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NEST-LOCATION AND NEST-SURVIVAL OF BLACK-CHINNED HUMMINGBIRDS IN NEW MEXICO: A COMPARISON BETWEEN RIVERS WITH DIFFERING LEVELS OF REGULATION AND INVASION OF NONNATIVE PLANTS

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ABSTRACT—We compared plants used as sites for nests and survival of nests of black-chinned hummingbirds (*Archilochus alexandri*) along two rivers in New Mexico. Along the free-flowing Gila River which was dominated by native plants, most nests were constructed in boxelder (*Acer negundo*). Along the flow-restricted Middle Rio Grande which was dominated by nonnative plants, most nests were constructed in nonnative plants such as Russian olive (*Elaeagnus angustifolia*) and saltcedar (*Tamarix*). Mean nest height varied among species of plants used as nesting sites but was about 4 m at each study area. Logistic exposure-estimates of survival of nests were considerably higher along the Middle Rio Grande (52%) than the along the Gila River (23%). Survival of nests was influenced by nest height and species of plant used as nesting site, with survival rates of nests greatest at mean heights in Russian olive and saltcedar. Our results highlight considerable variation in nesting characteristics between two study areas and show that subcanopy nest-sites are essential components of productive habitat for this species.

RESUMEN—Comparamos plantas usadas como lugares para nidos y supervivencia de nidos del colibrí barbinegro (*Archilochus alexandri*) a lo largo de dos ríos en Nuevo México. En el río Gila, que fluye libremente y tiene predominio de plantas nativas, la mayoría de los nidos fueron construidos de arce negundo (*Acer negundo*). A lo largo de la parte media del río Bravo, cuyo flujo es restringido y tiene predominio de plantas no nativas, la mayoría de los nidos fueron construidos con plantas no nativas, como el árbol del paraíso (*Elaeagnus angustifolia*) y el pino salado (*Tamarix*). La altura media de los nidos varió entre las diferentes especies de plantas usadas como lugares para anidar, pero en cada área de estudio fue de aproximadamente 4 m. Las tasas logísticas de supervivencia incluyendo la exposición de los nidos fueron considerablemente más altas en la parte media del río Bravo (52%) que en el río Gila (23%). La supervivencia de los nidos fue influida por la altura de los nidos y la especie de planta usada como lugar para anidar, con las tasas de supervivencia de nidos más altas en las alturas medias en el árbol del paraíso y el pino salado. Nuestros resultados destacan una variación considerable en las características de anidación entre las dos áreas de estudio y muestran que los lugares de anidación en el subdosel son componentes esenciales del hábitat productivo de esta especie.

The American Southwest hosts the largest populations of breeding hummingbirds in the United States (Wethington and Russell, 2003; Wethington et al., 2005). Within this region, riparian forests provide important resources, such as nest-sites and food, for several species of hummingbirds (Baltosser, 1986; Durst et al., 2008). Despite the widespread appeal of hummingbirds, relatively little is known about geographic variation in their use of riparian habitats or the contributions of various species of plants to demographic rates such as survival of nests (S. M. Wethington et al., in litt.). This information is particularly important in the Southwest, where many streams are heavily regulated and riparian forests are invaded by nonnative woody vegetation.

The black-chinned hummingbird (*Archilochus alexandri*) is the most abundant and widespread of the southwestern riparian-nesting hummingbirds (Baltosser and Russell, 2000; Wethington and Russell, 2003). The plants used as nesting sites and survival of nests have been measured for this species at some sites in Arizona and New Mexico, revealing variation among the locations studied (Baltosser, 1986; Brown, 1992; Smith et al., 2009; Greeney and Wethington, 2009). Differences in use of plants for nesting sites likely result from differences in composition of native woody plants and extent of invasion of nonnative plants among study sites. Measurements of nesting success vary as well, with estimates of survival of nests from central New Mexico greater than those from southeastern Arizona and southwestern New Mexico (Smith et al., 2009). Predation is the primary source of failure of nests for hummingbirds in the Southwest and risk of predation likely varies among nest-sites (Baltosser, 1986). Rates of nesting success should, therefore, vary between species of plants used as nesting sites and levels of river-regulation, which influences composition of riparian forests (Webb et al., 2007). Comparisons of plants used for nesting sites and survival at multiple sites are needed to determine if composition of plants or other factors limit nesting success of black-chinned hummingbirds. We report results from studies monitoring nests at two river systems that differed in extent of modification by humans and composition of riparian forest. Our objective was to identify patterns of nest-survival and use of plants for nest-sites by black-chinned hummingbirds at each study site to gain insight on the effects of river-regulation on these reproductive characteristics.

