



Research Article

Western Yellow-Billed Cuckoo Nest-Site Selection and Success in Restored and Natural Riparian Forests

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ABSTRACT The western distinct population segment of yellow-billed cuckoo (*Coccyzus americanus*; western cuckoo) has been extirpated from most of its former breeding range in the United States because of widespread loss and degradation of riparian cottonwood (*Populus* spp.)-willow (*Salix* spp.) forests. Restoration and management of breeding habitat is important to the recovery of this federally threatened species, and identification of high-quality breeding habitat can help improve the success of recovery. In 2005, the Lower Colorado River Multi-Species Conservation Program, a long-term, multi-agency effort, was initiated to maintain and create wildlife habitat within the historical floodplain of the lower Colorado River (LCR) for federally endangered and threatened species, including western cuckoos. We conducted an empirical, multi-scale field investigation from 2008–2012 to identify habitat characteristics selected by nesting western cuckoos along the LCR. Multiple logistic regression models revealed that western cuckoos selected nest sites characterized by increased densities of small, native, early successional trees measuring 8–23 cm diameter at breast height, and lower diurnal temperature compared to available habitat in restoration and natural forests. Nesting cuckoos selected sites with increased percent canopy closure, which was also important for nest success in restoration sites along the LCR. Our results show habitat components selected by nesting western cuckoos in restoration and natural riparian forests and can help guide the creation, enhancement, and management of riparian forests with habitat conditions necessary to promote nesting of western cuckoos. © 2021 The Wildlife Society.

KEY WORDS *Coccyzus americanus*, cottonwood-willow forest, habitat creation, lower Colorado River, microclimate, relative humidity, riparian restoration, southwestern United States, temperature.

Riparian forests in the southwestern United States were historically dynamic ecosystems (Stromberg 1993), where frequent floods created ever-changing vegetation structure and composition, providing abundant nesting habitat for many riparian-obligate species including Bell's vireos (*Vireo bellii*), willow flycatchers (*Empidonax traillii*), and yellow-billed cuckoos (*Coccyzus americanus*; Bell 1997). Over the last century, however, >90% of the original mixed-age stands of riparian forest have been lost or degraded because of agriculture and urban development, damming, diversion,

regulation of surface flow, and groundwater pumping (Lite and Stromberg 2005, Poff et al. 2011), with the remaining riparian areas experiencing varying degrees of indirect effects and degradation. Concomitantly, the western distinct population segment of the yellow-billed cuckoo (western cuckoo) experienced significant population declines across the western United States (Grinnell and Miller 1944, Gaines 1974, Gaines and Laymon 1984, Laymon and Halterman 1987) and is listed as federally threatened (U.S. Fish and Wildlife Service [USFWS] 2014b).

Knowledge of western cuckoo breeding habitat has stemmed largely from general habitat use and occupancy studies (Gaines 1974, Gaines and Laymon 1984, Greco 2013, Sechrist et al. 2013). Such studies reveal that western cuckoo territories consist primarily of relatively large (20–80 ha) intact stands of riparian cottonwood (*Populus* spp.)-willow (*Salix* spp.) forest (Laymon and Halterman 1989), characterized by dense canopy closure and foliage volume (Laymon et al. 1997, Hughes 2020). Although the characteristics of breeding habitat are generally understood

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(USFWS 2014*b*), information on specific habitat components important for nest placement and nesting success are still needed to assist with recovery actions, including habitat restoration and management. To fill this knowledge gap, we conducted an empirical multi-scale habitat selection study to determine characteristics associated with western cuckoo nest sites and nest success in restoration and natural riparian forests along the lower Colorado River (LCR).

Our objectives were to identify vegetation and microclimate habitat characteristics that influence western cuckoo nest-site selection and nest success in both restoration and natural forests, identify differential habitat characteristics that influence nest-site selection between natural and restoration sites, and develop recommendations for creating nest-site characteristics selected by western cuckoos when creating, enhancing, or managing riparian vegetation. We predicted that increased canopy closure and increased densities of native trees would be important in nest-site selection and nest success because they would provide concealment and protection from predators (S. A. Laymon, California Department of Fish and Game, unpublished report). Increased canopy closure can also provide thermal protection (e.g., shade) necessary for nestling survival (Rangel-Salazar et al. 2008). Temperatures in the LCR desert environment during the breeding season often exceed 40°C; thus, we also predicted that, like southwestern willow flycatchers (*E. t. extimus*) along the LCR (McLeod et al. 2008), lower mean and maximum diurnal temperature and higher relative humidity would be selected for nest sites.

STUDY AREA

We conducted this study from 2008–2012 along a 250-km reach of the LCR in Arizona and California in the United States from Havasu National Wildlife Refuge (34°46'N, 114°32'W) to the Cibola National Wildlife Refuge (33°21'N, 114°41'W). This area contains the Bill Williams River tributary and lies within the larger LCR region where the Lower Colorado River Multi-Species Conservation Program (LCR MSCP), a long-term, multi-agency effort, mandates the creation of 3,278 ha of riparian land cover for ≥7 federally listed species, of which 1,639 ha are for western cuckoos (LCR MSCP 2004). The LCR MSCP was established by United States Department of Interior agencies; water, power, and wildlife resource agencies from Arizona, California, and Nevada; indigenous American tribes; and environmental and recreational interest groups to form a partnership to develop and implement a long-term endangered species compliance and management program for the historical floodplain of the LCR. These partners form the LCR MSCP Steering Committee and the program is implemented by the Bureau of Reclamation, LCR region, Boulder City, Nevada. Riparian restoration efforts began in 2005. Prior to this effort, naturally occurring riparian forest along the lower Bill Williams River supported the largest, and one of the only remaining breeding populations of western cuckoos within the LCR watershed (Laymon and Halterman 1989, Johnson et al. 2007).

