

TUFTED TITMICE, BLACK-CRESTED TITMICE, AND THEIR HYBRIDS OCCUPY  
DIFFERENT TYPES OF HABITAT WITHIN THEIR HYBRID ZONE

by

Carli Renae Martinez, B.S.

A thesis submitted to the Graduate Council of  
Texas State University in partial fulfillment  
of the requirements for the degree of  
Master of Science  
with a Major in Population and Conservation Biology  
December 2022

Committee Members:

Joseph Veech, Chair

James R. Ott

Noland Martin

**COPYRIGHT**

by

Carli Renae Martinez

2022

## **FAIR USE AND AUTHOR'S PERMISSION STATEMENT**

### **Fair Use**

This work is protected by the Copyright Laws of the United States (Public Law 94-553, section 107). Consistent with fair use as defined in the Copyright Laws, brief quotations from this material are allowed with proper acknowledgement. Use of this material for financial gain without the author's express written permission is not allowed.

### **Duplication Permission**

As the copyright holder of this work I, Carli Renae Martinez, authorize duplication of this work, in whole or in part, for educational or scholarly purposes only.

## **ACKNOWLEDGEMENTS**

First and foremost, I would like to thank my advisor Dr. Joseph Veech for allowing me a place in his lab back in 2020, and for all his guidance and efforts. I greatly appreciate the freedom and trust he has granted me throughout the development and application of my research. By working with him, I have emerged a more confident and skilled researcher. Much thanks to my other committee members, Dr. James Ott and Dr. Noland Martin, for their thoughtful and acute advice that helped shape this research into what it is today. I admire their work as scientists and as teachers greatly. A big thank you to Texas State University for their funding through the Thesis Support Fellowship, and to all the individuals who approved and facilitated my access to field sites: Sean Griffin (Lady Bird Johnson Wildflower Center), Matt McCaw and Patrick Chaiken (Indiangrass and Onion Creek Wildlife Sanctuaries, TPWD), Aaron Wallendorf (Meadows Center), Rebecca Berzewski (O'Kent private residence), and Franklin Olvera (Cepeda private residence). Finally, I would like to extend special thanks to my loving parents, wonderful partner, and incredible fellow graduate students who offered endless aid and support throughout my time in the Population and Conservation Biology M.S. program at Texas State University.

## TABLE OF CONTENTS

	<b>Page</b>
ACKNOWLEDGEMENTS .....	v
LIST OF TABLES .....	vii
LIST OF FIGURES .....	viii
LIST OF ABBREVIATIONS .....	ix
ABSTRACT .....	x
CHAPTER	
I. INTRODUCTION .....	1
Study Species .....	5
Thesis Objectives .....	8
II. ANALYZING HABITAT ASSOCIATIONS WITH eBIRD DATA .....	10
Methods .....	11
Results .....	19
Discussion .....	23
III. ANALYZING HABITAT ASSOCIATIONS WITH CAMERA-TRAP AND FIELD SURVEY DATA .....	31
Methods .....	32
Results .....	39
Discussion .....	40
IV. TABLES AND FIGURES .....	43
LITERATURE CITED .....	70

## LIST OF TABLES

<b>Table</b>	<b>Page</b>
1. Number of grid cells within relative abundance categories for the titmice types.....	43
2. AIC model comparisons at $10 \times 10$ km spatial scale.....	44
3. AIC model comparisons at the $5 \times 5$ km spatial scale.....	46
4. AIC model comparisons at the $2.5 \times 2.5$ km spatial scale.....	49
5. Importance values and regression coefficients of habitat variables.....	51
6. PCA factor loadings.....	52

## LIST OF FIGURES

Figure	Page
1. Estimate of the current extent of the Tufted Titmouse ( <i>Baeolophus bicolor</i> ) × Black-crested Titmouse ( <i>Baeolophus atricristatus</i> ) hybrid zone .....	53
2. Year-round geographic ranges of the Tufted Titmouse ( <i>Baeolophus bicolor</i> ) and the Black-crested Titmouse ( <i>Baeolophus atricristatus</i> ) in North America.....	54
3. Key Morphology of the Tufted Titmouse ( <i>Baeolophus atricristatus</i> ), Black-crested Titmouse ( <i>Baeolophus atricristatus</i> ), and Tufted × Black-crested hybrid.....	55
4. The study region in central Texas and southwest Oklahoma .....	56
5. Fishnet with 10 × 10 km grid cells over the study region.....	57
6. Number of grid cells within each relative abundance category .....	58
7. Means of habitat variables within grid cells .....	59
8. PCA including latitude and longitude at 10 × 10 km spatial scale .....	60
9. PCA excluding latitude and longitude at 10 × 10 km spatial scale .....	61
10. PCA including latitude and longitude at 5 × 5 km spatial scale .....	62
11. PCA excluding latitude and longitude at 5 × 5 km spatial scale .....	63
12. PCA including latitude and longitude at 2.5 × 2.5 km spatial scale .....	64
13. PCA excluding latitude and longitude at 2.5 × 2.5 km spatial scale .....	65
14. Phenotypic hybrid index .....	66
15. Titmice captured by Bushnell trail camera at camera trap site.....	67
16. 100, 250, and 500 m buffers created around camera trap points .....	68
17. 100 m buffers created around unique survey point.....	69

## LIST OF ABBREVIATIONS

<b>Abbreviation</b>	<b>Description</b>
TUTI	Tufted Titmice
BCTI	Black-crested Titmice
NLCD	National Landcover Database
USFS	United States Forest Service
WFC	Lady Bird Johnson Wildflower Center
TPWD	Texas Parks and Wildlife Department
MC	Meadows Center
HI	Dixon's Hybrid Index Score

## ABSTRACT

Habitat can play a key role in either facilitating or preventing hybridization between some species. Within a hybrid zone, differences in habitat requirements could spatially separate two species to reduce hybridization. However, hybrid individuals might be best adapted to an intermediate type of habitat also occupied by the parent species in which case hybridization might be facilitated. Tufted Titmice (*Baeolophus bicolor*) (TUTI) and Black-crested Titmice (*Baeolophus atricristatus*) (BCTI) are sister species that hybridize within a narrow east-west contact zone that extends from central Texas into southwest Oklahoma. The zone corresponds with an ecotone that transitions from closed-canopy deciduous forests in the east, occupied by TUTI, to arid and open woodlands in the west occupied by BCTI. Furthermore, the ecotone encompasses areas impacted by urban and suburban development. For the first objective of my study, I tested whether landscape-level habitat characteristics found within the TUTI  $\times$  BCTI hybrid zone influence the relative abundances of the two parent species and their hybrids. I predicted that the parent species would differ in their habitat associations and hybrids would associate with habitats intermediate between that of TUTI and BCTI and with human disturbed habitats. I used eBird data and high resolution GIS land cover data in a grid-based sampling design to analyze the habitat associations of the three titmice types throughout the hybrid zone, plus locations immediately outside the h zone only occupied by the parental species. Logistic regression and AIC model selection revealed that the relative abundances of the three titmice types were most closely associated with percent

evergreen forest, mixed forest, and shrub cover. BCTI was associated with higher percentages of evergreen forest, and lower percentages of mixed forest and shrub cover, whereas TUTI had the inverse associations. Further, PCA revealed that hybrids tended to occupy a habitat that was intermediate between that of TUTI and BCTI. Anthropogenic disturbance did not appear to influence relative abundances of BCTI, TUTI, or hybrids. The second objective of my study was to determine if there are differences in the habitat associations of titmice belonging to different phenotypic classifications. I used camera traps and conducted bird surveys at select locations within the hybrid zone to identify titmice using Dixon's hybrid index applied to plumage characteristics. Habitat associations were analyzed similar to the eBird data but at a finer spatial scale. Locations occupied by only pure BCTI phenotypes had more canopy cover and evergreen forest than locations with hybrid phenotypes. My study demonstrates that within the hybrid zone, BCTI and TUTI have different habitat associations. However, hybrid individuals appear to occupy an intermediate type of habitat shared by the parental species.

## I. INTRODUCTION

Hybrid zones are geographic regions where two species' distributions overlap with interbreeding occurring between the species due to incomplete reproductive isolation. In many cases, these regions exist within narrow bands of overlap between the wider geographic ranges inhabited by the "parental" species (Bigelow 1965, Moore 1977, Harrison and Larson 2016, Wielstra 2021). A given hybrid zone may include various proportions of "pure" individuals of the parent species, as well as F1, F2, and backcrossed hybrids and other individuals representing different genetic admixtures. When some degree of parapatry exists between the two populations, proportions of pure individuals can vary depending on the exact location within the zone and may result in a cline or multiple clines (spatial gradients) in genotypes and associated phenotypes (Endler 1977, Barton and Hewitt 1985). Thus differences in habitat requirements or associations between the two parental species can be instrumental in maintaining the spatial and genetic structure of a hybrid zone, particularly if the habitat occupied by hybrid individuals differs from that of either parent species (Anderson 1948, Wang et al. 1997, Rieseberg and Carney 2008). In fact, many hybrid zones form within ecotones, defined as narrow geographic regions where two different ecosystems or habitat types transition into one another (Meacham 1962, Zweifel 1962, Hubbard 1969, Jackson 1973, De Dios 2006). Individuals of parent taxa are potentially better adapted to and therefore associated with, one of the habitat types (Endler 1977, Moore 1977, Seehausen et al. 2008 ). The transition and mixing of habitat characteristics within ecotones allows the species to co-occur at some degree of sympatry, thus creating the opportunity for

hybridization (Moore 1977, Kark and Rensburg 2006). Additionally, novel niches that hybrids are able to exploit may be created by the heterogeneous environment of the ecotone (Anderson 1948, Grant 1971). For instance, with regard to birds, some form of vegetation structure intermediate between the respective habitats of the two parent species, might be utilized more efficiently for foraging by hybrids than by individuals of either parent species (Wood et al. 2015).

Similarly hybridization between taxa is sometimes correlated with disturbed habitat; that is, areas affected by human activity (e.g., urbanization and agriculture;(Wright and Lowe 1968, Urbanska 1987, Pierotti and Annett 1993).These disturbed areas break up natural habitats that the parent taxa normally associate with and in turn create fragmented or even novel habitat (Anderson 1948). In some cases, hybrid individuals appear to be better suited for, and numerically dominant in these disturbed settings (Wright and Lowe 1968, Grant 1971, Moore 1977, Pierotti and Annet 1993, Vila et al. 2000, Wood et al. 2015). Restriction of hybrids to anthropogenically modified environments has been documented for some plant and vertebrate species (Wright and Lowe 1968, Grant 1971, Urbanska 1987, Pierotti and Annett 1993, Wood et al. 2015).

Among vertebrates, hybridization in birds is particularly extensive with at least 16% of all bird species hybridizing in the wild Ottenburghs et al. (2015). Furthermore, many bird species are highly selective of habitats (Lack 1933, Svardson 1949, Wiens 1969, Fisher and Davis 2010). Habitat use by birds frequently depends on vegetation composition (e.g., deciduous vs. coniferous forest) and structure (e.g., density of foliage, canopy or tree height, and percent canopy cover) due to species traits such as diet, foraging strategy, courtship behavior, and nesting requirements (MacArthur and

MacArthur 1961, MacArthur et al. 1962, Wiens 1973). Additionally, habitat selection in birds is often influenced by the presence of other species that share similar ecological niches. In many of these cases where ecologically similar bird species occupy the same general habitat, competition may be reduced by use of different foraging strategies and habitats; i.e., habitat partitioning (MacArthur 1958, Terborgh 1971, Diamond 1972, Traba et al. 2015). Thus, the spatial distributions of habitat characteristics may influence the initiation and maintenance of hybridization between bird species that have overlapping habitat preferences.

Indicative of the primary role that habitat plays, many avian hybrid zones in North America occur along ecotones (Tanner 1952, Dixon 1955, Sibley and West 1959, Yang and Selander 1968, Hubbard 1969, Moore and Price 1993). For example, within the broad ecotone between the eastern edge of the Rocky Mountains and the western edge of the Great Plains, Rising (1969) found that hybridizing orioles differ in their habitat associations. Specifically, Bullock's Orioles (*Icterus bullockii*) are physiologically adapted (i.e., high tolerance to hyperthermia and water restrictions), to the relatively xeric environment of the Rocky Mountains, whereas Baltimore Orioles (*Icterus galbula*) are adapted (i.e., low tolerance to hyperthermia and water restrictions) to the mesic environment of eastern deciduous forests. Hybridization between these two wide-ranging species is therefore narrowly restricted to ecotonal areas where habitat features from both environments meet and become heterogeneous. Similarly, the distributions of two hybridizing subspecies of the Northern Flicker (*Colaptes auratus*) are correlated with precipitation patterns within this same mid-continental ecotone. The Red-Shafted form is associated with xeric western forests and the Yellow-Shafted with mesic eastern forests

(Moore and Price 1993). Within Colorado, hybrids of Steller's Jays (*Cyanocitta stelleri*), birds of primarily montane coniferous forests, and Blue Jays (*Cyanocitta cristata*), birds primarily of deciduous wooded prairies, have been found along ecotonal areas of pine and deciduous forests (Rising 1983). As another example, the Spotted Towhee (*Pipilo erythrophthalmus arcticus*) (western subspecies) and Unspotted towhee (*P. e. erythrophthalmus*) (eastern subspecies) hybridize where the open chapparral environment of the western plains meets deciduous forests in northern Colorado, Nebraska, and South Dakota (Sibley and West 1959, Rising 1983).

Hybridization of some bird species in North America also appears to be associated with and perhaps facilitated by anthropogenically disturbed habitats. For example, species of gulls (genus *Larus*) and species of ducks (genus *Anas*) frequently hybridize with other congeners across human disturbed habitats in North America, and some of these hybridizing lineages have even expanded their geographic ranges along with the anthropogenic alteration of habitats (Pierotti and Annett 1993). Although factors such as the dispersal abilities and assortative mating behavior of two distinct taxa are important in determining the geographic extent and maintenance of hybrid zones (Bigelow 1965, Moore 1977, Barton and Hewitt 1985, Hewitt 1988), habitat characteristics also appear to play a major role in shaping the dynamics of many avian hybrid zones in North America. Therefore, further investigation into similar systems should involve a close look at the habitat associations of the hybridizing taxa to more fully understand the importance of habitat in facilitating hybridization and the geographic location and extent of a hybrid zone. For this study, I focused on the Tufted Titmouse (*Baeolophus bicolor*) and Black-crested Titmouse (*Baeolophus atricristatus*) hybrid zone

that stretches across central Texas into the lower southwest corner of Oklahoma (Figure 1). The hybrid zone is associated with an ecotone that represents a transition from closed-canopy deciduous forests in the east to arid and open woodlands in the west (Curry and Patten 2014). Furthermore, the ecotone encompasses areas impacted by human disturbance and urbanization (Smith 1910, Dixon 1955, Brauning 1992). In this system I evaluated how the relative abundances of the parent species and hybrids across the hybrid zone are influenced by habitat characteristics.

### **Study Species**

Tufted Titmice (hereafter TUTI) are native throughout the eastern United States, with the southwestern limits of their range in central Texas (Phillips 1986, Howell and Webb 1995) (Figure 2). These small passerine birds (15 – 16 cm) are light gray on top and white below with a slight amount of peach-colored plumage along their flanks (Figure 3). The crests atop their head are an identical gray to their bodies and they have a black patch of plumage on their foreheads. No sexual dimorphism is present, but juveniles may have lighter dusky forehead patches (Pyle 1997). TUTI are mostly limited to deciduous forests but can occupy mixed deciduous-coniferous forests, although a dense canopy with many tree species is preferred (Dixon 1955, Conner et al. 1983, Brauning 1992). They utilize the canopy, mid-story, and ground but typically forage in the lower and interior spaces of trees (Gillespie 1930b, Dixon 1955, Watt 1972). While foraging they glean for a variety of food items such as larval and adult insects, seeds, and fruits (Bent 1946, Dixon 1955, Suthers et al. 2000). They typically live in pairs during the summer and form mixed species foraging flocks, during the winter (Brawn and Samson

1983, Contreras and Sieving 2011).

The more arid range of Black-crested Titmice (hereafter BCTI) extends from northeastern Mexico into parts of west and central Texas and southwest Oklahoma (Dixon 1955, Sutton 1967, Oberholser 1974, Curry and Patten 2014) (Figure 2). BCTI are typically smaller (~ 14 cm) than TUTI. Their plumage morphology is similar except that BCTI have more pronounced black crests and buffy white foreheads (Figure 3). Females and juveniles may exhibit dull black crests (Dixon 1955, Pyle 1997). The species occupies evergreen, semideciduous, or deciduous broadleaf forests and semi-wooded areas, but has an affinity for oak and mesquite trees (Smith 1910, Dixon 1955, Miller 1955, Carter 1986). Though less studied than TUTI, BCTI are assumed to have many of the same foraging habits and diet preferences as TUTI (Dixon 1961). Furthermore, they also occur in pairs during the breeding season (February to mid-July) and participate in mixed species foraging flocks when not breeding (Dixon 1961, Harrap and Quinn 1995). Neither species migrates.

BCTI and TUTI are considered to have diverged during the glaciations of the late Pleistocene (Dixon 1978, Avise and Zink 1988, Gill and Slikas 1992). Approximately 4,000 years ago, changes in climate and melting of glaciers led to geographic range expansion of both species and subsequent range overlap which created a secondary contact zone in what is largely restricted to central Texas (Dixon 1955, 1978). An additional secondary contact zone emerged about 100 years ago in southwest Oklahoma (Dixon 1955, Sutton 1967, Patten and Smith-Patten 2008, Curry and Patten 2014) after mesquite began spreading due to fire suppression and overgrazing. This habitat alteration facilitated range expansion of BCTI (Van Auken 2000, Callahan 2002, Curry 2014). The

new contact zone in Oklahoma is spatially continuous with the old contact zone in Texas (Figure 1), therefore, they will be herein referred to as a singular hybrid zone. Frequent interspecific mating, as reported by Dixon (1955), within the contact zone resulted in taxonomists initially lumping the two currently recognized species into one taxon for a period of time (Ritchison, et al. 2020). However, later molecular genetic studies revealed significant genetic differentiation between the two forms (Braun et al. 1984, Avise and Zink 1988, Sheldon et al. 1992) that justified re-establishing the two taxa as separate species and delineation of the the hybrid zone (Banks et al. 2002).

