PARTITIONING OF FORAGING HABITAT BY THREE KINGFISHER SPECIES

(ALCEDINIDAE: CERYLINAE) ALONG THE SOUTH LLANO RIVER, TEXAS

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ABSTRACT

A current northward expansion of Ringed (*Megaceryle torquata*) and Green Kingfishers (*Chloroceryle americana*) places them in aquatic systems with the temperate Belted Kingfisher (*Megaceryle alcyon*). I surveyed a 23.5km stretch of the South Llano River near Junction, TX to determine seasonal abundance and compare foraging perch characteristics among the species. Data was collected on 7 foraging perch characteristics for 250 kingfisher observations across 26 surveys. Mean encounter rate for Green, Belted, and Ringed Kingfishers per river kilometer was 0.48, 0.22, and 0.09, respectively. Seasonal presence varied among the species: Green Kingfishers were present year-round, while the Belted and Ringed Kingfishers were absent from mid-spring to mid-summer. Foraging perch characteristics were analyzed via permutational multivariate analysis of variance using distance matrices; characteristics of Green Kingfisher foraging perches were significantly different from those of Belted and Ringed Kingfishers, while there was no difference in foraging perch characteristics between Belted and Ringed Kingfishers.

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INTRODUCTION

Habitat-partitioning:

Ecologists have variously defined niche. Grinnell (1924) defined a niche as the ultimate distribution of a single species or subspecies, corresponding to what is known as habitat today. Elton (1927) defined niche as the functional role or job a species within a community. Essentially, the Eltonian definition corresponds to the trophic position occupied by a species within a food web. Hutchison (1957) defined a niche as a multi-dimensional hyper-volume whereby each of N-dimensions corresponds to a measure of the abiotic and biotic environment (e.g., humidity, temperature, prey availability). Under Hutchison's model, a species' niche was the N-dimensional volume created by the overlapping tolerance curves along all of N-axes. Logically, it follows that the more similar the niches of two or more species are, the more likely the species will compete when they spatially co-occur. Where niches of two species are highly similar or identical, persistence of both species is unlikely as demonstrated by the experiments of Gause (Gause & Witt 1935). Contemporarily, the exclusion of a species by another due to competition is termed competitive exclusion.

Several morphological or behavioral mechanisms may work to reduce competition between similar species and thus allow for coexistence. For example, character displacement of bill morphology among overlapping populations of Darwin's finches (Grant 1986) on the Galapagos Islands, allows different species of finch to exploit different seeds and thus avoid competition. Behaviorally, species may shift their activities away from potential competitors thus partitioning shared space.

Waterbirds

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MacArthur (1958) demonstrated that *Dendroica* warblers feed in different positions and display different behaviors within conifers, as a means of increasing exposure to more potential foods within the tree. Although there were slight overlaps in these activities, these slight differences in habitat preference allowed for the coexistence of multiple species in one habitat. Thus, the coexistence of multiple, like-niche species in a single habitat, due limited spatial (or other) overlap, is known as niche-packing (Mizera and Meszena 2003).

Kingfishers are a family of piscivorous birds in the order Coraciiformes with distinctive, yet conserved, morphology and behavior. This is reflective in their specialized diet and use of shorelines in riverine systems. As most kingfishers have comparable behavioral and ecological requirements, they make for useful models in understanding mechanisms of niche-separation among like-birds. Numerous studies have been conducted on kingfisher habitat-partitioning in tropical habitats, where multiple kingfisher species coexist in riverine systems (Remsen 1990 and Bittermann 2012). These studies aimed to quantify differences in habitat preferences that allow for "niche-packing" of three, or more, kingfisher species. Along the Kilombero River, Tanzania, Bonnington *et al.* (2007), showed that the larger two species of kingfisher, the Giant (*Megaceryle maxima*) and Pied Kingfishers (*Ceryle rudis*), preferred taller perches, as well wider stretches of river, than the other two, smaller species (Half-collared [*Alcedo semitorquata*] and Malachite Kingfishers [*Alcedo cristata*]). A similar study, conducted by Borah *et al.* (2012), in the Bhitarkanika mangroves of Odisha, India, found comparable results. Not only did the larger species prefer taller perches, but there were differences in selected foraging substrates as well. Farther east, along the Chikuma River in Japan, Kasahara and Katoh (2008) documented the habitat preferences of the widespread Common Kingfisher (*Alcedo atthis*), and the larger Crested

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Kingfisher (*Ceryle lugubris*). As before, the larger *C. lugubris* preferred taller perches available, such as trees and shrubs, to *A. atthis*, which utilized primarily aquatic plants. Flow rate associated with perches varied between the two species as well, with *C. lugubris* preferring faster flowing river sections than *A. atthis*. Within the Neotropics, Bittermann (2012) studied differences in habitat use of Green Kingfishers, Amazon Kingfishers (*Chloroceryle amazona*), and Ringed Kingfishers (*M. torquata*) in proximity to the La Gamba Tropical Research Station within Costa Rica's tropical lowlands. A clear gradient in perch height was observed among all three species, with larger birds favoring taller perches for foraging.

Though numerous studies pertaining to habitat partitioning of kingfishers have been conducted around the world, none have been conducted in temperate North America. This is due to the limited diversity of temperate kingfishers. Historically, only two species of kingfishers have been residents of temperate North America: The Belted Kingfisher (*M. alcyon*), the ubiquitous kingfisher of the United States and Canada, and the neotropical Green Kingfisher, which was largely restricted to the lower Rio Grande Valley and the Edward's Plateau region of Texas (Oberholser 1974), as well as southwestern Arizona. Recently, another species of neotropical kingfisher has expanded its range into Texas, the Ringed Kingfisher, which became listed as a permanent resident of the lower Rio Grande Valley in the 1950's (Oberholser 1974).

Both Green and Ringed Kingfishers have undertaken rapid range expansions north and eastward from the Lower Rio Grande Valley of Texas during the 1900's (Rappole *et al.* 2007). Continued expansion of both species is evidenced by vagrant Ringed Kingfishers observed as far north as Dallas Co., TX (Cook, G. 2007. eBird Checklist). Green Kingfishers

have been sighted consistently throughout the Edwards Plateau and as far north as Coryell Co., TX within the last decade (Rodriguez, W. 2009. eBird Checklist). This expansion of distributions for these two neotropical kingfishers subjects them to increased habitat overlap with the Belted Kingfisher. The purpose of this study was to examine the three species in an area of sympatry and identify potential differences in foraging perch selection and nearby water characteristics to determine how or if these birds are partitioning their habitats amongst themselves. According to Hutchinson and MacArthur (1959), if two mammals or birds of like-niches display a weight-to-weight ratio 1:1.3, then ordinarily competition should be avoided. As Amazon and Ringed Kingfishers, with a mass ratio of 1:2.4, were shown by Bittermann (2012) to partition their habitat by perch-height; one would infer that the Belted Kingfisher, cogenator to the larger Ringed Kingfisher, would also partition by perch-height with Ringed Kingfisher, as the mass ratio of the two species is 1:2.1 (masses provided by Dunning 1992). This is of course assuming that Hutchinson's idea of differential habitat-selection induced by differences in body mass between kingfishers holds true where their ranges are sympatric, within a temperate zone.