We selected 6 naturally occurring non-restoration sites (i.e., natural) and 11 restoration sites that encompassed similar sized areas (~400 ha) within Sonoran Desert riparian areas with elevation ranging from 72–170 m. From June to August average monthly high temperatures are 42°C. June regularly has no precipitation and monsoons typically start in early July and continue through September with average monthly rainfall <1 cm. The area remains dry (<1 cm of average monthly rainfall) and mild (73°C average monthly temperature) through fall (Oct and Nov). December to March is mostly sunny, with intermittent storms averaging <2 cm of monthly rainfall. April and May are characterized by dry, hot conditions (<0.2 cm of average monthly rainfall and average monthly high of 34°C). Dominant fauna include desert bighorn sheep (*Ovis canadensis*), coyote (*Canis latrans*), bobcat (*Lynx rufus*), raccoon (*Procyon lotor*), collared peccary (*Pecari tajacu*), striped skunk (*Mephitis mephitis*), western spotted skunk (*Spilogale gracilis*), beaver (*Caster canadensis*), snakes (*Lampropeltis* spp.), bats (*Myotis* spp.), rodents (*Neotoma* spp.), and various lizard and migratory bird species. Survey sites were located within state or federally protected areas used for recreational activities and consisted of early to mature native or mixed native and exotic riparian forest patches. Native species included seep willow (*Baccharis salicifolia*), mesquite (*Prosopis* spp.), coyote willow (*S. exigua*), Fremont cottonwood (*P. fremontii*), and Goodding's willow (*S. gooddingii*). Tamarisk (*Tamarix* spp.) was the most common non-native species.

Natural, unrestored sites occupied by western cuckoos were located in the floodplain of the lower Bill Williams River in Arizona, approximately 200 km northwest of Phoenix, and experienced monsoon floods and received simulated spring flooding through occasional managed water releases from Alamo Dam (34°13'N, 113°36'W). Natural sites contained saplings (<8 cm diameter at breast height [dbh]), early- (8–23 cm dbh), and mid- to late successional (>23 cm dbh) riparian trees. Non-native tamarisk invaded the natural sites prior to our study, and its density in these sites exceeded that of Fremont cottonwood and Goodding's willow (Table 1). Although tamarisk is one of the dominant tree species, it is found within a mosaic of some of the last remaining extensive stands of natural cottonwood and willow forests within the LCR watershed (van Riper et al. 2008). We conducted our study at these sites prior to colonization by tamarisk leaf beetles (*Diorhabda* spp.) and associated die-off of riparian trees attributed to regional drought (Udall and Overpeck 2017).

Restoration sites occupied by western cuckoos were located along the LCR up to 80 km north and 160 km south of the Bill Williams River in California and Arizona. These sites were located within the Palo Verde Ecological Reserve in California and the Cibola Valley Conservation Area, Cibola National Wildlife Refuge, and Havasu National Wildlife Refuge in Arizona. Restoration sites were subjected to consistent flood irrigation every 10–14 days (LCR MSCP 2007*b*, 2009, 2010) from May to September each year, and supported young riparian forests (2–7 yrs old) dominated by saplings (<8 cm dbh) and early-successional

Table 1. Comparing vegetation at restoration and natural sites occupied by western yellow-billed cuckoos with descriptive statistics and results of Mann-Whitney-Wilcoxon tests ($\alpha=0.01$) for vegetation variables recorded at randomly placed vegetation plots at restoration ($n=80$) and natural sites ($n=65$) along the lower Colorado River in Arizona and California, USA, 2008–2012.

Vegetation variable	Restoration ($n=80$)			Natural ($n=65$)			<i>P</i>
	Median	95% CI	Range	Median	95% CI	Range	
Native saplings (<8 cm dbh)/10 m ²	0.51	0.13, 1.53	0–12.35	0.13	0, 0.38	0–7.51	0.002
Small (8–23 cm dbh) native trees/10 m ²	0.38	0.13, 0.64	0–3.95	0.06	0, 0.13	0–3.95	<0.001
Medium-large (>23 cm dbh) native trees/10 m ²	0.00	0, 0	0–0.60	0.07	0.05, 0.10	0–0.70	<0.001
Gooding's willow/10 m ²	0.13	0, 0.25	0–12.35	0.02	0, 0.10	0–7.38	0.216
Fremont cottonwood/10 m ²	0.23	0.02, 0.76	0–5.98	0.00	0, 0.05	0–4.20	0.002
Tamarisk/10 m ²	0.00	0, 0	0–19.74	2.77	1.88, 3.34	0–18.59	<0.001
Canopy closure (%)	87	83, 92	4–100	87	82, 92	3–98	0.514

riparian trees (8–23 cm dbh) that were actively managed under the LCR MSCP (LCR MSCP 2004). The restoration sites contained variable densities of Fremont cottonwood and Gooding's willow; minimal amounts of tamarisk were present at these sites (Table 1).

METHODS

Bird Surveys

We conducted standardized broadcast call surveys for western cuckoos at all sites every 12–20 days from June to August following techniques used by Halterman et al. (2011) from 2008–2012. We located ≥ 1 nests at 6 natural sites and 11 restoration sites. During or immediately after each broadcast call survey, we searched for nests in woody vegetation accessible to surveyors on foot surrounding a detection location because western cuckoos may respond to broadcast calls from nests (Martin and Geupel 1993). We monitored areas with multiple detections for a dawn nest exchange because male western cuckoos predominantly incubate through the night and are replaced by their mate shortly after sunrise, with 1 or both birds often vocalizing during the exchange (Halterman 2009, Hughes 2020). Once we found a nest, we monitored it every 1 to 4 days and deemed it successful if ≥ 1 young fledged, which we determined by detecting a fledgling near the nest within 2 days of the estimated fledge date (\bar{x} number of days between nest visits = 2.75; Martin and Geupel 1993). We recorded a nest as failed when we observed the nest damaged or destroyed with eggs not indicative of hatching or large eggshell fragments or remains, or empty before the earliest possible fledge date (6 days after hatching) with no further juvenile or adult activity detected nearby. Field personnel followed pre-approved survey and nest searching protocols to ensure safe and effective techniques for approaching potential cuckoo nests, emphasizing minimization of disturbance to breeding birds (Halterman et al. 2011, 2015). Observers also checked for predators before visiting a potential nest and minimized time spent at nests. We obtained necessary site-specific permits from Havasu National Wildlife Refuge (SCP 09-2255-09-011), Bill Williams River National Wildlife Refuge (SCP 22551-09), and Cibola National Wildlife Refuge (SCP 22540-09-06) and scientific collecting permits from Arizona Game and Fish (SP759343)

and California Department of Fish and Game (SCP 10586) prior to the start of each field season.