Studies conducted by Dixon (1955, 1978, 1990) and Curry and Patten (2014), have shown that the frequency of co-occurrence and incidence of hybridization varies across the contact zone, with putatively pure (based on phenotypic characters) TUTI individuals occurring more frequently along the eastern edge of the zone and putatively pure (again based on phenotypic characters) BCTI individuals along the western edge. In relation to these spatial patterns, the morphology of hybrids also varies across the zone due to multi-generational hybridization and backcrossing events (Curry 2014). Nonetheless, the plumage morphology of hybrids of all admixture classes is intermediate between the two parent species as illustrated in Figure 3. Importantly, the spectrum of hybrid phenotypic classifications is often concordant with genotypic classifications (i.e., F1, F2, backcrossed hybrids). Therefore, plumage morphology is considered a reliable indicator of genetic admixture (Curry 2014).

Previous studies have focused on habitat associations of the two parent species separately, primarily outside of the contact zone (Smith 1910, Dixon 1961, Wauer 1971, Conner et al. 1983, Brauning 1992). Direct comparison of the habitat ecology of the two

species is difficult because no study has simultaneously examined habitat use of both species. Additionally, TUTI have been studied far more extensively than the sister species, which has caused many traits of TUTI, including habitat use, to be assumed for BCTI without strong supporting evidence. To date, research on the hybrids has focused on the extent of their geographic range and the morphological variation found throughout the range (e.g., Dixon 1990, Curry and Patten 2014), with no attention given to habitat use. Furthermore, human disturbed habitats (e.g., residential neighborhoods and city parks) are common across the hybrid zone (Smith 1910, Dixon 1955, Brauning 1992), yet no studies have directly tested for correlations between human disturbance and the incidence of hybridization in TUTI and BCTI. Therefore, the TUTI × BCTI hybrid zone provides an opportunity to investigate whether both habitat characteristics and anthropogenic disturbance have a significant effect on the current distributions of TUTI, BCTI, and their hybrids.

### **Thesis Objectives**

The primary goal of my study was to evaluate the influence of habitat characteristics across central Texas and southwest Oklahoma on the relative abundances of TUTI, BCTI, and their hybrids in the zone of hybridization. Specific objectives were to (1) determine if there are differences in habitat associations among TUTI, BCTI, and their hybrids. within the hybrid zone, and (2) determine if there are differences in the habitat associations of titmice belonging to different phenotypic classes. For my first objective, I used citizen science data from eBird, in conjunction with high resolution remotely-sensed land cover data, to describe and analyze the habitat associations of both

the parent species and hybrids within the hybrid zone and in allopatric locations immediately outside the zone. eBird does not classify hybrid individuals based on admixture (no information provided beyond “hybrid”). Thus, to obtain more detailed data on hybrid classifications (F1, F2. Etc.) and their habitat associations, I collected data using camera traps and field surveys in areas deemed suitable for hybrid occurrence. I determined the putative class of all observed titmice following Dixon’s (1955) plumage-based hybrid index as adapted by Curry and Patten (2014). I then analyzed the habitat associations of these titmice in a similar manner to the eBird data.

## II. ANALYZING HABITAT ASSOCIATIONS WITH eBIRD DATA

My study design and analyses tested whether the distinct habitat associations of TUTI and BCTI remain in the hybrid zone or if the two parent species overlap in habitat use. Additionally, I aimed to identify the habitat characteristics that hybrids most strongly associate with. This landscape level investigation used eBird count data, NLCD raster data (see below), and GIS analyses to examine the correlation between relative abundance of TUTI, BCTI, and hybrids with land cover types, percent canopy cover, and percent impervious surfaces (an indicator of anthropogenic disturbance) at different spatial scales. I hypothesized that the habitat preferences of the two putatively pure species identified in allopatry would be maintained within the hybrid zone such that (1) TUTI and BCTI would differ in their habitat associations and (2) hybrid individuals would associate with habitat characteristics that are intermediate between those of the parent species. Specifically, I predicted that relative abundance of TUTI would be positively correlated with areas of primarily deciduous forest and dense canopy cover, whereas relative abundance of BCTI would be positively correlated with coniferous and mixed forest habitats exhibiting moderate canopy cover. I predicted the relative abundance of hybrids would be highest within areas that contained intermediate values of the forest cover types and canopy cover. Furthermore, I predicted hybrids would have strong associations with novel anthropogenic habitats (comprised of moderate to high percentage of impervious surface). In general, hybrids were expected to be most common (though not necessarily more common than either parent species) in landscapes that could be considered intermediate between the types of landscapes occupied by each parent

species.

## **Methods**

### eBird Data and Study Region

The eBird database is a citizen science database administered and managed by the Cornell Lab of Ornithology that allows observers to upload sightings of bird species in the form of checklists. All survey checklists are geo-referenced to a single latitudinal/longitudinal point, often marking the starting or mid-point of a survey that may have involved some walking or vehicle travel by the surveyor. The bird species included on a checklist varies depending on the specific location of the survey, but the birder is given the option to add species not listed on the particular checklist. For each checklist, the surveyor tabulates a total count of each species identified during their survey. Additionally, when submitting checklists on the website portal, survey participants may include information on the environmental conditions, detailed descriptions of the birds' appearances, and/or specific behaviors. Unusual sightings or descriptions for an area are flagged and reviewed by eBird staff for data quality control.

I acquired count data for TUTI, BCTI, and their hybrids (three separate datasets) from checklists submitted within Texas and Oklahoma between the years of 2012 and 2020. The data came from checklists that listed both of the parent species and hybrids. The nine-year time period bracketed the 2016 land cover data (see next section) used in the habitat analysis. Analyzing the relative abundances and habitat associations of the three titmice types for each year separately would be redundant considering the habitat data did not change over time (i.e., data came from datasets that represented one year:

2016). Therefore, the count data across all years were combined to represent a total count of the nine-year time period for each titmouse type. Furthermore, pooling the count data across years provided a larger sample size and accounted for variation in sampling effort across survey locations from year to year. These total counts were then used to derive the relative abundance of TUTI, BCTI, and hybrids within grid cells of a specified size overlaying the hybrid zone (see GIS Analysis section below). To focus my analysis on the hybrid zone and establish my study region, I identified all Texas and Oklahoma counties that had checklists reporting hybrids along with one or both of the parent species. Counties bordering the hybrid zone (east and west of the zone) that did not include any observations of hybrids, but did report observations for the parent species, were also included in the study region to delineate habitat associations of the parent species outside of the zone (Figure 4). To ensure spatial accuracy of the eBird data, I eliminated checklists in which the observer reported travelling more than 10 km, although most checklists did not report traveling more than 1 km. The data was further filtered to guard against pseudo replication by removing all duplicate observations such as when two or more eBird participants submit the same checklist. It is important to note that hybrid individuals can vary greatly in their phenotypes, and some closely resemble one or the other parent species. eBird participants do not always identify and record TUTI  $\times$  BCTI hybrids, therefore counts of hybrids in my final dataset are likely underestimates and counts for the parent species may be overestimates.

### Landscape-Level Habitat Data

The National Land Cover Database (NLCD), provided by the United States Geological Survey was used to obtain landscape-level habitat data. Several different GIS raster layers derived from remote-sensing imagery of the Landsat satellites are publicly available on the NLCD website at a  $30 \times 30$  m pixel resolution. For my habitat analysis I used the 2016 Land Cover layer (CONUS), the 2016 USFS Tree Canopy Cover layer (CONUS), and the 2016 Percent Developed Imperviousness layer (CONUS). The Land Cover layer assigns each  $30 \times 30$  m pixel located within the continental United States to one of 16 different land cover categories that encompass a large array of habitat types. However, the majority of these land cover categories (N=12) were not included in the final analysis presented herein due to a priori knowledge of them being unsuitable habitat for titmice. The four land cover categories I used were deciduous forest, evergreen forest, mixed forest, and scrub/shrub land because TUTI and/or BCTI are known to have associations with these vegetation types outside of the hybrid zone. The correlation coefficients for these four variables were all between -0.3 and 0.3 at all spatial scales used in analyses (see sections below).

The Tree Canopy Cover layer was used to assess canopy structure considering there are known differences in the associations of TUTI and BCTI with canopy density. This layer assigns a percent canopy cover value in 1% increments to each  $30 \times 30$  m pixel. Similarly, the Percent Developed Imperviousness layer assigns the percentage of pavement and building cover (mainly asphalt and concrete) within a  $30 \times 30$  m pixel in 1% increment values. This GIS layer was incorporated because it more directly measures levels of anthropogenic disturbance than the developed land cover categories of the Land

Cover layer. Including the Percent Developed Imperviousness layer was important considering the two titmice species and hybrids have geographic ranges that overlap areas impacted by human development and have been noted to occur in developed areas (Smith 1910, Dixon 1955, Brauning 1992). To describe habitat affinities I analyzed six habitat variables from the NLCD raster layers: percent deciduous forest, percent evergreen forest, percent mixed forest, percent scrub/shrub cover, mean percent canopy cover, and mean percent impervious cover.

### Geographic Information System Analysis

ArcGIS Pro 2.8.2. (ESRI Software) was used to map and then analyze the relationships between eBird and NLCD data. Polygons of counties in Texas and Oklahoma were uploaded to visualize the boundaries of the study region (Figure 4). The three NLCD raster layers were then uploaded and the ‘Clip Raster’ tool was used to clip each layer to the extent of the study region (i.e. the selected counties). The three eBird datasets (TUTI, BCTI, and hybrid counts from 2012-2020) were imported as three separate point feature class layers over the NLCD raster layers. Each “point” corresponded to the latitude/longitude coordinates of a survey with the associated total count of the given species. The ‘Create Fishnet’ tool was then used to overlay a grid with cells of  $10 \times 10$  km across the study region (Figure 5). Each cell is an individual polygon that can be used to extract the associated data. This relatively large grid cell size was needed in order to meet the assumption that the actual coordinates of the eBird sightings were within the focal grid cell. At the same time the grid cell size was small enough to provide a sample size of several hundred grid cells across the study region. The

‘Aggregate Points’ tool was used to sum the total count of TUTI, BCTI, and hybrids within each  $10 \times 10$  km grid cell across the study region. These total counts were used to derive the relative abundance of TUTI, BCTI, and hybrids within each grid cell. By converting the counts of the three titmice types into relative abundances (within a grid cell) the variation in sampling effort (i.e., total number of titmice counted) across grid cells was removed.

I obtained estimates of the seven habitat variables within each grid cell through the use of various spatial analysis tools in ArcGIS Pro. For the NLCD Land Cover layer, I used the ‘Tabulate Area’ tool to calculate the total area (in meters) of each land cover class and the percentage of each land cover class within each  $10 \times 10$  km grid cell. For the NLCD Tree Canopy and the NLCD Percent Developed Imperviousness layers, I used the ‘Zonal Statistics as Table’ tool to calculate the mean percentages of canopy cover and impervious cover across all  $30 \times 30$  m pixels within each grid cell. These data extraction processes for both the eBird and NLCD data were repeated utilizing fishnets with  $5 \times 5$  km and  $2.5 \times 2.5$  km grid cells. The data extracted from the three different spatial scales were treated as three separate data sets and analyzed independently. The more highly resolved grids (smaller net size) were intended to examine differences in habitat associations at finer (more local) spatial scales and to test whether habitat associations varied with spatial scale (e.g., across the three net sizes). By reducing the grid cell size, some error in the total counts and corresponding relative abundances of the three titmice types was likely introduced due to the eBird data being spatially imprecise. However, most checklists did not report traveling more than 1 km, therefore error was likely minimal (Torgersen et al. 1999, Apps et al. 2002, Veech and Crist 2007, Muller et al.

2018). Lastly, I removed grid cells that had a total titmouse count of less than 50. This removal process was done at all spatial scales to ensure the relative abundances calculated had a precision level of at least 0.02. After removal, the final datasets had the following number of grid cells:  $10 \times 10$  km (N = 498),  $5 \times 5$  km (N = 784), and  $2.5 \times 2.5$  km (N = 1041).

### Statistical Analysis

Before testing for significant relationships between the relative abundance of the three titmice classes (i.e., TUTI, BCTI, and hybrid) and habitat variables, and differences in habitat associations among the titmice classes, summary statistics were first calculated to visualize general distribution patterns of the putative titmice classes and potential habitat associations. To characterize general distributions the number of grid cells within each relative abundance category in 0.1 increments were indexed for each titmouse type and spatial scale. Next, the number of grid cells that contained each of the six possible combinations of the three titmice types were counted for each of the three spatial scales. These combinations included: just BCTI, just TUTI, just hybrids, BCTI and TUTI, BCTI and hybrid, TUTI and hybrid, and all three titmice types. Lastly, for each spatial scale, the grid cells were sorted into more generalized groups: those with just BCTI, just TUTI, and a single group that presumably included all three titmice types which represented locations of hybridization. In this latter group, grid cells that contained only hybrids, hybrids with BCTI, hybrids with TUTI, BCTI and TUTI and all three titmice types were lumped. This pooling of grid cells was done under the assumption that hybrids cannot exist within an area without the presence of both parent species, and that hybrids likely

exist in areas where the two parent species co-occur even though no hybrids were reported. For each group, the means and standard deviations of each habitat variable across all grid cells were calculated.

The  $10 \times 10$  km,  $5 \times 5$  km, and  $2.5 \times 2.5$  km datasets were then statistically analyzed in RStudio 4.0.5 using the 'glm' function in the 'stats' package for all regression modeling. Multiple logistic regression was used to test for significant positive, negative, and intermediate relationships between the six habitat variables and the relative abundances of BCTI, TUTI and hybrids at the three spatial scales. Logistic regression was selected as it is appropriate for response variables that scale between 0 and 1 (e.g., relative abundance), and it is a generally powerful and flexible way to test for habitat associations (Veech 2021). The squared terms for each of the habitat variables were also included within the model building process. I had hypothesized that hybrids would associate with intermediate habitats, therefore the squared habitat variables were included so as to identify any relationships that would involve relative abundance being at a maximum (or minimum) at intermediate values of the habitat variable (Veech and Plappert, in review). All regression models created included latitude and longitude as predictor variables to help account for the effects that spatial autocorrelation may have had on relative abundance. Therefore, a total of 14 predictor variables were examined: latitude, longitude, mean percent imperviousness, mean percent canopy cover, percent deciduous forest, percent evergreen forest, percent mixed forest, percent shrub/scrub land, and the squared term for all six habitat variables.

I used a forward stepwise process to construct different sets of regression models for each combination of titmouse type and grid size, rather than conducting all possible

models for each combination (Sun et al. 1998, Ruengvirayudh and Brooks 2016, Zhou 2018). Interactions were not included in any of the models because I was most interested in the direct influence of each habitat variable and there was no a priori reason to suspect that interactions among predictor variables would be important. Furthermore, incorporating all possible interactions between the un-squared and squared habitat variables would make for complex and over-specified models. First, I constructed models that included latitude, longitude, one of the habitat predictor variables, and the squared term of the given habitat variable. If the habitat predictor and/or its squared term was found to be significant ( $P \leq 0.05$ ) or marginally significant ( $0.05 \leq P \leq 0.08$ ) in these models, then the predictor(s) were carried forward and included in the next step where various multi-factor models, with all combinations of the included predictor variables were created. For every titmouse type and spatial scale combination, the final model included latitude, longitude, and all habitat variables (unsquared and squared terms) that were found to be significant or marginally significant in the previous step. The variables included in the final models varied among the titmice types and across spatial scales. For a given titmouse type and spatial scale, all of the models were compared against each other with Akaike's Information Criterion (AIC) obtained using the 'model.sel' function within the 'MuMIn' package in R. Importance values were calculated for each habitat variable by summing the weights of the models that included the given variable. This was done for each titmouse type by spatial scale combination. This analysis identified habitat variables that BCTI, TUTI, and hybrids appear to associate with most commonly.

To more directly examine differences in habitat associations between the three titmice types, especially regarding hybrids associating with intermediate habitats between

those of BCTI and TUTI, I used Principal Components Analysis (PCA). At each spatial scale, a single PCA was conducted that included five habitat variables along with latitude and longitude, making for a total of seven factors. Mean percent imperviousness was not included due to its lack of significance in all regression modeling. Additionally, PCA was again applied at each spatial scale without latitude and longitude to determine if separation along PC axis among BCTI, TUTI, and hybrids remained when spatial components were allowed to confound patterns. Those PCAs had a total of five factors. For all PCAs, PC1 and 2 accounted for over half the variance in the data (Table 6), therefore, for each grid cell at each spatial scale, I only obtained the PC scores for PCs 1 and 2. For each titmouse group, I then weighted the PC scores by the relative abundance within the grid cell. The relative abundance weights were obtained by dividing the relative abundance of a particular titmouse type in a given grid cell by the sum of all relative abundance values for that titmouse type across all grid cells. I then constructed PC plots to visually examine and assess the extent that the three titmice groups were separated along PCs 1 and 2. To determine the significance of any separation observed in each PCA, single factor ANOVAs were conducted to test for differences in the means of the weighted PC 1 and 2 scores between the three titmice types. If ANOVAs were significant, Tukey's honest significance test was used to test for differences between each pairwise comparison.

## **Results**

For all three spatial scales, ( $10 \times 10$  km,  $5 \times 5$  km, and  $2.5 \times 2.5$  km) grid cells with a relative abundance of 1.0 for BCTI were most common, followed by TUTI, and

hybrids (Figure 6). In other words, more grid cells were exclusively BCTI than TUTI, and only a few grid cells ( $N = 2$  for  $10 \times 10$  km,  $3$  for  $5 \times 5$  km, and  $5$  for  $2.5 \times 2.5$  km) contained hybrids alone (Table 1). TUTI were absent (relative abundance (RA) = 0.0) from grid cells more often than BCTI or hybrids (Figure 6). In general, BCTI and TUTI were either the only titmice type present (RA = 1) within grid cells or absent (RA = 0) from grid cells in high frequencies (i.e., bimodal distributions), whereas hybrids tended to exist at lower relative abundance categories (RA = 0–0.2) across grid cells (Figure 6). Grid cells that contained both BCTI and hybrids occurred most frequently across the study region at all spatial scales (Table 1). Overall, BCTI was more common than both TUTI and hybrids (Table 1, Figure 6) across the study region.

