

ALL IN THE FAMILY: THE EFFECTS OF URBANIZATION AND WEATHER  
VARIABILITY ON THE BEHAVIOR, SOCIALITY, AND POPULATION  
DYNAMICS OF A KIN-STRUCTURED PASSERINE,  
THE BLACK-CRESTED TITMOUSE  
(*BAEOLOPHUS ATRICRISTATUS*)

by

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## **DEDICATION**

I dedicate this dissertation to Gary and Cathy Rylander, my father and mother who have taught me how to live life, how to overcome adversity, and how to love unconditionally, all without needing to say a word. Your faith and encouragement are second to none, and I would not be where I am today had you not already shown me the way. Thank you for believing in me.



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## ABSTRACT

There is much debate as to the proximate and ultimate causation of kin-structure in avifauna, as it is relatively rare among bird species. However, the research needed to understand causation of kin-structure begins with foundational work on population demographics and social dynamics. Without sound knowledge of dispersal behavior, survival rates, and reproductive metrics, one cannot begin to untangle how kin-selection favors the formation of family groups where members increase inclusive fitness through the passing of personal and shared genes. This is especially important considering how urbanization and shifting weather patterns may additionally effect species evolved to remain near kin.

One such species that forms extended family groups is the black-crested titmouse (*Baeolophus atricristatus*, BCTI), a non-migratory passerine in the Paridae family. My master's thesis research revealed that in a rural setting, large juvenile male BCTI often limit their natal dispersal and establish territories adjacent to their parents the following spring, forming kin-structured neighborhoods over time. Even though this was an interesting and novel discovery for the *Baeolophus* genus, my work prompted additional questions as to why BCTI maintain kin-structure and how urbanization influences extended family relations, topics which I addressed in this dissertation.

Because BCTI are commonly observed in rural and urban landscapes within their range, I first studied if BCTI residing in an urban environment form kin-structured

neighborhoods, and if so, to what extent. Additionally, I examined home range size, habitat composition of home ranges, and body conditional indices (BCI) of urban BCTI and compared them to a rural population. My study site was at four different locations in San Marcos, Texas, that all varied in degrees of urbanization. The rural site, where I also conducted my thesis research, was the Freeman Center (hereafter Freeman), a 1400-ha Texas State University property ~10 km from downtown San Marcos. The habitat at Freeman is a mosaic of native hill country vegetation with minimal man-made structures or roads. My urban sites included Texas State University campus (hereafter Campus), single-home residential neighborhoods in San Marcos (hereafter Residential), and public parks operated by the City of San Marcos (hereafter Parks). Thus, the rank of locations from highest to lowest in terms of urbanization is Campus > Residential > Parks > Freeman. My results revealed that BCTI in urban locations form kin-structured neighborhoods but to a lesser extent than their rural counterparts. Home range size of urban BCTI was influenced by habitat composition, where home ranges were larger on Campus (highly urbanized) and smaller in Residential areas and in Parks (low degrees of urbanization) compared to BCTI home range size at Freeman. Additionally, BCTI in urban and rural locations did not differ in BCI, but there was a high degree of variation of BCI within and among family groups.

Because there were differences in the extent of kin-structure neighborhood formation between urban and rural populations of BCTI, for my second study, I investigated if there were differences between the two in relation to productivity, nesting

success, and timing of reproductive cycle. I also accounted for differences in habitat composition and weather variability across the breeding season. My results provided evidence that urban BCTI begin first clutch initiation ~9 days before rural BCTI, and average February low temperatures were highly correlated with nest initiation date at Freeman. Though overall productivity was not different between urban and rural locations, nest fate and daily survival rates of nests were much lower for Residential nests than nests in any other location.

Results from my second study suggested that additional population demographics of the BCTI may be influenced by urbanization, therefore I addressed this in my third study. I examined if apparent survival of BCTI varied between urban and rural populations, between sexes and ages, as well as between breeding and non-breeding seasons (summer and winter, respectively). Additionally, I assessed if apparent survival increased when adult BCTI held territories near kin in kin-structured neighborhoods. Overall, apparent survival estimates were higher for males compared to females, as well as higher for adults compared to juveniles regardless of location or season. Urban males had a higher apparent survival than rural males during the summer but a lower apparent survival during the winter. Moreover, urban females had a lower apparent survival than rural females in both seasons. Thus, rural BCTI apparent survival was more stable over time for both age classes and sexes, indicating that urban BCTI may be more susceptible to population fluctuations due to inclement weather and habitat inconsistencies. Interestingly, apparent survival for rural BCTI surrounded by kin was lower than that

estimated for adults not surrounded by kin. Though this seems counterintuitive to kin-selection, I hypothesize that these estimates could indicate that once adults are established territorially, they tend to remain in kin-structured neighborhoods until they die, whereas adults not surrounded by kin may be younger, healthier, and still aiming to achieve kin-structured status.

Finally, in my fourth study, I investigated if there were potential inclusive fitness benefits for BCTI in kin-structured neighborhoods through the behavior of resource sharing. By using radio frequency identification (RFID) feeding stations, I was able to monitor a small population of BCTI equipped with passive integrated transponder (PIT) tags and could record when certain individuals aggregated to share food. Results revealed that both closely and distantly related kin may benefit through “quality over quantity” foraging bouts together (foraging time together versus frequency of foraging bouts together). Additionally, males accompany their mate to a high extent on foraging bouts during the breeding season as compared to any other season, likely indicating mate guarding behavior.

Overall, results from this dissertation indicate that though BCTI are still common and establish kin-structured neighborhoods in urban locations, they likely incur lower reproductive success and apparent survival due to certain stressors and threats that are not as prevalent in rural locations. Therefore, the differences in BCTI social dynamics and demographics between urban and rural populations may eventually lead to less kin-

structure in urban areas over time. This in turn could create a positive-feedback loop, where less kin-structure leads to lower survival and recruitment, which again influences kin-structure. Because it does not appear that resource sharing is a highly kin-selected behavior among BCTI, future work should examine other behaviors that potentially maintain extended family cohesion, such as joint territory defense, predator vigilance, or the availability of empty territories for juveniles to inherit. Thus, by determining what behaviors or traits are most important to maintaining BCTI kin-structure, future conservationists may be able to directly increase apparent survival and reproductive success should BCTI populations begin to decline.

# **I. GENERAL INTRODUCTION**

## **Background Information**

### ***Avian sociality***

The study of social behaviors among birds is a growing field that has gained much attention in the past few decades (Powell 1974, Ekman 2006, Wey et al. 2008, Silk et al. 2014). Group interactions typically occur due to advantages that flock members receive for participating in social gatherings (Pulliam 1973, Caraco et al. 1980). However, untangling the benefits of certain flocking behaviors can be difficult.

One of the main benefits birds receive from social flocks is in the foraging context (Pulliam 1973, Roberts 1996). In principle, intra- and interspecific flocks can gather information about resources through their knowledge of the area as well as their behavior of positively locating a food source (Sandlin 2000, Chaves-Campos 2011). In some species, particularly corvids, individuals within a flock share the location of resources with other members, expecting that when resources become scarce, another member will do the same, suggesting that there can be benefits of reciprocal altruism (Marzluff et al. 1996). Similarly, migratory birds cue in on signals of foraging residential species that are familiar with the landscape and thus provide clues as to where potential resources may be located (Morse 1970, Harrison and Whitehouse 2011). However, there are costs associated with group foraging; as group membership increases past a certain threshold, competition for resources increases, as well as the time and energy spent moving to and from foraging patches (MacArthur and Pianka 1966, Ens et al. 1995). Therefore, it depends upon the species and the surrounding habitat matrix as to what the ideal

membership number is for foraging flocks to be optimal (Gluck 1987, Shochat et al 2004).

Though foraging in a group may be beneficial to predator detection and locating resources, there also are costs to such behaviors. Resources are limited and often dispersed, and all members of a flock will not receive the same net gain from sharing (Cimprich and Grubb 1994, Lange and Leimar 2001). Thus, fighting and chasing are common in foraging flocks, resulting in extra energy expenditure and potential injury depending upon how valuable a resource is for survival (Pravosudov et al. 1999). Each individual is subjected to the fitness costs and benefits of sharing resources within a flock, or they experiencing the alternative of foraging alone and risking greater chances of predation (Waite 1987, Dhondt 2012).

A more recent area of study on avian sociality focuses on family flocking dynamics, a relatively rare phenomenon occurring in < 9% of bird species (Ekman 2006). Familial social groups are typically comprised of a male and female pair that is accompanied by some number of offspring after the breeding season for an extended period (Condee 1970, Cockburn 2006). Juveniles in this situation either: 1) Delay dispersal and provide no alloparental care to the family group; 2) Delay dispersal and participate in cooperative breeding; or 3) Limit dispersal and establish a territory of their own parallel to parents the following year (Ekman 2006, Rylander et al. 2020). Depending upon the species, the fate of retained offspring may be obligate or facultative in nature, where current biotic and abiotic factors influence the family flocking structure for the next year (Emlen 1995, Cockburn 2006). When resources are scarce or when the surrounding habitat matrix is saturated with dominant conspecifics, juveniles may alter

their dispersal behavior until an opportunity to become independent arises (Emlen 1982, Komdeur 1992).

For familial flocks to exist, selection must produce positive fitness gains for all individuals within the family unit (Hatchwell 2009). When social groups are comprised of related individuals, both direct and indirect fitness benefits contribute to an individual's inclusive fitness. Direct fitness is measured as the inheritance of genes directly from parent to offspring, while indirect fitness is measured as the extra survival of kin (weighted by the degree of relatedness) due to an individual's altruistic behavior that comes at a price to the individual (Hamilton 1964, Smith and Ridpath 1972, Sherman 1977, Ekman 2006). The prolonged brood care hypothesis suggests that both parents and juveniles positively benefit from remaining in a social flock (Ekman and Rosander 1992). Parents are less aggressive towards offspring which may aid in keeping juveniles on their natal territories (Dickinson et al. 2009). In other case studies of familial sociality, the breeding parents' fitness is decreased when their young are experimentally removed from the flock (Hatchwell et al. 2001).

For juveniles exhibiting philopatry, typically both direct and indirect fitness benefits can influence their overall inclusive fitness within the familial unit. Direct benefits to fitness can be described as either current or future net gains. Resource sharing (Marzluff et al. 1996), heightened predator vigilance (Powell 1974, Caraco et al. 1980, Lima 1995), and decreased aggression levels (Pravosudova et al. 1999) are common ways in which an individual's direct fitness is boosted in present time by surrounding itself with relatives (Dickinson et al. 1996). Future direct benefits for juveniles remaining in a flock can be described as potential admittance to a neighboring territory for breeding



purposes, as well as learning certain valuable behaviors that elder flock members exhibit (Koenig et al. 1992, Kokko and Ekman 2002). All potentially lead to successful passing of genes directly to offspring if the juveniles establish their own territory the following year and mate.