Vegetation Sampling

We sampled trees, shrubs, and canopy closure within circular plots centered on each nest and a paired randomly placed plot within respective cuckoo territories (i.e., availability plots). To delineate approximate territories, we calculated 20-ha polygons of suitable riparian land cover centered on each nest using ArcGIS Pro (version 2.6.3) geographic information software (Esri, Redlands, CA, USA). We measured habitat characteristics based on the current understanding of western cuckoo nesting habitat (Laymon et al. 1997, Hughes 2020). To account for the late-season breeding of western cuckoos (e.g., frequently late July) and to avoid disturbance to nesting birds, we collected vegetation data from late August and September when nests were no longer active. We assumed that this brief period between nesting and data collection had little effect on a mismatch in timing and was constant among sites.

We measured vegetation characteristics at the plot level within 2 nested plots: a 5-m-radius circular plot centered within a 11.3-m-radius circular plot. Within each 5-m plot, we recorded the number of vertical stems at 10 cm above the ground separately for each species (i.e., counted a stem branching >10 cm as 1 stem). We estimated canopy closure at the plot center using averaged model-A spherical densiometer readings (Forest Densimeters, Bartlesville, OK, USA) taken from the 4 cardinal directions. Although estimates from densimeters can differ from those obtained by other canopy measurement instruments (e.g., moosehorn, hemispherical photography, and line-intercept; Cook et al. 1995, Fiala et al. 2006), we used this wide-angle cover estimator because it more closely characterizes the perception of cover experienced by an animal compared to other instruments (Nuttle 1997). In addition to considering the angle of view of the densiometer (Fiala et al. 2006), we used the same model of densiometer and equal sample sizes ($n=4$) to estimate canopy closure in all plots and sites.

We based live tree categories on height, dbh, species, and the number of vertical stems ≥ 50 cm tall. Within the 11.3-m-radius circle, we counted the number and species of medium and large tree stems. We classified stems <8 cm dbh and >1.4 m tall as shrubs and saplings, 8–23 cm

dbh and stems >1.4 m tall as small (early successional) trees, and >23 cm dbh as medium to large (mid- or late-successional) trees. We used these measurements to estimate densities of shrubs and saplings, small native trees, and medium to large native trees. We grouped all sizes by species to estimate densities of Goodding's willow, Fremont cottonwood, and tamarisk, which were the most common riparian tree species in our study area.

Microclimate Sampling

We deployed data loggers at randomly selected habitat availability plots in early June and at nest plots within a few days of discovery. Data loggers recorded hourly temperature (model DS1921G Thermocron iButton®; Embedded Data Systems, Lawrenceburg, KY, USA) and hourly temperature and relative humidity (model DS1923; hereafter called data loggers or loggers). The loggers recorded temperature to the nearest 0.5°C, and relative humidity to the nearest 0.6%. We placed temperature and relative humidity data loggers at 166 locations within restoration sites (113 in availability plots [33 recording temp only] and 53 at nests [5 recording temp only]) and 145 locations in natural riparian sites (125 availability plots [58 recording temp only] and 20 nests [6 recording temp only]).

In nest plots, we placed loggers directly below nests 2 m above ground for consistency and to minimize disturbance to nesting birds. In availability plots, we suspended data loggers 2 m above the ground in a tree closest to the center of each plot determined by handheld global positioning system units (Garmin, Olathe, KS, USA). To reflect solar gain and provide shade, we covered each data logger with a 7.62-cm square of nylon mesh (2008) or suspended them from a 5.1-cm × 5.1-cm × 1-cm painted plastic housing (2009–2012). After 2008, we replaced the mesh with plastic shading because the mesh was sometimes removed by rodents. A *t*-test of various housings, including the mesh and plastic container, found no significant differences ($\alpha = 0.05$) in temperature or relative humidity readings among the housings. We retrieved loggers between early and mid-September after the end of the nesting season. The June–September temperature and relative humidity hourly measurements recorded by the data loggers created a repeated measures dataset.

Statistical Analyses

To assess whether differences in the number of nests counted in natural and restoration sites were attributed to

differences in nest detection rates, we calculated the average number of nests detected per survey hour as a catch per unit effort (CPUE; Skalski et al. 2005). The CPUE is also viewed as an index of density (Skalski et al. 2005). We used data from 2010 and 2011, which were the only years we recorded the amount of effort (time spent in the field) at all sites, and examined CPUE point estimates and confidence intervals.

To characterize site types and test for differences in vegetation and microclimate, we used data from all availability plots, including those random sites not restricted to within western cuckoo territories. We tested for differences in vegetation variables between site types (restoration, natural) using a Mann-Whitney-Wilcoxon test (R package stats) because of the non-parametric data (Table 1); we used $\alpha = 0.01$ to reduce the probability of Type 1 errors that can arise from multiple univariate tests. To test for differences in microclimate between site types and to account for measurements through time, we used repeated measures analysis of variance with $\alpha = 0.01$ (Table 2). We performed subset analyses (natural, restoration) on site types because of significant differences found between natural and restoration sites that could confound a collective analysis (Tables 1 and 2). Additionally, we assessed the 2 site types separately because a main objective was to determine if there were different factors selected for during nest-site selection at each site type, and if so, to be able to make type-specific management recommendations.

We used multiple logistic regression mixed-effects models (R package lme4; Bates et al. 2015) to assess habitat characteristics important to nest-site selection and nest success. We analyzed vegetation and microclimate variables separately for nest-site selection and nest success analyses because vegetation data included 1 estimate per plot for each variable, whereas temperature and relative humidity data were collected as time series and contained many data points per plot. We used the R statistical software for all data analyses (R Core Team 2020).

Nest-site selection analysis: vegetation.—We used a multiple logistic regression model framework to assess differences in vegetation characteristics between nest and availability plots separately in restoration and natural sites. To test the same set of competing hypotheses regarding habitat selection in each site type, we performed parallel analyses by constructing and fitting an identical candidate set of *a priori* models to each dataset (Table 3). Logistic

Table 2. Comparing microclimate variables at restoration and natural sites occupied by western yellow-billed cuckoo with descriptive statistics and results of repeated measures analysis of variance tests ($\alpha = 0.01$) for availability plots along the lower Colorado River in Arizona and California, USA, 2008–2012.