The means of the six habitat variables across grid cells for each titmice category (just BCTI, just TUTI, and all types/hybridization present) were fairly consistent across all three spatial scales (Figure 7). Although this was a preliminary examination, some apparent differences in habitat associations were observed between the two parent species, and some intermediate associations were found for the hybrids as predicted. Grid cells with just BCTI had higher means in percent shrub coverage ( $10 \times 10$  km: 52.3 %,  $5 \times 5$  km: 41.1 %, and  $2.5 \times 2.5$  km: 34.14%) than those with just TUTI (3.5 %, 2.0%, and 2.2 %). Grid cells with both parents and/or hybrids present were intermediate for shrub coverage (16.1 %, 13.6 %, and 10.5 %). Grid cells with just TUTI had higher means in mean percent imperviousness (14.3 %, 19.7 %, and 17.8 %) and percent mixed forest coverage (1.6 %, 1.5 %, and 2.0 %) than grid cells with just BCTI (imperviousness: 2.1 %, 5.9 %, and 9.9% ; mixed forest: 0.6 %, 0.5 %, and 0.6 %). Grid cells with both parents and/or hybrids had intermediate means for mean percent imperviousness (1.5 %,

1.4 %, and 1.1 %,).

The logistic regression models provided support for some of my predictions and the putative habitat associations mentioned above. Through AIC model selection (Tables 2 - 4) and calculation of importance values (Table 5), the three titmice types were found to be associated (either positively or negatively) with some of the habitat variables. For both BCTI and TUTI at the  $10 \times 10$  km scale, percent evergreen, mixed, and shrub cover had the highest importance values (Table 5) and appeared most often in the highest ranked models (Table 2). Importantly, the regression coefficients for the un-squared terms of percent evergreen and percent mixed cover were significant and opposite in sign for BCTI and TUTI at all three spatial scales (Table 5), meaning an increase in evergreen forest led to an increase in grid cells occupied by BCTI and a decrease in grid cells occupied by TUTI, whereas an increase in mixed forest led to an increase in TUTI and a decrease in BCTI. The un-squared terms of percent shrub cover were significant and opposite in sign for BCTI and TUTI at the  $5 \times 5$  km spatial scale (Table 5), meaning an increase in shrub cover led to an increase in TUTI occupancy and a decrease in BCTI occupancy. This pattern was not found at the other spatial scales. Regression coefficients for hybrids were non-significant for most of the habitat variables although percent shrub cover had high importance values at all three spatial scales (Table 5).

Results from the PCAs with latitude and longitude were fairly consistent with one another across spatial scales. PCAs without latitude and longitude were also consistent with one another across spatial scales. For all PCAs, PC1 and PC2 accounted for over half the variance in the data (Table 6). The PCAs with latitude and longitude (at all spatial scales) revealed some separation along PC1, with hybrids being intermediate

between BCTI and TUTI, though more overlap occurred between TUTI and hybrids than BCTI and hybrids (Figure 8, 10, and 12). The highest factor loadings on PC1 were longitude, percent shrub, and percent evergreen (Table 6). The PCAs that did not include latitude and longitude (at all spatial scales) separated the titmice groups along PC2, where hybrids appeared intermediate with regard to the five habitat variables, though more overlap occurred with TUTI (Figure 9, 11, and 13). The highest factor loadings on PC2 were percent deciduous, percent shrub, and percent mixed forest (Table 6). For both PCAs (with and without latitude and longitude), overlap of hybrids with the parent species became more pronounced as the spatial scale decreased (for example, compare Figures 8, 10, and 12). The single factor ANOVAs revealed that separation of titmouse groups observed along PC axes was significant ( $P < 0.01$ ) at all three spatial scales when the PCA included latitude and longitude and when it did not. All pairwise comparisons (Tukey's tests) were significant ( $P < 0.01$ ) except TUTI vs. Hybrid at  $10 \times 10$  km for PC2 that included latitude and longitude (Figure 8) and BCTI vs. Hybrid at  $2.5 \times 2.5$  km for PC1 that did not include latitude and longitude (Figure 13). Therefore, for PCAs with latitude and longitude, PC1 factor loadings indicated that longitude, percent shrub cover, and percent evergreen cover had the strongest influence on the separation between titmice classes along PC1, and for PCAs without latitude and longitude, PC2 factor loadings indicated that percent deciduous cover, percent shrub cover, and percent mixed cover had the strongest influence on the separation between titmice classes along PC2.

## **Discussion**

The primary goal of my study was to evaluate the influence of habitat characteristics on the relative abundances of TUTI, BCTI and their hybrids across their hybrid zone. Such knowledge provides insight on whether habitat characteristics, in conjunction with species habitat affinities, plays a role in the formation and maintenance of hybrid zones. The role of habitat in either inhibiting or influencing hybridization and thus eventual speciation (or lack thereof) continues to be studied by evolutionary ecologists (Schluter 2001, Wolf et al. 2001, Seehausen et al. 2008, Pierce et al. 2017). Considering TUTI and BCTI share similar foraging and nesting strategies (Dixon 1961), and that habitat characteristics vary throughout the study region, I reasoned that habitat associations within the contact zone might differ between the parent species and thus reduce interspecific competition which in turn would decrease the probability of hybridization and promote the maintenance of species boundaries (Endler 1977, Seehausen et al. 2008). Specifically, I hypothesized that the different habitat associations of TUTI and BCTI known to exist outside of the hybrid zone would be maintained within the hybrid zone and that hybrids would associate with a habitat type considered to be intermediate between those habitats of the two parent species. This hypothesis was partially supported by the results obtained in my study.

Preliminary inspection of the six habitat variables revealed some differences in the habitats found within localities (grid cells) containing only BCTI observations, only TUTI observations, and those with observed or probable hybrids present (Figure 7). Grid cells that only contained BCTI individuals had higher percentages of shrub cover than TUTI, and lower percentages of mean impervious cover and mixed forest cover than

TUTI. Grid cells with observed or probable hybrids present had means for percent shrub cover and mean percent imperviousness that were intermediate between the two parent species. Some of these differences were further supported by the results found in the logistic multiple regression models and AIC model comparison. Percent cover of evergreen forest, mixed (deciduous and evergreen) forest, and shrub cover had consistently high importance values for the three titmice types at each of the three spatial scales. As expected, the direction and significance of the relationships varied among the titmice types. In the top models, BCTI nearly always had a significant positive relationship with percent evergreen cover, and a significant negative relationship with percent mixed and shrub cover, whereas TUTI was the inverse for all respective variables. Therefore, BCTI are more likely to be found in landscapes with higher proportions of evergreen forest and lower proportions of mixed forest and shrub cover, whereas TUTI are more likely to be found in landscapes with higher proportions of percent mixed forest and shrub cover, and lower proportions of evergreen forest.

Although these results demonstrated differences in habitat associations as I hypothesized, my prediction that BCTI would be associated with higher proportions of evergreen and mixed forest, and TUTI with higher proportions of deciduous forest across the study region, was not fully supported. Rather, relative abundance of TUTI was positively correlated with mixed forest whereas relative abundance of BCTI was negatively correlated with mixed forest. This finding is not entirely contrary to the prediction, however, considering the mixed forest cover type is a mixture of evergreen and deciduous vegetation. Therefore, it may reflect a strong aversion to deciduous vegetation by BCTI and TUTI's preference for such vegetation. Furthermore, no

significant associations or differences in mean canopy cover were detected among the grid cells occupied by the three titmice types contrary to the prediction that TUTI would occupy landscapes with much more canopy cover than those occupied by BCTI. This unexpected result may be due to the broad scale of the habitat analysis. Perhaps analysis at the territory or neighborhood scale (e.g., a few hectares surrounding a nest site) would better be able to reveal the importance of canopy cover in defining differences in the habitats of the three titmice types. However, it is possible that land cover types are more important in determining BCTI and TUTI abundance than is overall canopy cover. TUTI were not expected to have positive associations with shrub cover, however it is possible that TUTI show more variation in their habitat associations within the hybrid zone than they do outside the zone and have adapted to use shrubby land cover even though the vast majority of their geographic range in the eastern and southern USA is comprised of forest, not shrubland. Also, considering that woody shrub encroachment has increased throughout Texas and Oklahoma in the past century (Van Auken 2000) TUTI may have gradually adapted to that habitat type rather than being geographically displaced by it. In either case, further examination of the habitat associations of the parent species within and immediately outside of the hybrid zone should be conducted, especially at spatial scales that involve the territories of titmice, to draw stronger conclusions.

Percent shrub cover had high importance values for hybrids across all spatial scales but was not found to have a significant effect on hybrid relative abundance. In fact, the most evident result for hybrids was the overall lack of significance of the regression coefficients for all habitat variables. This implies that hybrids do not tend to occupy areas with particularly high or low proportions of the habitat variables analyzed. Furthermore,

the squared terms of the habitat variables were non-significant, which indicated that hybrid relative abundance is not significantly greater at intermediate values of the habitat variables as I predicted. Contrarily, results from the PCA analyses revealed that hybrids appear to occupy habitat that is intermediate between that of the two parent species

For both the PCAs conducted with and without latitude and longitude, the weighted PC scores for the three titmice types were significantly separated along the PC axes. In all cases, weighted PC scores for BCTI grouped together on one end of the given PC axis, and weighted PC scores for TUTI grouped on the opposite end. This pattern generally supports results of the regression modeling, relative abundances of BCTI and TUTI differ for some of the habitat variables. PC scores for the hybrids grouped along intermediate segments of the PC axes, demonstrating the intermediacy of hybrid habitat associations. The habitat variables with high importance in the regression modeling (percent evergreen, mixed, and shrub) were also some of the habitat variables with the highest factor loadings in the PCAs, which corroborates the influence of these variables on the distribution and abundance of the three titmice types. Including or excluding latitude and longitude within PCAs did not strongly affect the factor loadings. The overall similarity of PCAs with and without spatial variables further supports the hypothesized correlation between habitat characteristics and the abundances of the three titmice types across the hybrid zone because it demonstrated that the influence of the habitat variables remained strong even when spatial components were allowed to confound the relative abundance patterns. Grid cells that contained hybrids had much smaller sample sizes than grid cells that contained either of the parent species across all three spatial scales (Table 1). Therefore, it is likely that sample sizes of grid cells containing hybrids were too low

to detect significant relationships between hybrid relative abundance and the squared habitat variables in the regression analysis, despite the apparent presence of intermediate associations in the PCA analyses. With greater sampling effort focused on hybrid individuals, larger sample sizes may be obtained and more distinct associations may be discovered in future habitat analyses.

Results for the parent species and hybrids are in line with theory that emphasizes the importance of ecological variables contributing to the formation and maintenance of hybrid zones that arose through secondary contact (Endler 1977, Moore 1977, Seehausen et al. 2008) such as the BCTI  $\times$  TUTI hybrid zone. Taxa that genetically diverged in allopatry might have diverged in their ecological requirements due to local adaptation. These differing requirements that potentially evolved in allopatry, therefore limit the distributions of the parent species in their current sympatric ranges where hybridization occurs and helps maintain some degree of reproductive isolation. Hybrids are thus thought to be restricted, or perhaps even better adapted, to areas where ecological characteristics are intermediate or transitional between those preferred by either parent species (Rising 1969, Moore 1977, Hewitt 1988). Other recent studies regarding bird hybrid zones formed through secondary contact have found results similar to mine.

Carling and Thomassen (2012) found that hybridization rates of Lazuli Buntings (*Passerina amoena*) and Indigo Buntings (*Passerina cyanea*) were better explained by environmental variables, specifically associations with rainfall, than geographic distance between sampling localities within the Rocky Mountains/Great Plains Ecotone. This was in line with the hypothesis that Indigo Buntings are better adapted to mesic environments, Lazuli Buntings to xeric environments, and hybrids being limited to transitional areas. In

Northern New York, Wood et al. 2016 demonstrated that Golden-winged Warblers (*Vermivora chrysoptera*) occupy territories with higher vegetative structural heterogeneity, higher proportions of deciduous forest, lower proportions of shrub/scrub cover in adjacent habitats, and further distances from medium to high density urban areas than Blue-winged Warblers (*Vermivora cyanoptera*). Phenotypic hybrids and some cryptic hybrids were found to occupy territories with intermediate values for all respective variables. In a like manner, the study of Carpenter et al. (2022) revealed that the eastern subspecies of Warbling Vireo (*Vireo gilvus*) is associated with deciduous forests and non-forested areas and is replaced by the western subspecies in areas with greater proportions of mixed coniferous/deciduous forests. Hybrid genotypes were most common in transitional or intermediate areas with regard to types of land cover.

Mean percent imperviousness (variable indicative of disturbance) was not found to be significant for any of the titmice types throughout the regression modeling process and accordingly was not included in the PCAs. Therefore, I did not find support for hybrids being associated with anthropogenically disturbed landscapes as I had hypothesized. Nonetheless, the role of urbanization in possibly facilitating titmouse hybridization could be further explored. Perhaps, human disturbance and urban expansion does influence BCTI  $\times$  TUTI hybridization in some way, as has been documented for other avian hybrid zones. Graham et al. (2021) found admixture rates of four North American chickadee species (*Poecile*) to be highest in urban parkland and mixed habitats. Admixture rates were highest within species pairs that included Black-capped Chickadees (*P. atricapillus*), which are considered to be habitat generalists. Similarly, Wood et al. (2016) found that Blue-winged Warblers live in closer proximity to highly urbanized

areas and have less specialized habitat preferences than Golden-winged Warblers. They attribute recent increases in hybridization and respective decreases in Golden-winged Warbler populations to the spread of urbanization. Similar to Black-capped Chickadees and Blue-winged Warblers, BCTI are believed to have less specialized habitat preferences than their sister species (Smith 1910, Dixon 1955, Miller 1955, Carter 1986), and therefore may be more tolerant to habitat fragmentation produced by urbanization. Further study is needed to determine whether urban expansion in central Texas plays a partial role in the rates of hybridization between BCTI and TUTI

Previous studies of hybridization in birds have utilized some form of genetic testing on captured birds to determine their ancestry and degree of genetic admixture. Citizen science data (e.g., eBird) can be beneficial in obtaining large sample sizes for potentially more powerful statistical analyses and illustrating large scale patterns, but the risk of identification errors is larger, and it is difficult to measure the extent or direction of gene flow given that all observations are strictly phenotypic. Although phenotype is a fairly reliable determinant of genotype in titmice (Curry 2104), it is still possible for a bird that physically looks like either a pure BCTI or TUTI, to have alleles from the other parent species (cryptic hybrids). Therefore, hybrid individuals are likely more prominent within the hybrid zone than what my study detected. In fact, according to the eBird data, BCTI is the most common titmice type within the hybrid zone. Moreover, throughout the mapping process in ArcGIS Pro, I noticed that BCTI observations expanded eastward between 2012 and 2021. Granted, this could be due to an increase in sampling effort by birders, but it may imply that BCTI populations are expanding further east into TUTI populations and that TUTI alleles are spreading into BCTI populations . If so, then

cryptic BCTI and TUTI hybrids are likely common throughout the hybrid zone. Future studies of this system could use genotyping of captured birds to confirm the classification of titmice and produce more accurate estimates of their relative abundances across the hybrid zone although this would entail much effort and time.

Further examination of the magnitude and direction of the relationships between titmice ancestry and specific habitat characteristics may help determine whether habitat acts as a selective force on genotypes within the BCTI  $\times$  TUTI species complex. Such findings could help resolve questions over the initial formation of the hybrid zone and whether we could expect distributions of the parent species and hybrids to change as habitat continues to evolve within Texas and Oklahoma. In a greater context, a study combining detailed genetic data and habitat analyses could provide further insight into the role of habitat, anthropogenic disturbance, directionality of gene flow, and species range expansion in facilitating hybridization in birds and perhaps other species.

### **III. ANALYZING HABITAT ASSOCIATIONS WITH CAMERA-TRAP AND FIELD SURVEY DATA**

Given that eBird checklists do not report specific hybrid phenotypes (beyond simply “hybrid”), the objective of this study was to determine if titmice belonging to different phenotypic classifications differ in their habitat associations. Through the course of his studies on the TUTI × BCTI hybrid zone, Dixon (1955) developed a hybrid index (hereafter HI) that uses plumage coloration of the crest and forehead to classify titmice on a scale from 0 to 6. The method was also more recently used by Curry and Patten (2014). A score of 0 is assigned to phenotypically pure TUTI individuals and a score of 6 to phenotypically pure BCTI individuals, with hybrids scored somewhere in between depending on their degree of phenotypic intermediacy (Figure 14). I conducted birding surveys and set up camera traps at various sites that encompassed the eastern, western, and central portions of the hybrid zone to more closely identify titmice following Dixon’s HI. The habitat associations of these observed titmice were then analyzed in a GIS framework with the NLCD raster layers at a fine spatial scale (no more than 500 m radius buffers around each sighting). This fine scale was used to obtain information about habitat types located within the immediate vicinity of observed titmice and to compare with the habitat associations found at the landscape scale in the previous eBird study. I expected to find similar associations with land cover types as was found in the previous study, however, I expected that percentages of canopy cover and impervious surfaces would hold more significance at a spatial scale that focused on areas of immediate use by titmice. In these areas that titmice actively forage, nest, and guard, vegetation structure and ground cover may play a more important role in determining the occupancy and

abundance of different titmice classes. Therefore, I hypothesized that (1) titmice classified as TUTI or leaning towards TUTI (HI values 0-1) would associate with deciduous forest habitats and dense canopy cover, (2) titmice classified as BCTI or leaning towards BCTI (HI values 5-6) would associate with coniferous and mixed forest habitats with moderate to high canopy cover, and (3) titmice classified as distinctly hybrid (HI values 2-4) would be associated with intermediate habitats regarding land cover types, and habitats impacted by human development, that is areas with moderate to high proportions of impervious surfaces and moderate to low canopy cover.

## **Methods**

### Study Sites

From late March to mid-July of 2022, I collected data for titmice phenotypes at a total of ten sites across Austin, San Marcos, and San Antonio. Although these locations were partially chosen due to their close proximity to San Marcos, they were also of interest due to high hybrid occurrence discovered in the e-Bird data and the variety of habitat types they encompassed, including human disturbed habitats. The specific sites were chosen to include a variety of habitat types, levels of human disturbance, and locations within the hybrid zone (i.e. eastern, western, and central portions) although no sites were located along the edges of the zone. At all ten sites I conducted birding surveys. Additionally, camera traps were set up at six of the ten sites to aid in obtaining more data.