While it is uncommon for related individuals to remain in a flock for an extended period of time, it is even rarer for juveniles to limit dispersal and establish a breeding territory of their own next to or overlapping their parents (Ekman 2006, Dickinson et al. 2009). When this occurs, kin-structured neighborhoods are formed over time, where generations of related families all have established breeding territories adjacent to one another (Hatchwell 2001, Rylander 2015). Related neighbors typically receive increased direct and indirect fitness benefits even though they may not flock together at all times. Long-tailed tits (*Aegithalos caudatus*) and western bluebirds (*Sialia mexicana*) both establish kin-structured neighborhoods, and during times of limited food supply or predator intrusions, related members of different flocks gather to share resources and/or heighten the defense against threats (Hatchwell 2001, Dickinson et al. 2009).

### ***Effects of urbanization***

Anthropogenic habitat destruction and degradation is a global threat to biodiversity in both terrestrial and aquatic ecosystems (McKee et al. 2004, Wessely et al. 2017). Not only do humans directly affect the landscape through development and urbanization, they also indirectly leave their mark by releasing pollutants, over-exploiting natural resources, leaching soils, and contributing to the unstable and uncertain effects of climate change (Kennish 2002, Dirzo and Raven 2003, Wake and Vredenburg 2008). Many wildlife populations may not have suitable genetic variation or behavioral

plasticity needed to persist in a rapidly changing environment, leading to possible extirpation (Prugh et al. 2008, Mills 2013). Therefore, it is of utmost importance to understand the potential ramifications for organisms that reside within an urbanized landscape.

During the past half century, the human population has experienced an exponential growth rate that is debatably reaching, or is already beyond, the carrying capacity of Earth (Holdren and Ehrlich 1974, Van Den Bergh and Rietveld 2004). In the wake of such growth comes the need for more infrastructure, food, and water. To meet these demands, anthropogenic activities continue to spread through urbanization and agriculture (Crist et al. 2017). Though each human-made structure, such as buildings, bridges, and highways, may seem to have negligible impacts, all structures considered together across a landscape might have profound repercussions on both flora and fauna and should be assessed through sound scientific research.

Birds are used as indicators of ecosystem health (Burger and Gochfield 2001, Gregory et al. 2003, Smits and Fernie 2014). Most avifaunal species typically are easier to detect than mammals, herpetofauna, and invertebrates because they are readily observed throughout daylight hours and are present in nearly all habitat types. Auditory surveys can positively identify the presence of avian species and are inexpensive and efficient with little technology requirements (Bibby et al. 2000). Birds, unlike many other organisms, have vagility through powered flight if conditions become unfavorable for their survival (Gill 2007). Thus, in particular habitats, the presence/absence or richness of bird species can be used as an indicator for the status and health of other

organisms that may not be able to move to another location as easily (Burger and Gochfield 2001).

Many species have adapted over time to urban sprawl, some reaching extremes that appear to prefer or depend upon anthropogenic influence (Murgui and Hedblom 2017, Ravinet et al. 2018). Though this kind of “urban survival” can leave an impression of harmony and coexistence, individuals of many avian species able to exist within urban habitats may suffer decreases in fitness relative to individuals in non-altered habitats (Caizergues et al. 2018). This is due to a number of reasons:

- 1). Resource depletion and alteration – As urbanization continues, humans tend to over-exploit common resources such as water and timber and manipulate the landscape by removing native vegetation and replacing it with non-native exotic fauna and flora (Rottenborn 1999). This ultimately can lead to birds not having the necessities for reproduction (lack of nesting locations or nesting materials) or survival (food, water, and shelter) (Blewett and Marzluff 2005).

- 2). Habitat fragmentation – The consequences of removing vegetation and creating smaller discontinuous patches of suitable habitat can cause many problems. Some species have difficulty dispersing great distances from isolated habitat fragments and therefore end up with limited gene flow, while others attempt to disperse, only to fail and perish (Fernandez-Juricic 2000, Doherty and Grubb Jr 2002). Patches of habitat also may not be large enough for reproductive purposes and thus serve as sinks for particular species.

3). Exposure to elements – Urban areas create pockets of microclimates that are different from those in rural locations (Atchison and Rodewald 2006). Depending on the location, urbanization can alter temperature and precipitation. Any of these variations from the norm may impact avian communities (Doherty and Grubb Jr. 2002).

4). Inter- and intra-specific competition – Because suitable habitat typically is more limited in urban areas, competition for resources, mates, and space can be exacerbated due to an increase in density of individuals (Dhondt 2012). Not only are members of the same species competing for resources, but different species, which can be native or exotic, also are competing for these same resources. Exotic species usually are more aggressive than natives and frequently outcompete their typically smaller and more naïve counterparts (Case 1996).

5). Increased predation – Urbanized areas often experience shifts in predation rates, typically stemming from the extirpation of native top-tier predators (mountain lions, coyotes, bobcats) that can depress mesocarnivore (raccoons, opossums, skunks) populations (Mills 2013). Without this natural check in the ecosystem, mesocarnivores can flourish and consume more prey such as birds, their eggs, and nestlings (Rylander pers. obs.). Exotic predators also tend to be more abundant in urban areas, with feral and free-ranging domestic cats being one of the most prevalent, killing billions of birds every year (Beckerman et al. 2007, Marra and Santella 2016). Exotic rat species, which also can be numerous in urban areas, predate bird nests and serve as vectors for diseases like the Bubonic plague, Leptospirosis, Toxoplasmosis, and other diseases (Sorace 2002).

6). Diseases and stress – Exposure to exotic wildlife that typically occur within urban areas can increase transmission rates of diseases (such as toxoplasmosis and avian

pox) that can be transferred to native bird species (Dubey 2002). Birds within altered landscapes also pass on parasites, mites, and disease more frequently due to limited space and increased physical contact from competition (Hamer et al. 2012). Many urban avian communities have higher stress levels (seen in H:L blood ratios, breath rate, and more) when compared to their rural counterparts (Ruiz et al. 2002, Torne-Noguera et al 2014), which in turn weaken the natural immune system, leading to increased effects of parasites and disease on a bird's health (Murgui and Hedblom 2017).

Recent studies have revealed that projects associated with habitat restoration, green-space designation, and eco-friendly building design, can drastically alter and positively influence the presence and persistence of avian species in urban areas (Dobson et al. 1997, Murgui and Hedblom 2017). Thus, it is important to perform research and collect data on bird communities in more rural locations that have not been as altered, enhancing the understanding of managing wildlife in urbanized areas. It also is important to note that not all urban areas are “created equally,” with various degrees of urbanization existing; downtown zones can be drastically different from residential neighborhoods, which can, in turn, be different from urban parks and recreational fields (Rottenborn 1999, Conway et al. 2006). Birds use these areas differently and sometimes thrive in managed urban zones (Aurora et al. 2009), though each species have particular requirements and should be assessed on a case by case basis (Hedblom and Soderstrom 2012).

### ***Shifting demographics***

It may not be apparent how population dynamics of avian species are changing in time and space, particularly how human and human-made stressors affect survivorship,

fecundity, and other vital rates (Pearce-Higgins and Green 2014). While some populations may not be affected by anthropogenic pressures, it is likely that most are influenced to some extent (Robles et al. 2007). Thus, the exact way in which urbanization influences the demographics of a population needs investigation. In a recent study by Reidy et al. (2018), the endangered golden-cheeked warbler (*Setophaga chrysoparia*) responded negatively to edge habitat and lower canopy cover associated with habitat fragmentation near infrastructure. The number of fledglings produced per territory decreased as landscape woodland cover decreased. Another study by Stracey and Robinson (2012) demonstrated that the northern mockingbird (*Mimus polyglottos*) benefitted from urbanization. Breeding pairs produced more offspring and had increased apparent survival than those located in a nearby rural habitat patch. Yet Grodsky et al. (2016) revealed that the current levels of harvested woody biomass (habitat alteration) in southeastern forests did not affect territorial densities along with other demographic metrics in early-successional, breeding bird communities.

Species that establish complex social structures over many generations may experience population-level effects from urbanization, habitat fragmentation, and climate change on a more profound scale due to their necessity to remain together for persistence (Pearce-Higgins and Green 2014, Layton-Matthews et al. 2018). Avifauna that receive fitness benefits by living in a group could be more susceptible to anthropogenic stressors, especially if they disrupt membership recruitment for reproductive purposes (Griesser and Lagerberg 2012). Ryder and Sillett (2015) modeled predicted climate change patterns effects on the lekking behaviors of wire-tailed manakins (*Pipra filicauda*) in the Amazon rainforest. Over time, shifts in precipitation may disrupt male recruitment to established

leks, resulting in a less stable mating system for this species. Understanding how current and future anthropogenic stressors affect the vital rates and population dynamics of kin-oriented species that may not be able to adapt or emigrate to new locations as a group will allow for more specific management plans that can focus on the group of individuals as a functional entity.

### ***Study species profile***

To understand how urbanization and weather patterns influence a kin-structured bird, I studied a species of passerine that is common within its range in both urban and rural landscapes, the black-crested titmouse (*Baeolophus atricristatus*, hereafter BCTI). The BCTI is a small songbird that resides in the western half of Texas, southern portion of Oklahoma, and into Mexico at its southern extreme in Veracruz (Dunn and Alderfer 2011). This species is typically observed in woodland and edge habitats because it relies on mature trees for nesting cavities and much of its food sources. As an omnivore, the BCTI eats insects, berries, seeds and nuts, and its large eyes enable it to be constantly vigilant as it forages and sings (Patten and Smith-Patten 2008).

The BCTI is a social species that forms intra- and interspecific flocks during different times of the year (Dixon 1955, Rylander et al. 2020). During the fall and winter, titmice, chickadees, woodpeckers and warblers forage together while alarming and alerting each other of potential predators nearby (Dixon 1961). In the post-breeding season, BCTI usually form family flocks consisting of a territorial male and female pair, one or two of their offspring that delay dispersal, and sometimes unrelated floaters that are accepted into the flock (Rylander 2015, Patten and Smith-Patten 2008). Although uncommon, BCTI can cooperatively breed when the dominant (and typically heaviest)

male offspring from the previous year's clutch foregoes dispersal and assists his parents by feeding nestlings (Rylander 2015). Yet, it is more frequent that the dominant male offspring establishes a territory next to or overlapping his parents' territory, creating a kin structured neighborhood over time (Rylander et al. 2020).

Because the BCTI is a residential species where both adults and limited dispersing juveniles have high site-fidelity from year to year (Rylander 2015), it is possible to capture and color band individuals for focal monitoring through multiple seasons. BCTI also frequent human-made nestboxes, easing access to eggs, nestlings, and adults for banding and measurement purposes (Rylander 2015). Coupling the ease of capture and the lack of seasonal migration, the BCTI is a species that is ideal for research involving annual behavioral trends, particularly those involving social interactions that are not apparent without detailed observation on a marked population.

Until recently, the BCTI was considered a subspecies of the tufted titmouse complex (*Baeolophus bicolor*, hereafter TUTI) (Banks et al. 2002). Though these two species readily hybridize along a thin zone that runs north to south from Oklahoma to southeastern Texas (Dixon 1955), the BCTI has enough genetic differentiation to be considered a separate species (Braun et al. 1984, Avise and Zink 1988, Banks et al. 2002). Both biotic (certain premating isolation barriers) and abiotic (ecoregion vegetation and climate) factors maintain the reproductive isolation of TUTI and BCTI on either side of the contact zone, though it becomes complicated in areas of Oklahoma where TUTI-BCTI contact is historically more recent (Dixon 1955, Curry and Patten 2014). Therefore, past studies that combine BCTI with TUTI should be deciphered with caution, especially the inferences drawn from populations of TUTI nowhere near the contact zone with



BCTI (Patten and Smith-Patten 2008). Thus, the BCTI is a species that needs additional research comparing urban and rural population demographics, reproductive parameters, and social structure.