Microclimate variable	Restoration ^a				Natural ^b				P
	\bar{x}	SD	n	Range	\bar{x}	SD	n	Range	
\bar{x} diurnal temp (°C)	31.9	2.7	113	18.2–39.9	32.5	2.9	125	14.2–45.0	0.025
Max. diurnal temp (°C)	39.2	3.7	113	18.2–51.1	40.1	4.2	125	14.2–60.0	0.026
\bar{x} diurnal relative humidity (%)	56	14	80	18–100	48	13	67	12–100	<0.001
Max. diurnal relative humidity (%)	84	11	80	30–100	81	10	67	17–100	0.007

^a Restoration samples from 113 availability plots, 33 recording temperature only.

^b Natural site samples from 125 availability plots, 58 recording temperature only.

Table 3. List of candidate logistic regression models of nest-site selection by western yellow-billed cuckoos within restoration and natural sites along the lower Colorado River in Arizona and California, USA from 2008–2012. We did not include Goodding's willow density in the natural site analysis because of multicollinearity with small native tree density.

Candidate models
1. Canopy closure + small native tree density + medium-large native tree density + Fremont cottonwood density + Goodding's willow density + tamarisk density + sapling density ^b
2. Canopy closure + small native tree density + medium-large native tree density + tamarisk density + Fremont cottonwood density + sapling density ^a
3. Canopy closure + Fremont cottonwood density + Goodding's willow density + tamarisk density ^b
4. Canopy closure + small native tree density + medium-large native tree density ^a
5. Canopy closure + tamarisk density + medium-large native tree density ^a
6. Canopy closure + tamarisk density + small native tree density ^a
7. Small native tree density + medium-large native tree density ^a
8. Canopy closure + small native tree density ^a
9. Canopy closure + medium-large native tree density ^a
10. Canopy closure + Fremont cottonwood density ^a
11. Canopy closure + tamarisk density ^a
12. Canopy closure + Goodding's willow density
13. Small native tree density ^a
14. Medium-large native tree density ^a
15. Sapling density ^a
16. Canopy closure ^a
17. Tamarisk density ^a
18. Goodding's willow density ^b
19. Fremont cottonwood density ^a

^a Model used for restoration and natural site analyses.

^b Model used for restoration site analysis only.

regression analyses used a balanced dataset (Salas-Eljatib et al. 2018) of an equal number of nest and randomly selected availability plots. We used an information-theoretic approach to rank *a priori* models with Akaike's Information Criterion corrected for small sample size (AIC_c), the difference between each model compared to the model with the lowest AIC_c (ΔAIC_c), and Akaike weights (w_i ; Burnham and Anderson 2002). We used deviance residual goodness-of-fit tests to check the global model for overdispersion. We selected the most parsimonious model with $\Delta AIC_c \leq 2$ (Burnham and Anderson 2002) and calculated 95% confidence intervals of the odds ratio (OR); confidence intervals not containing 1 indicated conclusive estimates (Ott and Longnecker 2001). The candidate model set was based on combinations of variables hypothesized to contribute to nest-site selection. We did not include highly correlated variables with a variance inflation factor >5 in the same model (Belsley et al. 1980) or candidate set of models. Goodding's willow and small native tree densities were correlated in the natural site dataset; we removed Goodding's willow density from the natural site analysis and retained small native tree density for the natural site analyses to represent both variables. After comparing models with and without year and individual site as random effects (Bolker et al. 2009), we determined year and individual site were not useful to include in models.

Nest-site selection analysis: microclimate.—Daily mean and maximum temperatures and relative humidity were based on hourly data recorded by each data logger from 0500–1900, with truncated dates to match the active nesting period each year. We analyzed data from restoration and natural sites separately. Because microclimate variables were correlated (variance inflation factor >5), we retained a single metric (average diurnal temperature) for the analyses. To determine differences between nests and availability plots, we used a logistic regression mixed-effects model with day of year and year as random effects to account for measurements through time and to account for annual microclimate variation. We ran this model separately for natural and restoration sites. The random effect terms introduced a correlation structure between days and years that accounted for temporal correlations (Zuur et al. 2009). We used the OR from the output of the logistic models to evaluate daily average temperature at nest sites compared to availability plots and computed 95% confidence intervals of OR to assess coefficients of the microclimate variables.

Nest success analysis: vegetation and microclimate.—We modeled nest success as a binomial response in generalized logistic mixed-effects exposure models (Shaffer 2004), which account for variable nest-visitation intervals. Because nests located at natural sites had 100% apparent success, we analyzed only data from restoration sites to investigate the influence of habitat variables on nest success. We used combinations of variables that we hypothesized would influence nest success, constructed a candidate set of models, and used AIC_c to select the most parsimonious model using the same approach described above for the nest site selection analysis. Based on our predictions that canopy closure and small native tree density would be the main influences on nest success, we included additive effects of these 2 variables in our candidate models. We included individual site as a random effect to account for potential differences in predation rates between sites. We modeled average temperature separately because of differences in data collection methods.

RESULTS

We located 87 nests between 2008–2012, with the majority ($n=66$) found in restoration sites. The number of individual nests found in restoration sites increased from 2 nests in 2008 to 27 nests in 2012 (corresponding with a ~ 2.5 -fold increase in available habitat attributed to continued tree planting efforts), whereas the number of nests in natural sites were relatively fewer and more constant over time (annual $n=3, 3, 7, 7,$ and 1 nest(s) from 2008–2012, respectively; 5-yr $\bar{x}=4.2$ nests). We found no difference in nest detection rates between site types (natural: $n=16$ nests, CPUE = 0.08 [95% CI = 0.00–0.17]; restoration: $n=32$ nests, CPUE = 0.08 [95% CI = 0.00–0.20]), indicating that nest densities were similar in restoration and natural sites. Based on initial nest detections and fledging dates, the nesting season was longer in restoration sites (5-yr $\bar{x}=47$ days, 95% CI = 24–33) compared to natural sites (5-yr $\bar{x}=28$ days, 95% CI = 23–32). In 2012, we also confirmed

multiple double-brooding events (4 individuals with 7 nests) all occurring at the Palo Verde Ecological Reserve restoration sites.

