

## NESTING ECOLOGY OF THE NORTHERN BEARDLESS-TYRANNULET (*CAMPTOSTOMA IMBERBE*) IN THE LOWER RIO GRANDE VALLEY OF TEXAS, U.S.A.

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**Resumen.** – **Ecología reproductiva del Mosquero Imberbe Norteño (*Camptostoma imberbe*) en el Valle Bajo del Río Bravo de Texas, Estados Unidos de América.** – Durante el período 2002–2003, se estudió la ecología reproductiva del Mosquero Imberbe Norteño (*Camptostoma imberbe*), un residente permanente poco conocido y poco común en el Valle Bajo del Río Grande de Texas, Estados Unidos de América. Hemos encontrado 28 nidos en grupos de musgo español (*Tillandsia usneoides*) o musgo bola (*T. recurvata*), 93% de los cuales estaban en el olmo de cedro (*Ulmus crassifolia*) árboles. En promedio la construcción del nido llevó 7 días, la incubación 14 días y los pichones dejaron el nido 18,5 días luego de la eclosión. De los 28 nidos el 43% fue exitoso. El 38% de los nidos fracasados mostró signos evidentes de depredación. Los nidos se encuentran en zonas con denso crecimiento de *Tillandsia* y con árboles más altos que en las zonas no utilizadas cercanas. La disponibilidad de este hábitat puede limitar el tamaño de la población del Mosquero Imberbe Norteño en el Valle Bajo del Río Grande.

**Abstract.** – During 2002–2003, we studied the breeding ecology of the Northern Beardless-Tyrannulet (*Camptostoma imberbe*), a poorly known and rare permanent resident in the Lower Rio Grande Valley of Texas, United States of America. We found 28 nests in clusters of Spanish moss (*Tillandsia usneoides*) or ball moss (*T. recurvata*), 93% of which were in cedar elm (*Ulmus crassifolia*) trees. Nest-building, incubation, and nestling periods averaged 7.0, 14.0, and 18.5 days, respectively. Of the 28 nests, 43% were successful, while 38% of the failed nests showed obvious signs of depredation. Nests were located in areas with denser *Tillandsia* growth and with taller trees than nearby non-used areas. Availability of this habitat may limit the population size of Northern Beardless-Tyrannulets in the Lower Rio Grande Valley.

**Handling editor:** Jack Eitner; **Receipt:** 23 November 2014; **First decision:** 5 February 2015; **Final acceptance:** 13 March 2015.

**Key words:** *Camptostoma imberbe*, incubation period, Lower Rio Grande Valley, nesting habitat, nesting success, nestling period, Northern Beardless-Tyrannulet, Texas, United States of America.

### INTRODUCTION

The Lower Rio Grande Valley (LRGV) of southernmost Texas, U.S.A., consisting of

Cameron, Hidalgo, Willacy, and Starr counties, represents the northernmost range limit of several tropical bird species (Oberholser 1974, Brush 2005), including the Northern

Beardless-Tyrannulet (*Camptostoma imberbe*). Since the 1920s, about 95% of the LRGV's subtropical evergreen forest, riparian woodland, and scrublands (hereafter collectively referred to as riparian woodland) have been cleared for agricultural and urban development (Jahrsdoerfer & Leslie 1988). Even in protected areas, plant communities have been altered by the elimination of large-scale flooding due to significant water diversions along the Rio Grande, such as Falcon Dam (completed in 1953) and Amistad Dam (1968). Many riparian woodlands supporting subtropical deciduous forest or evergreen forest have become dry thorn-forest or thorn-scrub. This habitat change has been accompanied by corresponding shifts in avian communities (Lonard & Judd 2002, Brush 2005).

Northern Beardless-Tyrannulets (hereafter tyrannulets) inhabit arid to semi-humid woodlands, deciduous forest, gallery forest edges, and riparian thickets across their range, which extends from southeastern Arizona, southwestern New Mexico, and deep South Texas southward through Central America to northwestern Costa Rica (Gehlbach 1987, Howell & Webb 1995, Tenney 2000). They are year-round residents in most of their range, including the LRGV. Never common in the LRGV, tyrannulets have become much rarer since 1951, with accelerated loss and deterioration of native forests (Oberholser 1974). Tyrannulets now appear to be restricted to a small number of "island" tracts of habitat composed of remnant riparian woodland often supporting dense growth of the epiphytic bromeliads ball moss (*Tillandsia recurvata*) and Spanish moss (*T. usneoides*; Brush 1999, 2005; scientific names of plants from Richardson & King 2011). Tyrannulets have been listed as a 'Species of Conservation Concern' at the federal level (United States Geological Survey 2000) and as 'Threatened' on the Texas Threatened and Endangered

Species list (Campbell 2003, Texas Parks & Wildlife Department 2014).