MATERIALS AND METHODS—Our study area at the Gila River was composed of riparian forest patches in the Cliff-Gila Valley and the Gila Bird Area in Grant County, New Mexico. This section of the Gila River is free-flowing, apart from some irrigation diversions (Soles, 2008). In the Cliff-Gila Valley, boxelder (*Acer negundo*) was the numerically dominant species of tree, comprising >40% of woody plants (Stoleson and Finch, 2003). The forest canopy was largely composed of large Fremont cottonwoods (*Populus fremontii*), which comprised 3% of the woody plants. The most abundant nonnative tree was Russian olive (*Elaeagnus angustifolia*), which also comprised 3% of the woody plants (Stoleson and Finch, 2001). Riparian forest patches varied from 4.5–10.0 ha in area and were separated by a matrix of river channels, irrigation ditches, pastures, and hayfields (Brodhead, 2005). Land-cover bordering the riparian zone included grazed pastures, hay fields, and upland desert scrub.

Our study area at the Middle Rio Grande differed from that at the Gila River in river-regulation and composition of riparian forest. Streamflow was restricted by Cochiti Dam built in 1974 and was further altered by the construction of several smaller diversion dams south of Cochiti (Scurlock, 1998). The riparian forest of this site was largely characterized by a continuous canopy of Rio Grande cottonwood (*Populus deltoides* subspecies *wislizenii*) that exceeded 100 m in width in some locations (Howe and Knopf, 1991). Results from data collected in sampling plots of vegetation (Smith et al., 2009) showed that exotic woody species were numerically dominant throughout the study area and formed much of the woody understory, with Russian olive comprising 7.8% of woody plants and saltcedar (*Tamarix ramosissima*) comprising 76%. As a result of construction of levees, riparian vegetation was confined to dense, linear strips between the active streambed and low-flow conveyance canals (Whitney, 1996; Scurlock, 1998). We searched for nests at 4 plots below Cochiti Dam, north of Albuquerque, 10 plots located between Albuquerque and Socorro on land managed by the Middle Rio Grande Conservancy District, and 2 plots at Bosque Del Apache National Wildlife Refuge, south of Socorro. Size of plots ranged from 13.2–28.9 ha. Types of land-cover outside of the levees included agricultural fields, urban areas, grasslands, and desert scrub.

We located and monitored nests from 1997–2004 along the Gila River and from 2000–2008 along the Middle Rio Grande. At each study area, a crew of technicians visited each plot at least once per week from late April to late August to search for nests. Nests were relatively easy to find by following females, so there was little risk of bias in detection of nests among potential species of plants used for nesting sites. Upon finding a nest, we recorded the position with a global positioning system to allow revisits until the attempted nest was complete. Because of the large size of the study areas, we were unable to revisit nests at regular frequencies and the length of intervals between checks of nests averaged 5.7 days. To ensure that we determined fates of nests accurately, multiple observers visited each nest. We assumed that empty nests were successful if nestlings were observed in the nest within 4 days of fledging age during the last check of nests or fledglings were seen or heard in the area. We assumed that empty nests had not survived if they were empty >4 days prior to fledging, the nest was greatly disturbed, or egg or nestling fragments were seen in or near the nest. We chose 4 days within fledgling as a cutoff for success because, in our experience, nestlings are capable of flying from a nest if threatened by predation at this time. We omitted nests from our analyses of survival if they were abandoned during construction or failed due to human interference. When nests were no longer active, observers returned to measure nest height (distance from ground to nest) and characteristics of nest plants (plants used for nesting sites).