The apparent rate of nest success at restoration sites was 0.67, with predation determined to be the primary cause of nest failure (64% of failed nests attributed to predation). All 21 nests located in natural sites successfully fledged ≥ 1 young (apparent nest success = 1.0). Initial detections of active nests in natural sites (median = 10 days into incubation, $n = 21$) occurred significantly later in the nesting cycle compared to restoration sites (median = 3.5 days into incubation, $n = 66$, Wilcoxon signed-rank test; $P = 0.006$), which may have led to our not finding some early failed nests and a biased high estimate of nest survival in the natural sites.

All vegetation variables differed between natural and restoration sites (all $P < 0.002$) except for Goodding's willow density and canopy closure (Table 1). Restoration sites had 4 times the sapling density and 6 times the density of small (8–23 cm dbh) native trees compared to natural sites, whereas natural sites contained 7 times the density of large (> 23 cm dbh) native trees (Table 1). Tamarisk density was negligible in restoration sites but was the most common species in natural sites, whereas Fremont cottonwood occurred in low densities in natural sites and was the most common species in restoration sites (Table 1). Restoration sites also had lower mean and maximum temperatures compared to natural sites even though most of the restoration sites were situated farther south, where ambient temperatures are typically higher (Table 2). Restoration sites had higher average and maximum relative humidity than natural sites (Table 2). Canopy closure was negatively associated with average diurnal temperature ($\beta = -1.6622$, $t_{351} = -4.667$, $P \leq 0.001$).

Nest-Site Selection

The most parsimonious model for natural sites contained only small native tree density, whereas the most parsimonious model for restoration sites contained small native tree

density and canopy closure (Table 4). These models were competing with others ($\Delta AIC_c < 2$) but were nested within those competing models and therefore considered the most parsimonious. None of the top-ranked models had overwhelming support (i.e., $w_i > 0.9$; Table 4). Variables occurring more than once in the top models included density of small native trees and canopy closure (Table 4). Although tamarisk was the most common tree used for nest placement at natural sites (43% of nests), tamarisk nest trees occurred within a mosaic of native-dominated trees, and there was no support in our most parsimonious models for tamarisk density at the plot scale influencing nest-site selection by western cuckoos. The likelihood of a western cuckoo placing a nest at a location within a natural site increased 6.6 times with every increase by 1 small native tree (cottonwood or Goodding's willow) per 10 m^2 (OR = 6.63, 95% CI = 1.89–19.77; Fig. 1A). Similarly, western cuckoos were 1.8 times more likely to nest at a location within a restoration site with every increase in 1 small native tree per 10 m^2 (OR = 1.75, 95% CI = 1.15–2.77; Fig. 1B). The odds of nest placement increased 2% with every 1% increase in total canopy closure (OR = 1.02, 95% CI = 1.01–1.04) in restoration sites.

Within restoration and natural sites, nest locations averaged lower mean and maximum diurnal temperatures (Fig. 2) and higher mean diurnal relative humidity (Fig. 3) compared to conditions at availability plots. Odds of nest placement within natural sites increased 28% with every 1°C decrease in mean diurnal temperature (OR = 0.72, 95% CI = 0.69–0.76; $P \leq 0.001$; Fig. 4A). The odds of nest placement at restoration sites increased 22% with every 1°C decrease in mean diurnal temperature (OR = 0.78, 95% CI = 0.76–0.80; $P \leq 0.001$; Fig. 4B).

Nest Success

We used data from 65 of 66 nests found in 11 restoration sites to compare vegetation characteristics between

Table 4. Parallel model selection analyses of mixed effects logistic regression models for estimating western yellow-billed cuckoo nest-site selection in restoration ($n = 66$ nests) and natural sites ($n = 21$ nests) on the lower Colorado River in Arizona and California, USA, 2008–2012. Model selection was based on Akaike's Information Criterion corrected for small sample size (AIC_c), difference in AIC_c between each model compared to the model with the lowest AIC_c (ΔAIC_c), and relative Akaike weights (w_i); *indicates the selected best model from a group of competing models ($\Delta AIC_c < 2$) based on the principle of parsimony. Medium-large native trees = > 23 cm diameter at breast height, small native trees = 8–23 cm dbh, and saplings = < 8 cm dbh. We report models within 10% of w_i from the top model (Royall 1997).

Model	AIC_c	ΔAIC_c	w_i
Restoration sites			
8. Canopy closure + small native tree density*	173.06	0.00	0.33
4. Canopy closure + small native tree density + medium-large native tree density	175.03	1.97	0.12
1. Canopy closure + small native tree density + medium-large native tree density + Fremont cottonwood density + Goodding's willow density + tamarisk density + sapling density	175.09	2.03	0.12
6. Canopy closure + tamarisk density + small native tree density	175.19	2.13	0.12
13. Small native tree density	175.83	2.77	0.10
2. Canopy closure + small native tree density + medium-large native tree density + tamarisk density + Fremont cottonwood density + sapling density	176.14	3.08	0.07
Natural sites			
13. Small native tree density*	53.24	0.00	0.36
8. Canopy closure + small native tree density	54.29	1.05	0.21
7. Small native tree density + medium-large native tree density	55.18	1.95	0.14
6. Canopy closure + tamarisk density + small native tree density	55.94	2.71	0.09
15. Sapling density	56.37	3.14	0.08
4. Canopy closure + small native tree density + medium-large native tree density	56.51	3.28	0.07