Objectives:

1. Identify and compare differences in perch characteristics between the three native kingfisher species and quantify habitat partitioning habitat in along the South Llano River, Texas

2. Document encounter rate for each of the three species on a survey-to-survey basis along the South Llano River, Texas

METHODS

Sampling Site:

The study utilized kingfisher observations along a 23.5km segment of the South Llano River, located in Kimble Co., Texas (Fig. 1). The South Llano River is a spring-fed tributary of the Llano River, running northward through the Edwards Plateau, which is characterized by scrubland and limestone terrain. The study site consisted of two segments along the South Llano River. Segment one is a 14.3 km section of the river, starting at the upstream crossing of US Route 377 north of Telegraph, TX, to the South Llano River State Park in Junction, TX. Segment two is a 9.2km section of the river, beginning at the South Llano River State Park to Flatrock Lane in Junction, Texas. Surveys were conducted from March 2016 to December 2017 at three-week intervals along both segments of the South Llano River, completed in two consecutive days. Surveys were conducted by kayak. Surveys began no later than 08:30. Side-channels and other waters surrounding the main channel of the South Llano River were not sampled during the study. Using binoculars, location, species, sex, and perch characteristics were recorded under the first observed perch of an individual kingfisher. If the kingfisher flushed from its perch before the perch be located, the next perch to be observed for the individual was recorded. To limit double counting of individuals flushing downstream, I ignored individuals of the same species and sex encountered downstream for 30 minutes following an observation.

Encounter-rate and Seasonality:

Encounter-rate for each species was recorded for each survey as a measure of number of birds, of a species, observed per kilometer. Dissimilarity in encounter-rate between the species was tested with ANOVA. Due to the violation of homoscedasticity of the Ringed
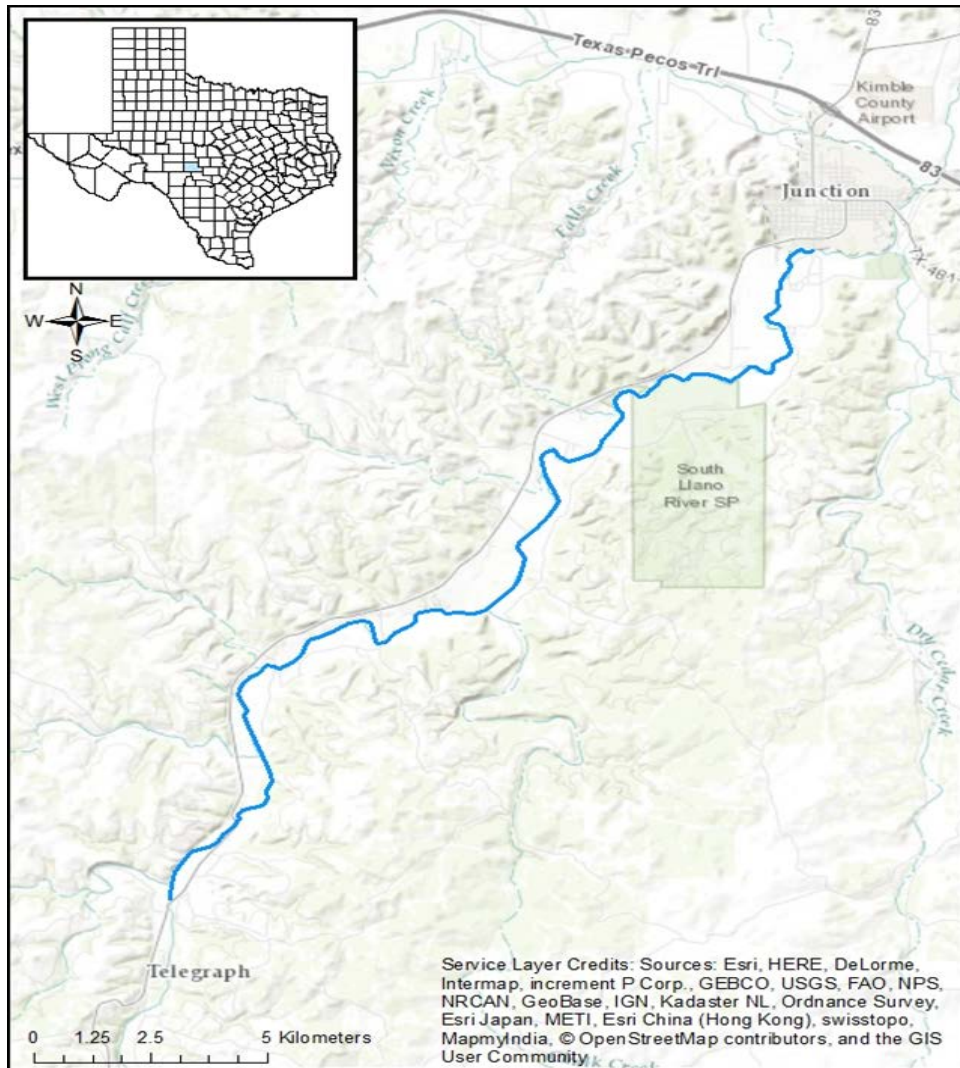
Figure 1. Map displaying distance and location of study-transect along the South Llano River, Kimble County, TX. Transect began at the US Route 377-crossing north of Telegraph, and ended at Flat Rock Lane, in Junction, TX.

Kingfisher data, differences in encounter-rate between the Ringed and the other two

kingfisher species were calculated using Welch's One-Way ANOVA (Jan & Shieh 2014).

Mean encounter-rate was recorded seasonally, with seasons corresponding to the periods

between the equinoxes and solstices. Any significant difference in seasonal encounter-rate

for each species was quantified using ANOVA, followed by Tukey's HSD for posthoc

testing. Each comparison was conducted using linear models, with assumptions of each linear

model being checked using global validation of linear model assumptions (GVLMA) within

the gvlma package (ver. 1.0.0.2) of the open-source program, R (R Development Core Team

2018).