We calculated the percentage of nests found in each species of plants, mean nest height, mean nest-plant height (height of plant with a nest), and relative nest height (nest height/nest-plant height) separately for each study area. We also calculated apparent nest survival (number of successful nests/total number of nests) for each study area and for species of plant in which we located at least 10 nests.

We used a two-stage information-theoretic model selection process to compare nest survival among study areas and species of nest plants. In the first stage, we constructed logistic exposure models (Shaffer, 2004) with study area, nest height, and effects of date as explanatory variables. We calculated Akaike's Information Criterion adjusted for sample size (AIC_c) to select which models best described variation in nest survival (Burnham and Anderson, 2002; Shaffer, 2004). We used the Nestsurvival R package to calculate AIC_c and Akaike weight (w_i), the relative strength of support for each model. We also estimated daily nest-survival rate using model-averaged coefficients of variables in the set of models (Shaffer and Thompson, 2007). In the second stage, we evaluated the effect of use of nest plants on nest survival by comparing daily nest-survival rate among species of nest plants in which at least 10% of the nests at a study area were constructed. We built a model-set containing only nests in species of plants that met the given criteria. Variables in this second model-set were nest height and species of nest plants. As in the first stage, we evaluated models using AIC_c, and we used model-averaged parameter-estimates to estimate daily nest-survival rate. We transformed daily nest-survival rate to predicted period survival (percentage of nests fledging at least one nestling during the study period) by raising daily nest-survival

TABLE 1—Characteristics of plants in which ≥10 nests were constructed by black-chinned hummingbirds (*Archilochus alexandri*) along the Gila River in southwestern New Mexico and along the Middle Rio Grande in central New Mexico from 1997–2004.

		Variable				
Site	Nest plant	Percentage used	Plant height (m)	Nest height (m)	Relative nest height (%)	Apparent survival (% successful)
Gila River	Boxelder	70.9	13.5	4.9	37.9	40.8
	Arizona alder	4.9	11.2	4.6	41.9	28.6
	Fremont cottonwood	4.9	21.1	6.0	36.3	33.3
	Goodding's willow	4.5	10.4	3.1	39.7	42.9
	Netleaf hackberry	4.9	6.3	2.4	44.0	50.0
Middle Rio Grande	Russian olive[a]	35.1	7.1	2.8	41.9	68.4
	Rio Grande cottonwood	28.8	17.5	8.0	48.1	48.7
	Saltcedar[a]	21.6	6.4	2.7	45.2	68.1
	White mulberry[a]	4.2	11.3	3.7	34.6	61.1
	Tree of heaven[a]	2.3	7.1	3.7	59.5	77.8

[a] Nonnative.

rate to the power of 38, the number of days in the nesting period of the black-chinned hummingbird at our study areas.

RESULTS—We found 192 nests at the Gila River and 527 nests at the Middle Rio Grande. More than 70% of the nests we found at the Gila River were constructed in boxelder; another 20% were constructed in Arizona alder (*Alnus oblongifolia*), Fremont cottonwood, Goodding's willow *(Salix gooddingii)*, and netleaf hackberry (*Celtis reticulate*; Table 1). The remaining nests were constructed in another eight species of woody plants. At the Middle Rio Grande, 35% of the nests were constructed in Russian olive, 29% were constructed in Rio Grande cottonwood, and 22% were constructed in saltcedar. We found another 6.5% of nests in white mulberry (*Morus alba*) and tree of heaven (*Ailanthus altissima*), both nonnative species (Table 1). The remaining nests at the Middle Rio Grande were constructed in another six species of woody plants. Mean nest height was similar between study areas (Gila River = 4.8 m, 95% confidence interval (CI) of 4.4–5.1 m; Middle Rio Grande = 4.4 m, 95% CI of 4.1–4.7 m) as was the range of nest heights (Fig. 1). Mean nest height was greatest in cottonwoods at each study area and lowest in netleaf hackberry, which was the shortest nest plant (Table 1). On average, nests constructed by hummingbirds were in the lower half of trees examined at both sites (Table 1).