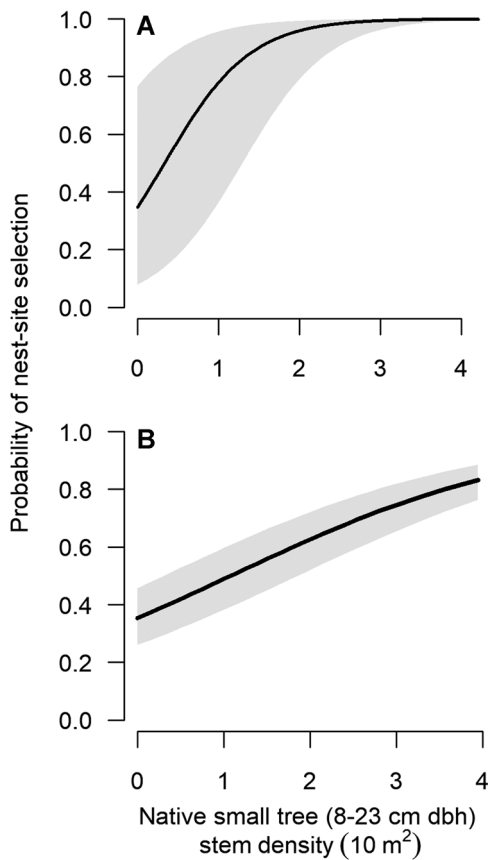


Figure 1. Probability of nest-site selection by western cuckoos on the lower Colorado River, in Arizona and California, USA, 2008–2012, relative to density of small (8–23 cm diameter breast height [dbh]) native trees per 10 m² at A) natural and B) restoration sites; 95% confidence intervals are shown as shaded areas.

successful and failed nests in those sites; 1 nest had an undetermined fate. Of these, 66% ($n=43$) fledged young, with the majority of successful nests (86%; $n=37$) containing >80% canopy closure. The most parsimonious model predicted nest fate as a function of canopy closure ($w_i=0.63$; Table 5). The odds of nest success at restoration sites increased 4% with every 1% increase in total canopy closure (OR = 1.04, 95% CI = 1.01–1.07).

At 9 restoration sites, we obtained temperature data from 49 nests (31 successful and 18 failed). Successful nests were more likely to have lower mean diurnal temperatures than failed nests. Nest success odds increased 5% with every 1°C decrease in mean diurnal temperature (OR = 0.95, 95% CI = 0.91–0.99; $P \leq 0.012$).

DISCUSSION

Nesting western cuckoos selected for specific habitat features when choosing nest sites along the LCR and tributaries. At restoration sites, western cuckoos selected nest sites with increased densities of small native trees and canopy closure. Cuckoos also selected for increased densities of small native trees in natural sites, although the correlation of this variable with willow density prevented us from testing whether selection differed between small

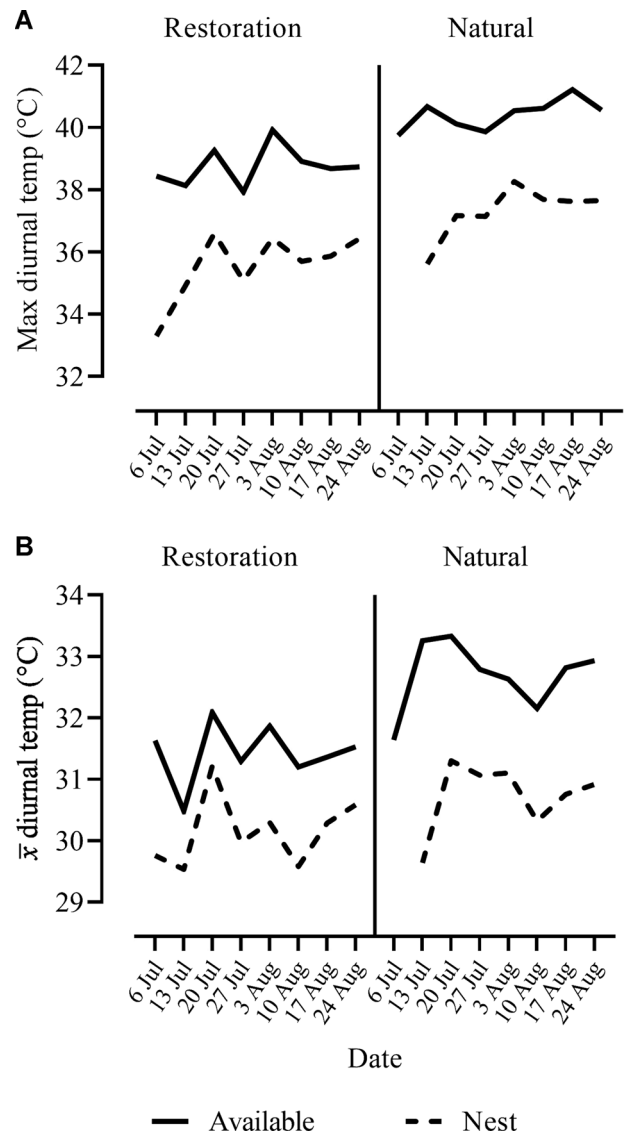


Figure 2. A) Maximum diurnal temperature (°C) and B) mean diurnal temperature averaged by week during the breeding season at western yellow-billed cuckoo nests (dashed lines) and availability plots (solid lines) at restoration sites ($n=53$) and natural sites ($n=20$) on the lower Colorado River in Arizona and California, USA, 2008–2012.

cottonwood or willow densities. The underlying factors for nest-site selection within young, dense trees may be a result of other characteristics within this type of riparian forest, such as optimal microclimate conditions (Hamilton and Hamilton 1965), increased prey availability (Pendleton et al. 2011), and increased canopy closure directly over the nest (Laymon et al. 1997). In our study, increased canopy closure was important for nest-site selection and nest success at restoration sites.