Perch Characteristics:

All perch characteristics were recorded underneath the identified perch. Perch type

was noted and categorizing as organic (trees/shrubs), inorganic (sunken rocks), and man-

made (fencing/utility wires). Water depth was measured in centimeters using a ~3m pole

graded into 10cm increments. Water depth was measured from the water surface underneath

the kingfisher's perch to the bottom of the river perpendicular to the surface. River width was

measured to the nearest 0.1 meter by a laser rangefinder at the location of the perch. The

river flow rate (meters/seconds) was calculated using a flow meter (Vernier, Beaverton,

Oregon), placing the flow meter approximately 30cm below the water's surface underneath

the perch, facing the direction of the river's flow. Flow was recorded for 20 seconds and then

averaged as m/s. I measured perch height (nearest cm) from the bottom of the perch to the

surface of the water using the graded pole. If the perch was greater than 3m in height, a

clinometer (Suunto, Vantaa, Finland) was used, to estimate perch height. Some of the perch

characteristics, such water velocity and water depth, can have a cause-and-effect relationship,

suggesting a high correlation across multiple variables (Colby 1961). To capture the effect of some of these perch characteristics on a coarser spatial-scale (Beisel 1998), the mesohabitat of each kingfisher's location was also recorded, as mesospatial heterogeneity might be indicative of aquatic indicator-species (Groeschel 2013). The survey transect was partitioned into the following three mesohabitat categories: riffle, run, or pool. Mesohabitats were defined by presence of visible depth, substrate, as well as surface-agitation (Groeschel 2013). Riffles were categorized by areas of the river with shallow depth, cobbled substrate, and extensive surface-agitation, induced by the substrate breaking the water's surface. Runs were categorized as areas of the river with moderate depth, cobbled or smooth limestone substrate, and reduced surface-agitation. Pools were categorized as areas of the river with great depth, silted or vegetated substrate, and zero or minimal surface-agitation. GPS waypoints were used to marking the start and end of each mesohabitat. These coordinates were used to delineate the river into stream segments and assign each kingfisher location to a given mesohabitat.

Statistical Analysis of Foraging-habitat:

Multivariate analyses are often used in community/guild studies, as they are regarded as robust tools useful for condensing variation in large, multiple-variable datasets (Wiens 1989). Data subsets were created consisting of species pairs (Ringed and Green Kingfishers, Ringed and Belted Kingfishers, Belted and Green Kingfishers) for comparison of perch characteristics. Permutational multivariate analysis of variance using distance matrices (ADONIS) was used to discern any dissimilarity between perch characteristics for the species-pair, being analogous to a permutational MANOVA. ADONIS was selected for statistical comparison of species as it allows for semi-metric or metric distance matrices

(Gutierrez-Galan 2016). To visualize patterns within the perch characteristics, non-metric multidimensional scaling (NMDS) was utilized to map species-dissimilarity onto an abstract ordination space. P-values for ADONIS were adjusted using the Holm-Bonferroni adjustment method.

Both ADONIS and NMDS data-matrices were constructed with Bray-Curtis distance metrics. As distances calculated are semi-metric, Bray-Curtis allows for the inclusion of qualitative variables, much like in documentation of community structures (Anderson 2001), with typical environmental variables used for ecological niche-separation (soil pH, air temperature, etc.). Analysis of stress (goodness-of-fit) were conducted via a permutational scree plot. The appropriate number of dimensions for display was selected by plotting out the successive reduction in stress with increasing dimensions, resampling the optimal stress of the Bray-Curtis data matrix for 1000 iterations (Ellison & Gotelli 2004). Post-analysis interpretation of NMDS ordination is commonly done by fitting variables as vectors to ordinal plots (Okansen et al. 2018). Perch variables were fitted to the NMDS plot as vectors, with length showing linearity of the variable gradient and proportional correlation between the variable and the ordination plot, and direction of the vector associated with the correlation of the variable with the axes. Similarity percentages (SIMPER) were calculated, using 1000 permutations, for each significantly-dissimilar species pair to identify the contribution of each perch characteristic to the overall dissimilarity (Clarke 1993). All above statistical methods were performed using the open-source program, Rstudio (R Development Core Team 2018) within the vegan package (ver. 2.4-6).

RESULTS

Encounter-rate and Seasonality:

From March 2016 to December 2017, a total of 408 kingfisher observations were collected across 27 surveys. Encounter-rate varied significantly between each of the three kingfisher species, with: Green vs. Belted Kingfishers (ANOVA: $F_{1,52}=18.17$, $p<0.001$), Green vs. Ringed Kingfishers (Welch's ANOVA: $F_{1,35}=71.188$, $p<0.001$), and Belted vs. Ringed Kingfishers (Welch's ANOVA: $F_{1,34}=7.04$, $p=0.012$). Mean encounter-rate of each species was shown to be inversely proportional to the sizes of each species, with: Green Kingfishers ($\bar{x}=0.49$, SD=0.218), Belted Kingfishers ($\bar{x}=0.22$, SD=0.229), and Ringed Kingfishers ($\bar{x}=0.10$, SD=0.094).

Encounter-rate varied significantly by season for Belted Kingfishers (ANOVA: $F_{3,23}=10.38$, $p<0.001$) with summer and spring surveys having significantly lower encounter-rates than winter or fall surveys (Fig. 2). Belted Kingfishers were absent from surveys during Mid-Spring till Mid-Summer both years. Absences for Belted Kingfishers correspond with surveys April 30th through July 30th, 2016 and May 18th through June 25th, 2017. There was no evidence to suggest that the encounter-rate for Green Kingfishers varied seasonally (ANOVA: $F_{3,23}=0.17$, $p=0.911$) (Fig. 3). The linear model for the Ringed Kingfishers failed the global stat for GVLMA, suggesting non-linearity within the data frame (Pena and Slate 2006), so no further testing over seasonality was conducted for the species.

Statistical Analyses:

Out of the 408 kingfisher observations, 250 observations were used for statistical comparisons, due to testing constraints of the post-hoc SIMPER analysis. This sample consisted of 149 Green, 67 Belted, and 34 Ringed Kingfishers.
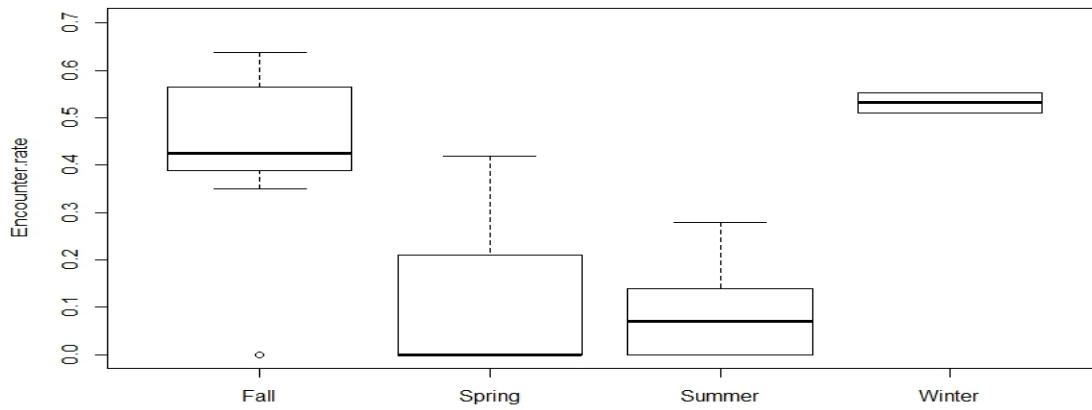
Figure 2. Box-plot displaying mean encounter-rate per survey (birds per kilometer) for the Belted Kingfisher by the seasons. Kingfisher encounters were most frequent in fall and winter; with significantly fewer kingfishers observed in spring or summer.
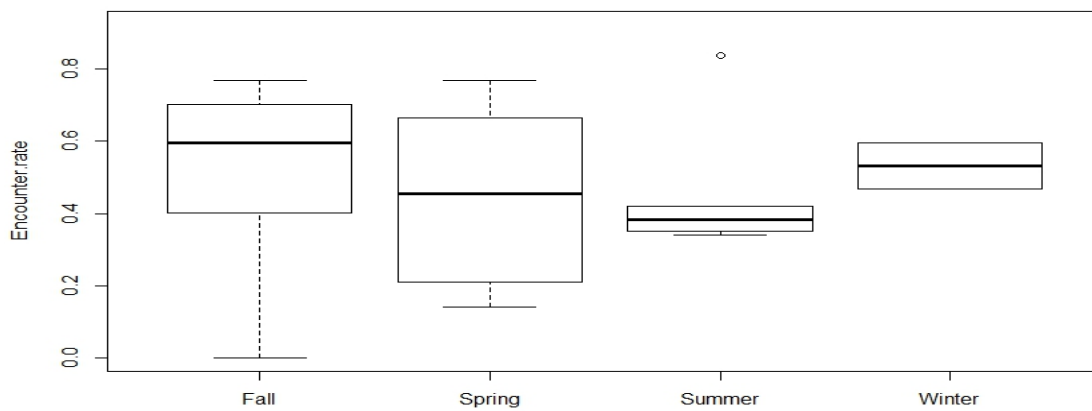
Figure 3. Box-plot displaying mean encounter-rate per survey (birds per kilometer) for the Green Kingfisher by the seasons. Kingfisher encounters did not vary significantly by the seasonality of the surveys.