We determined outcomes for 137 nests at the Gila River and 434 nests at the Middle Rio Grande. Apparent survival rate was 42 and 63%, respectively. Among nest plants at the Gila River, apparent survival rate was greatest in netleaf hackberry and lowest in Arizona alder (Table 1). At the Middle Rio Grande, apparent survival was greatest in tree of heaven and lowest in cottonwood (Table 1). The best-supported nest-survival model from the first selection stage, as determined by the lowest value of AIC, contained effects of nest height and study area (w_i = 0.38). Predictions based on model-averaged estimates from this model-set indicated that, at mean nest heights, nest survival was greater along the Middle Rio Grande (52%, 95% CI of 46–58%) than along the Gila River (23%, 95% CI of 12–36%). In the second stage of model-selection, we examined nests constructed in boxelder along the Gila River and nests in cottonwood, Russian olive, and saltcedar along the Middle Rio Grande. The best-supported model from this stage contained an interaction between species of nest plant and nest height (w_i = 0.67). Model-average predictions of period survival increased with increasing nest height in saltcedar but decreased with increasing nest height in boxelder, cottonwood, and Russian olive (Fig. 2a). At mean nest heights in each species of plant, model-averaged predictions of period survival were greatest in Russian olive and saltcedar, intermediate in cottonwood, and lowest in boxelder (Fig. 2b).

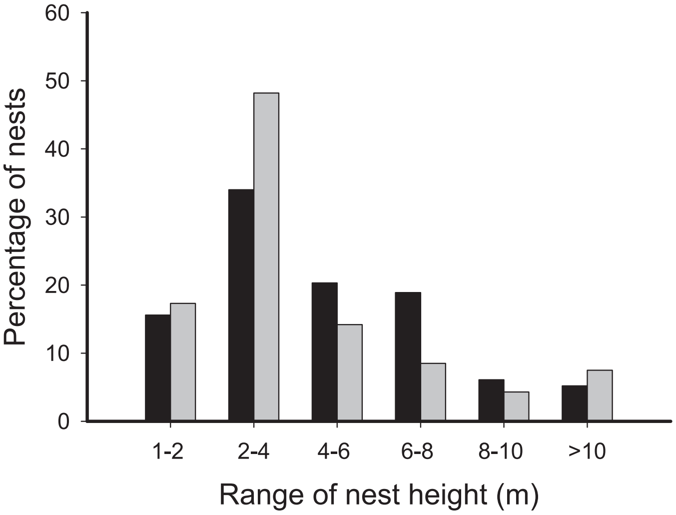

FIG. 1—Percentage of nests constructed by black-chinned hummingbirds in each height class at the Gila River (black bars) and Middle Rio Grande (gray bars) in New Mexico.