Even though tyrannulets have a large geographical range, many aspects of their breeding biology remain unknown (Tenney 2000, Brush 2005). Tyrannulets are small and drably colored, and they probably go undetected much of the time, unless the observer knows the unique vocalizations uttered by males and females (Brush 1999, Tenney 2000). There are no published data quantifying lengths of incubation and nestling stages and habitat selection (Werner 2004). The 11 nests found in 1996–1998 (Brush 1999) were the first records of nests in the LRGV since 1940. The nest itself is a domed or globular structure with a side entrance (Fig. 1), almost always in hidden locations, such as epiphytes, tent caterpillar (*Malacosoma* spp.) webs, clusters of mistletoe (*Phoradendron* spp.), and clusters of seed pods (Oberholser 1974, Rowley 1984, TB unpubl. data). In this study, our objectives were to (1) determine the nest success of the Northern Beardless-Tyrannulet, and (2) describe the habitat characteristics of nests, so that we could make recommendations for habitat conservation and management.

## METHODS

*Study area.* SMW conducted primary field work during March–August 2002 and 2003 along the Rio Grande in Hidalgo County, Texas (Fig. 2), on the US-Mexican border. The climate is semi-arid and subtropical with a highly variable annual rainfall, averaging 560 mm, mild winters with infrequent freezes, and long, hot summers with high temperatures regularly exceeding 35°C (1961–2001 data; National Climatic Data Center 2003). Abandoned river channels, locally called resacas, historically contained subtropical deciduous forest dominated by 15–20 m tall Mexican ash (*Fraxinus berlandieri*), cedar elm (*Ulmus crassifolia*), and sugar



FIG. 1. A) Nest of Northern Beardless-Tyrannulet (*Camptostoma imberbe*) in cluster of Spanish moss. B) Northern Beardless-Tyrannulet leaning in to deliver food to active nest in cluster of Spanish moss.

hackberry (*Celtis laevigata*) trees. Upland resaca-edge areas supported diverse subtropical evergreen forest and thorn-forest, dominated by anacua (*Ebretia anacua*), Texas ebony (*Chloroleucon* [*Ebenopsis*] *ebano*), honey mesquite (*Prosopis glandulosa*), coma (*Sideroxylon celastrium*), and brasil (*Condalia hookeri*). At the edges of resacas, evergreen forest reached 12–15 m in height, with shorter trees in drier upland

areas nearby. Thorny plants dominated the understory, and ground-level vegetation historically consisted of native herbaceous and semi-herbaceous broad-leaved species. In many areas, tall trees have died, and thorn-forest has replaced taller resaca-edge and deciduous riparian forest in many remnant tracts. Likewise, the diverse understory is often displaced by guinea grass (*Megathyrsus*