## **Research Objectives**

The following chapters of my dissertation addressed targeted questions through specific objectives using the BCTI as a model species.

### **II - Welcome to suburbia: the effects of urbanization on dispersal patterns of a kin structured songbird, the black-crested productivity**

Objectives:

1. I examined factors that influence urban BCTI home range size.
2. I assessed family flocking dynamics and dispersal behaviors of urban BCTI.
3. I compared body condition between urban and rural populations of BCTI adults and nestlings.

### **III. Whether city-slicker or country-bumpkin, black-crested titmice adapt to urbanization regarding nesting success and productivity**

Objectives:

1. I examined BCTI nesting characteristics, including initiation dates of first and second clutches, the frequency distribution of eggs, nestlings, and fledglings per nest, and factors influencing nest fate.
2. I assessed BCTI annual productivity across years and locations.
3. I calculated daily survival rates (DSR) of BCTI nests.

#### **IV. The big picture: assessing kin-selection in population demographics and dynamics of a social-structured passerine in rural and urban landscapes**

Objectives:

1. I assessed the effects of habitat composition and weather on apparent survival of adult and juvenile BCTI in rural and urban landscapes.
2. I examined if kin-selection influenced rural adult BCTI apparent survival.

#### **V. Living at home: assessing inclusive fitness benefits associated with resource sharing in a familial flocking songbird**

Objectives:

1. I documented differences in BCTI feeding behaviors among age groups, between sexes, and across seasons at reliable food sources.
2. I examined if kin-selection favors resource sharing between two separate, but related, BCTI family groups compared to two unrelated family groups.
3. I assessed if BCTI parents display nepotistic behaviors towards retained juveniles in relation to resource allocation.
4. I determined if BCTI mated pairs visit a common food resource more often in the presence or absence of the other.

#### ***Study site***

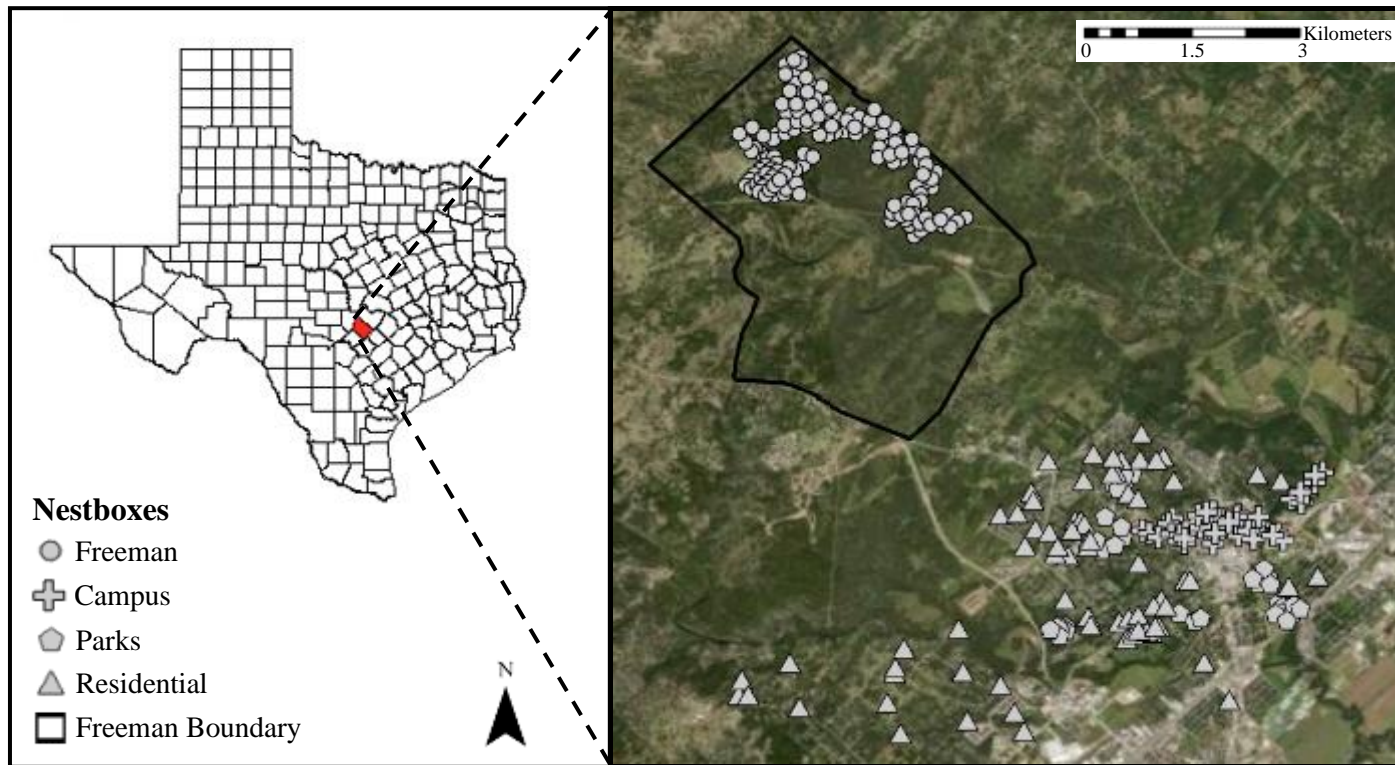
For all chapters of my dissertation, I used a series of 306 nestboxes installed across four locations San Marcos, Texas, USA (29.8833° N, -97.9414° W): 1) the Freeman Center; 2) Texas State University's main campus; 3) San Marcos public parks;

and 4) single-family home residential neighborhoods in San Marcos (Figure 1.1). The BCTI is common, conspicuous, and readily used nestboxes in all locations (Rylander pers. obs.), making it convenient to capture and individually color band entire family flocks during the nesting season (March – June).

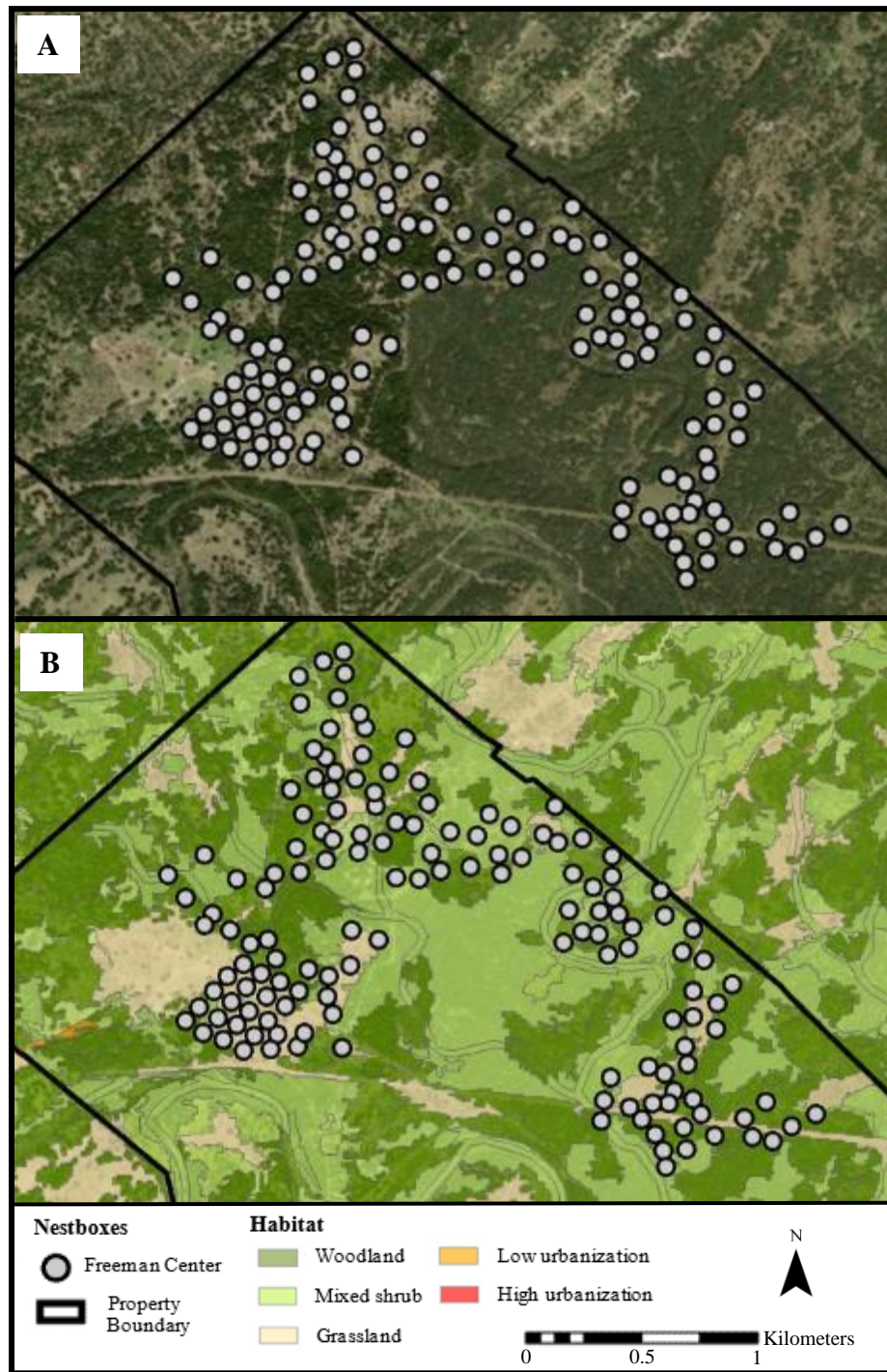
The northern half of the Freeman Center (hereafter ‘Freeman’) is a rural 1400-ha property owned by Texas State University and located ~10 km northwest of downtown San Marcos. The habitat is a mosaic of oak-juniper woodlands (*Quercus fusiformis*, *Q. buckleyi*, *Juniperus ashei*) (46%), open grassland savannahs (*Bothriochloa ischaemum*, *Schizachyrium scoparium*, *Diospyros texana*, *Forestiera pubescens*) (22%), and a mixture of grassland/woodland interface (32%). During the winter of 2012 and 2013, I installed 40 and 31 nestboxes, respectively, and during the winter of 2017, I installed an additional 75 nestboxes (Figure 1.2). I positioned all nestboxes ~3 m high on t-posts, and in the winter of 2015, I installed PVC-pipe style predator baffles on t-posts below the nestbox to maintain robust sample sizes of banded BCTI (Figure 1.3).

During the winter of 2016, I installed 40 nestboxes across Texas State University’s campus (hereafter ‘Campus’), a highly urbanized series of dormitories, large multistory buildings, parking lots, and parking garages. I also installed 34 nestboxes during this same time frame at public City of San Marcos parks (hereafter ‘Parks’) that contained > 2.5 ha of contiguous greenspace patches with old-growth trees (Dunbar, Crook’s Park, Prospect, Schulle Canyon, Children’s Park, and the San Marcos City Cemetery). Finally, I installed 86 nestboxes in single-family home residential areas of San Marcos (hereafter ‘Residential’) during the winter of 2017, where residential lots contained mature trees and other vegetation. In total, across the three “urban” sites, I

instead 160 nestboxes, with sites ranking from high to low urbanization (the amount of impervious cover) as follows: Campus > Residential > Parks (Figure 1.4). I affixed all urban nestboxes with screws or ratchet straps and placed them on various tree species > 15 cm diameter at breast height (DBH) between 2–4 m from the ground (Figure 1.3).



