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NESTING CHRONOLOGY, DENSITY AND HABITAT USE OF BLACK-CHINNED HUMMINGBIRDS ALONG THE COLORADO RIVER, ARIZONA

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Abstract.—Black-chinned Hummingbird (*Archilochus alexandri*) nests ($n = 119$) were located by means of systematic searches of two different riparian habitats along the Colorado River in Grand Canyon, Arizona, from April through July 1982–1987. Most nests (94%) were located in the introduced riparian shrub tamarisk (*Tamarix ramosissima*). Active nests were present from 22 March through 10 July, with ≥80% of all nests active during the peak of nesting in May. Black-chinned Hummingbird nests were located only in tamarisk-dominated habitats, where nesting density ranged from 0 to 3.5 active nests/ha, and no nests were found in native habitats dominated by honey mesquite (*Prosopis glandulosa*). Nests were found only in riparian habitat patches that were ≥0.5 ha in size, exhibited ≥69% vegetative cover and had a mean canopy height of ≥1.4 m. Maintenance of this Black-chinned Hummingbird population depends on the continued existence of tamarisk-dominated habitat with these minimal patch-size characteristics.

CRONOLOGÍA DE ANIDAMIENTO, DENSIDAD Y UTILIZACIÓN DE HABITAT POR PARTE DE *ARCHILOCHUS ALEXANDRI* A LO LARGO DEL RÍO COLORADO, ARIZONA

Sinopsis.—De abril a julio de 1982 a 1987, se localizaron nidos del zumbador *Archilochus alexandri*, a tráves de una búsqueda sistemática, en dos habitats riparios diferentes, a lo largo del Río Colorado, en el Gran Cañón de Arizona. La gran mayoría de los nidos (94%) fueron localizados en el arbusto introducido *Tamarix ramosissima*. Se encontraron nidos activos desde el 22 de marzo hasta el 10 de julio, con ≥ del 80% de los nidos durante el pico de la época reproductiva en mayo. Los nidos del zumbador, fueron encontrados únicamente en habitat dominados por el arbusto exótico, en donde la densidad de nidos varió de 0 a 3.5 nidos activos/ha. No se encontraron nidos del ave, en habitats dominados por vegetación nativa como *Prosopsis glandulosa*. Los nidos fueron encontrados solo en parches de habitat ripario cuyo tamaño era ≥ a 0.5 ha, con una cobertura de vegetación ≥ a 69% y que tenían una altura promedio del docel a 1.4 m. El mantener a esta población de zumbadores dependerá de la continua existencia de habitat dominado por *Tamarix ramosissima* y parches con las características mínimas previamente mencionadas.

The Black-chinned Hummingbird (*Archilochus alexandri*) is a fairly common summer resident of the southwestern United States, where it

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exhibits a preference for riparian habitat (Johnson et al. 1987). Most information on the nesting biology of this species is anecdotal (Bent 1964), and little is known of its nesting biology in dam-altered riparian habitats. Although tamarisk (*Tamarix ramosissima*), an introduced riparian shrub, dominates over 100,000 ha of riparian habitat in the southwestern United States (Horton 1977), no study of Black-chinned Hummingbird nesting biology has been conducted in tamarisk habitat. The purpose of my study was to describe the nesting biology of Black-chinned Hummingbirds in a recently created tamarisk habitat and contrast it with their use of native riparian habitat.

METHODS

The study area was the 389-km riparian corridor of the Colorado River through Grand Canyon National Park, Arizona, from Lees Ferry (920 m) to Diamond Creek (410 m). This area has been substantially modified by the completion in 1963 of Glen Canyon Dam, 24 km upriver of Lees Ferry, and subsequent dam operations (Turner and Karpiscak 1980).

Pre-dam riparian vegetation was dominated by honey mesquite (*Prosopis glandulosa*) and catclaw acacia (*Acacia greggii*) in the old high-water zone (OHWZ), which was adjacent to and just above the pre-dam scour zone. Annual floods maintained the pre-dam scour zone in essentially a vegetation-free state. Completion of the dam curtailed annual flooding and dam operation greatly reduced mean flows. The pre-dam scour zone was then quickly colonized by riparian vegetation, forming the new high-water zone (NHWZ). The NHWZ was dominated by the introduced shrub tamarisk, but also included native shrubs such as coyote willow (*Salix exigua*), Goodding's willow (*S. gooddingii*), arrowweed (*Tessaria sericea*) and seepwillow (*Baccharis* spp.). The OHWZ persisted as a relict habitat after dam construction, so that in many areas both habitat zones existed as immediately adjacent, sometimes discontinuous, parallel strands (Brown and Trosset 1989, Turner and Karpiscak 1980).