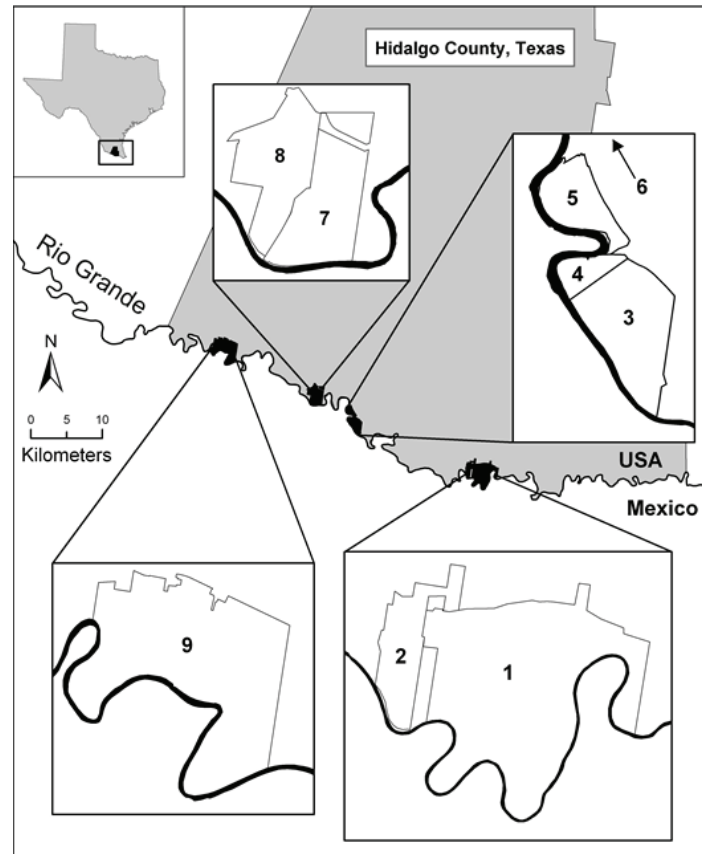


FIG. 2. Map of tracts surveyed for nests of Northern Beardless-Tyrannulets in Hidalgo County, Texas, U.S.A., during 2002–2003. Elevations range from 23–43 m a.s.l. From downstream to upstream, tracts are (1) Santa Ana National Wildlife Refuge (26°58'02"N, 98°08'54"W), (2) Marinoff tract, Lower Rio Grande Valley National Wildlife Refuge (LRGVNWR; 26°04'40"N, 98°10'01"W), (3) Gabrielson tract, LRGVNWR (26°07'51"N, 98°19'20"W), (4) Anzalduas County Park (26°08'20"N, 98°19'53"W), (5) Madero tract, LRGVNWR (26°09'03"N, 98°19'58"W), (6) Madero residential (26°10'09"N, 98°19'52"W), (7) El Morillo Banco tract, LRGVNWR (26°10'06"N, 98°22'25"W), (8) Bentsen-Rio Grande Valley State Park (26°10'24"N, 98°22'59"W), and (9) La Joya tract, LRGVNWR (26°13'55"N, 98°30'24"W).

*maximus*) and buffel grass (*Pennisetum ciliare*), non-native species introduced into livestock pastures (scientific names of grasses from Shaw 2012).

**Data collection.** SMW and 1–2 field assistants searched for nests from mid-March to mid-August 2002 and 2003, at Anzalduas County Park, Bentsen-Rio Grande Valley State Park

(hereafter, Bentsen), Santa Ana National Wildlife Refuge (hereafter, Santa Ana), and the Gabrielson and Madero tracts of Lower Rio Grande Valley National Wildlife Refuge, because they appeared to harbor the most tyrannulets during preliminary surveys and during a previous study (Brush 1999).

Territorial pairs were located by following otherwise inconspicuous tyrannulets; singing

males making the *pier-pier-pier* call and females making *pee-uk* calls (Brush 1999, Tenney 2000). Nests were found by following behavioral cues (Martin and Geupel 1993) and monitored from a distance with binoculars at least every 3 to 5 days, with more frequent visits during transition periods. Nesting attempts were considered successful if nests fledged at least one tyrannulet.

Territorial boundaries were determined at the sites by following nesting individuals and keeping track of simultaneously-active nests. Although no birds were color-banded, the rarity of the species meant that territories did not overlap, and territorial disputes were never observed. We defined a breeding pair as the same pair nesting on a territory during the same season, although we did not know if the unmarked birds maintained pair bonds through the whole season. Locations of nests were recorded using a handheld GPS device (Map 330M; Magellan Corporation, San Dimas, California, USA) and plotted on digital orthophoto quadrangles using ArcView 8.3 (ESRI 2002).

We calculated nest success according to Mayfield (1961, 1975) and Johnson (1979). For failed nests, we calculated the fail date as the half-way point between the last confirmed active date and the date on which the nest was confirmed not active (Martin *et al.* 1997). Clutch sizes could not be estimated due to the enclosed nature of the nests. We were occasionally able to estimate the minimum number of nestlings inside a nest visually or aurally, but many nests were located too high in the canopy to make this estimate. The number of fledglings was determined by observing begging individuals outside of the nest.

We took two groups of measurements at each tyrannulet nest. First, we recorded nest-placement variables, including tree species, nest tree height, diameter at breast height (DBH) of the nest tree, nest height at nest

opening, azimuth from the nest-tree trunk to the nest ("trunk-to-nest angle"), compass direction of the nest-opening ("nest-opening angle"), and horizontal distance from the nest-tree trunk to the nest. Compass bearings were corrected for magnetic declination and recorded for true north. Heights below approximately 8.5 m were measured with a telescopic pole, and heights above 8.5 m were measured with a clinometer.