**Figure 1.1** Nestbox placement across four study locations in Hays County, San Marcos, Texas, 2013–2021. Nestboxes were installed at one rural location, the Freeman Center (“Freeman”) and three urban locations: Texas State University campus (“Campus”), City of San Marcos parks (“Parks”), and single-family home residential neighborhoods (“Residential”).

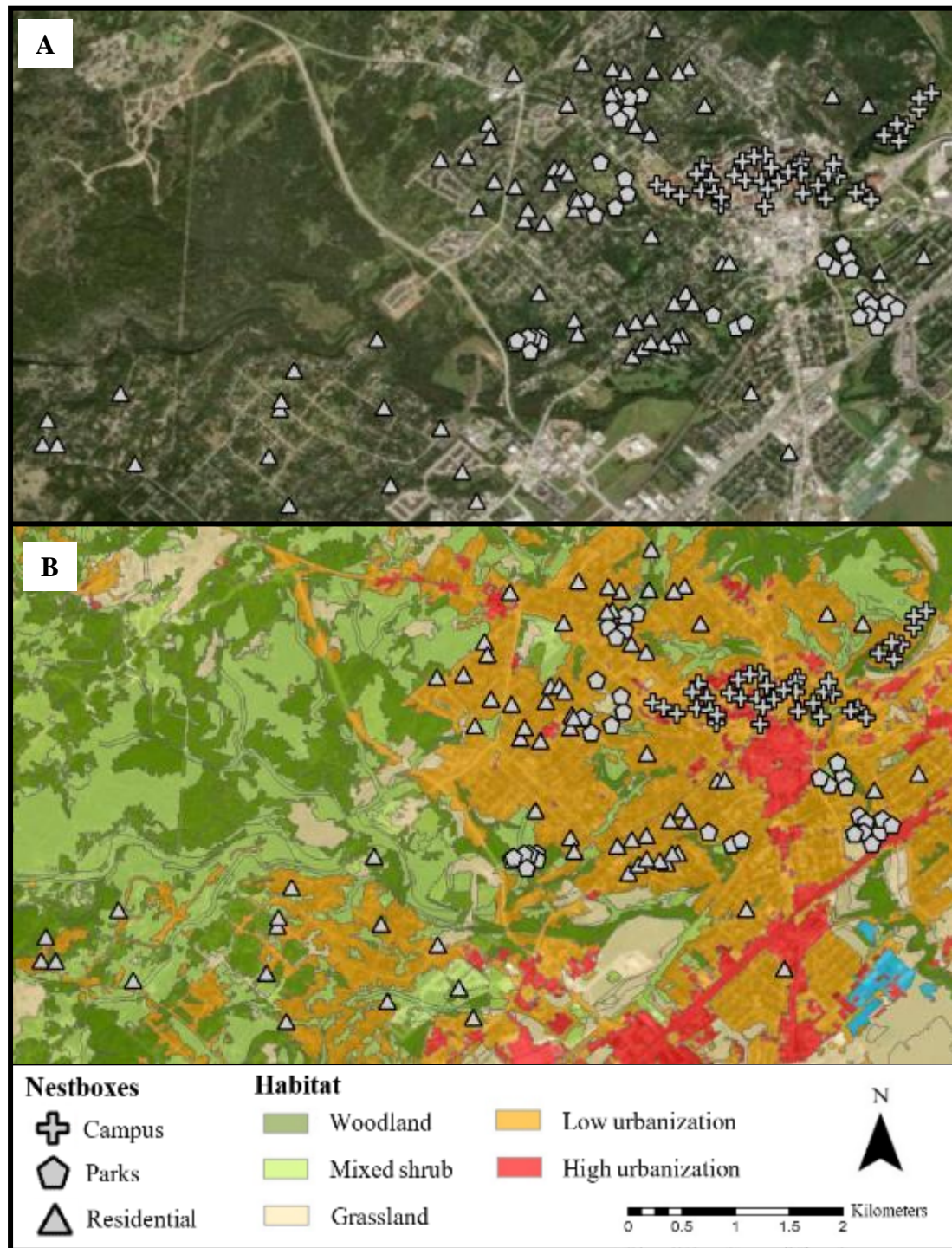


**Figure 1.2** Nestbox placement on the Freeman Center in San Marcos, Texas, 2013–2017. **A.** Aerial imagery of vegetation surrounding nestboxes. **B.** Arc GIS vegetative layer (TPWD 2020) used in habitat composition analyses.





**Figure 1.3** Nestbox installation methods at urban and rural study locations in San Marcos, Texas. **A.** An urban nestbox mounted directly to a tree using ratchet straps (or screws). **B.** A rural nestbox mounted to a 3-m t-post with PVC-style predator baffle below. Though both nestboxes are slightly different in appearance, both had the same dimensions.



**Figure 1.4** Nestbox placement across three urban locations, Campus, Parks, and Residential areas, in San Marcos, Texas, 2016–2017. **A.** Aerial imagery of vegetation surrounding nestboxes. **B.** Arc GIS vegetative layer (TPWD 2020) used in habitat composition analyses.



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## II. WELCOME TO SUBURBIA: THE EFFECTS OF URBANIZATION ON DISPERSAL PATTERNS OF A KIN-STRUCTURED SONGBIRD, THE BLACK- CRESTED TITMOUSE

### Abstract

Urbanization is altering avian behavior and survival. Depending on the life-history and behavioral plasticity of the population, demographics may shift causing population declines or increases. To assess the influence of anthropogenic landscapes on avian home range, dispersal patterns, and body condition, I studied a kin-structured passerine, the black-crested titmouse (*Baeolophus atricristatus*, hereafter BCTI) in urban areas of San Marcos, Texas. I color-banded and monitored  $n = 35$  urban BCTI families between 2017 – 2019. Urban BCTI home range size was (mean  $\pm$  SD)  $9.11 \pm 5.06$  ha and was positively correlated with the proportion of high urbanization (areas dominated by impervious cover) within the home range (95% CI = [2.66-5.69]). Limited dispersal (when juveniles eventually establish a territory adjacent to their father's) was negatively influenced by the proportion of low urbanization habitat (areas of non-industrial infrastructure and some impervious cover) (95% CI = [-2.25--0.33]), as well as by sex (95% CI = [1.12 – 24.36]) and mass-rank (95% CI = [0.21 – 1.28]), indicating heavier male-biased philopatry. I conducted a similar study on a rural population of BCTI in San Marcos in 2013 – 2015. BCTI nestling and adult body condition did not differ between urban and rural populations, year, or fledge date, but adult males had a higher body condition (higher standardized mass to tarsus length ratio) (95% CI = [0.57 – 1.13]) in both populations. Similar to rural populations, urban BCTI construct kin-structured

neighborhoods, though urban landscapes are influencing home range and the proportion of juveniles able to establish territories near family.

## **Introduction**

Human-caused habitat destruction is threatening biodiversity around the world, especially through the conversion of natural landscapes into urbanized terrain (McKee et al. 2004, Dirzo and Raven 2003, Wessely et al. 2017). Although wildlife has long coexisted with humans, noticeable anthropogenic impacts on the environment have accelerated in the last half century (Holdren and Ehrlich 1974, Van Den Bergh and Rietveld 2004). Many species cannot tolerate rapid land conversion and are either forced to emigrate or suffer fitness consequences (Prugh et al. 2008, Mills 2013). Some avian species may provide an exception. Because most species are capable of flight, birds can temporarily or permanently emigrate from an area if it is not suitable for their survival (Murgui and Hedblom 2017). Therefore, overall species richness of native avian communities often indicates the status and health of other wildlife taxa that cannot disperse to another location as easily (Burger and Gochfield 2001).

The effect of urbanization on a given avian species is unpredictable, yet many bird species thrive in urbanized landscapes, even if some individuals suffer decreases in fitness relative to members that reside in natural habitats (Rottenborn 1999, Chamberlain et al. 2009). Fitness may be compromised by, for example, resource depletion (Blewett and Marzluff 2005), exposure to elements (Atchison and Rodewald 2006), increased predation (Sorace 2002, Marra and Santella 2016), and increased inter- and intra-specific competition (Case 1996, Dhont 2012). These consequences stem from increased habitat fragmentation and conversion of land for anthropogenic use (Doherty and Grubb Jr 2002,

Murgui and Hedblom 2017). By contrast, urbanized areas with ample greenspace may provide avifauna with an abundance of food and other valuable resources, increasing individual fitness and survival (Aurora et al. 2009, Hedblom and Soderstrom 2012). In such instances, greenspaces are important resources for populations of some species, especially if they are interconnected with wildlife corridors and migratory flyways (Fernandez-Juricic 2000, Murgui and Hedblom 2017).

It is an open question as to which bird species may be able to thrive in an urbanized landscape. In particular, little is known about social species that depend upon kin for survival or reproduction (Beck and Heinsohn 2006, Griesser and Lagerberg 2012). Not only do family-oriented species experience the same pressures from human-cause stressors, but they possibly are subject to additional fitness consequences when family members are not able to reside nearby (Layton-Matthews et al. 2018). The retention of juveniles that ultimately form kin groups is altered in urbanized landscapes when dispersal patterns are disrupted (Ekman 2006, Griesser and Lagerberg 2012). Juveniles that otherwise reside near kin may be forced to disperse if urbanized landscapes lack resources, available mates, and suitable habitat patches (Komdeur 1992, Beck and Heinsohn 2006, Dickinson et al. 2009). In short, compounded effects on kin-structured social species may accrue due to their inability to cope as the landscape changes.

The black-crested titmouse (*Baeolophus atricristatus*, hereafter BCTI) is a kin-structured passerine in the Paridae family that is common in urban and rural landscapes within its range (Patten and Smith-Patten 2008). It resides in semi-arid woodlands of Texas, Oklahoma, and Mexico, and it breeds in early spring and summer (March – June) (Dixon 1978). After the breeding season, BCTI often are observed in family groups of

three (sometimes four), with membership comprised of a male and female territorial pair and one of their offspring from the same year (Rylander 2015). These family groups typically remain cohesive until the beginning of the following breeding season, when the retained juvenile either: 1) disperses into a neighboring territory with a mate of his own, thus creating a kin-structured neighborhood; 2) becomes a helper at his parents' new nest; or 3) disappears altogether due to either predation or complete dispersal (difficult to distinguish between the two) (Rylander et al. 2020). For these reasons the BCTI is a good candidate to address effects of urbanization on juvenile dispersal behavior and individual fitness of a kin-structured passerine.