The delayed initial detections of active nests in natural sites may have contributed to the shorter observed nesting season in these sites, and could have led to our missing some early failed nests and therefore a biased high estimate of nest survival. Possible explanations for delayed initial detections at natural sites may be asynchronous vocal behaviors and

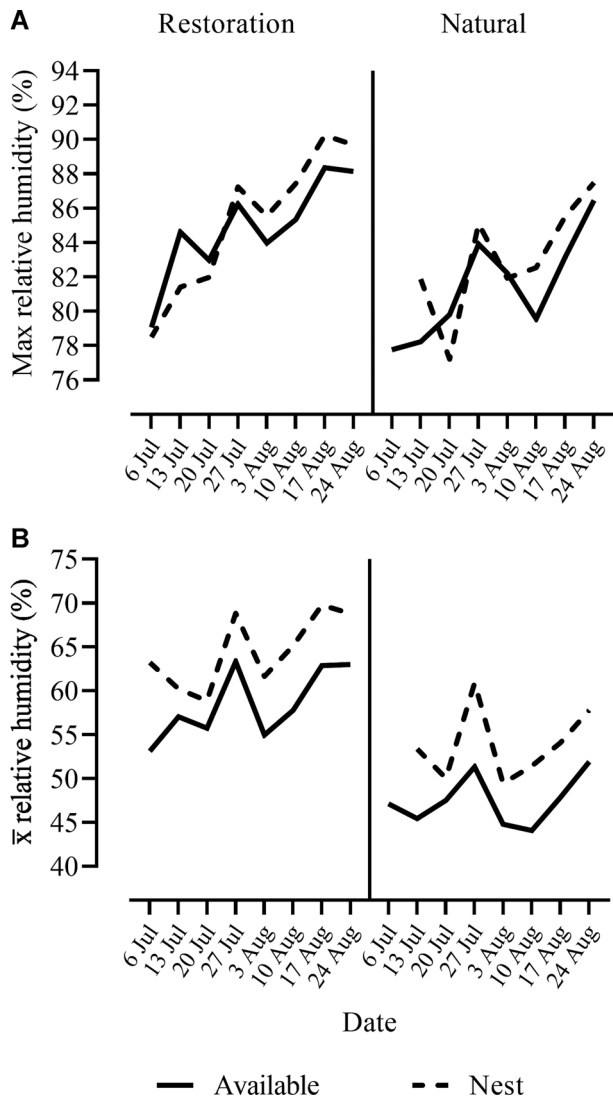


Figure 3. A) Maximum diurnal relative humidity and B) mean diurnal relative humidity averaged by week during the breeding season at western yellow-billed cuckoo nests (dashed lines) and availability plots (solid lines) at restoration sites ($n = 48$) and natural sites ($n = 14$) on the lower Colorado River in Arizona and California, USA, 2008–2012.

activity patterns attributed to differential risks of predation (Lima 2009), abundance and availability of high-quality prey, age structure of breeding individuals (Martin 1995, Murphy 2004), and stage of the breeding cycle. Although we did not record or compare predator populations in natural and restoration sites, we did observe a higher nest predation rate in restoration sites (64%) compared to natural sites (0%), and our standardized sampling protocols that included predator checks before visiting a potential nest and minimized time spent at nests should not have contributed to this difference.

The higher total abundance of nests in restoration sites (76% of 87 nests) was not surprising given that we observed a longer nesting season and double brooding in restoration sites. These differences emerged despite our CPUE estimates indicating equal nest detection rates and densities in

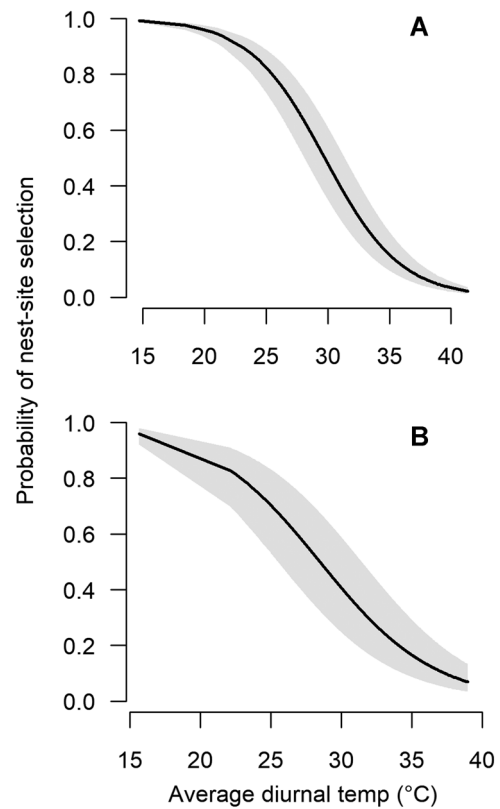


Figure 4. Probability of nest-site selection by western cuckoos on the lower Colorado River, in Arizona and California, USA, 2008–2012, relative to mean diurnal temperature at A) natural sites and B) restoration sites; 95% confidence intervals are shown as shaded areas.

both site types. At natural sites cuckoos tightly synchronized their nest timing with the local summer peak in cicada abundance and thereafter became less vocal and detectable, whereas at restoration sites cuckoos predominantly relied on other prey species and bred asynchronously for a longer period of time at restoration sites compared to natural sites. Considering this, future population monitoring efforts should incorporate methods that can account for spatial and habitat-specific differences in breeding phenology within and among local populations.

Our results suggest that the strategic placement of small native trees in a specific site or the management of riparian forests for patches of early successional native trees could improve or increase nesting habitat for western cuckoos. For example, our

Table 5. Logistic exposure model selection based on Akaike's Information Criterion corrected for small sample size (AIC_c) for nest success from 65 western yellow-billed cuckoo nests (43 successful, 22 failed) within 11 restoration sites on the lower Colorado River in Arizona and California, USA, 2008–2012; we present AIC_c values, the relative AIC_c difference (ΔAIC_c), and the relative Akaike weights (w_i); *indicates the selected best model from a group of competing models ($\Delta AIC_c < 2$) based on the principle of parsimony. Small native trees = 8–23 cm diameter at breast height.

Model	AIC_c	ΔAIC_c	w_i
Nest success at restoration sites			
Canopy closure*	122.34	0.00	0.62
Canopy closure + small native tree density	123.62	1.29	0.40
Small native tree density	127.65	5.32	0.04

results indicate that for every 1 small (8–23 cm dbh) tree planted per 10 m² within a restoration site, the odds of a western cuckoo placing a nest at that localized site can be nearly doubled (1.7 times). The median density of small native trees within restoration sites (0.38 trees/10 m² [380 trees/ha]) was greater than at natural sites (0.06 trees/10 m² [60 trees/ha]), including nest locations within natural sites (median = 0.25 trees/10 m² [250 trees/ha]), possibly explaining the greater number of nesting cuckoos at restoration sites (27 nests in 2012). Laymon and Halterman (1989) defined nesting habitat as dense broad-leaved forest patches at least 0.5–1 ha in size or even up to 4.5 ha (Johnson et al. 2017) within older stands ≥ 20 ha (Laymon and Halterman 1987). Similarly, Theimer et al. (2018) reported that the southwestern willow flycatcher, another federally listed riparian-obligate bird, is also an early successional-dependent species. The study suggested that different stages of riparian forest regeneration including early successional stands would benefit their populations.