Second, we measured nest-site variables, using a 0.04-ha circular plot (James & Shugart 1970, Martin *et al.* 1997) centered at the nest, and compared with a nearby non-use plot. We used a paired, random-plot design to identify features of the vegetation that were more likely to be associated with tyrannulet nests. The center of the 0.04-ha circular non-use plot was located at a random compass direction and a random distance between 20 and 50 m from each nest, to avoid moving into a different habitat (Werner *et al.* 2007). We recorded the number, DBH, and species of small trees (DBH < 15–30 cm), large trees (> 30 cm), and snags (dead trees with DBH > 15 cm and height > 1.4 m), and the number of fallen logs (diameter > 15 cm and length > 3 m). Canopy cover was measured using a concave densiometer at the center of the plot. Within each plot we placed four 10-m transects in the cardinal directions emanating from the center of the plot. At point intervals of 2 m along the transects, we placed a 7.6-m telescopic pole and counted the number and species of vegetation hits (Wiens & Rotenberry 1981) in each 1-m vertical layer. Thus the total number of points sampled with the pole in the plot was 21 (five points per cardinal transect and one center point). The maximum number of *Tillandsia* hits per 1-m layer was 10 for simplicity (hits of other species could exceed 10 per layer, but this rarely happened). Hits above 7.6 m were estimated after obtaining the nest and tree heights, usually with a clinometer. At each of the 21 points we

measured the maximum canopy height within 10 cm of the pole, and the maximum of these heights was the maximum height variable for the plot. To determine if *Tillandsia* species were more common at nest plots, we summed the totals of *T. usneoides* and *T. recurvata* foliage hits in all vertical layers and included this number as an overall measure of *Tillandsia* foliage density.

We used two indices of structural heterogeneity at the plot. We calculated height variation using the heterogeneity index of Wiens and Rotenberry (1981), where height variation = (maximum vegetation height – minimum vegetation height) / mean vegetation height. We calculated vertical structural diversity among the three vegetation layers using a Simpson diversity index (Hill 1973) following Braden (1999) by the formula  $1 / \sum (p_i)^2$  where  $p_i$  is the proportion of foliage hits in vertical layer  $i$  on a plot. Additional information on methodology can be found in Werner (2004).

**Data analysis.** We used Matched-pairs Logistic Regression (MPLR) to explore habitat preferences for nest placement (Hosmer and Lemeshow 2000). We present only those models with AIC differences ( $\Delta$ ) less than 10, using SPSS for Windows, versions 11.0 and 12.0 (SPSS 2001, 2003). An alpha level of 0.05 was used for all tests unless noted otherwise (Werner *et al.* 2007). Means other than nesting stage lengths are presented as  $\pm 1$  SE.

## RESULTS

We found 13 nests in 2002 (5 breeding pairs) and 15 nests in 2003 (7 breeding pairs). Nests were found during various stages: 64% ( $n = 18$ ) during building, 6% ( $n = 1$ ) during laying, 21% ( $n = 6$ ) during incubation, and 7% ( $n = 2$ ) during the nestling stage (the remaining nest was found during either the incubation or nestling stage). The first nests of each year were under construction by 1 April 2002 and

17 March 2003, and the latest active dates for known nests during each year were 30 August 2002 and 23 July 2003. The mean of the minimum observed building times rounded to the nearest whole day was 7 days ( $n = 13$ , range 2–15). Estimated mean lengths of the incubation and nestling stages were 14.0 days ( $n = 8$ , range 12–15.5) and 18.5 days ( $n = 9$ , range 16–21), respectively. We were able to see females brooding inside the nest at most nests that reached the incubation stage.

Twelve (43%) of the 28 nesting attempts were successful and 16 (57%) failed. Of the failed nests, four (25%) failed during incubation, seven (44%) failed during the nestling stage, and one nest failed during either the incubation or nestling stages. Four (25%) of the failed nests appeared completely built but were abandoned before incubation began. These nests could not be closely inspected but we included them in the analysis to maximize the sample size.

Nestlings could be heard softly begging ('bee-bee' call; Tenney 2000) from the nests as early as 11–12 days of age, and could sometimes be seen from a distance with binoculars at this point. Older nestlings often begged loudly from the nest and their heads sometimes protruded from the nest entrance when adults arrived with food. The mean number of fledglings for successful nests was  $2.1 \pm 0.2$  ( $n = 9$ , range 1–3). This could have been an underestimate, because some fledglings could have gone undetected. The maximum number of successful broods from what appeared to be the same nesting pair was two, and the maximum number of nesting attempts was four. On two occasions we observed females re-building 1–2 days after a single chick had fledged from a nearby nest and was still being fed in the area.

Causes of nest failure were difficult to ascertain because few of the 16 failed nests could be closely inspected. Six nests appeared to be ripped open or ripped down. Of these

nests, four had nestlings, one had eggs, and the sixth had either eggs or young chicks. Six failed nests appeared intact but could not be closely inspected. Three of these failed during possible egg-laying, one failed during incubation, and two failed during the nestling stage. Of the two nests that apparently failed from severe weather, one failed during a severe storm with golf-ball sized hail during incubation. The other nest was partially disintegrated after a heavy thunderstorm during the previous night, also during incubation.