In this study, I: 1) examined factors that influence urban BCTI home range size; 2) assessed family flocking dynamics and dispersal behaviors of urban BCTI; and 3) compared body condition between urban and rural populations of BCTI adults and nestlings. I predicted that BCTI home ranges would be larger in highly urbanized locations (Salinas-Melgoza et al. 2013, Clement et al. 2020), and that kin-structured neighborhood formation would be lower (due to forced juvenile dispersal) in patchier habitat (Layton-Matthews et al. 2018). I also predicted that body condition of both adults and nestlings would be lower in highly urbanized areas (Meillere et al. 2017, Seress et al. 2020), and that sexes would have similar body conditions as both participate in feeding nestlings and territorial defense which require high energy expenditure (Clutton-Brock 1991, Liker and Szekly 2005, McNamara and Houston 2008).

## Methods

### *Study site*

I monitored BCTI dispersal and flocking behavior across varying landscapes in San Marcos, TX, USA (29.8833° N, -97.9414° W), which is located within the Edwards Plateau Ecoregion (Figure 1.1). Because of human population growth, San Marcos makes an ideal location to perform research on avian species in response to effects of urbanization (Davila 2015). During the winter of 2016, I installed 40 nestboxes across Texas State University's campus (hereafter 'Campus') which comprises large multistory buildings, parking garages, dormitories, and parking lots. Also, during the winter of 2016, I installed 34 nestboxes within public City of San Marcos parks (hereafter 'Parks'; Schulle Canyon, Crook's Park, Children's Park, Dunbar, Prospect, and the San Marcos City Cemetery) that contained large (7+ acres) contiguous patches of greenspace and old-growth trees. During the winter of 2017, I installed an additional 86 nestboxes in single-family home residential areas of San Marcos (hereafter 'Residential'), where residential lots contained mature trees and other vegetation (as opposed to houses located in more recent clear-cut areas). Thus, the 160 nestboxes placed within San Marcos (Figure 1.4) rank from high to low urbanizations as follows: Campus > Residential > Parks. Due to logistics and university/city restraints, I was unable to completely randomize nestbox installation locations across the three sites. However, I intentionally placed nestboxes across a variety of habitats, vegetation classes, and degrees of urbanization. I affixed all nestboxes either with screws or ratchet straps between 2-4 m from the ground on various tree species > 15 cm diameter at breast height (DBH) (Figure 1.3).



For body condition comparisons, I incorporated banded BCTI from the Freeman Center, a rural 1400-ha Texas State University property located 10 km northwest of San Marcos, Texas. The northern half of the Freeman Center consists of a mosaic of oak-juniper woodlands (*Quercus fusiformis*, *Q. buckleyi*, *Juniperus ashei*) (46%), open grassland savannahs (*Bothriochloa ischaemum*, *Schizachyrium scoparium*, *Diospyros texana*, *Forestiera pubescens*) (22%), and a mix of grassland/woodland interface (32%) (Barnes et al. 2000). In previous years, researchers installed 40 (winter 2012) and 31 (winter 2013) nestboxes at the Freeman Center (hereafter ‘Rural’) for eastern bluebird (*Sialia sialis*) and BCTI studies. During the winter of 2017, I installed an additional 75 nestboxes, bringing the total of nestboxes on property up to 146 (Figure 1.2). Nestboxes were placed in both random roadway and grid arrangements, and all boxes were installed ~ 3 m high on t-posts (Figure 1.3). I installed PVC-pipe style predator baffles during the fall and winter of 2015 as to maintain robust sample sizes of banded BCTI that successfully fledged for other research projects on Freeman. Thus, there were 306 nestboxes between the three urban (Campus, Parks, Residential) and Rural study locations.

### ***Capture, banding, and measurements***

Between February and July of 2017–2019, I monitored nestboxes twice a week to identify those containing BCTI nesting substrate (moss, fur, and typically snakeskin; Patten and Smith-Patten 2008). Once BCTI were confirmed nesting, I documented nesting stage (incubation, hatchlings), nest age, and confirmed either successful fledging or failure (depredation, abandonment, unknown) for each nest. When hatchlings were  $\geq 5$  days old, I captured adults within the nestbox by hand as they fed young (Rylander et. al

2020). I affixed adults with a registered United States Geological Service (USGS) aluminum band and a unique combination of 1 to 3 Darvic color bands (Avinet Research Supplies, Portland, Maine). I determined sex of adults (cloacal protuberance on males, brood patch on females), recorded their mass using a 60-g Pesola Micro-Line spring scale, and measured lengths of tarsus length, wing chord (hereafter “wing”), and culmen (mm) before release. Between 10 and 14 days post-hatching, I color-banded nestlings with individual combinations and recorded tarsus (mm) and mass (g) to the closest 0.01 g. Because I was unable to band and measure all broods on the same day post-hatch, I assigned individuals within a brood a mass-rank score (Caro et al. 2016, Rylander et al. 2020) with heaviest individuals as 1, next heaviest as 2, and so on. I recorded fledging date as the first date in which no nestlings were present in the nest (using the Julian calendar) and determined brood size as the number of individuals banded within the nest, given that all individuals eventually fledged.

At the time of banding, I was unable to determine the sex of nestlings because BCTI are not sexually dimorphic. However, in instances when juvenile BCTI remained in the vicinity of their natal home ranges, I assigned each individual to a particular sex based on behaviors such as singing, courtship displays, and on occasion nesting behaviors if the individual was observed the following spring (Patten and Smith-Patten 2008). When this occurred, I updated the banding records with the new sex code retrospectively.

Though no genetic work was performed on our BCTI population, I determined familial relationships (father, mother, offspring) after repetitive and detailed focal monitoring at nestboxes during the entirety of the nesting cycle. Because adults were captured, banded, and sexed at nestboxes while feeding young, I repeatedly recorded the

same male and female entering the nestbox, as well as the same adults feeding their fledglings outside of the nest. Though I acknowledge that actual paternity is not known for these family groups, I assume that the BCTI experiences similarly low rates of extra-pair copulations as its sister taxa, the tufted titmouse, which had been recorded at 8.8% (*Baeolophus bicolor*, Pravosudova et al. 2002).

### ***Home range monitoring and habitat composition***

Through focal monitoring of banded individuals, I delineated BCTI home ranges by recording specific GPS locations (60CSx, Garmin Ltd., Olathe, KS). Once every two weeks ( $\geq 5$  days between visits with positive detections), I searched for family groups and identified individuals within each family flock. I varied the times of day I searched for family groups (0700 to 1800) to account for potential bias in BCTI behavior around dawn and dusk near roosting sites (Bibby et al. 2000). Once located, I followed banded BCTI groups for  $\geq 30$  min from  $\geq 20$  m to reduce any potential influence on their movement. If family groups were not positively detected or identified while searching, I returned to the same site within 1–4 days to relocate. However, if I was unable to detect banded groups over a 4-week period ( $\geq 5$  negative detections), I removed this BCTI group from our analyses. I followed the territory-holding male if groups split during observation periods. In summary, I recorded location and family flock membership  $\geq 10$  times throughout the breeding season each year (March–July), and continued following the same flock once every two weeks during the non-breeding season for the remainder of the year (August–February; Bibby et al. 2000, Rylander et al. 2020).

To assess habitat composition of BCTI home ranges, I used ArcGIS Pro 2.6.1 (Environmental Systems Research Institute 2020) to construct minimum convex

polygons from recorded GPS locations for each banded family each year, thus providing me with a delineated home range. I utilized a Texas Parks and Wildlife Department (TPWD 2020) 30-m by 30-m pixel vegetation geographic information system (GIS) layer to provide habitat composition within each BCTI home range. Due to the large number of detailed vegetation categories provided by this GIS layer, I reclassified vegetation into five broad categories: woodland, grassland, mixed shrub (i.e., a mix between woodland and grassland), low urbanization, and high urbanization. Vegetation polygons containing < 25% woodlands were classified as grasslands, < 75% and  $\geq$  25% woodlands were classified as mixed, and  $\geq$  75% woodlands were classified as woodlands (Rylander et al. 2020). I did not need to reclassify low urbanization and high urbanization polygons as they were already stand-alone categories in the original GIS layer. As described by TPWD, low urbanization is defined as “areas that are built-up but not entirely covered by impervious cover and includes most of the non-industrial areas within cities and towns.” TPWD describes high urbanization as “built-up areas and wide transportation corridors that are dominated by impervious cover.” Once all vegetation polygons were reclassified, I calculated the percentage of each of the five vegetation categories per total family group home range area, allowing for vegetation to be analyzed across all home ranges.

To examine if there were differences in the available versus occupied vegetation categories being used by urban BCTI, I used ArcGIS Pro to pair each occupied nestbox with a randomly generated point 400 – 500 m from the nestbox, representing a distance far enough to be considered a separate territory but not outside of reasonable BCTI foraging range (Rylander 2015, Rylander et al. 2020). I then created a 9.07-ha buffer around each random point, and within each buffer, extracted the percentage of each of the

five previously listed vegetation categories. I used 9.07 ha as the chosen buffer size because previous work on a nearby population of BCTI documented home range size averaging 9.07 ha (Rylander et al. 2020).

### ***Dispersal***

I placed fledged young into three categories based on their dispersal or lack thereof: “Complete dispersers” included offspring that were no longer present or near their natal home ranges ( $\geq 400$  m; Hatchwell 2009, Rylander et al. 2020). “Delayed dispersers” included offspring that remained near their natal home range for  $> 7$  months post-fledge but dispersed before the next breeding season (February the following year). Finally, “limited dispersers” included offspring that delayed their dispersal and eventually established a territory near their natal home range the following year ( $\leq 400$  m; Ekman 2006; Sharp et al. 2008, Rylander et al. 2020). Because “limited dispersers” and “delayed dispersers,” contain some of the same individuals (some delayed dispersers eventually changed status to limited dispersers if they remained near natal home ranges the following season), I never incorporated these two categories in a single model due to violating independence of samples. However, I performed analyses on “delayed dispersers” and “limited dispersers” separately to examine if there was a difference between individuals that remain but eventually disperse and those that remain permanently.

Because I could not determine the absolute fate of all dispersing offspring in this study, many “complete dispersing” BCTI juveniles may have died instead of dispersing. In many social avian species, dispersing juveniles tend to exhibit increased mortality rates compared with offspring that exhibit philopatry (Griesser et al. 2006). However,

because I was not interested in absolute dispersal fate for our study, I still examined factors involved in delayed and limited dispersal behavior of BCTI.

The methods used in this study were conducted in accordance to Institutional Animal Care and Use Committee (IACUC) (#201532811), federal Master Banding Permit (#24108), U.S. Fish and Wildlife Permit (MB121162-2), and Texas Parks and Wildlife Collection Permit (#SPR-0417-107). All birds were handled professionally as advised by the Ornithological Council's Guidelines for wild avifauna in research.

## **Data Analyses**

### ***Home range***

I used software R (version 4.0.2, R Development Core Team 2020) for all statistical analyses in this study. I first used a chi-squared test of independence to assess if there were differences in occupied versus available habitat of urban BCTI for the five vegetation categories. I then examined if there was a difference in habitat composition (specifically high urbanization habitat) within each BCTI home range across the three urban locations. For this analysis, I conducted an analysis of variance (ANOVA) with percent high urbanization within each home range as the response variable and location (Campus, Parks, and Residential) as the three-level categorical predictor. I then assessed if BCTI home range size (ha) was influenced by percentage of high urbanization habitat within the home range, by percentage of high urbanization habitat within the home range, location (Campus, Parks or Residential), fledge date, brood size, and year using generalized linear regression. The response variable, home range size, followed a gamma distribution, and all covariates were plotted against the response variable to confirm

linear relationships. I omitted variables with a variance inflation factor ( $VIF > 3$ ).