Although not extensively investigated here, hydrological processes (e.g., flooding) may give insight into small tree distribution and densities within naturally occurring riparian forests. For example, along unregulated and semi-unregulated rivers in naturally occurring riparian forests, disturbance cycles, ground water depth, and surface floods dictate the distribution and density of willow and cottonwood establishment and growth (Stromberg 1993, 2001; Webb and Leake 2006), where newly established trees typically occur in patches with densities of 400–1,500 trees/ha (Brady et al. 1985, Laymon et al. 1997, Stromberg 1997). Densities of this magnitude are similar to the median densities found in restoration sites (380 trees/ha) during this study.

Western cuckoos selected cooler nest locations along the LCR at restoration and natural sites compared to available sites where nesting birds are exposed to extreme temperatures that often exceed 40°C in July. There are currently no data on whether the preference for cooler nest sites holds true within northern parts of the range of western cuckoos (e.g., in Colorado or Idaho). The selection of cooler nest sites along the LCR is similar to that reported in southwestern willow flycatchers in the same area (McLeod et al. 2008). Additionally, dense riparian forests typically have lower temperatures compared to areas with less vegetative cover (Brososke et al. 1997), and a relatively cooler microclimate is likely the result of vegetation structure and local hydrology, where microclimate may be selected indirectly.

Canopy closure around nests has been reported to be important in predicting western cuckoo nest-site suitability. Laymon et al. (1997) suggested that sites with less than 40% canopy closure are unsuitable, those with 40–65% are marginal to suitable, and those with greater than 65% are optimal. At restoration sites in our study, we estimated 23% of failed nests had canopy closure <40%, the minimum necessary suggested by Laymon et al. (1997), whereas just 5% of successful nests had <40% canopy closure. The majority of our successful nests (86%) contained >80% canopy closure, and our

models revealed that nest success increased linearly with increased canopy closure (Table 5) and decreased temperature, further implicating the importance of these conditions on western cuckoo nest success and probably lifetime fitness.

Prior to the restoration initiative by the LCR MSCP, naturally occurring riparian forest along the lower Bill Williams River supported the largest and one of the only remaining breeding populations of western cuckoos on the LCR and tributaries (Laymon and Halterman 1989, Johnson et al. 2007). As of the final year in our study (2012), however, the LCR MSCP restoration sites supported the highest densities of breeding western cuckoos in the region. During that time, western cuckoos predominantly nested at newly planted restoration sites as early as 2 years post-planting. The restoration planting designs of the LCR MSCP aimed to mimic the natural tree composition and density found in the LCR native riparian landscape, with sections of restoration units planted with riparian tree densities of 1,000–5,000 trees/ha and mass transplanted cottonwoods and willows having an in-line spacing of 1.2–1.8 m and 1-m rows in between (LCR MSCP 2007a, b, 2009, 2010, 2011, 2012). The LCR MSCP irrigation regimes at restoration sites were not intended to restore hydrological conditions (Bunting et al. 2013) but instead to grow riparian forests and provide moist surface soils to promote conditions for invertebrate communities.

Along with the increase in available habitat from tree planting efforts during our study (from ~160 ha in 2008 to ~400 ha in 2012), we observed increased numbers of nests at restoration sites: from 2 nests in 2008 to 27 nests in 2012. This coincided with our observed increase in the length of the nesting season and observed double brooding in restoration sites. Thus, restoration sites during this study appeared to provide high-quality habitat to breeding western cuckoos. In terms of plant structure, the density of small native trees most likely to be selected by nesting cuckoos in natural sites (1.5–3 trees/10 m² [1,500–3,000 trees/ha]; Fig. 1A) was similar to both cottonwood and willow densities planted at the Palo Verde Ecological Reserve restoration sites (1,000–5,000 trees/ha), which as of 2018 had the largest population of breeding western cuckoos on the LCR and in California (McNeil et al. 2019). Although we did not investigate prey in this study, prey availability is also likely an important component of habitat quality and a factor underlying second- and third-level habitat selection (e.g., territory and nest-site selection; Johnson 1980, Pendleton et al. 2011, USFWS 2014a, Spiller and Dettmers 2019). A reasonable next step would be to investigate the effects of prey abundance and diversity on nest-site selection and nest success in this system and areas throughout the range of the western cuckoo.

Based on our findings, the LCR MSCP restoration actions have been successful at creating breeding habitat for western cuckoos; however, it is unknown whether the quality of this breeding habitat will persist if flood irrigation ceases and as the current trees mature without further

recruitment of young trees into these sites. As such, the methods we present here should be used to continue monitoring of restoration sites along the LCR to determine the long-term effectiveness of this type of habitat restoration as a recovery action for western cuckoos. We recommend that future research on nest success and nest-site selection by western cuckoos focus range-wide, and in particular within the core of their range in Arizona, western New Mexico, California, and northern Mexico.

MANAGEMENT IMPLICATIONS

Our results can be used with adaptive management practices to help maintain critical nesting habitat for the western cuckoo by providing specific restoration guidelines that create early successional (age 2–7 yrs) patches of dense (1,500–3,000 trees/ha) riparian forest. Incorporating dense patches of small native trees can be achieved through mass planting or by encouraging natural tree regeneration through disturbance and flooding, although it is desirable to base habitat management decisions on site conditions and proximity to resources (e.g., soil type and water availability) when creating this level of tree density. For example, a mature riparian forest within an altered river system could be managed to incorporate water releases during appropriate time frames that promote natural tree regeneration or by creating high tree density through mass plantings that receive water from an existing irrigation structure. Early successional forest patches that contain high tree density could also provide desired increases in canopy closure important for nest success, where patches of dense riparian trees in combination with >80% canopy closure can be attained simultaneously.

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