Searches for hummingbird nests were conducted from 10 Apr. through 1 Jul. 1982–1987, throughout the river corridor. In addition, intensive nest searches were made in nine paired study sites from 1984 to 1987 (Table 1). The nine paired study sites were chosen to include the largest and most well-developed habitat patches in each of nine selected river segments between Lees Ferry and Diamond Creek. Each study site was designed to contain both an OHWZ and an NHWZ patch. Time spent searching each habitat patch was proportional to the extent of each habitat zone in the study site. For example, the OHWZ:NHWZ ratio of nest searching time was 1:3 at sites whose vegetation consisted of one-fourth honey mesquite in the OHWZ and three-fourths tamarisk in the NHWZ (Brown and Trosset 1989). Systematic ground searches of both OHWZ and NHWZ paches were conducted by up to six skilled observers, and each habitat patch was thoroughly searched at least once each season. The number of nests/ha in each study site was calculated from concurrently active nests only. Female hummingbirds often indicated nest lo-

TABLE 1. Area, percent vegetative cover and mean canopy height of nine paired study sites searched for Black-chinned Hummingbird nests along the Colorado River in Grand Canyon, 1984–1987.

Study site	Area (ha)		Percent cover		Mean canopy height (m)	
	OHWZ[1]	NHWZ[2]	OHWZ	NHWZ	OHWZ	NHWZ
Saddle Canyon	1.6	2.8	80	88	1.6	3.7
Cardenas Creek	1.5	1.7	71	94	1.5	4.7
Bass Camp	0.1	0.1	31	50	0.3	0.9
Forster Canyon	0.6	0.4	50	40	0.7	0.8
National Canyon	2.2	0.4	60	38	1.8	0.9
Stairway Canyon	1.7	0.7	78	94	1.5	2.3
Parashant Canyon	1.4	0.5	89	84	3.0	3.0
Granite Park	5.6	1.0	72	69	1.9	1.4
220-Mile	0.9	0.1	58	35	1.5	2.1
Total or overall mean	15.6	7.7	64	66	1.5	2.4

[1] Old high-water zone.
[2] New high-water zone.

cations by exhibiting conspicuous agitation behavior when observers approached.

Data recorded on each nest included the date, number of eggs or young present, age of young (if applicable), study site (if applicable) and habitat zone within which the nest was located, nest substrate plant, and nest height. Both active nests and those that were vacated within the current season, in addition to those vacated the previous year but still identifiable, were included in the analysis of habitat zone, nest substrate plant and nest height. Only active nests containing eggs or young, or nests that had been active during the year of analysis but were discovered without eggs or young, were included in the density analysis. Only active nests containing eggs or young were included in the analysis of nesting chronology. All nest locations were tagged by placing colored surveyor's tape a known distance and direction from the nest to facilitate its future relocation and preclude the possibility of duplicating data from the same nest.

Percent cover was the proportion of a study area covered by the vertical projection of shrub crowns to the ground (Schemnitz 1980). Only cover provided by living woody plants >0.5 m in height was included in the analysis. Percent canopy cover was measured in April 1984 along 60 m of unbiased line-intercept vegetation transects in both habitat zones in each study site (after Canfield 1941). Maximum canopy height was measured to the nearest 0.5 m at 4-m intervals along each 60-m length of transect.

Nesting chronology was calculated from data collected on active nests (those containing eggs or young) during one to two visits per season, although 95% of nests were only visited once. The egg-laying period was the number of days between the laying of the first and last egg; the incubation period was the number of days from the laying of the last egg

to the hatching of the last egg; and the nestling period was the number of days from the hatching of the first egg to the fledging of the last young (Pettingill 1970). Each nest was assumed to be active for 39 d: 1 d for egg-laying, although two eggs normally constituted a completed clutch; 16 d for incubation; and 22 d for the nestling period (Bent 1964, Demaree 1970). I assumed that no delay existed between the termination of egg-laying and the initiation of incubation, hence the designation of the egg-laying period as being only 1 d even though this period occurred over 2 d. The average duration of each nesting phase was used to reconstruct the chronology of each nest, based on nest contents. Nests containing one egg were assumed to be in the egg-laying phase. Nests containing two eggs were assumed to be at the midpoint (day 8) of incubation. The greatest potential source of error in reconstructing nest chronology occurred for nests containing two eggs. Nests with two eggs that were laid the previous 2 d or were recorded on the last day of incubation would introduce an error of ±7 d into the overall accuracy of nesting chronology. This error was reduced to ±2 d for that 5% of the nest sample which was visited twice, since nestling age was determined to the nearest 4 d after descriptions of nestling development by Bent (1964) and Demaree (1970).

