faced warblers and yellow-eyed juncos (perhaps by providing more nest-area concealment than other plant species; C. Kirkpatrick, personal observation).

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