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Results from ADONIS displayed no changes in significance when using the subset of 250 kingfisher observations and all 408 kingfisher observations. Testing suggests significant evidence for the partitioning of foraging-habitat between Green and Belted Kingfishers (ADONIS: $F_{1,214}=77.432$, p-adj.<0.001), as well as between Green and Ringed Kingfishers (ADONIS: $F_{1,181}=51.743$, p-adj.<0.001). However, there is no evidence to suggest partitioning of foraging-habitat between Belted and Ringed Kingfishers (ADONIS: $F_{1,99}=2.036$, p-adj.=0.106).

The NMDS plot used contained 2-dimensions, based on the optimal stress of 0.08 (Clarke 1993), yielded by the permutational scree-plot (Fig. 4). NMDS ordination displays that separation of Green Kingfishers from the two *Megaceryle* sp. occurs primarily along the NMDS axis 1 (Fig. 5). Fitting of the perch characteristics to ordinal NMDS space shows that perch height has the strongest correlation with NMDS axis 1 (Fig. 6) and the most defined gradient (Fig. 6 and 7). Due to the relatively short length of most of the perch characteristic vectors, gradients are weakly correlated with the NMDS plot, making it difficult to interpret any specificity or variance among the kingfishers (Fig. 8). This suggests that perch height is primary discriminating perch characteristic between the three species of kingfisher; with the *Megaceryle* sp. selecting taller foraging-perches than Green Kingfishers. This is supported by SIMPER-testing; with 79% of the dissimilarity between Green and Belted Kingfishers (R=1.83, p<0.001) (Table 1) and 80% of the dissimilarity between Green and Ringed Kingfishers (R=1.65, p<0.001) (Table 2) explained by perch height within the data matrix. Water depth explains the second-most dissimilarity in the data matrix (Table 1a&b); with