RESULTS

Sample sizes and nest placement.—Of the 119 Black-chinned Hummingbird nests located during the study, 106 were new nests constructed during the year of discovery and 13 were old nests constructed in the previous year that had not been detected during earlier annual searches for nests. Most nests (n = 112; 94%) were located in the introduced shrub tamarisk. Native shrubs used for nest placement included: arrowweed (n = 5; 4%), Emory seep willow (*Baccharis emoryi*; n = 1; 1%), and desert broom (*Baccharis sarathroides*; n = 1; 1%). No nests were found in coyote willow, honey mesquite, or other native shrubs. Mean nest height above ground was 183 cm (range 76–450 cm, SD = 70 cm, n = 118).

Nesting chronology.—Eighty-five active nests containing eggs or young were located between 19 Apr. and 24 Jun. 1982–1987. Reconstruction of the nesting cycle indicated the mean date of the earliest egg laid was 1 April (SD = 9.3 d, earliest egg laid on 22 March). The mean date of latest fledging occurred on 25 June (SD = 10.7 d, latest fledging on 10 July). The peak of nesting activity was in May, when ≥80% of all nests contained eggs or young (Fig. 1).

Structural habitat differences.—NHWZ sites exhibited a slightly higher mean percent vegetative cover than OHWZ sites (Table 1). This difference was not statistically significant when compared on a site-by-site basis, however (two-tailed Wilcoxon signed rank test, $P > 0.1$). Mean canopy height was also greater in NHWZ sites (Table 1), but not significantly so (two-tailed Wilcoxon signed rank test, $P = 0.8$).

Habitat use and nesting density.—All nests found were located in post-dam NHWZ sites, and no nests were found in pre-dam OHWZ sites,

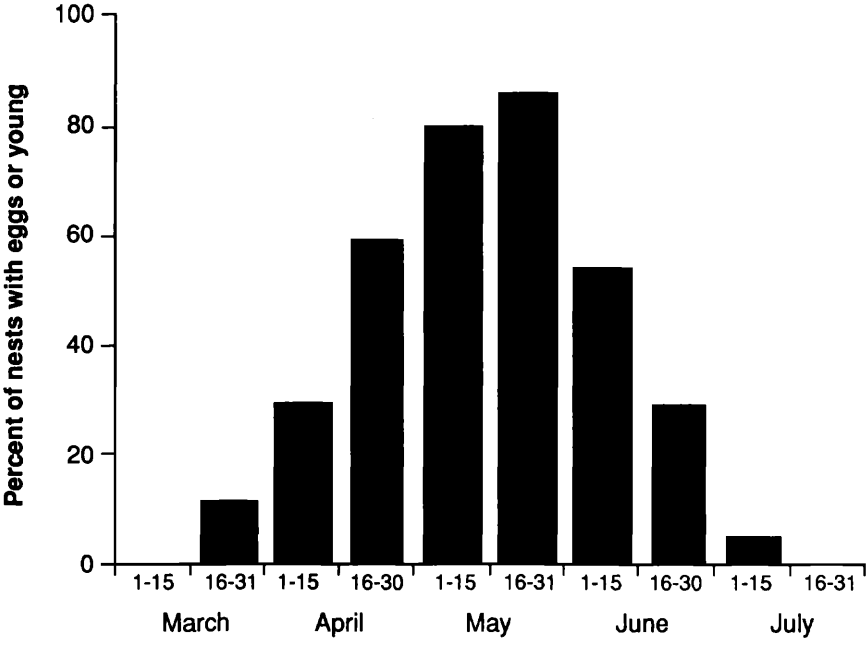

FIGURE 1. Percent of Black-chinned Hummingbird nests containing eggs or young (n = 85) by 2-wk intervals along the Colorado River in Grand Canyon, Arizona, 1982–1987.

even though twice as much OHWZ habitat was searched (Table 1). Nesting density ranged from 0 to 3.5 active nests/ha in NHWZ sites (Table 2). No nests were found in NHWZ sites that were <0.5 ha in size, exhibited <69% vegetative cover and had a mean canopy height of <1.4 m. The exception was one site (220-Mile) in which no nests were found. This site was only 0.1 ha in size and had 35% vegetative cover, but had a mean canopy height of 2.1 m.

DISCUSSION

Black-chinned Hummingbirds in the deserts of the southwestern United States make use of a wide variety of riparian trees and shrubs for nesting. Native nest substrate plants include hackberry (*Celtis reticulata*), cottonwood (*Populus fremontii*), sycamore (*Platanus wrightii*), oak (*Quercus* sp.), arrowweed, willows, and others (Bent 1964, Pitelka 1951). Trees in fruit orchards and introduced shrubs and vines in urban areas are also used (Bent 1964, Demaree 1970). This study provides the first documented instance of the use of the introduced tamarisk shrub as a nest substrate plant.