Continuous covariates were scaled and centered. Though BCTI inhabit woodlands more than other vegetation categories in the study (Patten and Smith-Patten 2008), I was interested in the effects of urbanization on BCTI home range size. Therefore, I made an *a priori* decision to include % high urbanization and % low urbanization in the models after assessing their correlation. I used backwards selection to remove factors that were not significant in the global model (confidence intervals overlapping 0) to create the most parsimonious model (Zuur et al. 2009).

### ***Delayed and limited dispersal***

I examined the influence of dispersal behavior on home range size (ha) of the natal group, percentage of low and high urbanization habitat within the home range, location, brood size, fledge date, and year using logistic regression. “Dispersal” was the binomial response variable, where (0) indicated all juveniles within a family unit completely dispersed away from their natal home range, and (1) indicated  $\geq 1$  juvenile(s) within a family unit delayed dispersal. I also performed a separate logistic regression (with the same covariates) where (1) indicated  $\geq 1$  juvenile(s) within a family unit limiting dispersal from their natal home range. I again utilized VIF to assess multicollinearity among independent covariates, as well as scaled and centered all continuous covariates. I then used backwards selection to create the most parsimonious model.

### ***Mass and sex***

To assess if BCTI dispersal was influenced by mass-rank of nestlings within a brood, I used a two-tailed Fisher's exact test of independence (Fisher 1934). I examined if a nestling's mass-rank being either "below" (heavier) or "above" (lighter) than the median mass-rank value of the entire brood affected if an individual "dispersed" or "delayed dispersal." I also conducted a separate Fisher's exact test to assess if mass-rank influenced "dispersed" or "limited dispersal" behavior of BCTI juveniles.

I performed additional two-tailed Fisher's exact tests to examine the influence of sex on juvenile BCTI delayed and limiting dispersal behavior. I assumed that if philopatry is not biased towards male or female BCTI, then a 1:1 ratio of males to females that either delay or limit their dispersal should be observed. If philopatry is sex-biased, however, then I predicted that one sex, specifically males, will have a greater frequency of delayed/limiting dispersal behavior over the other (Rylander et al. 2020).

### ***Morphology and conditional indices***

To compare body condition of both nestling and adult BCTI in urban and rural landscapes, I used tarsus (mm) and body mass (g) measurements to generate body conditional indices (hereafter BCI) which can be indicative of overall BCTI health (Peig and Green 2009, Borowske et al. 2018). To calculate BCI, I used case-resampling bootstrap regression to account for error associated with tarsus measurements (Sahinler and Topuz 2007). I then computed the residual value for each individual as the raw data point for mass subtracted from the bootstrapped regression (raw mass - predicted regression mass = BCI). Once BCI residuals were calculated, I used a linear mixed



effects model to assess if body condition of BCTI nestlings was influenced by location (Campus, Parks, Residential, Rural), Julian date when measurements were taken, year, bander who recorded the measurements, and random effect “family” due to a lack of independence of nestlings within the same nest. I also used a linear regression to examine if nestling BCI influenced limited or delayed dispersal of juveniles for 2018 and 2019 urban BCTI. In addition, I calculated BCIs for adult BCTI captured in 2018 and 2019 using a separate case-resampling bootstrap regression to examine if Julian date of capture, location, year, or sex influenced body condition using a linear regression.

## **Results**

### ***Capture and banding***

Between 2017–2019, I color-banded 468 individual BCTI in urban locations (136 on Campus, 129 in Parks, and 203 in Residential; Table 2.1). This included 84 adults and 384 nestlings that comprised 75 family units. However, some nests failed due to depredation, abandonment, or unknown causes, thus I used 47 family units for mass/sex analyses and 35 family units for home range and habitat composition analyses. In addition, for the body condition analyses, I collected data from 52 urban nests and 57 rural nests (548 total BCTI in the rural population; 91 adults, 457 nestlings) (Table 2.2).

### ***Home range and habitat composition***

Home range size for urban BCTI ( $n = 35$ ) was (mean  $\pm$  SD)  $9.11 \pm 5.06$  ha (Figure 2.1), with home range size ranging from 3.38–22.47 ha. Low urbanization habitat was represented the most within home ranges (mean  $\pm$  SD) ( $6.29 \pm 4.02$  ha), followed by high urbanization ( $1.09 \pm 1.90$  ha), woodland habitat ( $0.84 \pm 1.76$  ha), mixed ( $0.68 \pm 0.94$

ha), and finally grassland ( $0.38 \pm 1.06$  ha) (Figure 2.2). By location, home range size was the largest among Campus BCTI ( $14.04 \pm 4.55$  ha), followed by Parks ( $6.87 \pm 2.85$  ha), and Residential ( $6.10 \pm 2.45$  ha). Additionally, there was no difference in the percentages of each vegetation category between available and occupied habitat for urban BCTI ( $\chi^2 = 1.73, p = 0.79$ ).

There was a difference in the percentage of high urbanization habitat within home ranges across our three urban locations (ANOVA;  $F_{(2,32)} = 24.65, p < 0.01$ ). Tukey's post-hoc test revealed that Campus ( $17.82 \pm 10.90\%$ ) differed from both Parks ( $1.27 \pm 2.08\%$ ) and Residential ( $0.72 \pm 1.84\%$ ) locations significantly (both  $p < 0.01$ ). Residential and Parks did not differ in their percentages of high urbanization habitat within home ranges (Tukey's;  $p = 0.98$ ) (Figure 2.3).

The most parsimonious generalized linear regression model explaining home range size included predictors low urbanization and high urbanization (Table 2.3). A 10% increase in the proportion of low urbanization habitat decreased BCTI home range by 0.3 hectares (Figure 2.4). A 10% increase in the proportion of high urbanization habitat increased BCTI home range by 4.4 hectares (Figure 2.5). I removed covariate "Location" as it was highly correlated with percent high urbanization ( $VIF = 4.07$ ), which also can be explained by the previous ANOVA.

### ***Delayed and limited dispersal***

Due to limited sample size of family units ( $n = 5$  in 2017,  $n = 15$  in 2018, and  $n = 15$  for 2019), I performed an ANOVA to examine if pooling data across years was possible ( $n = 35$ ). The proportion of families with delayed and limited dispersers was the

response variable, and the fixed effect was each of the three years. There was no difference among the three years in regard to the proportion of families containing a delayed disperser (ANOVA,  $F_{(2,32)} = 0.05$ ,  $p = 0.96$ ) or a limited disperser (ANOVA,  $F_{(2,32)} = 0.14$ ;  $p = 0.87$ ), thus I proceeded using the pooled sample size with further analyses.

Of the 35 BCTI family groups monitored, 26 (74%) retained  $\geq 1$  juvenile during the delayed dispersal time period (9 months post-fledge), and 18 (51%) had  $\geq 1$  juvenile limit its dispersal and establish a territory adjacent to its natal home range the following year. I was unable to observe the absolute fate of the 8 juveniles that delayed but failed to limit their dispersal.

Based on the logistic regression models, urban BCTI delayed dispersal behavior was not influenced by any habitat or environmental predictors (Table 2.4, Figure 2.6). However, the proportion of low urbanization within BCTI home range influenced limited dispersal behavior ( $n = 35$ ;  $\beta = -1.16 \pm 0.48$ ;  $z = -2.43$ ; 95% CI =  $[-2.25, -0.33]$ ;  $p = 0.02$ ) (Figure 2.7). As the percentage of low urbanization decreased within a BCTI home range, the family group was more likely to have a juvenile limit its dispersal.

### ***Mass and sex***

Delayed and limited dispersal were influenced by urban BCTI mass-rank and sex. Of the 270 nestlings sampled from 38 nests, 37 individuals delayed their dispersal, 24 of which were assigned a mass-rank below the median mass-rank of their family unit ( $n = 270$ ; 95% CI =  $[0.17 - 0.82]$ ;  $p = 0.01$ ). 27 individuals limited their dispersal, 16 of which were assigned a mass-rank below the median mass-rank of their family unit ( $n = 270$ ;

95% CI = [0.21 – 1.28];  $p = 0.15$ ) (Table 2.5). On average, juveniles that delayed their dispersal were 0.86 mass-ranks lower than juveniles that completely dispersed, and those that limited their dispersal were 0.91 mass-ranks lower than those that completely dispersed.

Sex influenced delayed and limited dispersal behavior of urban BCTI. I was able to determine the sex of 29 of the 37 individuals that delayed their dispersal. Of those 29 juveniles, 25 were male and 4 were female ( $n = 29$ ; 95% CI = [1.43 – 28.05];  $p < 0.01$ ). I determined the sex of 25 of the 27 limited dispersing individuals; 21 were male and 4 were female ( $n = 25$ ; 95% CI = [1.12 – 24.36];  $p = 0.03$ ) (Table 2.6)). Of those that limited dispersal, males were on average 1.50 mass-ranks lower than females.

### *Conditional indices*

Because mass was not recorded using the same scale during 2017 for both BCTI nestlings and adults, I used only the measurements collected during 2018 and 2019. I first determined that the relationship between BCTI nestling tarsus and mass was linear ( $n = 684$ ; 2-tailed Student's t-test:  $T_{(682)} = 0.95$ ;  $p = 0.34$ ). Thus, I did not need to use a scaling factor when calculating nestling BCI. My linear mixed effects model revealed that none of the fixed predictors influenced BCTI nestling BCI (Table 2.7). However, random predictor 'Family' accounted for 55% of the variation of BCI in the global model, whereas the fixed predictors only accounted for 1.4% of the variation (conditional  $R^2 = 0.564$ , marginal  $R^2 = 0.014$ ) (Figure 2.8). Limited ( $\beta = 0.13 \pm 0.22$ ; 95% CI = [-0.31 – 0.56];  $p = 0.57$ ) and delayed ( $\beta = 0.21 \pm 0.19$ ; 95% CI = [-0.16 – 0.59];  $p = 0.27$ ) juvenile BCTI dispersal was not influenced by the BCI of individuals during the nestling stage.

For adult BCTI, I used the measurements from  $n = 146$  individuals (83 females and 63 males). I determined that the relationship between tarsus and mass was linear (2-tailed Student's T-test:  $T_{(144)} = -1.05$  ;  $p = 0.20$ ). Therefore, I did not use a scaling factor for calculating BCI and proceeded with a linear relationship. In the linear regression, sex was the only significant predictor of BCTI BCI ( $\beta = 0.85 \pm 0.14$ ; 95% CI =  $[0.57 - 1.13]$ ;  $p < 0.01$ ), whereas factors Julian date, year and location were not influential. On average, males had a BCI of 0.48 and females a BCI of -0.37, a difference of 0.85 between the sexes. The average actual mass of males (mean  $\pm$  SD) ( $19.3 \pm 0.68$  g) was greater than the average predicted mass ( $18.82 \pm 0.48$  g), and the average actual mass of females ( $17.89 \pm 0.98$ g) was less than the average predicted mass ( $18.25 \pm 0.53$  g).