Green Kingfishers selecting significantly shallower waters than Ringed Kingfishers (R=1.07, p=0.009) (Table 2).
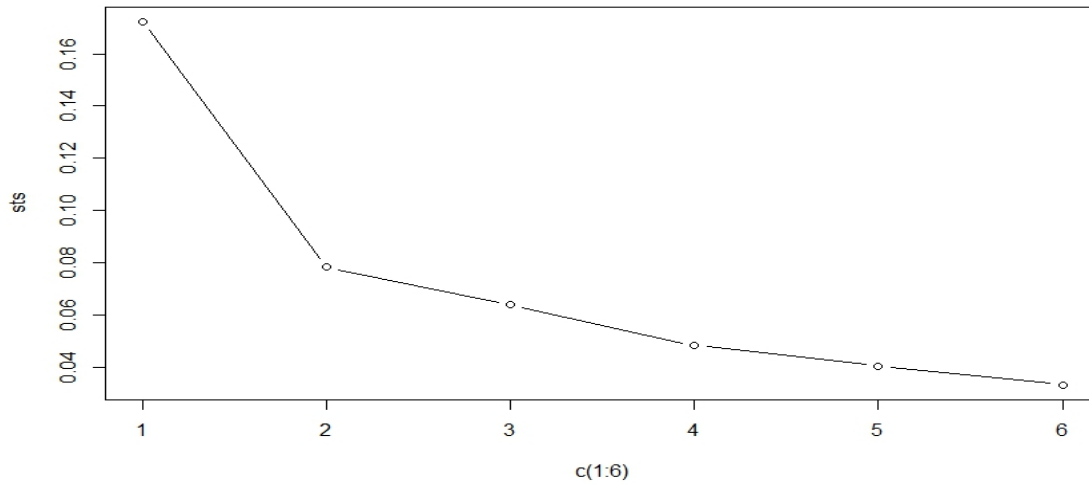
Figure 4. Stress-plot for NMDS data-matrix displaying drops in overall ordinal stress (y-axis) with added dimensionality to the ordination plot (x-axis). The most significant decrease in stress occurs with the addition of a 2nd dimension, with a stress value of 0.08.
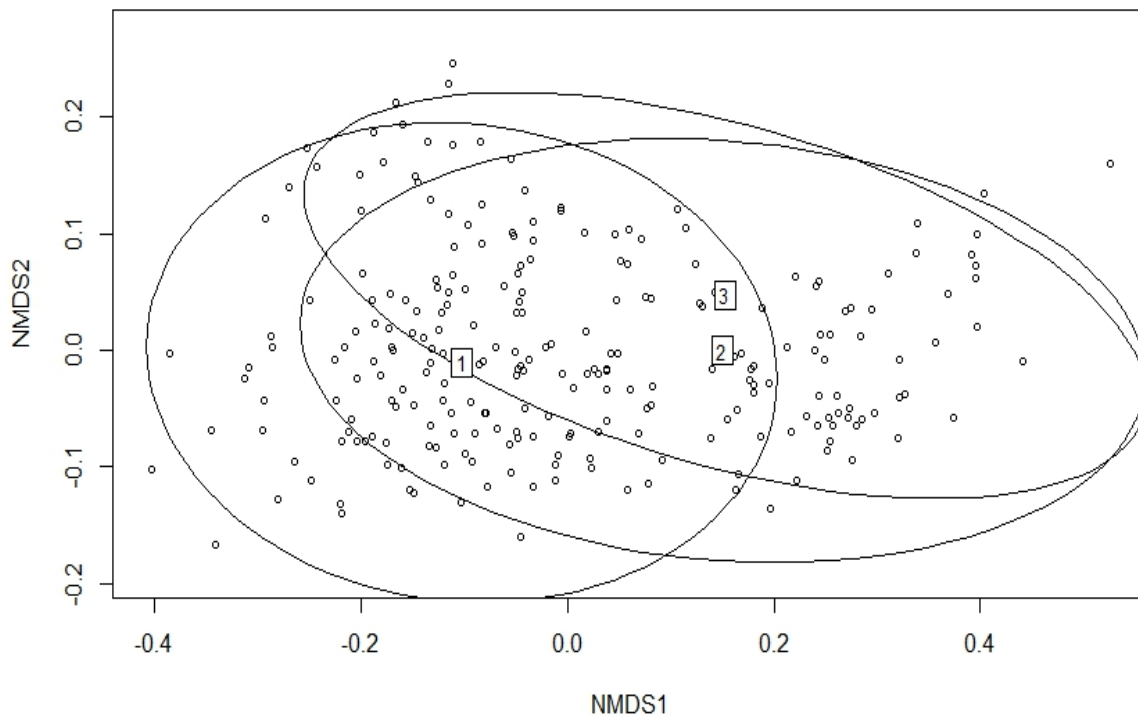
Figure 5. NMDS ordination-plot displaying kingfisher observations as points. The overall spread of each kingfisher species' foraging-niche is captured using a 95% confidence-envelope. Separation of the foraging-niches is primarily along axis NMDS1. 95% Confidence-envelopes are numbered at their centroid, with Green Kingfisher=1, Belted Kingfisher=2, Ringed Kingfisher=3.
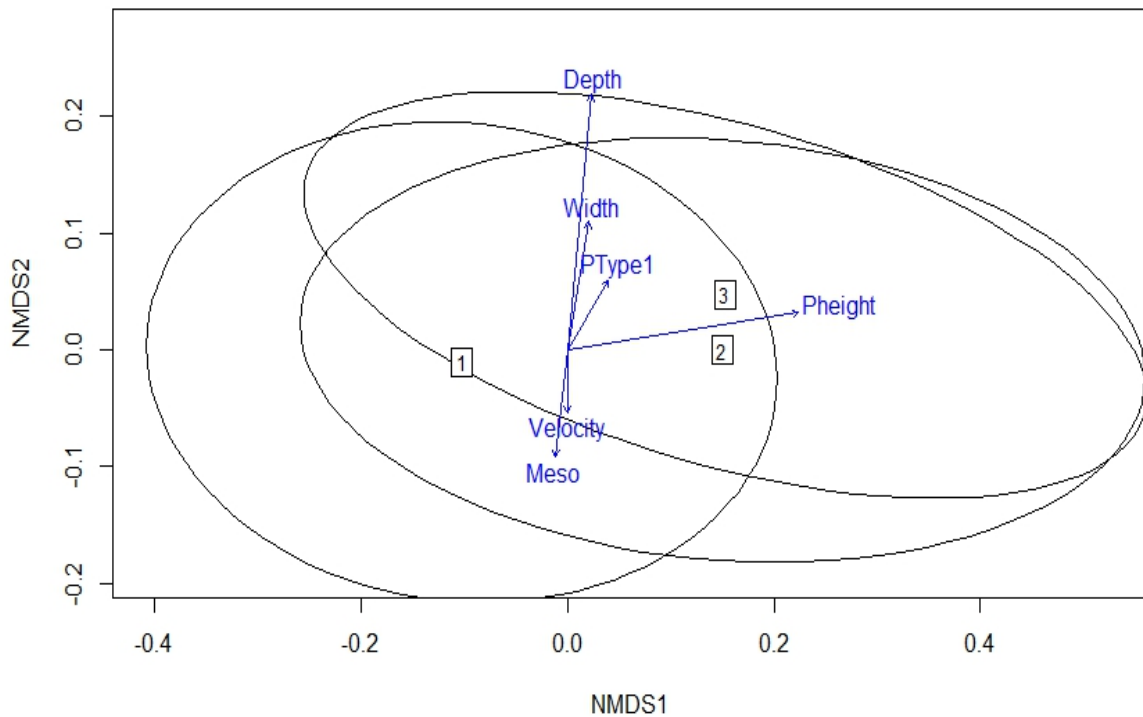
Figure 6. NMDS ordination-plot displaying perch characteristics as fitted-vectors. Depth=water depth, Width= river width, PType1= perch type, Velocity=water velocity, Meso= mesohabitat, Pheight=perch height. The perch characteristic mostly strongly-correlated with axis NMDS1 is Pheight. The overall spread of each kingfisher species' foraging-niche is captured using a 95% confidence-envelope. 95% Confidence-envelopes are numbered at their centroid, with Green Kingfisher=1, Belted Kingfisher=2, Ringed Kingfisher=3.
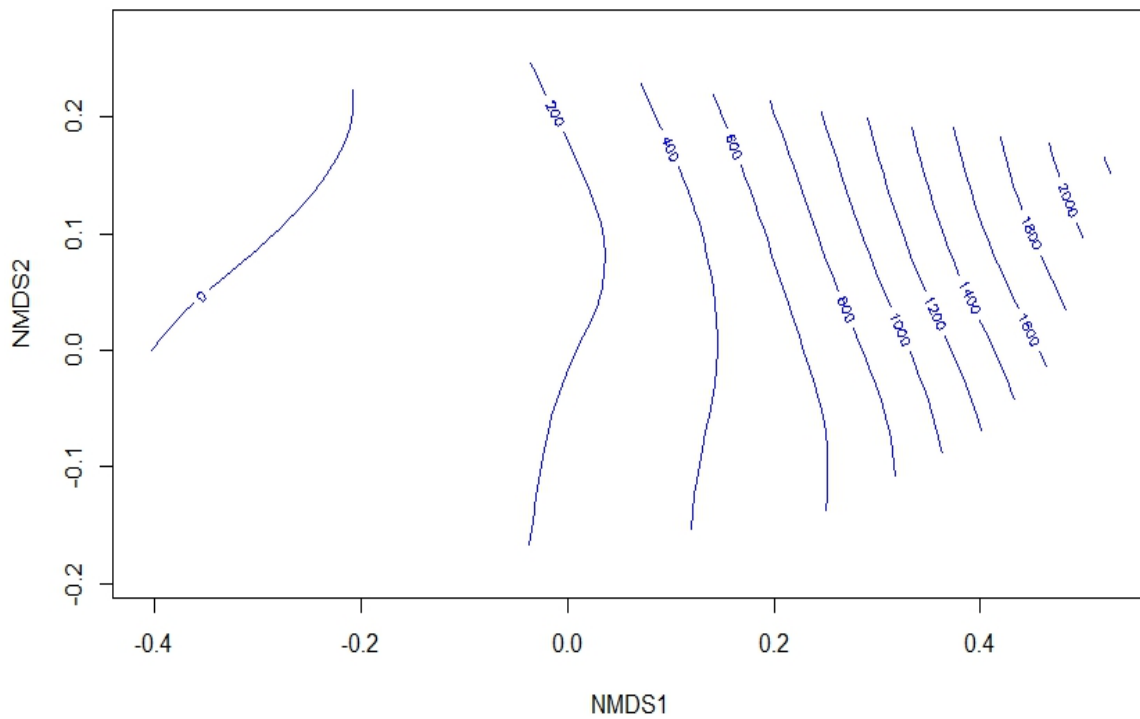
Figure 7. NMDS displaying environmental gradient of perch height in centimeters. Gradients follow the path of vectors in Fig 6; with the longer-length of the perch height vector displaying as being highly linear and correlated with axis NMDS1.
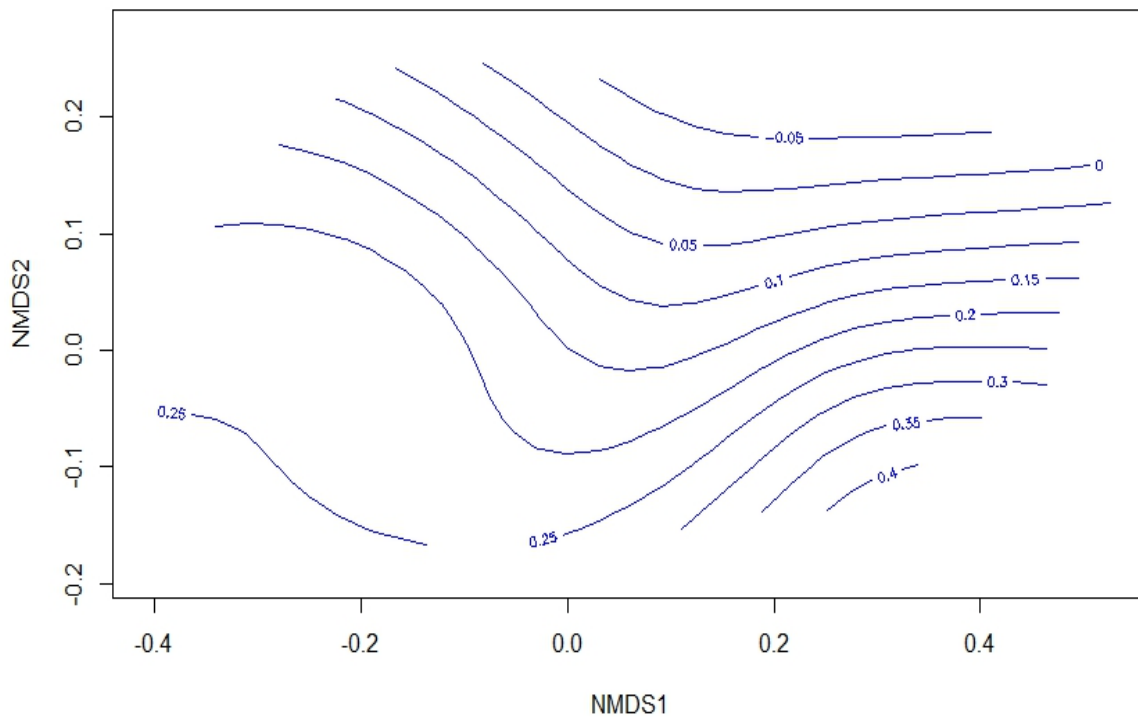
Figure 8. NMDS displaying environmental gradient of water velocity in meters per second. Gradients follow the path of vectors in Fig 6; with the shorter-length of the water velocity vector being weakly correlated with NMDS plot. Weakly-correlated variables display more non-linear gradients and decreased variance in niche-space.