Three camera trap sites were established in Austin: The Lady Bird Johnson Wildflower Center (hereafter WFC), Louis Rene Barrera Indiangrass Wildlife Sanctuary

(hereafter Indiangrass), and Onion Creek Wildlife Sanctuary (hereafter Onion Creek). The WFC is located among the suburbs of southwest Austin (western portion of hybrid zone). It is a botanical garden and research center owned by the University of Texas at Austin. The property has a substantial amount of natural habitat with numerous hiking trails. The trails cut through a heterogenous landscape made up of grasslands and dense tree stands composed of oak, mesquite, and juniper trees along with a wide variety of herbaceous flowering plants. I utilized these trails to conduct a majority of my walking bird surveys and to access camera traps (see next section). Indiangrass is a sanctuary maintained by Texas Parks and Wildlife (TPWD) and is located adjacent to Lake Walter E. Long in northeast Austin (eastern portion of hybrid zone). The surrounding areas are primarily rural and the sanctuary is not accessible to the public. The majority of the preserve is composed of wooded grassland prairie similar to that of the WFC though it contains less herbaceous plants and has a higher proportion of shrubs. Onion Creek is another private sanctuary maintained by TPWD. It is located in southeast Austin (eastern portion of hybrid zone) adjacent to a metropolitan park and is surrounded by semi suburban landscapes. The preserve is primarily composed of dense juniper and mesquite tree stands interspersed with tall grass.

In San Marcos (central portion of hybrid zone), one camera trap site was established at the Meadows Center (hereafter MC) owned by Texas State University and located on Spring Lake, near the main campus. A highly suburbanized landscape made up of major roads and small neighborhoods surrounds the center. A variety of habitat types exists within the property such as dense riparian vegetation surrounding Spring Lake that eventually thins into sparsely wooded grassland. Furthermore, there are steep

hill slopes with fairly dense stands of oak, mesquite, and juniper trees.

In the San Antonio area, I established camera trap sites at two private residences. One was on Cepeda Street in Helotes, a small town on the western outskirts of San Antonio (western portion of hybrid zone). The property (hereafter Cepeda) is a 8 ha plot of land situated in a semi-rural neighborhood. The property has large oak and juniper trees that create substantial canopy cover, although the understory is diffuse, and a small open meadow that transitions into dense juniper tree stands. I also conducted surveys in a semi-rural neighborhood off of Highway 281 near Bulverde on the far north-central side of San Antonio (western portion of hybrid zone). I set up a camera trap on a 0.4 ha property (on O’Kent Street) and conducted surveys by walking the entirety of the surrounding neighborhood. O’Kent is comprised of large, well-spaced oak trees that form moderate canopy cover. Small shrubs and herbaceous plants surround the perimeter of the house on the property. This is the general vegetative composition of all the properties within the neighborhood but dense juniper tree stands exist on properties that are not occupied (i.e., no house).

The four sites that did not have camera traps were all located within San Marcos to obtain more data from the central portion of the hybrid zone, which was under sampled by the camera trap sites. These sites included Blanco Shoals Natural Area, Schule Canyon Natural Area and the surrounding neighborhood, Rio Vista Park, and the Texas State University campus.

## Data Collection

Across all sites (camera trap and non-camera trap sites), I conducted a total of 26 birding surveys. The surveys took place between 0600 and 1100 hours, to coincide with increased bird activity in the morning. For the six sites with camera traps, I performed three surveys in Spring 2022: mid-late April, mid-late May, and mid-late June. Due to unforeseen equipment and weather setbacks, O'Kent was an exception, as it was surveyed only twice, mid-June and early July. The schedule was similar for the four non-camera trap survey sites although some sites did not get three repeated visits due to the sudden or opportunistic nature of their inclusion. The surveys were conducted similar to eBird traveling surveys, in that I would slowly travel on foot in one direction within the designated survey area for no more than two hours. Whenever I encountered a titmouse, typically by listening for singing, I observed the bird through binoculars and recorded their HI score (Figure 14) along with the GPS coordinates of the sighting. Often more than one titmouse would be spotted at the same point. In these cases, the single latitude/longitude point would have multiple titmice observations.

For each of the camera trap sites, I mounted a single Bushnell HD motion capture trail camera to a tree at least 3 m above the ground and recorded the GPS coordinates. All trees selected were surrounded by vegetation deemed suitable for titmice (i.e., moderate to high canopy cover with mixed forest and/or shrub cover). A platform bird feeder was then hung level with the camera within a distance of 5 m from the camera to ensure higher resolution photographs (Figure 15). These feeders were secured with a gridded wire covering to deter squirrels and filled with a mixture of black-oil sunflower seeds, and safflower seeds to attract titmice. The cameras were set to take a photograph every

three seconds upon triggering to increase the likelihood of capturing information for phenotypic classification.

The camera traps were deployed for two weeks at a time before I returned to download photographs, replace batteries, and replenish bird seed. I then examined photographs and used Dixon's HI to classify any titmice that were photographed (Figure 15). These were recorded as counts for each phenotypic category ( HI values 0-6) at the given site for the particular two-week time period. The data were binned into two-week sampling periods to help track my sampling schedule. Each camera trap site, except for O'Kent, had a total of six two-week sampling periods. For a given sampling period, I carefully observed the time stamps of the images that contained titmice to prevent recounting individuals. If within the same hour of the same day I repeatedly saw a titmouse of the same HI value, I would not add to the count of that category. Furthermore, to prevent observation bias, I did not attempt to classify or count a titmouse if I was unable to see both its crest and forehead patch coloration in the photographs.

#### GIS characterization of habitat

At the end of the data collection period, the walking surveys and stationary camera trap data were treated as two separate datasets because of differences in data collection methods. For the camera trap dataset, a total count of birds of each HI value identified over the four month data collection period (i.e., all two week periods) was counted for each site. Summing of counts was not done for the walking survey dataset because all observation points were unique. ArcGIS Pro 2.8.2. (ESRI Software) was used to map and analyze the survey and camera trap data in relationship to habitat

characteristics. The habitat variables of interest were the same as those used in the eBird study: percent deciduous forest, percent evergreen forest, percent mixed forest, percent shrub/scrub, mean percent canopy cover, and mean percent imperviousness. To more accurately depict current habitat characteristics I used the most recent GIS raster data sets released by the NLCD: 2019 Land Cover (CONUS), 2016 USFS Tree Canopy Cover (CONUS), and 2019 Percent Imperviousness (CONUS). The latitude/longitude coordinates of survey observations and camera traps were imported as individual points over the NLCD raster layers.

For each camera trap site, the 'Buffer' tool was used to create circular buffers around each camera trap point to extract habitat data from the NLCD raster layers. Three size buffers were created for each point: 100 m, 250 m, and 500 m radius (Figure 16). The 'Clip Raster' tool was used to clip the three NLCD raster layers within the bounds of each buffer size. Using the NLCD Land Cover layer, I used the 'Tabulate Area' tool to calculate the total area (in square meters) of each land cover class within each buffer at each scale. I then calculated the percent of the land cover for each habitat class (deciduous forest, evergreen forest, mixed forest, and shrub/scrub). For the NLCD Tree Canopy and the NLCD Percent Developed Imperviousness layers, I used the 'Zonal Statistics as Table' tool to calculate the mean percentages of canopy cover and impervious cover across all  $30 \times 30$  m pixels within each buffer at all three spatial scales.

Within the data collection sites, many of the unique points from the walking surveys were within 250 m of one another. The creation of 250 and 500 m buffers around each point would therefore result in extreme overlap of buffers from individual points and cause a lack of independence in the habitat values obtained across buffers. Thus, only

100 m buffers were created around the walking survey points (Figure 17). Although infrequent, if there was an overlap of 50% or more between any of the 100 m buffers, points were removed. If this degree of overlap occurred between two points, one point was randomly deleted. Within the dataset, HI counts from the deleted point were then added to the remaining point. When more than two points had significantly overlapping buffers, the point that existed within the most central part of the overlapping region was chosen to remain and all other points were deleted. The HI counts from the deleted points were then added to the remaining point. The same process used for the camera trap points was then used to extract the percentage of deciduous forest, evergreen forest, mixed forest, and shrub/scrub cover within each 100 m buffer, along with the mean percentages of canopy cover and imperviousness.

### Statistical Analysis

The goal with both the survey and camera trap datasets was to compare habitat associations of titmice belonging to different phenotypic classes (i.e., HI values). However, the sample sizes for both datasets were too small to conduct rigorous statistical analyses to test for differences in mean habitat values across each phenotype classes, or to test for significant relationships between hybrid index values and the various habitat variables. Furthermore, no titmice were classified as hybrid index value 0 (purely TUTI phenotype) or 1 during the data collection period. Therefore, a much simpler approach to detect patterns was adopted. Considering multiple titmice were classified at walking survey points a mean hybrid index value (0-6) based on all sightings was calculated for each 100 m buffer surrounding individual sighting points. A high proportion of these

mean hybrid index values were within the 5-6 range. Therefore the buffers, which also included the extracted values of all six habitat variables, were categorized into two groups: mean hybrid index value = 6, and mean hybrid index value < 6. Buffers that had a mean value of 6 included only BCTI phenotypes, and buffers that had a mean value of less than six included hybrid phenotypes. Welch's t-tests (two-tailed) were then conducted to test for significant differences in the means of the six habitat variables between the two groups. For the camera trap dataset, the mean hybrid index value were also calculated for each camera trap site. These mean values were the same across all three buffer sizes. No titmice were photographed at the Onion Creek camera trap so it was dropped. Due to small sample size and a lack of variation in mean HI values across sites, statistical analyses were not warranted for the camera survey data.

## **Results**

Of the six habitat variables, mean percent canopy cover and percent evergreen forest were significantly different between locations that had mean HI values of six (purely BCTI phenotypes) ( $n = 13$  locations), and locations that had mean HI values of less than six (presence of hybrid phenotypes) ( $n = 23$  locations). Locations with purely BCTI phenotypes had more canopy cover (48% vs. 33%,  $t = 2.14$ ,  $p = 0.04$ ) and greater evergreen coverage (38 % vs. 18%,  $t = 2.14$ ,  $p = 0.04$ ). Although there was not enough replication of the camera trap data ( $n = 5$ ) to conduct statistical analyses, it should be noted there was little variation in mean phenotypes across sites. All camera trap sites had mean HI scores between 5 and 6, leaning towards a purely BCTI phenotype.

## Discussion

Within the Tufted Titmice and Black-crested Titmice hybrid zone there is substantial variation in the plumage phenotypes of hybrid individuals presumably due to variation in genetic admixture. The primary goal of the Chapter 3 study was to determine if titmice belonging to different phenotypic classifications differ in their habitat associations. Assuming plumage phenotype is concordant with genotype, I hypothesized that titmice classified with HI values that leaned towards either parent species (0-1 for TUTI, and 5-6 for BCTI) would associate with the habitat characteristics found to be preferred by the parent species in allopatry, and that titmice classified as distinct hybrids (HI = 2-4) would associate with intermediate or human disturbed habitat types.

Unfortunately, insufficient data were collected from the walking surveys and camera trap surveys to produce reliable evidence for or against my hypothesis. In particular, TUTI was not observed at any site. However, some of the resulting patterns based on BCTI and hybrid observations were in line with the results from my eBird study. Locations (100 m buffers) with strictly BCTI phenotypes had higher percentages of evergreen forest than locations with hybrid phenotypes. This aligned with results from the eBird study where I found BCTI relative abundance to be positively related to percent evergreen forest across all landscape spatial scales. Thus, BCTI individuals have been associated with greater percentages of evergreen forest at both the landscape and local scale. These results imply that within the hybrid zone, BCTI prefer to reside in forests comprised primarily of evergreen vegetation. Additionally, locations with strictly BCTI phenotypes had higher mean percent canopy cover than locations with hybrid phenotypes, a result that was not found in the eBird study. This result may imply that

higher percentages of canopy cover play an important role in determining the occupancy and abundance of BCTI at the local scale, but not at the landscape scale.

A larger sample size for all HI classes may have been needed in the walking surveys to detect differences in associations with the vegetation types (evergreen, deciduous, mixed, and shrub). However, it may also be that vegetation structure such as canopy cover plays a larger role in determining BCTI, TUTI, and hybrid abundances at the local scale than does the type of vegetation. Regarding habitat selection, preferences in vegetation structure is exhibited by many different bird species. Wood et al. (2016) found that Golden-winged Warblers occupied territories with greater structural heterogeneity than Blue-winged Warblers, and that hybrids were intermediate regarding this habitat variable. Similar to warblers, BCTI and TUTI are species that form territories which are utilized year round for foraging and breeding (Pielou 1957, Sherry 1989, Brawn and Samson 1983, Harrap and Quinn 1995). Because territories influence foraging efficiency and reproductive success, titmice are likely very selective of the territories they choose to occupy (Hasselquist 1998, Franklin et al. 2000, Part et al. 2017). Canopy cover and fine-scale heterogeneity of vegetation may be more direct determinants of food availability and variety, along with nesting sites, within territories than are broad-scale land cover categories such as the type of forest (Fuller and Henderson 1992, Hill et al. 2004). In future studies, a combination of remotely-sensed and ground-sourced habitat data could be used to more accurately describe the vegetative structure of territories utilized by titmice so as to test for differences among BCTI, TUTI, and hybrids. The mapping of titmice territories could follow the methods of Rylander (2015), who delineated the territories of BCTI at Freeman Ranch in San Marcos, Texas. This would

require color banding adult titmice and observing their movements and habitat use for a prolonged period. A GPS unit could be used to mark various points where the focal bird stopped to forage or sing during the observation period, and these points can be used to create territory polygons in a GIS where percentages of land cover types, mean canopy cover, and variation in vegetation height (i.e., structural heterogeneity) can be calculated.

Throughout the data collection process, no titmice were identified as HI 1 or 0, even though the eastern sampling sites were located well within the range of TUTI. Furthermore, mean HI values across most sites (survey sites and camera trap sites) skewed towards a BCTI phenotype. This may imply an increased spread of BCTI eastward into TUTI populations and introgression of TUTI alleles into BCTI, as was discussed in the eBird study of Chapter 2. Again this cannot be determined without genetic analyses of individuals and adequate range wide sampling. Future studies of genetic introgression and the role of habitat in the process should increase the number of sites surveyed and ensure survey sites cover more of the hybrid zone, (i.e., including sites further north, south, east, and west). The studies should use genetic information to identify titmice and develop a HI based on genotype. This will provide a more accurate understanding of geneflow within the hybrid zone and how ancestry is related to habitat associations at different spatial scales.

## V. TABLES AND FIGURES

Table 1. The number of grid cells that contain different combinations of BCTI, TUTI, and/or hybrids at each spatial scale as based on eBird data (2012-2021).

<u>Combination</u>	<u>Spatial Scale (km)</u>		
	<u>10 × 10</u>	<u>5 × 5</u>	<u>2.5 × 2.5</u>
BCTI	128	234	337
TUTI	94	154	170
hybrid	2	3	5
BCTI, TUTI	4	6	6
BCTI, hybrid	157	276	408
TUTI, hybrid	59	70	73
BCTI, TUTI, hybrid	54	44	42

Table 2. Comparison of the multiple logistic regression models examining the relationship between the relative abundance of the three titmice types and habitat variables (mean canopy cover, percent deciduous forest, percent evergreen forest, percent mixed forest, and percent shrub) at the  $10 \times 10$  km spatial scale<sup>1</sup>. Results are only shown for models in which the weight ( $w$ ) was  $> 0.001$ .

---

Black-crested Titmouse

<u>Model</u>	<u>k</u>	<u>AIC</u>	<u>ΔAIC</u>	<u>Log-likelihood</u>	<u>w</u>
Evergreen + Mixed + Shrub	9	162.18	0	-72.09	0.5302
Evergreen + Mixed	7	162.95	0.76	-74.47	0.3608
Evergreen + Shrub	7	166.64	4.46	-76.32	0.0570
Mixed	5	168.06	5.88	-79.03	0.0280
Mixed + Shrub	7	169.2	7.02	-77.60	0.0159
Evergreen + Canopy	7	171.48	9.30	-78.74	0.0051
Evergreen	5	172.52	10.34	-81.26	0.0030

Tufted Titmouse

<u>Model</u>	<u>k</u>	<u>AIC</u>	<u>ΔAIC</u>	<u>Log-likelihood</u>	<u>w</u>
Evergreen + Mixed + Shrub	9	119.64	0	-50.82	0.5926
Evergreen + Mixed	7	121.04	1.40	-53.52	0.2943
Mixed + Shrub	7	124.01	4.37	-55.01	0.0667
Mixed	5	124.73	5.09	-57.37	0.0465

Hybrid

<u>Model</u>	<u>k</u>	<u>AIC</u>	<u>ΔAIC</u>	<u>Log-likelihood</u>	<u>w</u>
--------------	----------	------------	-------------	-----------------------	----------

Evergreen + Shrub	7	317.02	0	-151.51	0.8108
Evergreen + Mixed + Shrub	9	320.19	3.16	-151.09	0.1662
Shrub	5	324.79	7.77	-157.39	0.0167
Shrub + Mixed	7	327.88	10.85	-156.94	0.0036
Evergreen	5	330.13	13.11	-160.07	0.0012
Canopy	5	330.78	13.76	-160.39	0.0008
Canopy + Evergreen	7	331.87	14.84	-158.93	0.0005
Evergreen + Mixed	7	33.48	16.46	-159.74	0.0002
Deciduous	5	335.68	18.65	-162.84	0.0001

---

<sup>1</sup> The squared term of each habitat variable, latitude, and longitude of grid cell center were also included in all models.

Table 3. Comparison of the multiple logistic regression models examining the relationship between the relative abundance of the three titmice types and the habitat variables (mean canopy cover, percent deciduous forest, percent evergreen forest, percent mixed forest, and percent shrub) at the  $5 \times 5$  km spatial scale<sup>1</sup>. Results are only shown for models in which the weight ( $w$ ) was  $> 0.001$ .