## Discussion

BCTI in urbanized habitats form kin-structured neighborhoods through limited natal dispersal behavior of heavier juvenile males. Though previous work by Rylander et al. (2020) described this kin-structured neighborhood formation in a rural population of BCTI, it has never been documented in urban BCTI populations. Thus, to my knowledge, the BCTI is the first documented New World Paridae to have multi-generational family structure analyzed across a variety of habitat types. Other members of the Paridae family have been scarcely documented displaying limited natal dispersal and cooperative breeding behavior, including bridled titmice (*Baeolophus wollweberi*) (Nocedal and Ficken 1998) and tufted titmice (Brackbill 1970). Yet, among the *Poecile* and *Baeolophus* species, BCTI are the only parid with extensive documentation on kin-structured neighborhood formation.

BCTI kin-structured neighborhoods are formed in urban habitats through limited natal dispersal by juveniles, although they are formed less frequently than in rural BCTI populations (51% of families containing a limited disperser in urban habitats compared to 68% in rural, Rylander et al. 2020). Urban juveniles may attempt to form kin-structured neighborhoods but cannot for various reasons given that the percentage of urban BCTI family groups that contained a juvenile that delayed natal dispersal was greater than the percentage that ultimately limited their dispersal (74% compared to 51%, respectively). The lack of suitable habitat or mates (Pruett-Jones and Lewis 1990, Kokko and Lundberg 2001) or the lack of natural resources (food, water, and roosting cavities; Mortberg 2001, Coetzee et al. 2018) may force urban BCTI juveniles farther from their natal home ranges. Verhulst et al. (1997) discovered that high quality habitat facilitates natal dispersal in great tits (*Parus major*), and juvenile males are more likely to be observed closer to their natal home ranges in less patchy environments. Young male Seychelles warblers (*Acrocephalus sechellensis*) are less likely to disperse into neighboring habitat when territories are fully occupied by more dominant males (habitat saturation hypothesis; Komdeur 1992). In addition, landscapes that contain greater percentages of urbanization also may lead to higher mortality rates by both native and non-native predators, as well as through collisions with infrastructure and vehicles (Dunn 1993, Rottenborn 1999, Murgui and Hedblom 2017).

As in other songbirds, including members of the Paridae family, urban BCTI follow the pattern of male-biased philopatry (Greenwood et al. 1979, Pruett-Jones and Lewis 1990, Rylander et al. 2020). However, in urban areas, I observed that 16% of limited dispersing juveniles were female. Though I may have overlooked philopatric

females in the rural study, I could have observed a greater percentage in urban San Marcos due to constraints on dispersal behavior. Some species, such as the brown jay (*Cyanocorax morio*), exhibit female-biased philopatry (Williams and Rabenold 2005) when females locate nearby social groups that contain few members of the same sex. Marsh tits (*Parus palustris*) display a mixture of male and female-biased philopatry (Nilsson 1989). Though BCTI may be adapting to urban environments with different dispersal strategies, it is unlikely because female-biased philopatry is relatively rare in avian species (Williams and Rabenold 2005).

My results agree with previous studies examining natal dispersal behavior and the positive influence of nestling mass (Naef-Daenzer et al. 2001, Ekman 2006, Rylander et al. 2020). It is hypothesized that heavier siblings have a competitive advantage over lighter individuals due to their larger size and possible increased fitness (Fitzpatrick and Woolfenden 1984, Mumme et al. 2015). In the great tit, Drent (1983) and Tinbergen and Boerlijst (1990) discovered through different approaches that lighter nestlings have a lower likelihood of acquiring a territory compared to heavier nestlings once fledged. However, previous work composed by Perrins (2001) demonstrated that great tit nestling weight, when coupled with fledging date and year, influences recruitment and survival. Because I was unable to determine lay date for every BCTI nest in my study, nestling mass on was not recorded the same day post-hatch across nests. Thus, additional research using actual nestling BCTI mass, instead of relative mass-rankings, could prove useful in disentangling limited dispersal behavior when other factors like fledge date and year are considered.

For the BCTI and other avian species, home range size tends to be positively correlated with proportions of highly urbanized habitat (Redpath 1995, Hindmarch 2017). It is speculated that birds travel further in patchy, less suitable habitat to obtain sustainable resources (Sol et al. 2013). Clement et al. (2020) observed home range sizes of barred owls (*Strix varia*), a woodland-dwelling species, increases with the proportion of urbanization and treeless area within the home range. Salinas-Melgoza et al. (2013) also observed this same trend in yellow-naped parrots (*Amazona auropalliata*), where patchy vegetation results in individuals moving ten times further than those within concentrated, suitable vegetation. Results from previous work with BCTI in an unfragmented landscape display family groups with smaller home ranges (mean  $\pm$  SD) ( $9.14 \pm 4.18$  ha) than those of Campus BCTI ( $14.04 \pm 4.55$  ha) which had the greatest proportion of highly urbanized habitat (Rylander et al. 2020). In contrast, home ranges for Parks ( $6.87 \pm 2.85$  ha) and Residential ( $6.10 \pm 2.45$  ha) BCTI were smaller, on average, than those of rural BCTI. It is hypothesized that supplementary food and water, often in the form of bird feeders and tended gardens, may lead to smaller home range size (Brittingham and Temple 1992, Chamberlain et al. 2009, Coetzee et al. 2019). A study involving dark-eyed juncos (*Junco hyemalis*) revealed that home range size and movement rates decrease when individuals are exposed to supplementary feeders (Roth and Vetter 2008). However, Santangeli et al. (2012) suggests supplemental feeders did not alter home range size of boreal owl (*Aegolius funereus*) males but did restrain conspecific female's movements. Thus, mapping the location of supplemental feeders could fill knowledge gaps on behavioral plasticity of BCTI inhabiting varying grades of urbanized habitat (Wilson 1994).



It is not uncommon for males and females to differ in BCI during various part of the annual cycle (Clutton-Brock 1991, McNamara and Houston 2008, Harrison et al. 2013), especially if females are more invested during reproduction (Liker and Szekly 2005). Though male and female BCTI provide bi-parental care to offspring, females are solely involved in nest building and incubation (Patten and Smith-Patten 2008, Rylander pers. obs.) which could result in females having a lower BCI than males. Female seaside sparrows (*Ammodramus maritimus*), a species that provides bi-parental care to offspring, and female saltmarsh sparrows (*Ammodramus caudacutus*), a species that the female is the only sex involved rearing young, both had consistently lower body mass and body condition (scaled mass index method (SMI), Peig and Green 2009) than their male counterparts during all stages of the annual cycle (Borowske et al. 2018). Thus, it has been proposed that breeding body condition, especially of females, among other indicators of fitness and health, may carry-over into winter and result in lower survival (Liker and Szekly 2005, Harrison et al. 2013). However, many ecologists warn that more than one index for body condition should be examined when relating physicality to survival or individual fitness. Therefore, more work is needed assessing BCI of BCTI during the non-breeding season to examine potential carry-over effects impacting survival and reproductive output.

Contrary to other studies, differences in BCI were not detected between BCTI nestlings in urban and rural populations. Extensive work performed on a food-supplemented control populations of urban and forest-dwelling great tits demonstrated that un-supplemented urban nestlings have lower body mass and body condition than un-supplemented forest nestlings (Seress et al. 2020). This same experiment also concluded

that food-supplemented urban nestlings have similar body condition to un-supplemented forest nestlings, arguing that food may be the limiting resource altering young bird health. Similarly, Meillere et al. (2017) measured lower BCI (SMI method) and poorer feather condition in urban fledgling house sparrows (*Passer domesticus*) compared to rural fledglings. Though nestling titmice did not differ in BCI between urban and rural populations, I may have overlooked the effect of sex on nestling BCI and mass (Oddie 2000, Nicolaus et al. 2009), given the difference of adult BCTI body condition. I was unable to perform genetic testing on nestlings, and therefore the high amount of variation of BCI observed within clutches could be more of an effect from sex than location.

The importance of supplemental cavities in highly urbanized areas has been discussed in recent decades (Newton 1998, Martin and Eadie 1999, Mortberg 2001, Tomasevic and Marzluff 2017). The greatest density of breeding BCTI consistently using nestboxes each year were in the Campus location (refer to Figures 5 & 6), which also was the most urbanized landscape in the study. This is consistent with Gladalski et al. (2016) observing that great tits occupy more nestboxes at a greater density in a highly urbanized park in Poland when compared to a contiguous forest patch 10 km away. Tomasevic and Marzluff (2017) discovered that native secondary cavity nesters (those that do not excavate their own cavities) are more likely to inhabit highly urbanized areas with few natural snags if nestboxes are present. They hypothesized that many primary cavity nesting species (those that excavate their own cavities) are less common in highly urbanized areas, and thus cavities may be a limited resource for secondary cavity nesting species. However, research performed on house sparrows demonstrated that pairs occupy a greater number of nestboxes in rural compared to urbanized habitat (Angelier and

Brischoux 2019). Thus, understanding the life history and breeding behavior of the study species is important when implementing management practices, such as supplementary cavity provisioning (Chamberlain et al. 2009, Sol et al. 2014).

Though results suggest that BCTI kin-structured neighborhoods are less likely to form in urbanized environments, there are still knowledge gaps regarding the effects of kin-structure on individual survival, fecundity, and population persistence. As a generalist species that frequents bird feeders and utilizes man-made structures for nesting (Patten and Smith-Patten 2008), the BCTI may be adapted, and even well-suited, for life in the city. A study of European great tits discovered that urban-dwelling individuals have an increased survival rate compared to rural individuals, possibly due to food supplementation or milder microclimates (Horak and Lebreton 1998). A meta-analysis on multiple avian species suggested that though urban populations tend to have lower clutch size and lower productivity per nesting attempt, the presences of human-provided food resources may increase adult survival and overall population densities within cities (Chamberlain et al. 2009). However, this study also emphasized that their analyses are biased towards generalist species that tend to be well-adapted to anthropogenic disturbance. Thus, the pattern they discovered may not apply to family-oriented species. Layton-Matthews et al. (2018) revealed that habitat fragmentation alters demography and dispersal patterns of Siberian jay (*Perisoreus infaustus*) family groups, ultimately leading to localized population decline. Therefore, future work should focus on the interactions between environmental and social factors that are potentially disrupting kin-structured neighborhood formation of the BCTI.

**Table 2.1** The number of nestling and adult black-crested titmice (*Baeolophus atricristatus*) banded and measured across four locations in San Marcos, Texas, 2017–2019.

	Urban						Rural	
	Campus		Parks		Residential		Freeman	
	<u>Nestlings</u>	<u>Adults</u>	<u>Nestlings</u>	<u>Adults</u>	<u>Nestlings</u>	<u>Adults</u>	<u>Nestlings</u>	<u>Adults</u>
<b>2017</b>	23	7	23	9	--	--	89	9
<b>2018</b>	47	5	37	7	90	28	163	51
<b>2019</b>	49	6	45	8	70	15	205	32
<b>Total</b>	119	18	105	24	160	43	457	91

**Table 2.2** Morphometric measurements and calculated body conditional indices (BCI) recorded for adult black-crested titmice (*Baeolophus atricristatus*) captured during the spring of 2018 & 2019 in San Marcos, Texas.