	Average	SD	R	Ava	Avb	Cumsum	p
Pheight	4.267e-01	0.2331	1.8305	142.28	550.82	0.8101	0.0009
Depth	7.431e-02	0.0750	0.9902	58.932	79.283	0.9512	1.0000
Width	2.433e-02	0.0241	1.0097	26.391	28.417	0.9974	1.0000
Meso	8.972e-04	0.0011	0.7765	1.476	1.417	0.9991	1.0000
Velocity	3.893e-04	0.0004	0.8848	0.213	0.214	0.9998	0.9940
Ptype1	8.808e-05	0.0035	0.2496	1.020	1.119	1.0000	0.3846

Table 1. Similarity percentages (SIMPER) for the separation of foraging-niches explained in the data-matrix by each variable, comparing the Green to the Belted Kingfisher. The column "Cumsum" is the cumulative sum of dissimilarity explained within the data matrix with each additional variable added. Perch height (Pheight) explains 81% of the cumulative dissimilarity between the two species. Ava=average for Green Kingfishers, Avb=average for Belted Kingfishers.

	Average	SD	R	Ava	Avb	Cumsum	p
Pheight	4.044e-01	0.2449	1.6507	142.281	555.117	0.7518	0.0009
Depth	1.005e-01	0.0943	1.0653	58.932	115.323	0.9388	0.0089
Width	3.190e-02	0.0292	1.0893	26.391	41.117	0.9981	0.3996
Meso	2.809e-04	0.0010	0.6548	1.4765	1.1470	0.9994	1.0000
Velocity	2.809e-04	0.0003	0.7441	0.2131	0.0585	0.9999	1.0000
PType1	5.901e-05	0.0003	0.1965	1.0201	1.0294	1.0000	0.7022

Table 2. Similarity percentages (SIMPER) for the separation of foraging-niches explained in the data-matrix by each variable, comparing the Green Kingfisher to the Ringed Kingfisher. The column "Cumsum" is the cumulative sum of dissimilarity explained within the data matrix with each additional variable added. Perch height (Pheight) and water depth (Depth) explaining 75% and 18%, respectively, of the cumulative dissimilarity between the two species. Ava=average for Green Kingfishers, Avb=average for Ringed Kingfishers.

DISCUSSION

Habitat-partitioning:

I observed perch height to be the primary discriminating factor among kingfishers selecting perches along the South Llano River, TX. The importance of perch height has been highlighted in previous studies of tropical kingfishers in the Amazon Basin of South America, Costa Rica, India, Japan, and Tanzania (Bittermann 2012, Bonnington et al. 2007, Borah et al. 2012, Kasahara & Katoh 2008, Remsen 1991). Perch height is known to positively-correlate with kingfisher size and prey size (Remsen 1991). There is some evidence suggesting that Green Kingfishers' selection of perches displays some plasticity with the fluctuating presence of Belted Kingfishers along the river. During the absence of Belted Kingfishers during summer months, Green Kingfishers seem to select significantly higher perches than when Belted Kingfishers are present (ANOVA: $F_{36,129}=14.94$, $p<0.001$). This suggests that Belted Kingfishers exert competitive pressure on Green Kingfishers during their presence, forcing them to perch heights that might be less than ideal. Another possibility is that the food resources shift in Green Kingfishers with shifting seasonality, and the association with Belted Kingfishers is largely spurious. Differential selection of habitat-characteristics in the absence of competitors is seen in other faunal communities, such as communities of *Lepomis* sunfish, known prey of *Megaceryle* sp. (Werner & Hall 1976). Interpretation of these results should be made with caution however, as the summer sample-size for Green Kingfishers is much less smaller than that of the other seasons.