In this study, tyrannulets were found in areas with high abundance of *Tillandsia* and with tall trees, nesting almost exclusively in cedar elm. Ninety-three percent (26 of 28) of nests were built in cedar elm, 11 of which were dead. The two other nests were built in Texas ebony (at Bentsen only). Mean nest height was  $9.1 \pm 0.4$  m (range 4.9–14.0), mean nest tree height was  $13.0 \pm 0.5$  m (range 8.5–18.0), mean nest tree DBH was  $37.1 \pm 2.8$  cm (range 20.8–74.3), and mean horizontal distance from the nest to the nest-tree trunk was  $3.5 \pm 0.4$  m (range 0.3–7.9).

All active tyrannulet nests were built in or on *Tillandsia* epiphytes. There were two general types of nests: (1) those built among two or more ball moss clumps, appearing to have a more stationary base such as a branch or a ball moss clump; and (2) those built inside hanging Spanish moss clumps that were often suspended from branches. Fifty-seven percent (16 of 28) of the nests were in ball moss, and 43% (the remaining 12) were in Spanish moss. The nests in ball moss had a large amount of Spanish moss incorporated into their walls. Distribution of the two nest substrates between live cedar elm and dead cedar elm was not significantly different than expected (Pearson  $\chi^2 = 2.1$ , d.f. = 1,  $P = 0.15$ ). Mean trunk-to-nest angle was 271 degrees, but the distribution was random ( $\chi^2 = 2.8$ ,  $0.10 > P > 0.05$ ). Distribution of the nest-opening angles was also random (276 degrees;  $\chi^2 = 1.5$ ,  $P > 0.2$ ).

Nest plots on average had a lower foliage frequency in the 1–7 m strata than non-use plots, and nest plots generally had taller vegetation than non-use plots (Fig. 3). Five of the 15 nest-site MPLR variables were significant in univariate analyses (Table 1). Height variation was negatively correlated with canopy cover (Spearman  $r_s = -0.72$ ,  $P < 0.001$ ) and shrub-layer foliage frequency ( $r_s = -0.63$ ,  $P < 0.001$ ), and was therefore separated from these variables in the multivariate analysis. The best final MPLR model contained only one variable and indicated that the total amount of *Tillandsia* foliage hits best predicted nest-site selection (Table 2). The *Tillandsia* MPLR model had nearly five times the predictive power of the next best model, which included canopy cover and maximum vegetation height. The residual analysis indicated that all three models fit the data well.

Nest plots had much higher amounts of both epiphytic *Tillandsia* (Fig. 4). Nest plots had about six times the amount of Spanish moss (1843 vs. 303 hits) and about 10 times the amount of ball moss (202 vs. 21 hits), compared to non-use plots. The proportion of ball moss tended to be greater on nest plots than was Spanish moss, but the difference was not significant (Pearson  $\chi^2 = 3.8$ , d.f. = 1,  $P = 0.052$ ).

## DISCUSSION

Our nesting data add to the sparse natural history information for the Northern Beardless-Tyrannulet. The heavy use of cedar elms, particularly dead trees, complements Brush's (1999) data. The mean nest height of 9.1 m, with significant variation, reflects the uneven canopy height of woodlands in the LRGV, and would probably be lower in non-riparian habitats, as well as in areas where shrubby species such as palmettos were used as nest sites (Thayer 1906). The mean of seven days for nest-building falls within the anecdotal