---

Black-crested Titmouse

<u>Model</u>	<u>k</u>	<u>AIC</u>	<u>ΔAIC</u>	<u>Log-likelihood</u>	<u>w</u>
Evergreen + Mixed + Shrub	9	262.39	0	-122.20	0.6045
Evergreen + Mixed + Shrub + Deciduous	11	265.13	2.74	-121.57	0.1536
Evergreen + Mixed	7	265.33	2.94	-125.67	0.1390
Evergreen + Mixed + Deciduous	9	266.33	3.93	-124.16	0.0843
Evergreen + Shrub	7	271.48	9.09	-128.74	0.0064
Evergreen + Shrub + Canopy	9	272.62	10.23	-127.31	0.0036
Mixed	5	273.16	10.76	-131.58	0.0028
Mixed + Deciduous	7	273.88	11.49	-129.94	0.0019
Mixed + Deciduous + Shrub	9	273.95	11.56	-127.98	0.0019
Mixed + Shrub	7	273.97	11.58	-129.99	0.0018
Deciduous + Evergreen	7	279.96	17.56	-132.98	0.0001

Tufted Titmouse

<u>Model</u>	<u>k</u>	<u>AIC</u>	<u>ΔAIC</u>	<u>Log-likelihood</u>	<u>w</u>
--------------	----------	------------	-------------	-----------------------	----------

Evergreen + Mixed + Shrub	9	134.94	0	-58.47	0.7296
Evergreen + Mixed + Shrub + Deciduous	11	137.63	2.69	-57.81	0.1901
Evergreen + Mixed	7	140.04	5.12	-63.02	0.0568
Evergreen + Mixed + Deciduous	9	142.26	7.32	-62.13	0.0188
Mixed + Shrub	7	145.90	10.97	-65.95	0.0030
Mixed	5	148.32	13.38	-69.16	0.0009
Mixed + Shrub + Deciduous	9	149.29	14.35	-65.64	0.0006
Mixed + Deciduous	7	151.31	16.37	-68.65	0.0002

Hybrid

<u>Model</u>	<u>k</u>	<u>AIC</u>	<u>ΔAIC</u>	<u>Log-likelihood</u>	<u>w</u>
Canopy + Shrub	7	465.21	0	-225.69	0.4165
Canopy + Shrub + Evergreen	9	466.30	3.16	-224.15	0.2406
Shrub	5	467.63	7.77	-228.81	0.1242
Shrub + Evergreen	7	468.24	10.85	-227.12	0.0913
Shrub + Mixed	7	468.88	13.11	-227.44	0.0662
Shrub + Mixed + Evergreen	9	470.31	13.76	-226.15	0.0325
Shrub + Deciduous	7	472.31	14.84	-229.16	0.0119
Shrub + Deciduous + Mixed	9	473.56	16.46	-227.78	0.0064
Shrub + Deciduous + Mixed + Evergreen	11	474.50	18.65	-226.25	0.0040
Canopy	5	475.67		-232.83	0.0022

Mixed	5	476.43	-233.22	0.0015
Canopy + Evergreen	7	476.74	-231.37	0.0013
Evergreen	5	478.23	-234.11	0.0006
Deciduous	5	479.33	-234.67	0.0004
Mixed + Evergreen	7	480.45	-233.23	0.0002
Mixed + Deciduous	7	481.19	-233.59	0.0001
Deciduous + Evergreen	7	482.39	-234.20	0.0001

---

<sup>1</sup> The squared term of each habitat variable, latitude, and longitude of grid cell center were also included in all models.

Table 4. Comparison of the multiple logistic regression models examining the relationship between the relative abundance of the three titmice types and the habitat variables (mean canopy cover, percent deciduous forest, percent evergreen forest, percent mixed forest, and percent shrub) at the  $2.5 \times 2.5$  km spatial scale<sup>1</sup>. Results are only shown for models in which the weight ( $w$ ) was  $> 0.001$ .

---

Black-crested Titmouse

<u>Model</u>	<u>k</u>	<u>AIC</u>	<u>ΔAIC</u>	<u>Log-likelihood</u>	<u>w</u>
Evergreen + Mixed + Shrub + Deciduous	11	397.95	0	-187.98	0.6970
Evergreen + Mixed + Shrub	9	399.73	1.78	-190.87	0.2863
Evergreen + Mixed + Deciduous	9	406.74	8.78	-196.37	0.0086
Evergreen + Mixed	7	407.81	9.86	-194.91	0.0050
Evergreen + Shrub	7	408.84	10.89	-197.42	0.0030

Tufted Titmouse

<u>Model</u>	<u>k</u>	<u>AIC</u>	<u>ΔAIC</u>	<u>Log-likelihood</u>	<u>w</u>
Evergreen + Mixed	7	149.71	0	-67.86	0.5531
Evergreen + Mixed + Deciduous	9	151.59	1.88	-66.79	0.2163
Evergreen + Mixed + Shrub	9	152.14	2.43	-67.07	0.1638
Evergreen + Mixed + Shrub + Deciduous	11	154.64	4.93	-66.32	0.0469

Mixed	5	157.53	7.81	-73.76	0.0111
Mixed + Deciduous	7	158.77	9.06	-72.38	0.0060
Mixed + Shrub	7	161.02	11.31	-73.51	0.0019
Mixed + Shrub + Deciduous	9	162.64	12.93	-72.32	0.0009
<u>Hybrid</u>					
<u>Model</u>	<u>k</u>	<u>AIC</u>	<u>ΔAIC</u>	<u>Log-likelihood</u>	<u>w</u>
Shrub + Deciduous	7	649.34	0	-317.67	0.5434
Shrub	5	650.68	1.35	-320.34	0.2768
Shrub + Mixed + Deciduous	9	653.39	4.05	-317.70	0.0716
Shrub + Evergreen	7	654.50	5.16	-320.25	0.0411
Shrub + Mixed	7	654.51	5.17	-320.25	0.0499
Shrub + Mixed + Evergreen + Deciduous	11	657.05	7.71	-317.52	0.0115
Deciduous	5	658.24	8.91	-324.12	0.0063
Shrub + Evergreen + Mixed	9	658.25	8.92	-320.13	0.0063
Deciduous + Mixed	7	662.29	12.96	-324.15	0.0008
Mixed	5	663.54	14.20	-326.77	0.0004
Deciduous + Evergreen	7	663.85	14.51	-324.93	0.0004
Evergreen	5	665.25	15.92	-327.63	0.0002
Canopy	5	666.90	17.57	-328.45	0.0001

---

<sup>1</sup> The squared term of each habitat variable, latitude, and longitude of grid cell center were also included in all models.

Table 5. Importance values and coefficients (from un-squared terms) of five habitat variables at each of the three spatial scales ( $10 \times 10$  km,  $5 \times 5$  km, and  $2.5 \times 2.5$  km grid cells) for each titmouse type as derived from the multiple logistic regression models (Tables 2 – 4). The importance values represent the summed model weights that included the given variable. Coefficients shown are those that were significant from the top model of the given spatial scale by titmouse type combination.

	<u>BCTI</u>		<u>TUTI</u>		<u>Hybrids</u>	
	<u>Coefficient</u>	<u>Importance</u>	<u>Coefficient</u>	<u>Importance</u>	<u>Coefficient</u>	<u>Importance</u>
$10 \times 10$						
Canopy	—	0.005	—	0	—	0.001
Deciduous	—	0	—	0	—	0
Evergreen	<b>0.089</b>	0.956	<b>-0.146</b>	0.887	0.092	0.979
Mixed	<b>-0.362</b>	0.935	<b>0.736</b>	1	—	0.170
Shrub	—	0.603	—	0.659	—	0.997
$5 \times 5$						
Canopy	—	0.004	—	0	0.101	0.661
Deciduous	—	0.241	—	0.210	—	0.023
Evergreen	<b>0.059</b>	0.992	<b>-0.067</b>	0.995	—	0.371
Mixed	<b>-0.307</b>	0.990	<b>0.681</b>	1	—	0.111
Shrub	<b>-0.072</b>	0.772	<b>0.183</b>	0.923	—	0.994
$2.5 \times 2.5$						
Canopy	—	0	—	0	—	0
Deciduous	—	0.706	—	0.270	—	0.634
Evergreen	<b>0.046</b>	1	<b>-0.053</b>	0.980	—	0.060
Mixed	<b>-0.209</b>	0.997	<b>0.580</b>	1	—	0.141
Shrub	-0.080	0.986	—	0.214	—	1

Table 6. Results of the Principal Components Analysis applied to five habitat variables at each of the three spatial scales ( $10 \times 10$  km,  $5 \times 5$  km, and  $2.5 \times 2.5$  km grid cells). The percent of the total explained variation among the variables is given along with factor loadings for PCAs that included latitude and longitude and PCAs that excluded these two variables.

Factor loadings								
	<u>% var.</u>	<u>Lat.</u>	<u>Lon.</u>	<u>Canopy</u>	<u>Deciduous</u>	<u>Evergreen</u>	<u>Mixed</u>	<u>Shrub</u>
$10 \times 10$								
PC 1	35.6	-0.350	-0.514	0.328	-0.269	0.430	-0.116	0.485
PC 2	26.4	0.059	-0.225	-0.601	-0.497	-0.431	-0.305	0.243
PC 1	38.5	—	—	0.706	0.183	0.670	0.063	0.124
PC 2	31.0	—	—	-0.068	-0.648	0.197	-0.511	0.535
$5 \times 5$								
PC 1	34.5	-0.390	-0.504	0.392	-0.149	0.4774	-0.076	0.429
PC 2	25.3	-0.107	-0.276	-0.566	-0.526	-0.401	-0.229	0.318
PC 1	38.7	—	—	0.700	0.239	0.664	0.045	0.098
PC 2	27.1	—	—	-0.042	-0.625	0.230	-0.537	0.517
$2.5 \times 2.5$								
PC 1	31.2	-0.391	-0.533	0.344	-0.204	-0.466	-0.104	0.418
PC 2	25.4	-0.113	-0.272	-0.2613	-0.437	-0.461	-0.211	0.300
PC 1	37.2	—	—	0.708	0.212	0.670	0.068	0.014
PC 2	26.0	—	—	-0.020	-0.627	0.269	-0.585	0.438

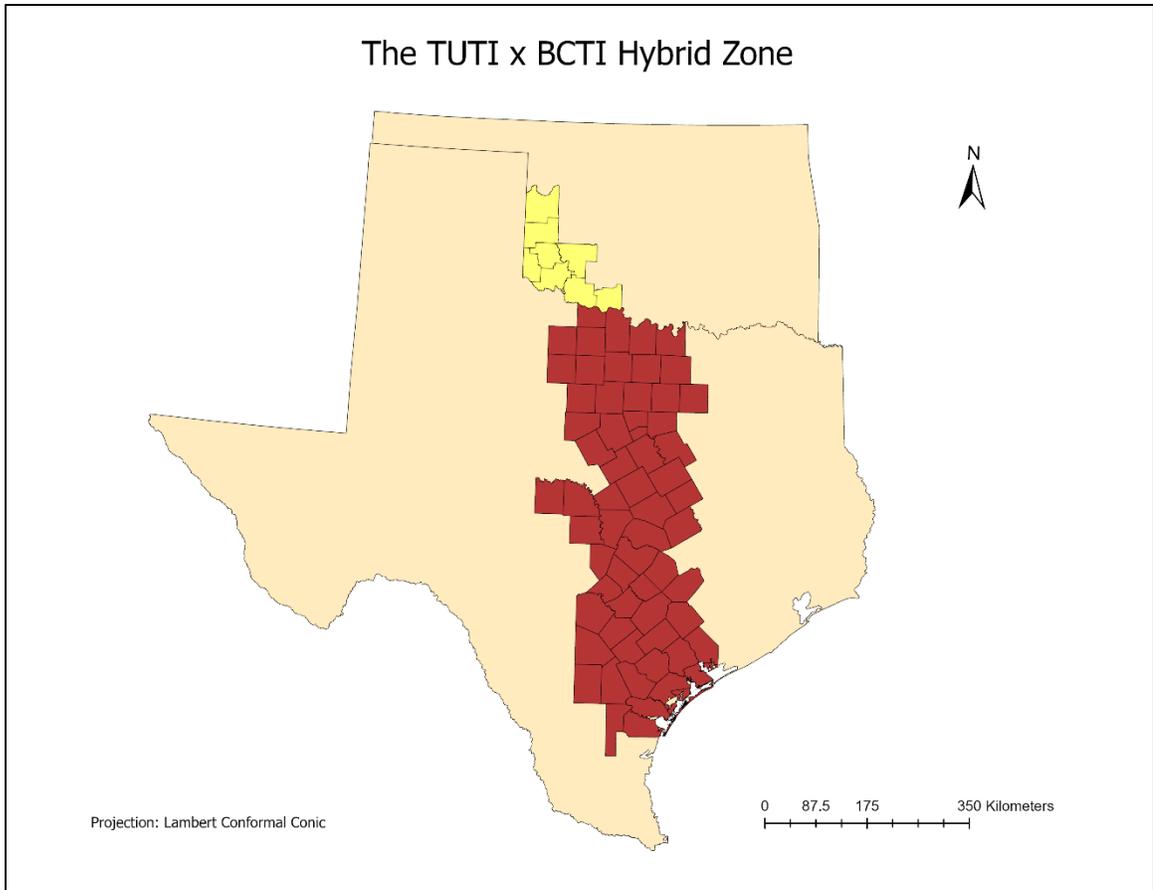


Figure 1. An estimate of the current extent of the Tufted  $\times$  lack-crested titmouse hybrid zone that spans central Texas (red portion) and southwest Oklahoma (yellow portion). The map includes counties that have recorded hybrid sightings in the eBird database (2012-2020).

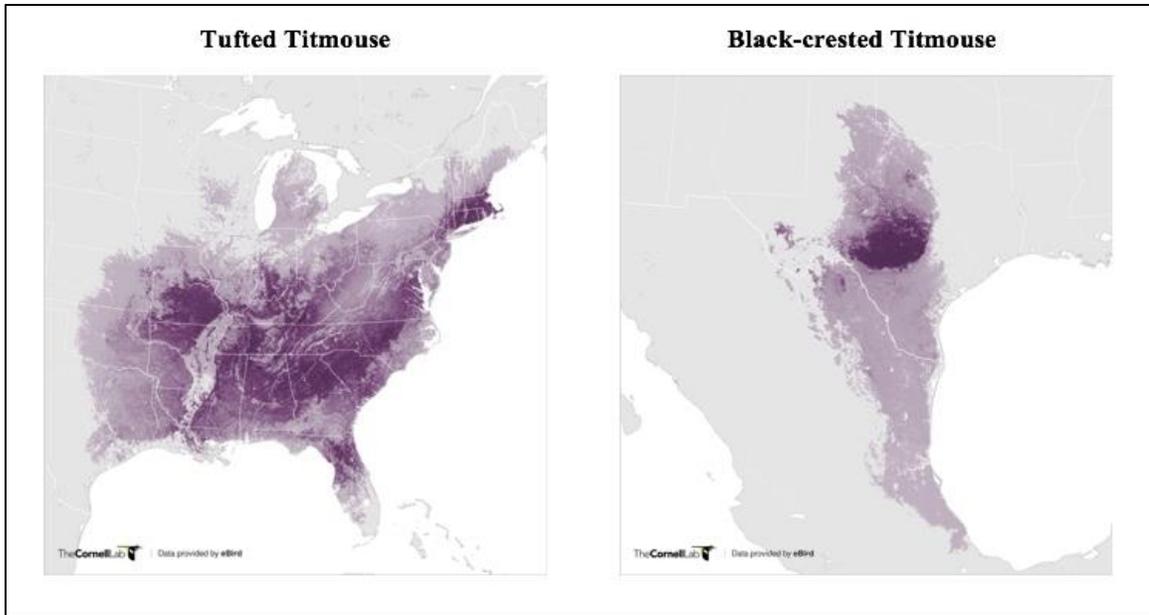


Figure 2. The year-round geographic ranges of the Tufted Titmouse and the Black-crested Titmouse in North America. Darker shades of purple indicate higher relative abundance. Maps provided by the Cornell Lab of Ornithology with data from eBird (Fink et al. 2020).

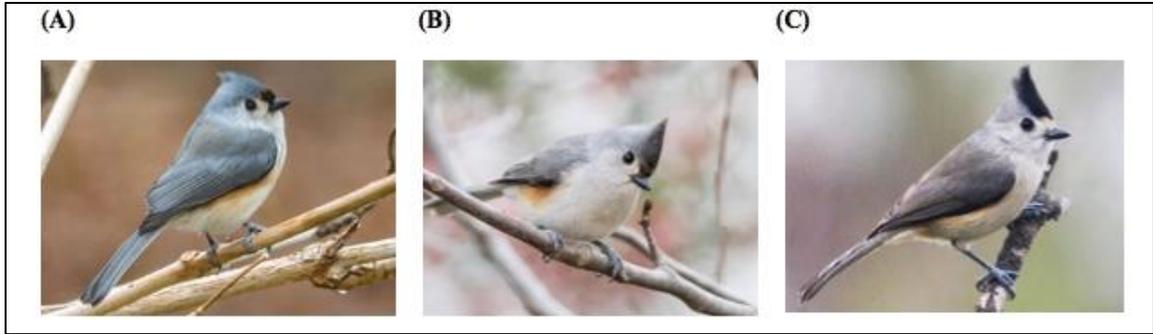


Figure 3. Adult plumage morphology of the (A) Tufted Titmouse (McGann 2016), (B) Tufted Titmouse  $\times$  Black-crested Titmouse hybrid (Lasley 2018), and (C) Black-crested Titmouse (Richards 2017).