The lack of evidence supporting partitioning of perch characteristics between Belted and Ringed Kingfishers might be due to physical limitations in the river's characteristics. Land- and homeowners, along with cervid species, can reduce the vegetative complexity of

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the South Llano River, resulting in less diversity of foraging perches. With Belted

Kingfishers having a ubiquitous distribution across North America and all its various aquatic

systems, the assumption was that it would display greater selection for higher-gradient

mesohabitats than the two Neotropical species that are most common in tropical lowlands

(Remsen 1991). Even though the results do not reflect this, it might indicate an inappropriate

method of quantifying mesohabitats and its application in NMDS ordination. Additionally, it

is possible that Belted and Ringed Kingfishers partition resources not measured in this study

(e.g., prey) and not features associated with perches. I chose to investigate perch

characteristics rather than food resources because animals are predicted to partition habitat

resources first and food resources second (Shoener 1974).

Hovering as a means of sighting prey was never observed during the survey period,

with all birds scanning the water's surface for prey. As birds rarely submerge themselves

while seizing prey from a perch, water depth might only have significance for avoiding

injury while foraging (Bitterman 2012). The substantial size difference between Green and

Ringed Kingfishers would explain the difference in favored water depth, with Ringed

Kingfishers requiring significantly deeper water to avoid harm. It's also possible that the

large prey Ringed Kingfishers require to meet its metabolic demands can only be found in

sufficient numbers in deeper water. River width might lack significance in kingfisher habitat-

partitioning as more open waters are under-sampled by foraging kingfishers. As kingfishers

forage from a perch, water closer to the perch (i.e. the adjacent shoreline) is more likely to be

scanned, and hunted over than waters near the river's midline. Insignificant partitioning with

water-velocity could be indicative of the limited range of flow rate on the river. Although

portions of the river have notable flows, flow near banks, with increased contact with

surrounding substrate, often is slowed or forced into eddies which have negligible flow rates. Available inorganic perches, such as rock shelves or sunken boulders, were relatively abundant; but their lack of use across all kingfishers (except for a few occasions by Green Kingfishers) suggests the lower overall height of rocks adjacent to the water might not meet the requirements of a kingfisher surveying for prey. Man-made perches along the river are minimal (fencing, utility lines, etc.) due to the limited development in a predominantly rural county.

Anecdotal evidence supports the notion that there isn't sufficient niche separation between Belted and Ringed Kingfishers to avoid interspecific conflict. The only observed interspecific aggression between any of the three species has been between the two *Megaceryle* sp., noted on three separate occasions. The larger Ringed Kingfisher acted as the aggressor, chasing off an individual Belted Kingfisher within the vicinity. The infrequency of conflict between the two *Megaceryle* sp. is likely due to the low linear density of Ringed Kingfishers on the river. Observations of intraspecific conflict in Green Kingfishers were noted on several occasions as well, most frequently during early-spring surveys. Kingfishers have been shown to be typically territorial towards conspecifics, as well as kingfishers smaller, yet comparably-sized, to themselves (Reyer et al. 1988, Remsen 1991, and Bittermann 2012).

Encounter-rate and Seasonality:

The absence of Belted Kingfishers during the majority of the summer months might provide Belted Kingfishers some relief from competitive pressure, as it breeds in northern waters where its cogenator doesn't occur. Such relief could come in the form of decreased competition for food, nest-sites, or the elimination of aggressive encounters. My

observations of the Belted Kingfishers' absence from the South Llano River during the summer months conflict with historical records which state the species to be a year-round resident (Buechner 1946). Some have suggested that Belted Kingfishers migrate northward after nesting due to rising temperatures, being only wintering residents south of 35th parallel (Grinnell 1917). Even if this is not the case for the pre-1950's distribution of the Belted Kingfisher, more studies are being conducted on the impact of climate change on the phenology of migratory and semi-migratory birds, both in temperate and neotropical regions (Crick 2004 and Rappole et al. 2007).

An overall decline in observations across all kingfisher species during spring and summer months could be correlated with multiple conditions. As density of foliage declines with the onset of winter, foraging kingfishers could become more conspicuous for surveyors. Spring in Texas is typically associated with kingfisher nesting for all 3 sp. (Oberholser 1974), with both adults assisting with incubation. In Green Kingfishers, both parents can spend up to 4 hours incubating during a single rotation, with Ringed Kingfishers rotating turns incubating approximately every 24 hours (Skutch 1957). Lack of observations for Ringed Kingfishers during spring and summer might also be in part due to the low infrequency at which Ringed Kingfishers were encountered on any given survey, rarely exceeding 3 individuals on any survey. This makes it highly likely that any Ringed Kingfishers on the river were simply not observed on spring or summer surveys. Foraging kingfishers also return frequently to nest cavities to feed nestlings; with case studies reporting Belted Kingfishers returning to nest cavities 1.6 times every hour (Kendeigh 1952). Another factor that might play a role in the decline of kingfisher observations during spring and summer is the increase in recreational usage of the South Llano River during the summer months. Presence of piscivorous birds are

known to be negatively-impacted, to some degree, by the human disturbance within foraging grounds (Newbrey et al. 2005).

Future Research:

Further sampling of Belted and Ringed Kingfisher perch characteristics along the South Llano River is advisable to confirm the results of the comparison of foraging-niches. As the South Llano River is only one of numerous tributaries that feed into the Colorado River alone, another study could be conducted analyzing niche-partitioning of the 3 kingfisher sp. in Central Texas river systems where all three species of kingfisher are present. Rivers vary in their physical and chemical composition based on their age and surrounding land-characteristics. A comparison of kingfisher guilds across river systems might yield species altering their niches and subsequent partitioning based on these differences in physical composition. Sampling for selected prey-items across the species of kingfishers along the South Llano River might reveal differences in favored prey between Ringed and Belted Kingfishers.

Certain kingfisher species are known to vary temporally for their peak activity (Borah et al. 2012). To see if any temporally partitioning occurs in the 3 species found in Texas, ethograms could be conducted on a weekly/bi-weekly basis, at a small study-site where all three sp. are known to forage. Due to small, and unequal sample-sizes across spring and summer surveys, efforts put towards testing if Green Kingfishers displays niche plasticity during times when Belted Kingfishers are in lower densities yielded inconclusive results. To see if Green Kingfishers truly display behavioral plasticity in habitat-selection in respect to the movement of Belted Kingfishers, continued sampling during summer months could yield insight of this phenomena.