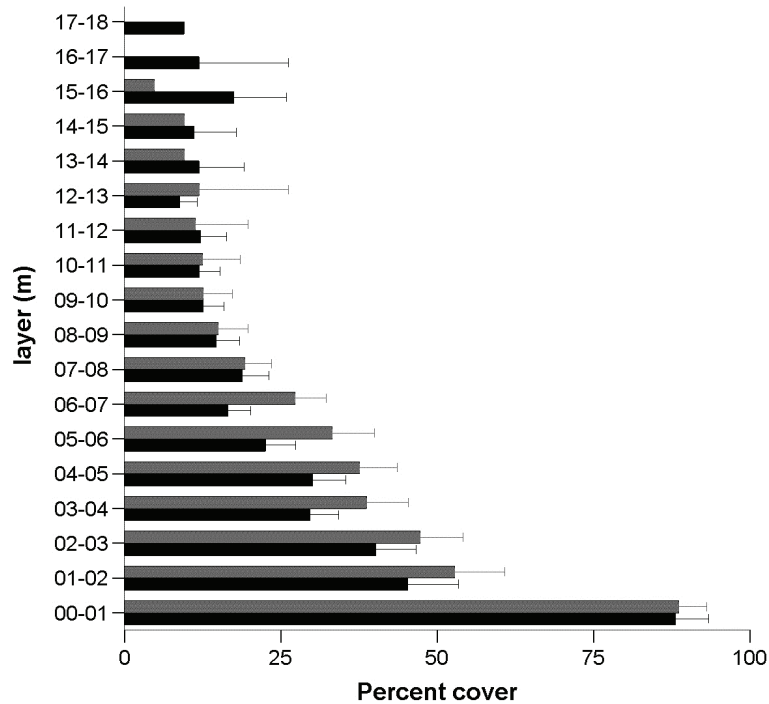


FIG. 3. Foliage frequency for each vertical meter layer obtained from vegetation hits on a vertical pole placed at 21 points within nest plots ( $n = 28$ ; black bars) and non-use plots ( $n = 28$ ; gray bars) for Northern Beardless-Tyrannulet nests in the Lower Rio Grande Valley, Texas, 2002–2003. Error bars represent 2 SE.

estimates summarized by Tenney (2000). Our estimate of 14 days for incubation is within the 14–16 day range of the Southern Beardless-Tyrannulet (*Camptostoma obsoletum*) (Skutch 1997) and the 13–14 days of the Gray-crowned Tyrannulet (*Serpophaga griseiceps*) (Mezquida & Marone 2000), although somewhat shorter than the 16–18 days of other small flycatchers in Costa Rica (Skutch 1960). The somewhat small clutch size of one to three eggs inferred from the number of fledglings and from Tenney's (2000) review is typical of tropical species that have likely adapted to greater levels of nest predation in the tropics compared to temperate zones (Stiles & Skutch 1989). Given our small sample sizes, we need more data on the nesting

biology of the Northern Beardless-Tyrannulet, particularly in areas where it is more abundant.

Brush's (1999) study is the only one we are aware of that presents nest success results of multiple Northern Beardless-Tyrannulet nests. Six of his 11 nests likely fledged, three nests were abandoned or depredated, and two nests' outcomes were unknown. His 55% (six of 11) raw success rate is slightly larger than the 43% we observed, but the significance is difficult to evaluate due to the small sample size. The long nesting season (Brush 1999), typical of tropical bird species, allows tyrannulets to re-nest after failures to increase their annual nesting success. Since we saw no evidence of male tyrannulets displaying before



TABLE 1. Summary of mean differences of nest-site variables between paired nest plots and non-use plots for Northern Beardless-Tyrannulet nests ( $n = 28$ ) in the Lower Rio Grande Valley, Texas, 2002–2003. Likelihood Ratio Test statistic (LRS  $\chi^2_1$ ) and  $P$  values are from univariate matched pairs logistic regression (MPLR). Asterisks denote significance for inclusion in the multivariate MPLR ( $P < 0.25$ ). <sup>a</sup> Matching letters indicate variables that were significantly correlated (Spearman Rank Correlation;  $|r_s| \geq 0.60$ ,  $P < 0.001$ ) and thus were not included in the same multivariate model.

Variable	$\bar{x}$ difference	SE	LRS $\chi^2_1$	$P$	Correlations <sup>a</sup>
% canopy cover	-8.9	5.1	3.0	0.09*	A
Large trees (15–30 cm DBH)	0.1	0.3	0.0	0.8	
Small trees (> 30 cm DBH)	-0.8	0.8	1.0	0.3	
Snags	0.5	0.6	0.6	0.4	
Logs	0.5	0.6	0.6	0.5	
Maximum height	2.7	0.5	21.0	< 0.001*	
Height variation	0.3	0.2	3.6	0.06*	AB
Foliage frequency, 0–1 m (%)	-0.6	2.6	0.0	0.8	
Foliage frequency, 1–3 m (%)	-7.8	3.2	5.6	0.02*	B
Foliage frequency, > 3 m (%)	-3.9	4.9	0.6	0.4	
Foliage density, 0–1 m	10.1	7.3	2.0	0.16*	
Foliage density, 1–3 m	-7.7	10.8	0.5	0.5	
Foliage density, > 3 m	11.4	13.3	0.8	0.4	
Vertical structural diversity	0.0	0.1	0.1	0.8	
Total <i>Tillandsia</i> hits	61.5	11.2	27.7	< 0.001*	

partially or completely built nests, and since only apparent females built nests, we speculate that the nests abandoned before incubation had been disturbed by a potential predator or nest-robbing bird (TB pers. observ.) and were not display nests.