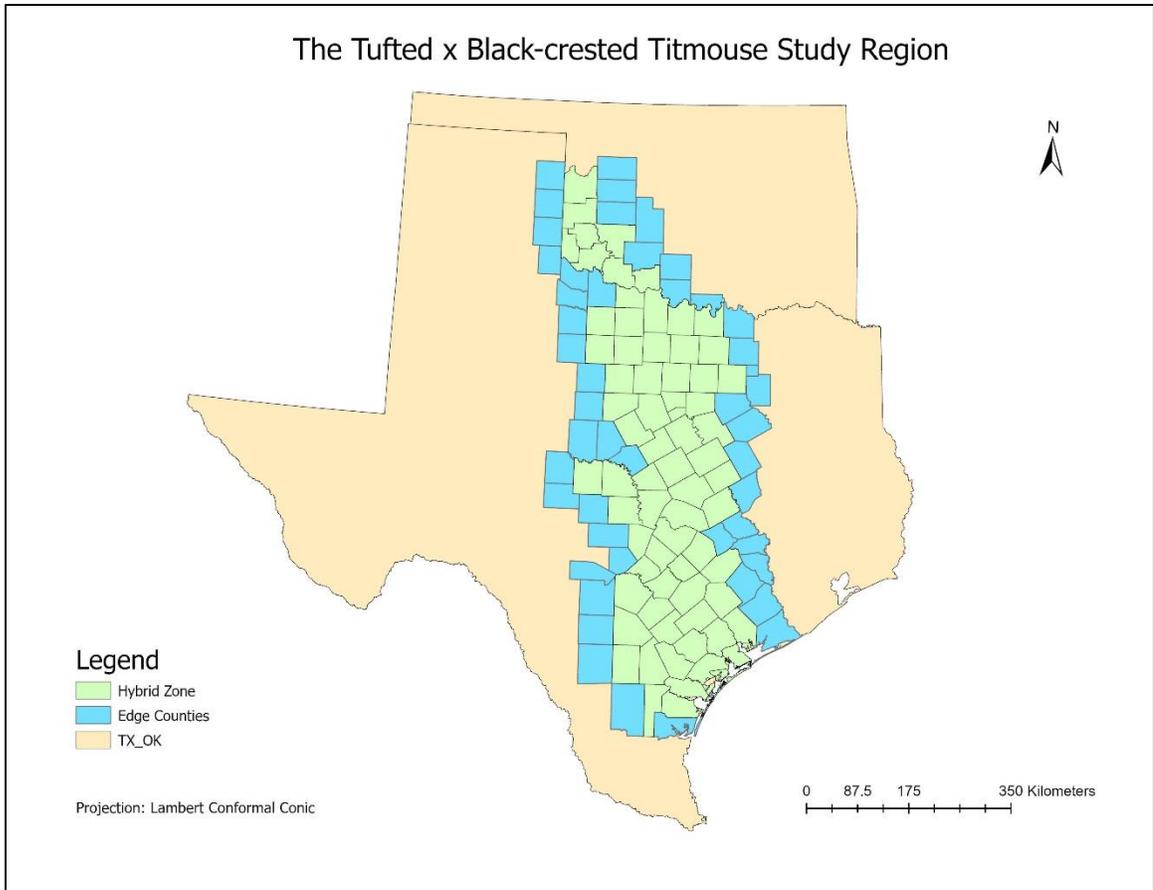


Figure 4. The designated study region that contains the hybrid zone (green portion) along with a narrow band of surrounding counties that have recorded sightings for either parent species but not both (blue portion).

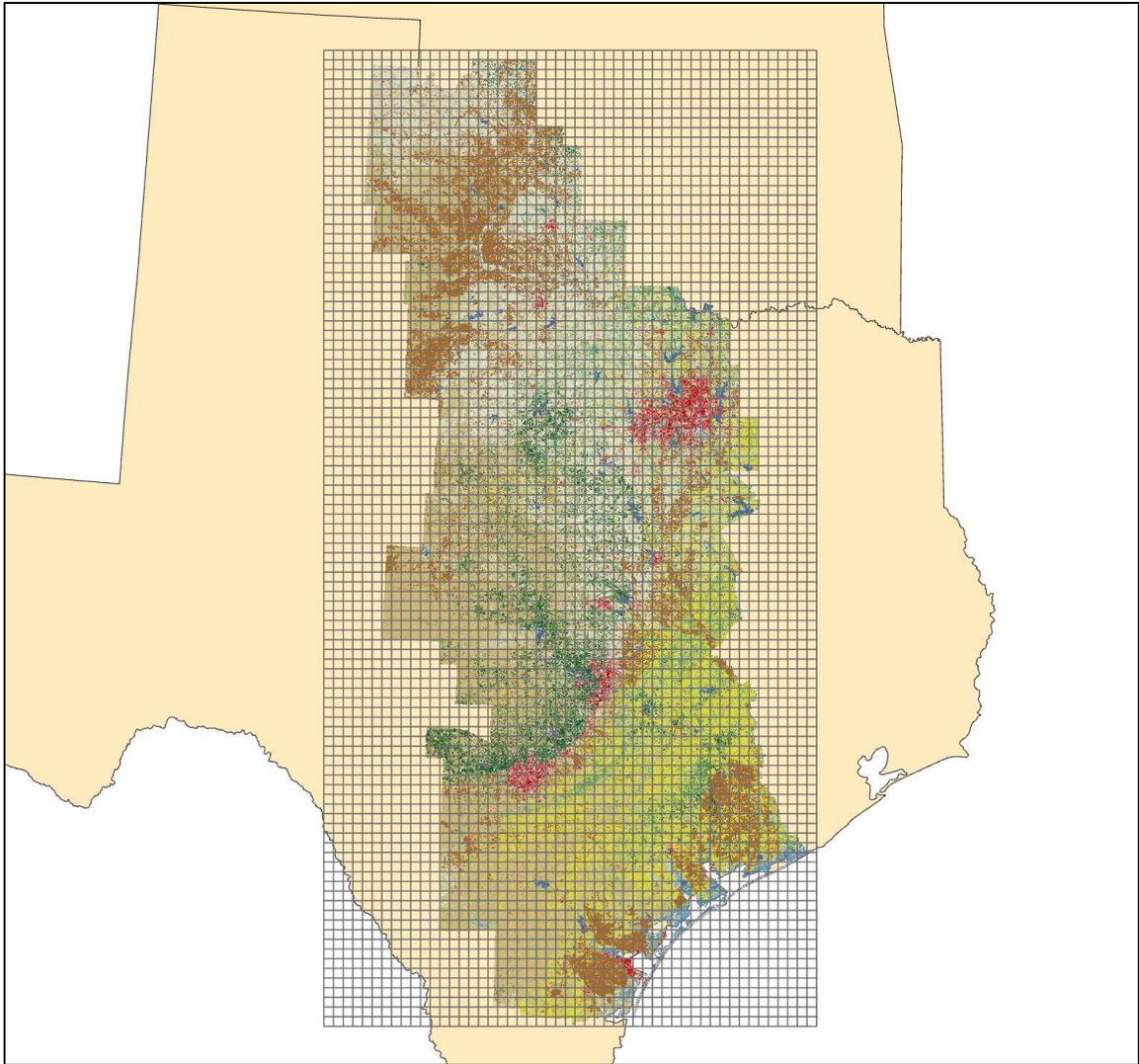


Figure 5. The  $10 \times 10$  km grid made with the 'Create Fishnet' tool in ArcGIS Pro. Each grid cell is a  $10 \text{ km}^2$  polygon that can be used to extract and analyze data. Here the grid is laid over the NLCD 2016 Land Cover layer that was clipped to the study region.

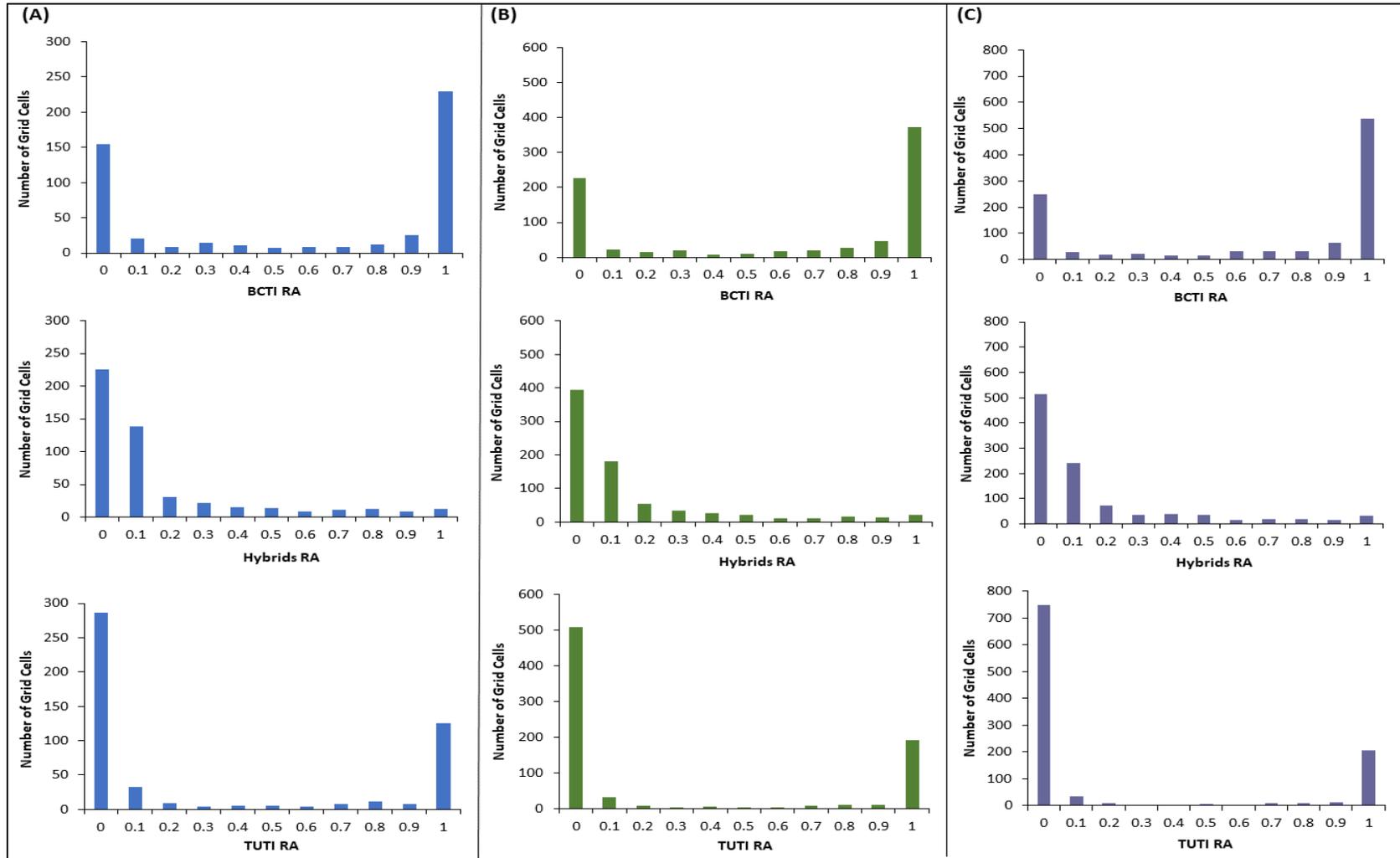


Figure 6. The number of grid cells within each relative abundance category (0.1 increments) for BCTI, TUTI, and hybrids at the (A)  $10 \times 10$  km, (B)  $5 \times 5$  km, and (C)  $2.5 \times 2.5$  km spatial scales as based on eBird data (2012-2021)

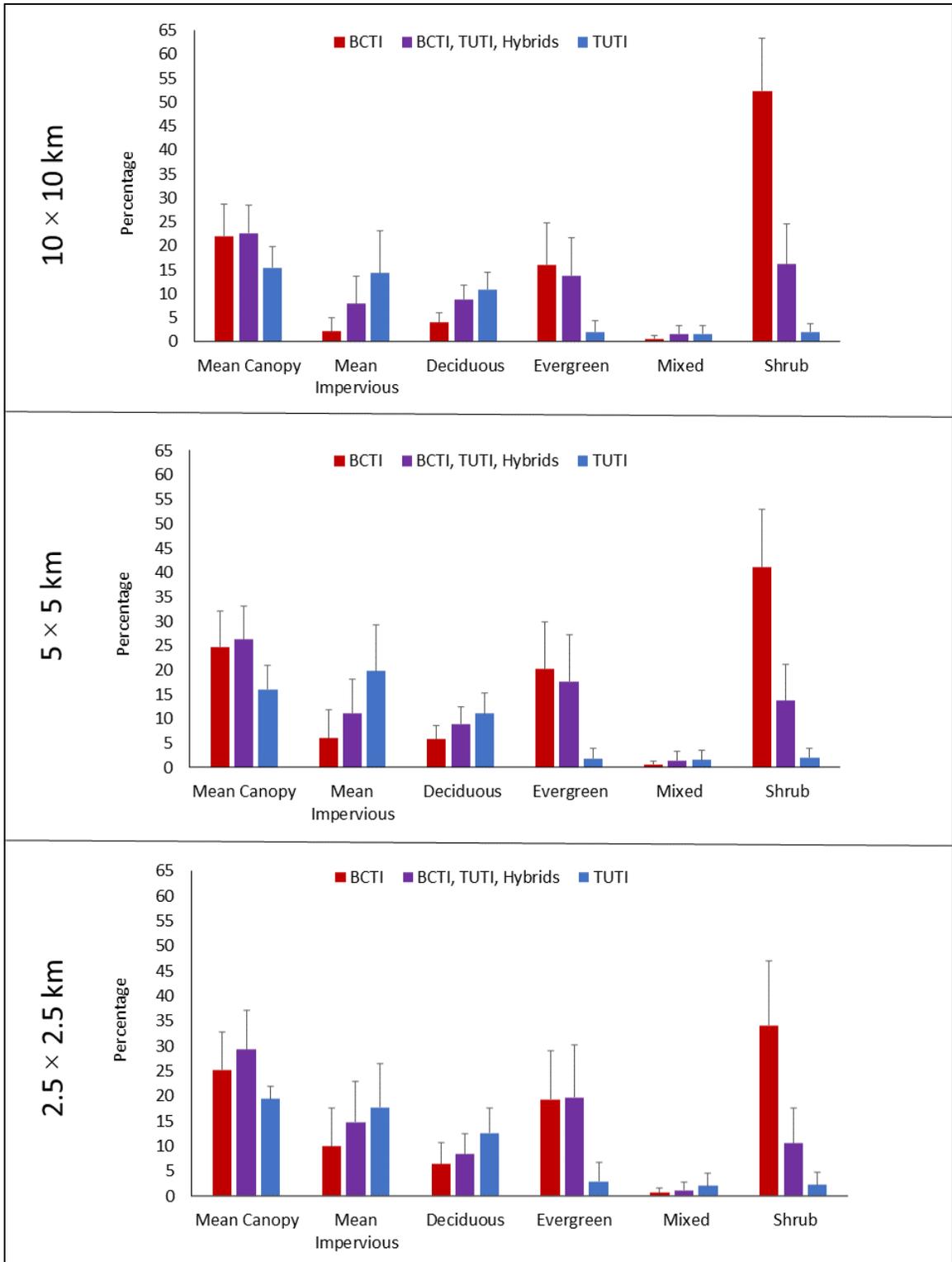


Figure 7. Mean values of the habitat variables across grid cells at the three different spatial scales categorized as only BCTI present, only TUTI present, or both parents and/or hybrids present as based on the eBird data. The standard deviation (SD) bars are set to 0.5 x SD for display purposes.

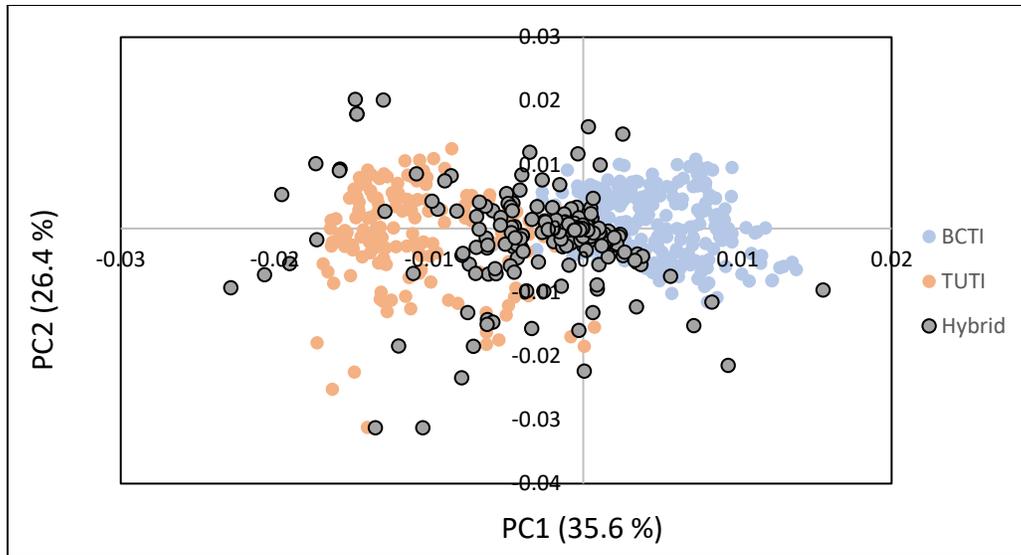


Figure 8. PCA at the  $10 \times 10$  km spatial scale including latitude, longitude, and five habitat variables: mean canopy cover, percent deciduous forest, percent evergreen forest, percent mixed forest, and percent shrub. PC1 is on the x-axis and PC2 is on the y-axis.

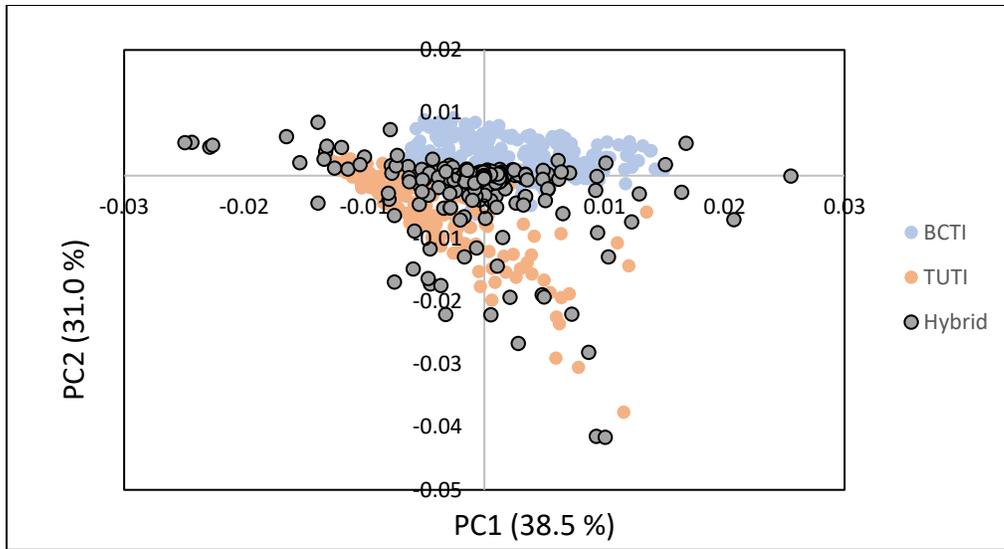


Figure 9. PCA at the  $10 \times 10$  km spatial scale including five habitat variables: mean canopy cover, percent deciduous forest, percent evergreen forest, percent mixed forest, and percent shrub, but with latitude and longitude removed. PC1 is on the x-axis and PC2 is on the y-axis.