LITERATURE CITED

Anderson, M. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecology 26: 32-46

Asokan, S. and Ali, A. 2010. Time-activity Budget of White-breasted Kingfisher *Halcyon smyrnensis* in Cauvery Delta Region, Tamil Nadu, India. Advances in Biological Research 4: 288-291

Beisel, J., Polatera, P., Thomas, S., and Moreteau, J. 1998. Stream community structure in relation to spatial variation: the influence of mesohabitat characteristics. Hydrobiologica 389: 74-88

Bittermann, F. 2012. Habitat use and niche segregation in Kingfisher species in the Pacific lowlands of Costa Rica. University of Vienna

Bonnington, C., Weaver, D., Fanning, E. 2007. The habitat preference of four kingfisher species along a branch of the Kilombero River, southern Tanzania. African Journal of Ecology 46: 424-427

Borah, J. Ghosh, M. Harihar, A., Pandav, B., Gopi, J.V. 2012. Food-niche partitioning among sympatric kingfishers in Bhitarkanika Mangroves, Odisha. Journal of the Bombay Natural History Society 109: 72-77

Buechner, H. 1946. Birds of Kerr County, Texas. Transactions of the Kansas Academy of Science. 49: 357-364

Clarke, K. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology 18: 117-143

Colby, B. 1961. United States Department of the Interior. Effect of depth of flow on

    discharge of bed material. Studies of flow in alluvial channels.

Cook, G. 2007. eBird Checklist: http://ebird.org/ebird/view/checklist/S27434694. eBird: An

    online database of bird distribution and abundance [web application]. eBird, Ithaca,

    New York. Available: http://www.ebird.org. Accessed: April 28th, 2016

Crick, H. 2004. The impact of climate change on birds. Ibis 146: 48-56

Dunning, J.B. 1992. CRC Handbook of Avian Body Masses. CRC Press LLC. Boca Raton,

    Florida 33431.

Elton, C. 1927. Animal Ecology. The Macmillan Company. New York City, NY

Gause, G. and Witt, A. 1935. Behavior of mixed populations and the problem of Natural

    Selection. The American Naturalist 69: 596-609

Grant, P. 1986. Ecology and Evolution of Darwin's Finches. Princeton University Press.

    Princeton, NJ

Grinnell, J. 1924. Geography and Evolution. Ecology 5: 227

Groeschel, J. 2013. Evaluations of growth and habitat use by Guadalupe Bass at a riverscape

    scale in the South Llano River. Submitted to Texas Tech University, Junction, Texas

Gutierrez-Galan, A., Gonzalez, C., and Maroto De Mercado, J. 2016. Woodpigeon Columba

    palumbus Diet Composition in Mediterranean Southern Spain. Ardeola 64: 17-30

Hutchinson, G. 1957. Concluding remarks. Cold Spring Harbor Symposia on Quantitative

    Biology 22: 415–427

Hutchinson, G.E. and MacArthur, R.H. 1959. A Theoretical Ecological Model of Size

    Distributions among Species of Animals. The American Naturalist 93: 117-125

Jan, S. and Shieh, G. 2014. Sample size determinations for Welch's test in one-way
heteroscedastic ANOVA. British Journal of Mathematical and Statistical
Psychology 67: 72-93

Kasahara, S. and Katoh, K. 2008. Food-niche differentiation in sympatric species of
kingfisher, the Common Kingfisher *Alcedo atthis* and the Greater Pied Kingfisher
Ceryle lugubris. Ornithological Science 7: 123-134

Kendeigh, S. 1952. Parental care and its evolution in birds. The University of Illinois Press.
Champaign, Illnois.

MacArthur, R.H. 1958. Population Ecology of some Warblers of Northeastern Coniferous
Forests. Ecology 39: 599-619

Mizera, F. and Meszena, G. 2003. Spatial Niche Packing, Character Displacement and
Adaptive Speciation along an Enivronmental Gradient. International Institute of
Applied Systems Analysis. Laxenburg, Austria. IR-03-062

Morgan, R., David, G. 1977. Breeding, Mortality and Movements of Kingfishers. Bird Study
24: 15-24

Newbrey, J., Bozek, M. and Niemuth, N. 2005. Effects of lake characteristics and human
disturbance on the presence of piscivorous birds in Northern Wisconsin, USA.
Waterbirds 28: 478-486

Oberholser, H. C. 1974. The Bird life of Texas. University of Texas Press, Austin, TX

Okansen, J., Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.,
O'Hara, R., Simpson, G., Solymos, P., Stevens, M., Szoecs, E., Wagner, H. 2018.
Vegan: Community Ecology Package. R package version 2.4-6

Pena, E. and Slate, E. 2006. Global Validation of Linear Model Assumptions. Journal of the American Statistical Association 101: 341

Rappole, J. H., Blacklock, G. W., Norwine, J. 2007. Apparent rapid Range change in South Texas Birds: Response to climate change? *In* Texas Climate 2100 (J. Norwine and K. John, eds.). Texas A&M University, Kingsville, TX.

Remsen, Jr., J.V. 1991. Community ecology of Neotropical Kingfishers. University of California Publications in Zoology 124: 2-4

Reyer, H., Migongo-Bake, W., Shmidt, L. 1988. Field studies and experiments on distribution and foraging of pied and malachite kingfishers at Lake Nakuru (Kenya). Journal of Animal Ecology 57: 595-610

Rodriguez, W. 2007. eBird Checklist: https://ebird.org/ebird/view/checklist/S28097122. eBird: An online database of bird distribution and abundance [web application]. eBird, Ithaca, New York. Available: http://www.ebird.org. Accessed: November 13th, 2017

Shoener, T. 1974. Resource partitioning in Ecological Communities. Science 185: 27-39

Skutch, A. 1957. Life History of the Amazon Kingfisher. The Condor 59: 217-229

Werner, E. and Hall, D. 1976. Niche shifts in Sunfishes: Experimental evidence and significance. Science 191: 404-406

BIOGRAPHY

Griffin Daniel Chodacki was born in Darien, Illinois on August 7th, 1994. He spent the first several years of his life in Darien, displaying the first signs of desire to become a naturalist as he explored surrounding woods and wetlands. At the age of 7, Griffin and his family moved to Leander, in the hill country of Central Texas.

Griffin enrolled in numerous advanced courses going through primary-school in Leander, in preparation for a life dedicated to studying the natural world. Griffin attended Angelo State University for his undergraduate career in Biology, where he exceled in academics and participated in educational seminars teaching local children about local fauna. Griffin participated in multiple undergraduate research projects in both the departments of Chemistry and Biology, honing his skills in scientific-writing and experimental design. During the summer months, Griffin spent his time assisting with fellow students in research and presenting curriculum to children over teachings acquired from ASU. Griffin graduated with a Bachelor's degree in Biology with a minor in Chemistry on December 2015.

After graduating, Griffin returned to Angelo State University to attend graduate school in Biology, under the tutelage of Dr. Ben Skipper. Griffin continued applying himself in rigorous courses aimed at improving his abilities to interpret his natural surroundings, as well as collaborating with other graduate students in their field work. Griffin earned his Master's degree in Biology on May 2018.

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