We found that tyrannulets build their nests in areas with more *Tillandsia* than nearby unused habitat, and nests were placed in clumps of *Tillandsia*. Ball moss and Spanish moss were relatively common within suitable riparian woodland in our study areas. However, both epiphytes are uncommon to rare across other woodlands across the LRGV, and they are essentially absent from reforested tracts, which make up an increasing percentage of riparian woodland (Brush 1999, 2005). The rarity of tyrannulets in the LRGV (Brush 2005) may be due in part to the rarity of Spanish moss and ball moss. *Tillandsia* abundance may be a factor both in habitat selection and nesting success, which would both affect pop-

ulation persistence. Even nests in *Tillandsia* may be depredated, as we saw, but presumably any more exposed nests outside *Tillandsia* clusters would be even less successful.

Forcey (2002) noted tyrannulets nesting in other *Tillandsia* species in Oaxaca, southern Mexico. The factors controlling *Tillandsia* abundance are poorly known, but may include tree size and bark roughness (Bernal *et al.* 2005, Lopez-Villalobos *et al.* 2008). This may explain why cedar elm, a large, rough-barked tree, which appeared to support a greater amount of *Tillandsia* than other LRGV trees, was the main tree species selected by tyrannulets for nesting in this study. Cedar elm had the highest overall abundance of trees in tyrannulet nesting habitat, but mesquite, seldom supporting *Tillandsia*, was most abundant in unused areas (Werner 2004).

Large and presumably old cedar elms, most often used as nest-sites in this study, are a declining resource in the LRGV, as drought

TABLE 2. Final MPLR models describing nest-site selection for Northern Beardless-Tyrannulet nests ( $n = 28$ ) in the Lower Rio Grande Valley, Texas, 2002–2003. LRS = Likelihood Ratio  $\chi^2$  Statistic;  $K$  = number of parameters;  $AIC_c$  = Akaike Information Criterion;  $\Delta_i$  = AIC differences;  $w_i$  = Akaike weights. <sup>a</sup>The LRS of the full model vs. null model is shown on the first row for each model, and the LRS for the full model versus the model without the variable is shown next to each variable. For univariate models 1 and 3, both LRS tests described above are the same. <sup>b</sup>\* $P < 0.05$ ; \*\* $P < 0.001$ .

Model # and Variable(s)	Coefficient	SE	LRS <sup>a,b</sup>	$K$	$AIC_c$	$\Delta_i$	$w_i$
1			27.7**	2	15.6	0.0	0.805
Total <i>Tillandsia</i> hits	0.095	0.043	27.7**				
2			27.1**	3	18.8	3.2	0.167
Canopy cover	-0.087	0.052	6.0*				
Maximum height	1.100	0.462	24.1**				
3			21.0**	2	22.3	6.7	0.029
Maximum height	0.919	0.338	21.0**				

and lack of flooding continue to take their toll in existing mature woodlands (Brush 2005). Since dead cedar elms retain few branches after 2–4 years (TB pers. observ.), dead trees used in a given nesting season would not be available within a few years. Most reforested tracts do not contain mature cedar elms, since they are mostly less than 25 years old, and revegetation with cedar elm has been difficult (TB unpubl. data).

Although our results show that *Tillandsia* is the most important variable distinguishing between nest areas and unused areas, tyrannulets in this region may not be strictly dependent upon *Tillandsia* for nest placement. SMW (2004) observed a female constructing a nest of dead leaves and webbing, possibly of a tent caterpillar, in an area with virtually no *Tillandsia*, within 10 km of Bentsen. In 2014, a nest was built in and of lichens in a dead tree with no *Tillandsia*, in a small wooded tract ca. 18 km ENE of Santa Ana NWR (TB unpubl. data). Tyrannulets have been observed in a few other reforested tracts along the Rio Grande within 12 km of Bentsen or Santa Ana where there is little if any *Tillandsia* (SMW, TB pers. observ.), although we do not

know if they nested there. Future studies should include tyrannulet nesting surveys at sites that have little or no *Tillandsia* to determine its importance as a limiting habitat component for nesting.