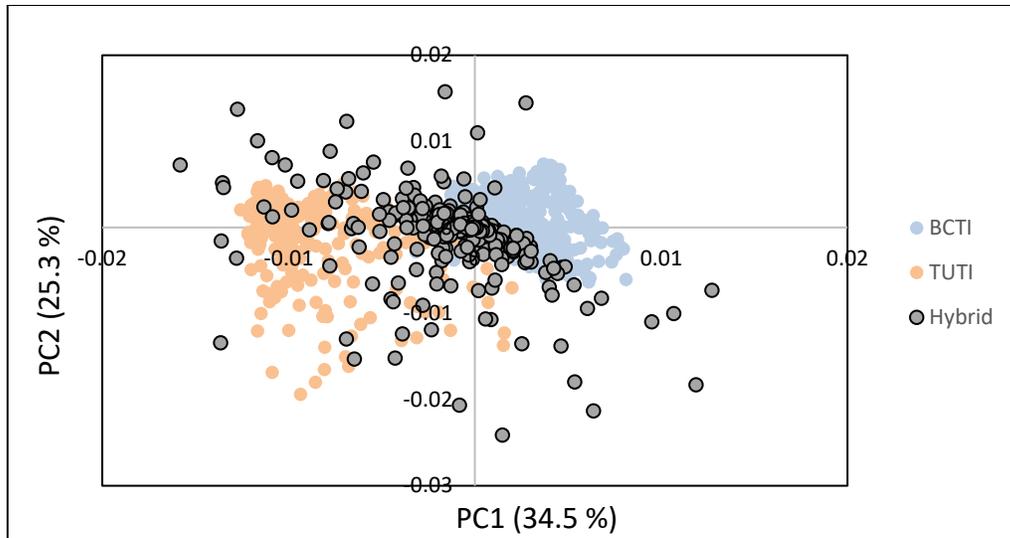


Figure 10. PCA at the  $5 \times 5$  km spatial scale including latitude, longitude, and five habitat variables: mean canopy cover, percent deciduous forest, percent evergreen forest, percent mixed forest, and percent shrub. PC1 is on the x-axis and PC2 is on the y-axis.

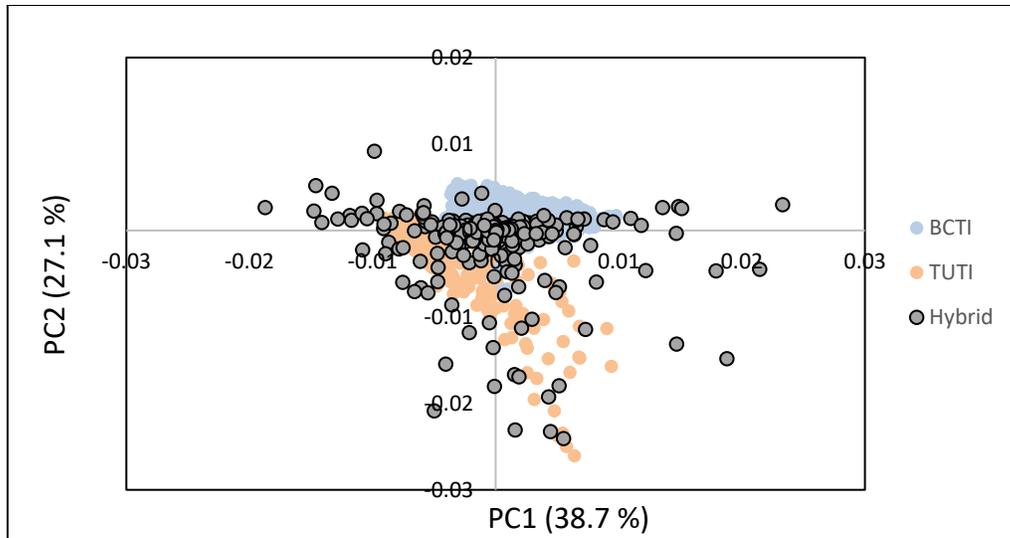


Figure 11. PCA at the  $5 \times 5$  km spatial scale including five habitat variables: mean canopy cover, percent deciduous forest, percent evergreen forest, percent mixed forest, and percent shrub, but with latitude and longitude removed. PC1 is on the x-axis and PC2 is on the y-axis.

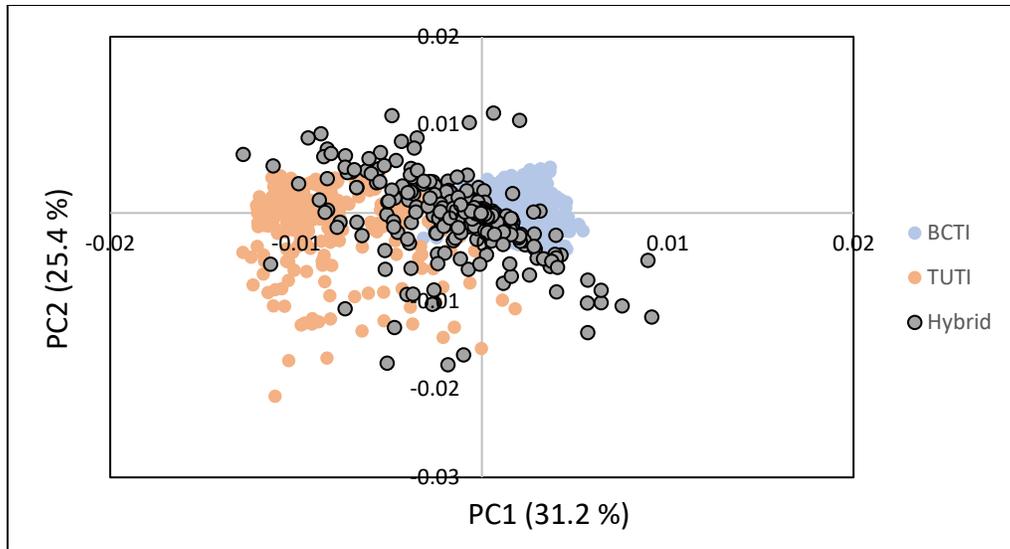


Figure 12. PCA at the  $2.5 \times 2.5$  km spatial scale including latitude, longitude, and five habitat variables: mean canopy cover, percent deciduous forest, percent evergreen forest, percent mixed forest, and percent shrub. PC1 is on the x-axis and PC2 is on the y-axis.

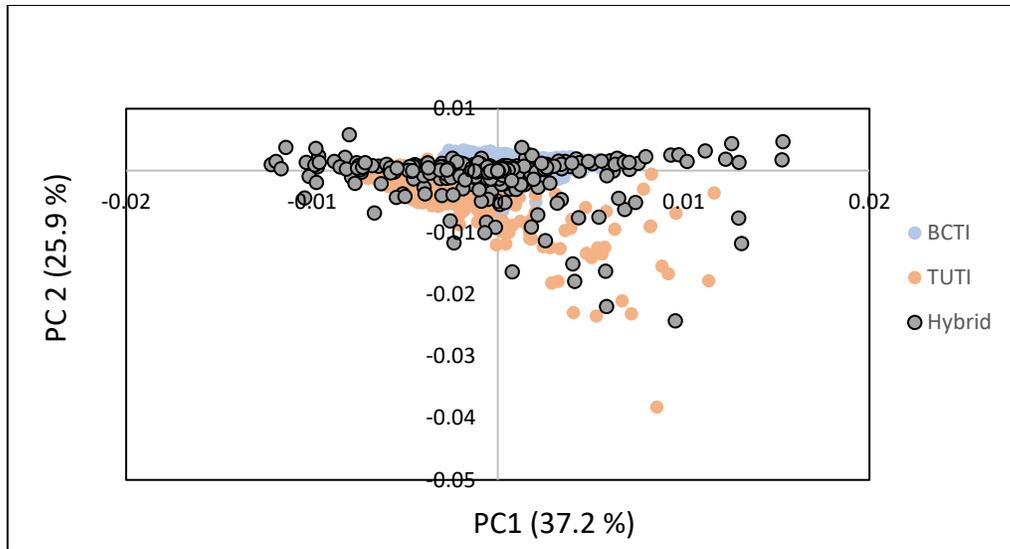


Figure 13. PCA at the  $2.5 \times 2.5$  km spatial scale including five habitat variables: mean canopy cover, percent deciduous forest, percent evergreen forest, percent mixed forest, and percent shrub, but with latitude and longitude removed. PC1 is on the x-axis and PC2 is on the y-axis.

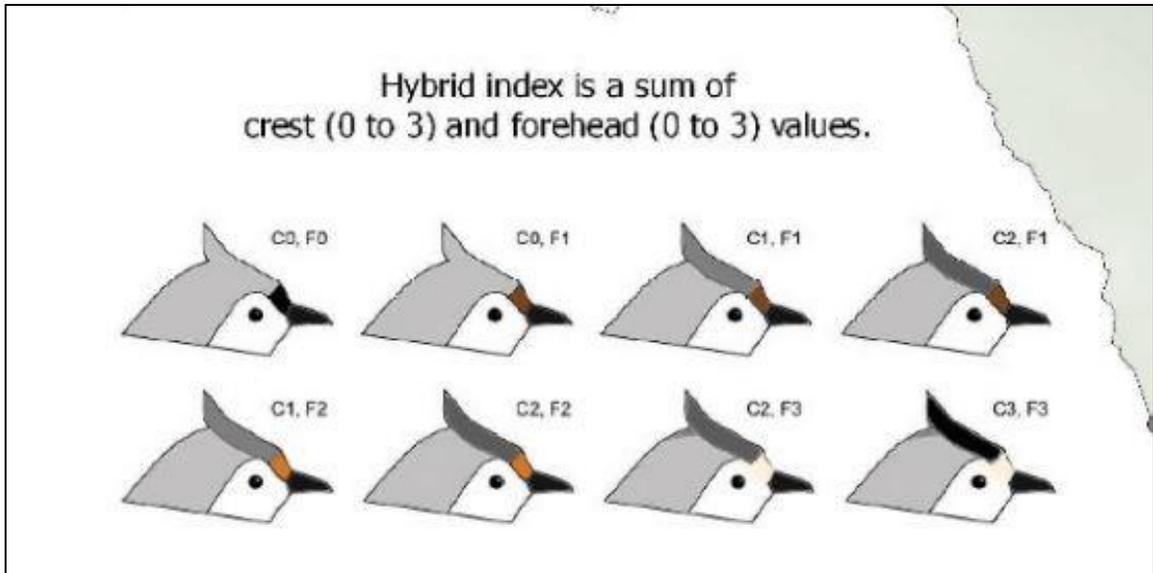


Figure 14. The phenotypic hybrid index developed by Dixon (1955) is a sum of crest (0-3) and forehead values (0-3). Crest values summarized by Curry and Patten (2014): 0 = Gray, same as coloration of the neck and back (TUTI); 1 = Dark gray, distinct from neck and back coloration; 2 = Dull black or very dark gray that blends at the edges; 3 = Shiny black crest with a definite margin (BCTI). Forehead values summarized by Curry and Patten (2014): 0 = Black with minimal brown along the edges (TUTI); 1 = Dark chestnut or dark brown; 2 = Light brown or chestnut; 3 = White or beige color that blends with the facial coloration (BCTI).



Figure 15. Two Black-crested Titmice (HI = 6) photographed by a Bushnell HD motion capture trail camera at the Ladybird Johnson Wildflower Center camera trap site in Austin, Texas.

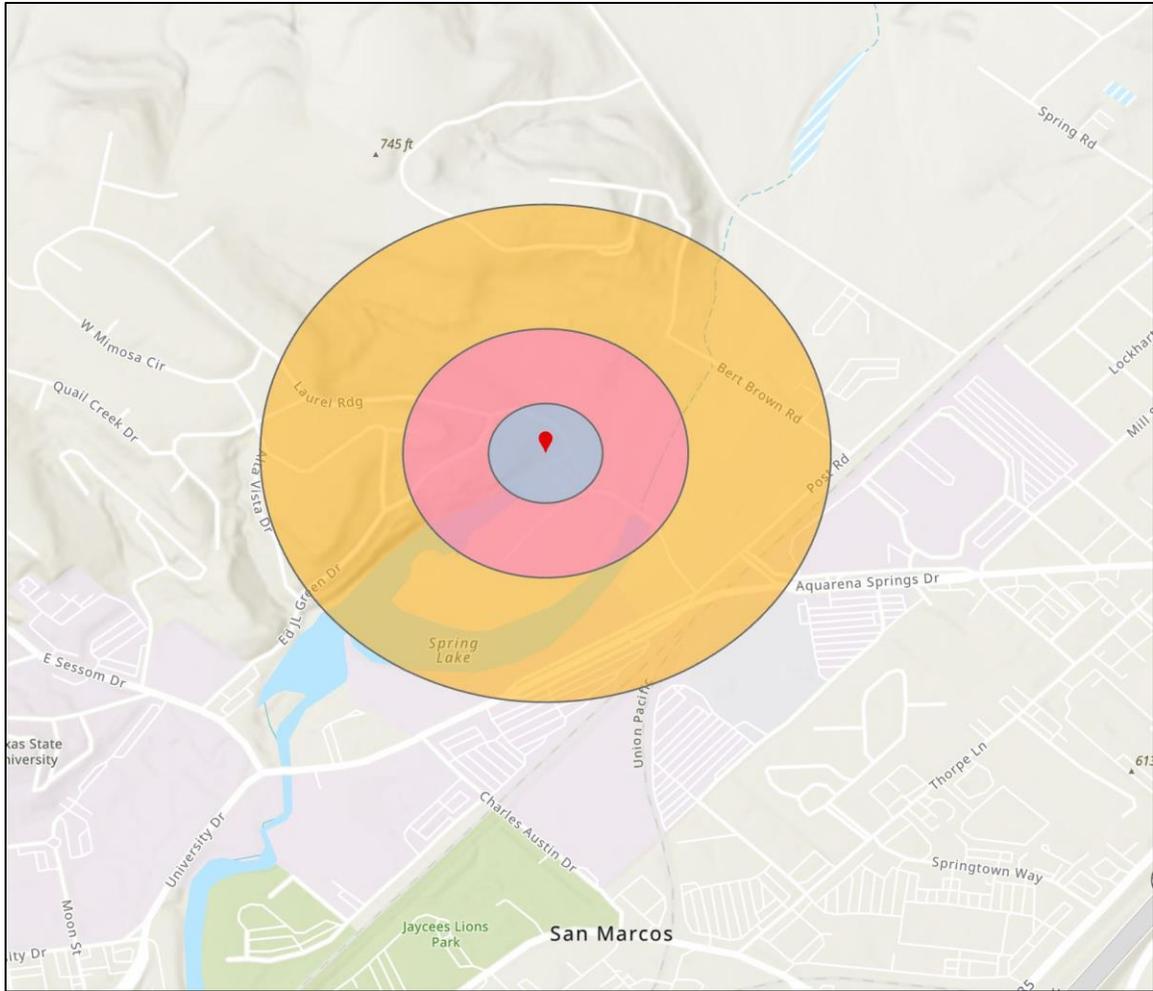


Figure 16. Buffers of 500 m radius (orange), 250 m radius (pink), and 100 m radius (blue) were created around each camera trap location to aid in extracting habitat data from the NLCD raster layers (not shown here). The camera trap depicted was located at the Meadows Center in San Marcos, Texas.

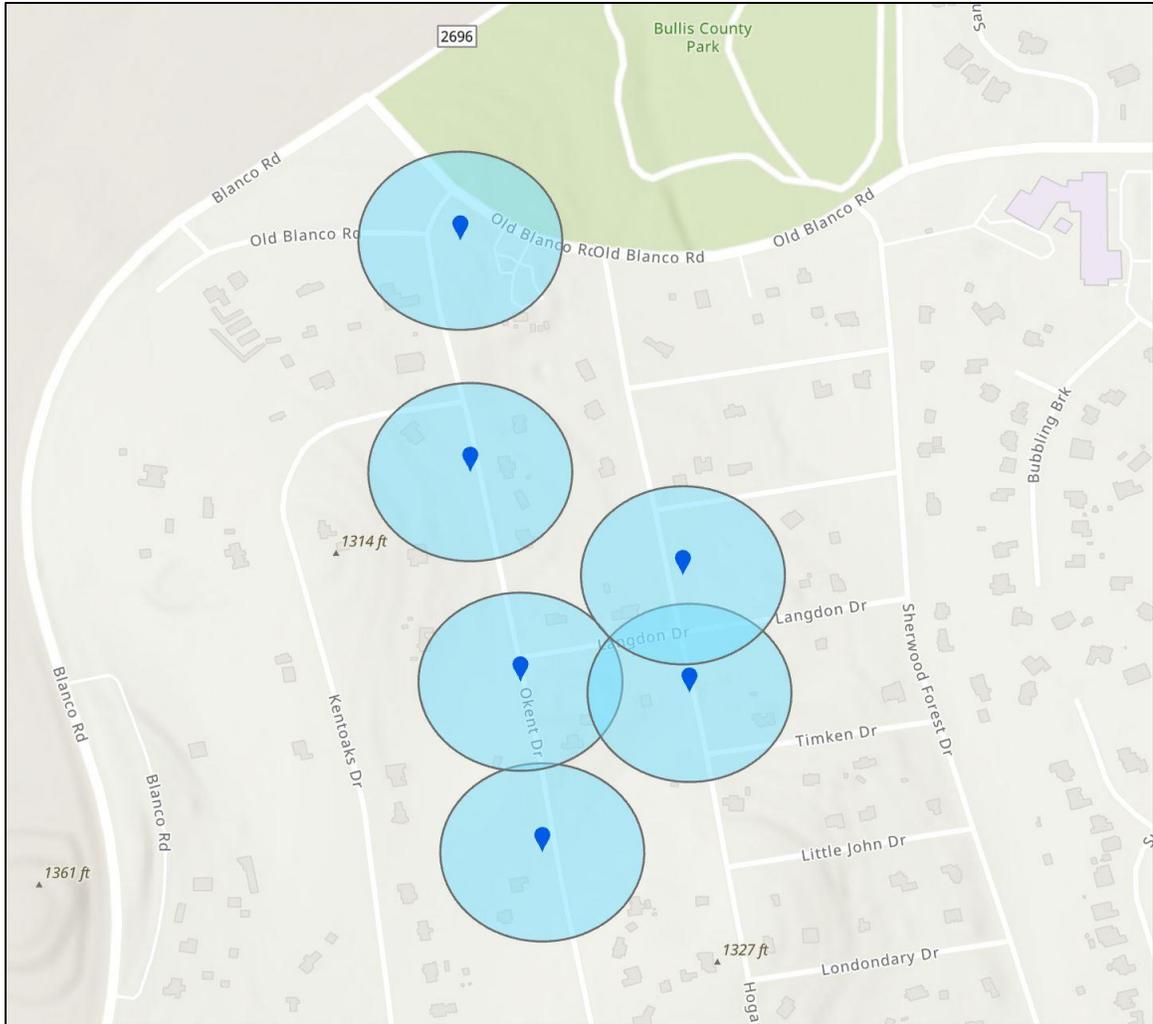


Figure 17. Buffers of 100 m radius were created around the unique walking survey points to aid in extracting data from the NLCD raster layers (not shown here). The survey points depicted are from the O'kent site in San Antonio, Texas.