Pitelka (1951) reported the nesting season of Black-chinned Hummingbirds near Santa Barbara, California (34°N), to extend from 15 April to 30 June, with the peak of nesting activity from 5 to 10 May.

TABLE 2. Number of active Black-chinned Hummingbird nests/ha found in the tamarisk-dominated new high-water zone study sites along the Colorado River in Grand Canyon, Arizona, 1984–1987.

Study site	Active nests/ha			
	1984	1985	1986	1987
Saddle Canyon	—[1]	2.1	1.4	1.8
Cardenas Creek	2.9	3.5	2.4	2.4
Bass Camp	0	0	0	0
Forster Canyon	0	0	0	0
National Canyon	0	0	0	0
Stairway Canyon	0	1.4	2.9	1.4
Parashant Canyon	2.0	0	0	2.0
Granite Park	1.0	0	2.0	1.0
220-Mile	0	0	0	0

[1] A nest-search was not conducted.

The nesting season along the Colorado River in Grand Canyon (36°N) was initiated earlier and lasted later, and the peak of nesting activity extended over the entire month of May.

The other species of hummingbird found nesting in the study area was Costa's Hummingbird (*Calypte costae*). Three active nests were found during May in the OHWZ at the National Canyon study site: one in catclaw acacia, one in graythorn (*Condalia globosa*), and the other on the flowering stalk of a Utah agave (*Agave utahensis*). Nest heights were 160, 150 and 230 cm, respectively. Costa's Hummingbird was rare in the study area while Black-chinned Hummingbird was common to abundant. Nest placement of Costa's Hummingbird was in areas of the OHWZ exhibiting relatively sparse vegetative cover, whereas Black-chinned Hummingbirds nested exclusively in areas of the NHWZ exhibiting dense vegetative cover.

I repeatedly observed female Black-chinned Hummingbirds leaving their nests in the NHWZ to forage ≥200 m away in the OHWZ, adjacent desert scrub habitats, or across or even over the river. These observations, combined with the nest-search findings, strongly indicate that searches for Black-chinned Hummingbird nests, while time-consuming, may more accurately reflect comparative nesting densities in adjacent (within 300 m) but different habitats censused by traditional methods (i.e., Emlen 1971, Kendeigh 1944). This possibility was also suggested by Stamp (1978), who censused a riparian bird community using the spot-map method (Kendeigh 1944) but used the nest-search method to determine conservatively the nesting density of Black-chinned Hummingbirds.

The development of the tamarisk-dominated NHWZ, as brought about by the construction and operation of Glen Canyon Dam, has apparently benefitted Black-chinned Hummingbirds by increasing the extent of available nesting habitat. Black-chinned Hummingbirds may have colonized the new habitat of the NHWZ from riparian areas along unaltered

perennial tributaries to the river, where they were fairly common nesting summer residents during the study period. An alternate possibility is that Black-chinned Hummingbirds nested more commonly in the OHWZ prior to establishment of the NHWZ.

In contrast, Costa's Hummingbird has apparently not been influenced by the new habitat created by the construction and operation of Glen Canyon Dam. Although pre-dam information on the density and habitat use of Costa's Hummingbird is also lacking, its contemporary use of the OHWZ suggests that it also used this habitat prior to dam construction.

The nesting density of Black-chinned Hummingbirds along the Colorado River in Grand Canyon was comparatively high, although other studies reporting hummingbird densities used different survey techniques. The 1–3.5 nests/ha discovered in this study, when transformed for comparison, become 40–140 pairs/40 ha. This contrasts with the 4–40 pairs/40 ha reported by Stamp (1978) in mesquite and cottonwood habitats, respectively, along the Verde River of Arizona using the nest-search method. Baltosser (1986) reported 7–18 individuals/40 ha in cottonwood habitat along the Gila River of New Mexico using the spot-map method, while Hunter et al. (1988) reported 14 individuals/40 ha in cottonwood habitat along the Pecos River of Texas using the Emlen (1971) technique.

The finding that Black-chinned Hummingbirds nested exclusively in the tamarisk-dominated NHWZ, although the OHWZ exhibited similar vegetative structure, has implications for habitat management in the study area. As nests were found only in patches $\geq$0.5 ha in size with $\geq$69% vegetative cover and a mean canopy height of $\geq$1.4 m, maintenance of the Black-chinned Hummingbird population depends on the continued existence of NHWZ habitat with these minimal patch-size characteristics. Fluctuating flows from Glen Canyon Dam are apparently causing substrate erosion and subsequent riparian habitat loss in the study area (Carothers and Brown 1991), in a long-term process that could accelerate habitat fragmentation along the river. This would reduce the future usefulness of tamarisk-dominated NHWZ habitats to nesting Black-chinned Hummingbirds.

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