Without some sort of flooding or a few years with above-normal rainfall, most of the forested areas will likely continue to degrade into habitat unfavorable to tyrannulets. Most of the remnant riparian and thorn forest in the LRGV has been preserved (Jahrsdoerfer & Leslie 1988), so future restoration efforts should include planting of species such as cedar elm, in cases where local moisture regimes are suitable, and more drought-tolerant trees in drier areas. At the same time, factors affecting establishment of *Tillandsia* on more drought-tolerant trees such as Texas ebony, coma, and brasil should be studied. *Tillandsia* abundance should be monitored, as there is some evidence it may decline due to climate change (Cach-Perez *et al.* 2013). Since many reforested tracts are used by woodland-dependent species, such as White-tipped Dove (*Leptotila verreauxi*), Long-billed Thrasher (*Toxostoma longirostre*), Olive Sparrow (*Arremonops rufivirgatus*), and Altamira Oriole

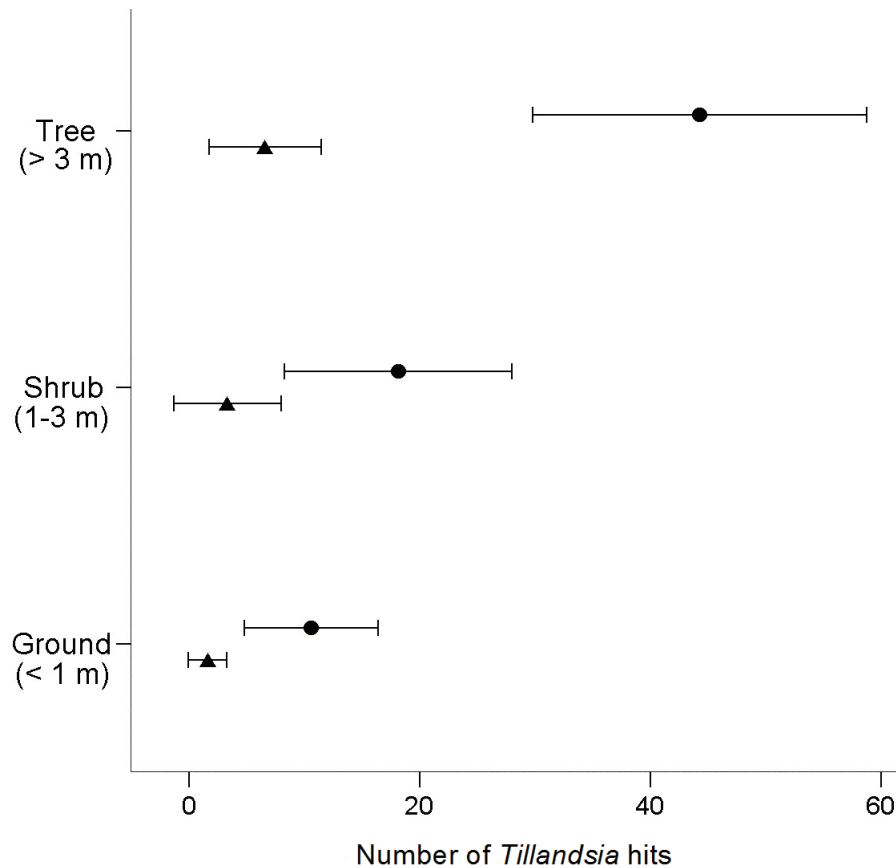


FIG. 4. Differences in total *Tillandsia* hits at nest plots (circles) and non-use plots (triangles) among three strata for Northern Beardless-Tyrannulet nests in the Lower Rio Grande Valley, Texas, 2002–2003. Nest plots had more *Tillandsia* in all three layers (Mann-Whitney U-tests: Ground,  $U = 226.5$ ,  $P < 0.01$ ; Shrub,  $U = 198$ ,  $P < 0.001$ ; Tree,  $U = 72$ ,  $P < 0.001$ ). Error bars represent 2 SE.

(*Icterus gularis*) (Brush 2005), re-vegetation that benefits tyrannulets will likely benefit other woodland birds of the LRGV.

#### ACKNOWLEDGMENTS

We thank the U.S. Geological Survey/U.S. Fish and Wildlife Service Species at Risk Program and the Texas Parks and Wildlife Conservation Action Grant program for funding this research. Personnel at the Santa Ana/Lower Rio Grande Valley National Wildlife

Refuge complex and Bentsen-Rio Grande Valley State Park were very generous in providing access to the study sites and lodging for field personnel. L. Drabek, V. Pedro, and J. Dale provided field assistance. We also thank D. Blankinship, M. Sternberg, J. Rupert, D. Stolley, S. Winter, C. Best, P. Alexander, G. Proudfoot, and K. Granillo for advice and support during the project. We thank C. R. Tenney, S. R. McGehee, and an anonymous reviewer for their comments on an earlier draft.

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