## LITERATURE CITED

- Anderson, E. 1948. Hybridization of the habitat. *Evolution* 2:1-9.
- Apps, C. D., N. J. Newhouse, and T. A. Kinley. 2002. Habitat associations of American Badgers in southeastern British Columbia. *Canadian Journal of Zoology* 80:1228-1239.
- Avise, J. C., and R. M. Zink. 1988. Molecular genetic divergence between avian sibling species: King and Clapper Rails, Long-billed and Short-billed Dowitchers, Boat-tailed and Great-tailed Grackles, and Tufted and Black-crested Titmice. *The Auk* 105:516-528.
- Banks, R. C., C. Cicero, J. L. Dunn, A. W. Kratter, P. C. Rasmussen, J. D. Rising, and D. F. Stotz. 2002. Forty-third supplement to the American Ornithologists' Union Checklist of North American Birds. *The Auk* 119:897-906.
- Barton, N. H., and G. M. Hewitt. 1985. Analysis of hybrid zones. *Annual Review of Ecology and Systematics* 16:113-148.
- Bent, A. C. 1946. Life Histories of North American jays, crows, and titmice, Part I. United States National Museum Bulletin 191.
- Bigelow, R. S. 1965. Hybrid zones and reproductive isolation. *Ecology* 19:449-458.
- Braun, D., G. B. Kitto, and M. J. Braun, 1984. Molecular population genetics of Tufted and Black-crested forms of *Parus bicolor*. *The Auk* 101:170-173.
- Brauning, D. 1992. Atlas of Breeding Birds in Pennsylvania. University of Pittsburgh Press, Pittsburgh, PA, USA.
- Brawn, J. D. and F. B. Samson. 1983. Winter behavior of Tufted Titmice. *The Wilson Bulletin* 95:222-232.

- Callaghan, P. H. 2002. Progress from grassland to shrubland: woody encroachment in North American grasslands. M.S. Thesis, Norman: University of Oklahoma.
- Carling, M. D., and H. A. Thomassen. 2012. The role of environmental heterogeneity in mating reproductive isolation between hybridizing *Passerina* (Aves: Cardinalidae) buntings. *International Journal of Ecology* 2012:1-11.
- Carpenter, A.M., B. A. Graham, G. M. Spellman, and T. M. Burg. 2022. Do habitat and Elevation promote hybridization during secondary contact between three genetically distinct groups of warbling vireo (*Vireo gilvus*)? *Heredity* 128:352-363.
- Carter, M. D. 1986. The parasitic behavior of bronzed cowbird in south Texas. *The Condor* 88:11-25.
- Conner, R. N., J. G. Dickson, B. A. Locke, and C. A. Segelquist. 1983. Vegetation characteristics important to common songbirds in east Texas. *Wilson Bulletin* 95: 349-361.
- Contreras, T. A., and K. E. Sieving. 2011. Leadership of winter mixed-species flocks by Tufted Titmice (*Baeolophus bicolor*): are titmice passive nuclear species? *International Journal of Zoology* 2011.
- Curry, C. M. 2014. The evolution of reproductive isolation in a temporally complex Passerine hybrid zone. Doctoral Dissertation, Norman: University of Oklahoma.
- Curry, C. M., and M. A. Patten. 2014. Current and historical extent of phenotypic variation in the Tufted and Black-crested Titmouse (Paridae) hybrid zone in southern Great Plains. *The American Midland Naturalist* 171:271-300.

- De Dios, R. S., M. Benito-Garzón, and H. Sainz-Ollero. 2006. Hybrid zones between two European oaks: a plant community approach. *Plant Ecology* 187:109-125.
- Diamond, J. M. 1972. The avifauna of the eastern highlands of New Guinea. Nuttall Ornithology Club., Cambridge, MA.
- Dixon, K. L. 1955. An ecological analysis of inter-breeding of crested titmice in Texas. *University of California Publications in Zoology* 54:125-206.
- Dixon, K. L. 1961. "Habitat distribution and niche relationships in North American species of *Parus*" In *Vertebrate Speciation.*, edited by W. F. Blair, 179-216. Austin: University of Texas Press.
- Dixon, K. L. 1978. A distributional history of Black-crested Titmouse. *The American Midland Naturalist* 100:29-42.
- Dixon, K. L. 1990. Constancy of margins of the hybrid zone in titmice of the *Parus* bicolor complex in coastal Texas. *The Auk* 107:184-188.
- Endler, J. A. 1977. Secondary or primary intergradation? In *Geographic Variation, Speciation and Clines.*, 152-178. New Jersey: Princeton University Press.
- Fisher, R. J., and S. K. Davis. 2010. From Wiens to Robel: a review of grassland habitat Selection. *The Journal of Wildlife Management* 74:265-273.
- Franklin, A. B., D. R. Anderson, R. J. Gutiérrez, and K. P. Burnham. 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. *Ecological Monographs* 70:539-590.

- Fuller, R. J., and A. C. B. Henderson. 1992. Distribution of breeding songbirds in Bradfield Woods, Suffolk, in relation to vegetation and coppice management. *Bird Study* 39:73-88.
- Gill, F. B., and B. Slikas. 1992. Patterns of mitochondrial DNA divergence in North American crested titmice. *The Condor* 94:20-28.
- Gillespie, M. 1930. Behavior and local distribution of tufted titmice in winter and spring. *Bird Banding* 1:113-127.
- Graham, B. A., I. Gazeley, K. A. Otter, and T. Burg. 2021. Do phylogeny and habitat influence admixture among four North American chickadee (family: Paridae) species? *Journal of Avian Biology* 52.
- Grant, V. 1971. *Plant Speciation*. Columbia University Press, New York.
- Harrison, R. G., and E. L. Larson. 2016. Heterogenous genome divergence, differential introgression, and the origin and structure of hybrid zones. *Molecular Ecology* 25: 2454-2466
- Harrap, S., and D. Quinn. 1995. *Chickadees, Tits, Nuthatches and Treecreepers*. Princeton University Press, Princeton, New Jersey.
- Hasselquist, D. 1998. Polygyny in great reed warblers: a long-term study of factors contributing to male fitness. *Ecology* 79: 2376-2390.
- Hewitt, G. M. 1988. Hybrid zones-natural laboratories for evolutionary studies. *Trends in Ecology and Evolution* 3:158-167.
- Hill, R. A., S. A. Hinsley, D. L. A. Gaveau, and P.E. Bellamy. Cover: predicting habitat quality for Great Tits (*Parus major*) with airborne laser scanning data. *Remote Sensing* 25:4851-4855.

- Howell, S. N. G., and S. Webb. 1995. A Guide to the Birds of Mexico and Northern Central America. Oxford University Press, New York, NY, USA.
- Hubbard, J. P. 1969. The relationships and evolution of the *Dendrocia coronata* complex. The Auk 86:393-432.
- Jackson, J. F. 1973. The phenetics and ecology of a narrow hybrid zone. Evolution 27:58-68.
- Kark, S., and B. J. Rensberg. 2006. Ecotones: marginal or central areas of transition? Israel Journal of Ecology and Evolution 52:29-53.
- Lack, D. 1933. Habitat selection in birds. With special reference to the effects of afforestation on the Breckland avifauna. Journal of Animal Ecology 2:239-262.
- MacArthur, R. Ah. 1958. Population ecology of some warblers of northeastern coniferous Forests. Ecology 39:599-619.
- MacArthur, R. H., and J. MacArthur. 1961. On birds species diversity. Ecology 42:594-598.
- MacArthur, R. H., J. W. MacArthur, and J. Preer. 1962. On bird species diversity II. Prediction of bird censuses from habitat measurements. American Naturalist 96:167-174.
- Meacham, W. R. 1962. Factors affecting secondary integration between two allopatric populations in the *Bufo woodhousei* complex. American Midland Naturalist 67:282-304.
- Miller, A. H. 1955. The avifauna of the Sierra de Carmen of Coahuila, Mexico. The Condor 57:154-178.

- Moore, W. S. 1977. An evaluation of narrow hybrid zones in vertebrates. *The Quarterly Review of Biology* 52:263-277.
- Moore, W. S., and J. T. Price. 1993. Nature of selection in northern flicker hybrid zone and the implications for speciation theory. In *Hybrid Zones and the Evolutionary Process.*, edited by R. G. Harrison, 196-225. New York: Oxford University Press.
- Muller, J. A., J. A. Veech, and R. M. Kostecke. 2018. Landscape-scale habitat associations of Sprauge's pipits wintering in the southern United States. *Journal of Field Ornithology* 89:326-336.
- Oberholser, H. C. 1974. *The Bird Life of Texas*. University of Texas Press, Austin, TX, USA.
- Ottenburghs, J. R., C. Ydenburg, P. Van Hooft, S. E. Van Wieren, and H. T. Prins. 2015. The avian hybrids project: gathering the scientific literature on avian Hybridization. *International Journal of Avian Science* 157:892-894.
- Pärt, T., J. Knappe, M. Low, M. Öberg, and D. Arlt. 2017. Disentangling the effects of date, individual, and territory quality on the seasonal decline in fitness. *Ecology* 98:2102-2110.
- Patten, M. A., and B. D. Smith-Patten. 2008. Black-crested Titmouse (*Baeolophus atricristatus*). In *The Birds of North America*, no. 717. (A. Poole, Ed.) Cornell Lab of Ornithology, Ithaca, NY.
- Philips, A. R. 1986. *The Known Birds of North and Middle America, Part I. Hirundinidae to Mimidae; Certhiidae*. Denver Museum of Natural History, Denver, CO, USA.
- Pielou, W. P. 1957. A life-history study of the Tufted Titmouse, *Parus bicolor* Linnaeus. Ph.D. dissertation, Michigan State University, East Lansing, MI, USA.

- Pierce, A. A., R. Gutierrez, A. M. Rice, and K. S. Pfennig. 2017. Genetic variation during range expansion: effects of habitat novelty and hybridization. *Proceedings of the Royal Society B: Biological Sciences* 284.
- Pierotti, R., and C. A. Annet. 1993. Hybridization and male parental investment in birds. *The Condor* 95:670-679.
- Pyle, P. 1997. *Identification Guide to North American Birds, Part I: Columbidae to Ploceidae*. Slate Creek Press, Bolinas, CA, USA.
- Rieseberg, L. H., and S. E. Carney. 2008. Plant hybridization. *New Phytologist* 140:599-624.
- Rising, J. D. 1969. A comparison of metabolism and evaporative water loss of Baltimore And bullock orioles. *Comparative Biochemistry and Physiology* 31:915-925.
- Rising, J. D. 1983. The Great Plains hybrid zones. *Current Ornithology* 1:131-157.
- Ritchison, G., T. C. Grubb Jr., and V. V. Pravosudov. Tufted Titmouse (*Baeolophus Bicolor*), version 1.0. In *Birds of the World* (P. G. Rodewald, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA.
- Ruengvirayudh, P., and G. P. Brooks. 2016. Comparing stepwise regression models to The best-subsets models, or, the art of stepwise. *General Linear Model Journal* 42.
- Schluter, D. 2001. Ecology and the origin of species. *Trends in Ecology and Evolution* 16:372-280.
- Seehausen, O., G. Takimoto, D. Roy, J. Jokela. 2008. Speciation reversal and biodiversity Dynamics with hybridization in changing environments. *Molecular Ecology* 17: 20-44.

- Sheldon, F. H., B. Slikas, M. Kinnarney, F. B. Gill, E. Zhao, and B. Silverin. 1992. DNA-DNA hybridization evidence of phylogenetic relationships among major lineages of *Parus*. *The Auk* 109:173-185.
- Sherry, D. F. 1989. Food storing in Paridae. *Wilson Bulletin* 101:289-304.
- Sibley, C. G., and D. A. West. 1959. Hybridization in the rufous-sided towhees of the Great Plains. *The Auk* 76:326-338.
- Smith, A. P. 1910. Miscellaneous bird notes from the lower Rio Grande. *The Condor* 12:93-103.
- Sullivan, B. L., C. L. Wood, M. J. Iliff, R. E. Bonney, D. Fink, and S. Kelling. 2009. eBird: a citizen-based bird observation network in the biological sciences. *Biological Conservation* 142:2282-2292.
- Sun, N-Z., S. Yang, and W. W-G. Yeh. 1998. A proposed stepwise regression method for model structure identification. *Water Resources Research* 34:2561-2572.
- Suthers, H. B., J. M. Bickal, and P. G. Rodewald. 2000. Use of successional habitat and fruit resources by songbirds during autumn migration in central New Jersey. *Wilson Bulletin* 112:249-260.
- Sutton, G. M. 1967. *Oklahoma Birds, their Ecology and Distribution with Comments on The Avifauna of the Southern Great Plains*, University of Oklahoma Press, Norman, OK, USA.
- Svardson, G. 1949. Competition and habitat selection in birds. *Oikos* 1:157-174.
- Tanner, J. T. 1952. Black-capped and Carolina chickadees in the southern Appalachian mountains. *The Auk* 69:407-424.

- Terborgh, J. 1971. Distribution on environmental gradients: theory and preliminary interpretation of distributional patterns in the avifauna of the Cordillera Vilcabamba, Peru. *Ecology* 52:23-40.
- Torgersen, C. E., D. M. Price, H. W. Li, and B. A. McIntosh. 1999. Multiscale thermal Refugia and stream habitat associations of chinook salmon in northeastern Oregon.
- Traba, J., M. B. Morales, C. P. Carmona, and M. Paula Delgado. 2015. Resource partitioning and niche segregation in a steppe bird assemblage. *Community Ecology* 16:178-188.
- Urbanska, K. M. 1987. Disturbance, hybridization and hybrid speciation. In *Disturbance of Grasslands* (J. van Andel, J. P. Bakker, and R. W. Snaydon, Eds.). Dr. W. Junk Publishers, Dordrecht, The Netherlands.
- Van Auken, O. W. 2000. Shrub invasions of North American semiarid grasslands. *Annual Review of Ecology and Systematics* 31:197-215.
- Veech, J. A., and T. O. Crist. 2007. Habitat and climate heterogeneity maintain beta-diversity of birds among landscapes within ecoregions. *Global Ecology and Biogeography* 16:650-656.
- Veech, J. A. 2021. *Habitat Ecology and Analysis*. Oxford University Press, Oxford, UK.
- Vila, M., E. Weber, and C. M. D'Antonio. 2000. Conservation implications of invasion by plant hybridization. *Biological Invasions* 2:207-217.
- Wang, H., E. D. McArthur, S. C. Sanderson, J. H. Graham, and D. C. Freeman. 1997. Narrow hybrid zone between two species of sagebrush (*Artemisia tridentata*): Asteraceae. IV: Reciprocal transplant experiments. *Evolution* 51:95-102.

- Watt, D. J. 1972. Comparison of the foraging behaviors of the Carolina Chickadee and Tufted Titmouse in northwestern Arkansas. M.Sc., University of Arkansas, Fayetteville.
- Wauer, R. H. 1971. Ecological distribution of the Chisos Mountains, Texas. *Southwestern Naturalist* 16:1-29.
- Wielstra, B. 2021. Quick Guide Hybrid Zones. *Current Biology* 31:R108-R109.
- Wiens, J. A. 1969. An approach to the study of ecological relationships among grassland Birds. *Ornithological Monographs* 8: 1-93.
- Wiens, J. A. 1972. Interterritorial habitat variation in grasshopper and savannah sparrows. *Ecology* 54:877-884.
- Wolf, D. E., N. Takebayashi, and L. H. Rieseberg. 2001. Predicting the risk of extinction through hybridization. *Conservation Biology* 15:1039-1053.
- Wood, E. M., S. E. Barker Swarthout, W. M. Hochachka, J. L. Larkin, R. W. Rohrbaugh, K. V. Rosenberg, and A. D. Rodewald. 2015. Intermediate habitat associations by hybrids may facilitate genetic introgression in a songbird. *Journal of Avian Biology* 47:508-520.
- Wright, J. W., and C. H. Lowe. 1968. Weeds, polyploids, and the geographical and Ecological distribution of all-female species of *Cnemidophorus*. *Copeia* 1968:128-138.
- Yang, S. Y., and R. K. Selander. 1968. Hybridization in the Grackle *Quiscalus quiscula* in Louisiana. *Systematic Zoology* 17:107-766.

Zhou, N., J. W. Pierre, and D. Trudnowski. 2012. A stepwise regression method for estimating dominant electromechanical modes. *IEEE Transactions on Power Systems* 27:1051-1059.

Zweifel, R. G. 1962. Analysis of hybridization between two subspecies of the desert Whiptail Lizard, *Cnemidophorus tigris*. *Copeia* 1962:749-766.