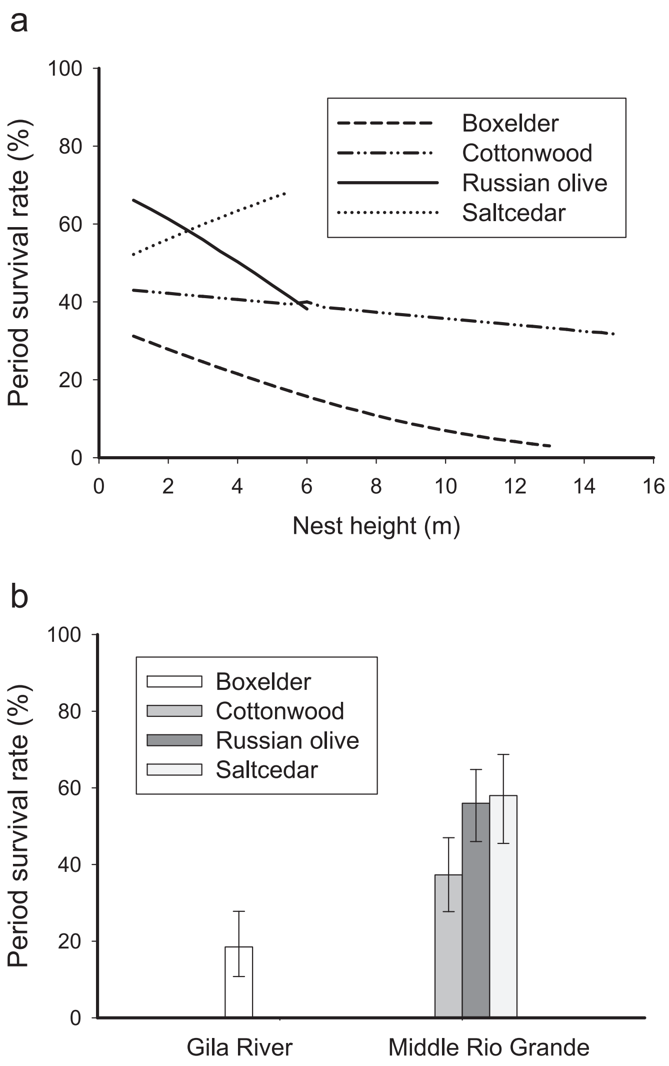

FIG. 2—Model-averaged predictions of nest-survival for black-chinned hummingbirds a) across the range of nest heights and b) at mean nest heights (error bars indicating 95% confidence intervals) in boxelder along the Gila River and in cottonwood, Russian olive, and saltcedar along the Middle Rio Grande, New Mexico.

DISCUSSION—At both study areas, black-chinned hummingbirds nested primarily in the subcanopy forest layer, about 4 m from the ground, but we found striking differences in patterns of nest plants used. Boxelder was used for over 70% of all nests at the Gila River, while use of nest plants at the Middle Rio Grande was spread more evenly across three species of trees, two of which were nonnative. Baltosser (1978) reported that 35 of 36 nests were constructed in boxelder along the Gila River near the town of Cliff. We documented use of a greater number of nest plants at the Gila River, which may be explained by the larger size of our study area, which included the Gila Bird Area, where boxelder is not as dominant (Brodhead et al., 2007).

Most of the nests at the Middle Rio Grande were constructed in nonnative trees or shrubs. Use of nest plants by black-chinned hummingbirds reflects the fact that, instead of one species dominating the subcanopy layer, which we observed at the Gila River, several species, most of them nonnative, composed the subcanopy at the Middle Rio Grande. Russian olive, the woody plant in which the greatest percentage of nests at the Middle Rio Grande were constructed, is frequently used as a nest-site by other riparian-nesting birds including mourning dove (*Zenaida macroura*), yellow-billed cuckoo (*Coccyzus americanus*), southwestern willow flycatcher (*Empidonax traillii* extimus), and yellow-breasted chat (*Icteria virens*; Knopf and Olson, 1984; Stoleson and Finch, 2001). Saltcedar was the primary nest plant for black-chinned hummingbird in the Grand Canyon, where few other native or nonnative trees and shrubs were present (Brown, 1992). Saltcedar was used less frequently than Russian olive and cottonwood by hummingbirds at the Middle Rio Grande despite the fact that it was the most abundant woody plant in the study area (Smith et al., 2009). These results indicate that, with regard to use of invasive plants, hummingbirds frequently nest in saltcedar when it is the only small tree present but prefer Russian olive. Interestingly, we did not find any nests in Russian olive at the Gila River, though this was the most frequently used species of plant along the Middle Rio Grande. This result mirrors those from other studies in which use of exotic vegetation by breeding birds varied among riparian sites (Hunter et al., 1988; Sogge et al., 2008). Because Russian olive composed only 3% of the community of plants at the Gila River (Stoleson and Finch, 2001), abundance of this nonnative tree may need to reach a threshold before it is selected by black-chinned hummingbirds as a substrate for nests. Further comparisons of selection of nest-sites within and between habitats with varying levels of nonnative vegetation are needed to clearly identify such thresholds for birds and nest plants.

The frequent use of the subcanopy layer by black-chinned hummingbirds may serve to minimize predation, which is the primary cause of failure of nests for hummingbirds (Baltosser, 1986). A variety of birds nest and forage in cottonwood canopy, and many are known to consume eggs or nestlings of hummingbirds (Rosenberg et al., 1982; Baltosser, 1986). By nesting at intermediate heights in the lower portion of trees, black-chinned hummingbirds may avoid predation by canopy-foraging birds. Indeed, nest survival decreased with height in most of the nest plants examined in this and previous studies (Baltosser, 1986; Smith et al., 2009). Saltcedar was the only nest plant in which nest survival increased with height. Nests at low heights in saltcedar may have been vulnerable to ground-dwelling mammalian predators, some of which are associated with invasion of saltcedar (Ellis et al., 1997). Based on these results, we conclude that a layer of woody vegetation offering intermediate nest heights (2–5 m) is needed to maintain productivity of hummingbirds in southwestern riparian forests.

Nest-survival rates for hummingbirds differed among the four frequently used species of nest plants, indicating that, along with structure of the forest, composition of woody plants influences productivity of hummingbirds. In a previous analysis (Smith et al., 2009), we found that nests constructed by black-chinned hummingbirds at low heights in nonnative vegetation along the Middle Rio Grande had higher survival rates than those constructed in cottonwoods. In our study, we found similar results comparing nest survival at mean nest heights among Russian olive, saltcedar, and boxelder. Though boxelder appears to be a preferred nest plant for black-chinned hummingbirds, nonnative plants along the Middle Rio Grande may provide nest sites with higher rates of survival than that of this native tree. Differences in nest survival could be explained by structural differences among species of nest plants. For example, Russian olive and saltcedar form dense thickets of vegetation with high densities of stems, leaves, and, in the case of Russian olive, thorns (Stoleson and Finch, 2001). Nests in boxelder and cottonwood may be easier for predators to locate and access than nests in Russian olive and saltcedar. If rates of predation on nests are in fact lower in nonnative trees and shrubs, this result would contrast strikingly with those from studies showing increased rates of predation in nonnative vegetation (Schmidt and Whelan, 1999; Borgman and Rodewald, 2004; Lloyd and Martin, 2005) or similar rates in native and nonnative vegetation (Schmidt et al., 2005; Sogge et al., 2008). Additional research, however, is necessary to disentangle effects of composition and structure of nest plants on survival of nests constructed by black-chinned hummingbirds in riparian forests of New Mexico.

Several mechanisms associated with study areas, not nest plants, could have caused the observed differences in survival of nests. In southeastern Arizona, survival of nests for black-chinned hummingbirds increased with increasing proximity to nests of Cooper's hawk (*Accipiter cooperii*) and northern goshawk (*Accipiter gentilis*; Greeney and Wethington, 2009). We encountered active nests for Cooper's hawk much more frequently at the Middle Rio Grande than at the Gila River, with at least one nest built by Cooper's hawk located each year in most plots at the Middle Rio Grande. Though we did not observe clustering of nests constructed by hummingbirds around nests used by accipiters as did Greeney and Wethington (2009), hummingbirds at the Middle Rio Grande may have benefited from a reduction in activity of mesopredators brought upon by the presence of these hawks as in southeastern Arizona. In addition, the spatial characteristics of our study areas differed, with plots at the Gila River arranged as discrete patches of vegetation while plots at the Middle Rio Grande were portions of a continuous gallery forest. Nests in patches at the Gila River may have been more vulnerable to avian, mammalian, or reptilian predators that are associated with fragmented agricultural landscapes (Chalfoun et al., 2002). Further observational and experimental data are needed to test these possible explanations as well as those involving differences in food resources, which likely varied between study areas.

Our results for black-chinned hummingbirds show considerable variation in use of nest plants and in survival of nests between our two study areas in New Mexico. This variation may be linked to river-regulation along the Middle Rio Grande, which led to changes in the spatial structure and composition of riparian vegetation. Despite these changes from the natural state, hummingbirds nesting along the Middle Rio Grande benefited from abundant nesting sites and high survival rates of nests relative to the Gila River. If one generality can be made from our comparison, it is the importance of subcanopy vegetation to nesting density and productivity of black-chinned hummingbirds in the American Southwest. Based on our results, riparian forests with mature trees and little woody subcanopy will support relatively low densities of nests for black-chinned hummingbirds, and these nests will have lower survival rates than those in subcanopy vegetation. To prevent declines of black-chinned hummingbirds and other species needing similar habitat, managers should maintain low-stature subcanopy vegetation beneath the canopy of mature riparian trees or in early-successional patches.

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