Measurement	Female				Male			
	Campus	Parks	Residential	Rural	Campus	Parks	Residential	Rural
<b>Body Mass (g)</b>	18.14 ± 1.07	18.05 ± 0.72	18.13 ± 1.05	17.71 ± 0.97	18.88 ± 0.63	19.30 ± 0.97	19.56 ± 0.68	19.22 ± 0.61
<b>Tarsus (mm)</b>	19.47 ± 0.73	19.22 ± 0.47	19.59 ± 0.71	19.18 ± 0.52	19.79 ± 0.47	19.72 ± 0.97	20.13 ± 0.51	19.91 ± 0.50
<b>BCI</b>	-0.25 ± 0.90	-0.13 ± 0.80	-0.38 ± 0.99	-0.43 ± 0.90	0.20 ± 0.72	0.68 ± 0.83	0.58 ± 0.84	0.44 ± 0.76
<b>Wing (mm)</b>	72.14 ± 1.07	70.80 ± 0.63	71.30 ± 1.89	71.72 ± 1.66	73.50 ± 0.58	75.20 ± 1.79	75.00 ± 2.72	75.22 ± 1.96
<b>Culmen (mm)</b>	10.61 ± 0.33	10.60 ± 0.65	10.47 ± 0.54	10.30 ± 0.38	10.50 ± 0.32	10.39 ± 0.40	10.39 ± 0.49	10.46 ± 0.41

**Table 2.3** The top generalized linear regression model for predicting home range size (ha) of urban black-crested titmice (*Baeolophus atricristatus*) in San Marcos, Texas, 2017–2019. Percent high and low urbanization are proportions of those vegetation categories located within each home range.

Covariate	$\beta \pm \text{SE}$	<i>t</i> -value	<i>p</i>	95% CI
(Intercept)	9.25 $\pm$ 0.56	16.41	< 0.01	8.24 – 10.46
% high urban	4.01 $\pm$ 0.78	5.18	< <b>0.01</b>	2.66 – 5.69
% low urban	-0.84 $\pm$ 0.41	-2.04	<b>0.05</b>	-1.65 - -0.12

**Table 2.4** The global model from the logistic regression where no factors significantly influenced delayed dispersal behavior in juvenile black-crested titmice (*Baeolophus atricristatus*) in urban San Marcos, Texas, 2017–2019. Percent low urbanization is the proportion of that vegetation category located within the home range, fledge number is the number of total nestlings per family unit that successfully left the nest, and Julian date is the calendar date in which nestlings were banded (a proxy for fledge date).

Covariate	$\beta \pm \text{SE}$	z-value	p	95% CI
(Intercept)	$1.48 \pm 0.54$	2.74	<0.01	0.56 – 2.76
Fledge number	$-0.89 \pm 0.54$	-1.64	0.10	-2.12 – 0.06
Home range	$0.71 \pm 0.61$	1.15	0.25	-0.33 – 2.15
% low urban	$-0.79 \pm 0.53$	0.53	0.14	-1.99 – 0.15
Julian date	$-0.36 \pm 0.50$	0.50	0.43	-1.48 – 0.57

**Table 2.5** The number of black-crested titmouse (*Baeolophus atricristatus*) nestlings in urban San Marcos, Texas that delayed or limited dispersal based on if their mass-rank fell below or above the median mass-rank for each nest. Delayed dispersal is defined as juveniles remaining in their natal home range for  $\geq 9$  months post-fledge but eventually dispersing after that. Limited dispersal is defined as juveniles remaining in their natal home range for  $\geq 9$  months post-fledge and eventually establish a territory adjacent to their father's the following spring.

<b>Mass-rank</b>	<b>Below</b>	<b>Above</b>
Delayed	24	13
Dispersed	96	137
Limited	16	11
Dispersed	106	137

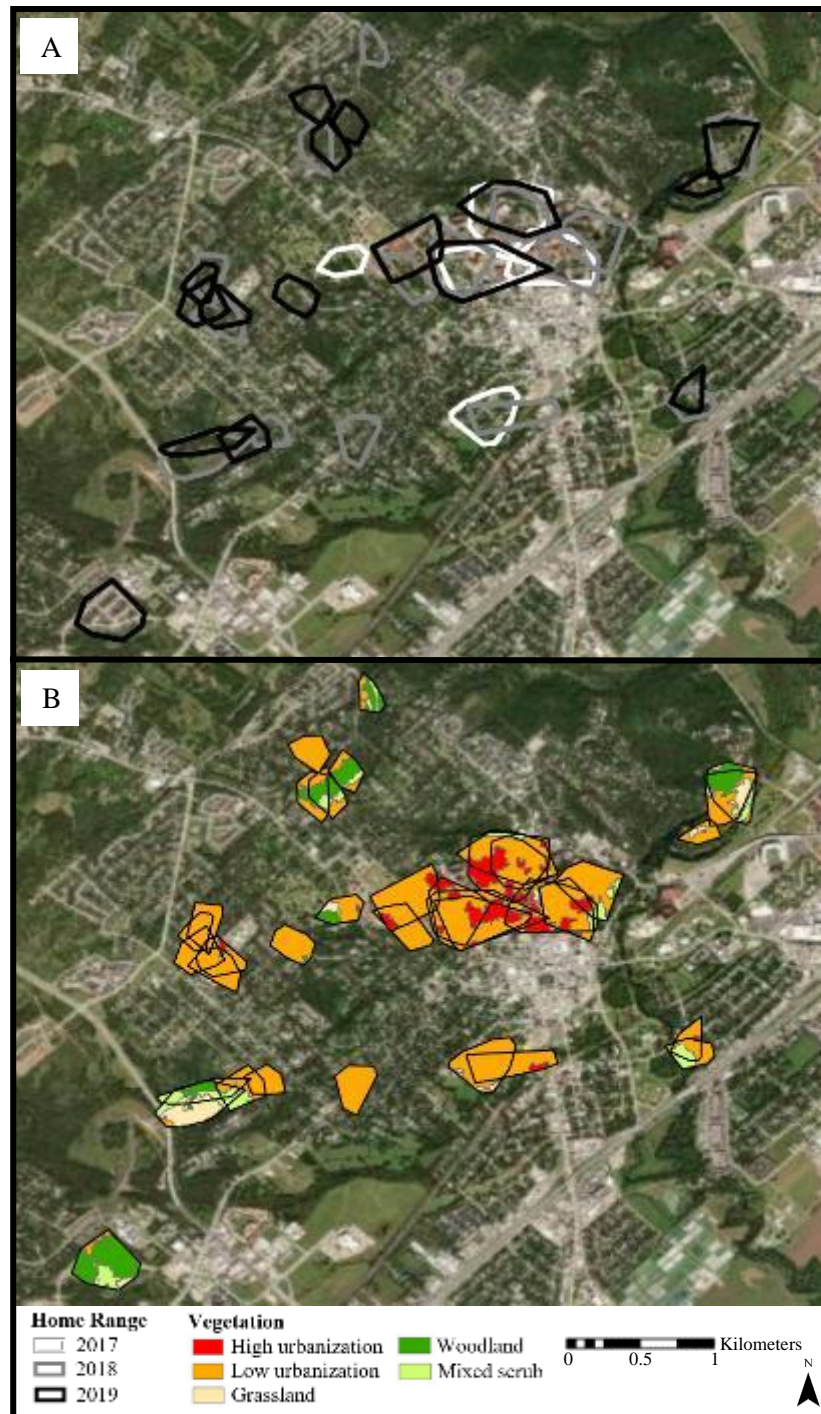


**Table 2.6** The number of observed versus expected juvenile male and female black-crested titmice (*Baeolophus atricristatus*) that delayed or limited their dispersal in urban San Marcos, Texas, 2017–2019. Delayed dispersal is defined as juveniles remaining in their natal home range for  $\geq 9$  months post-fledge but eventually dispersing after that. Limited dispersal is defined as juveniles remaining in their natal home range for  $\geq 9$  months post-fledge and eventually establish a territory adjacent to their father’s the following spring. The “expected” number is assuming that philopatry is not sex-biased, thus providing a 50:50 ratio of males to females that delay dispersal.

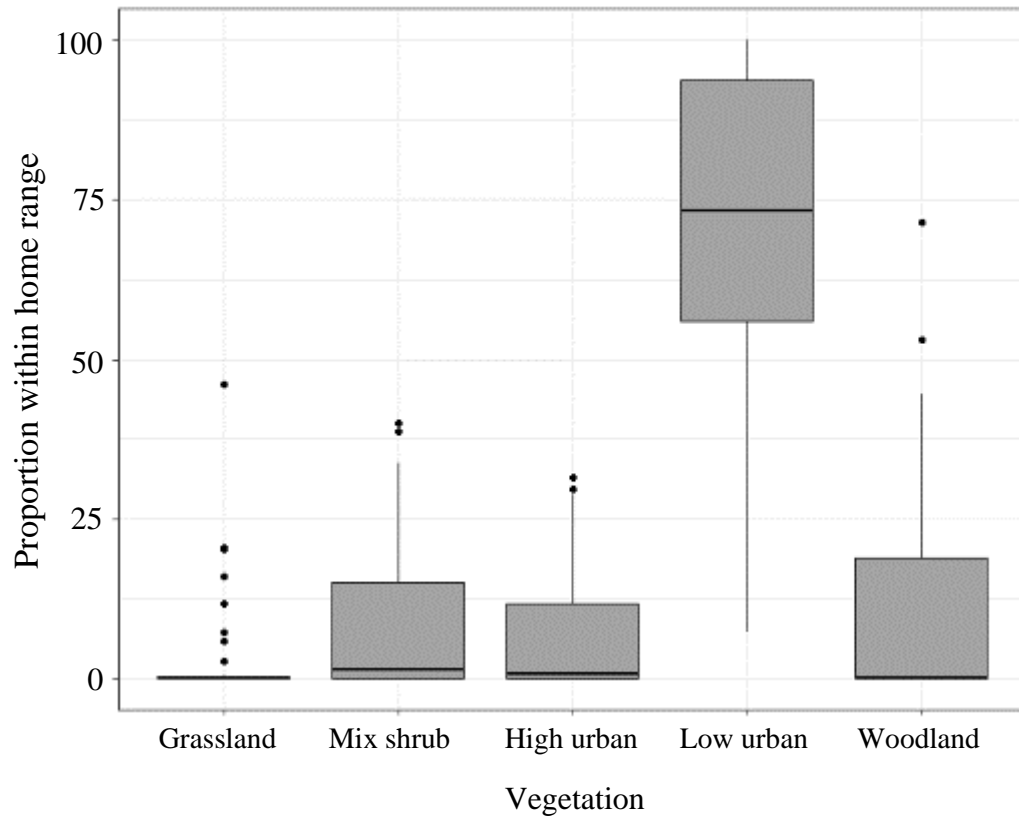
Dispersal	Sex	Observed	Expected
Delay	Male	25	15
	Female	4	14
Limit	Male	21	13
	Female	4	12

**Table 2.7** The global model for the linear mixed effects regression explaining that none of the fixed effects influence black-crested titmouse (*Baeolophus atricristatus*) nestling body conditional indices (BCI) in San Marcos, Texas, 2018–2019. However, random effect “Family” did significantly influence nestling BCI, as there was much variation (55% of total variation) among family units. Fixed factor Bander was the individual responsible for recording measurements, and Julian date is the calendar date in which measurements were recorded.

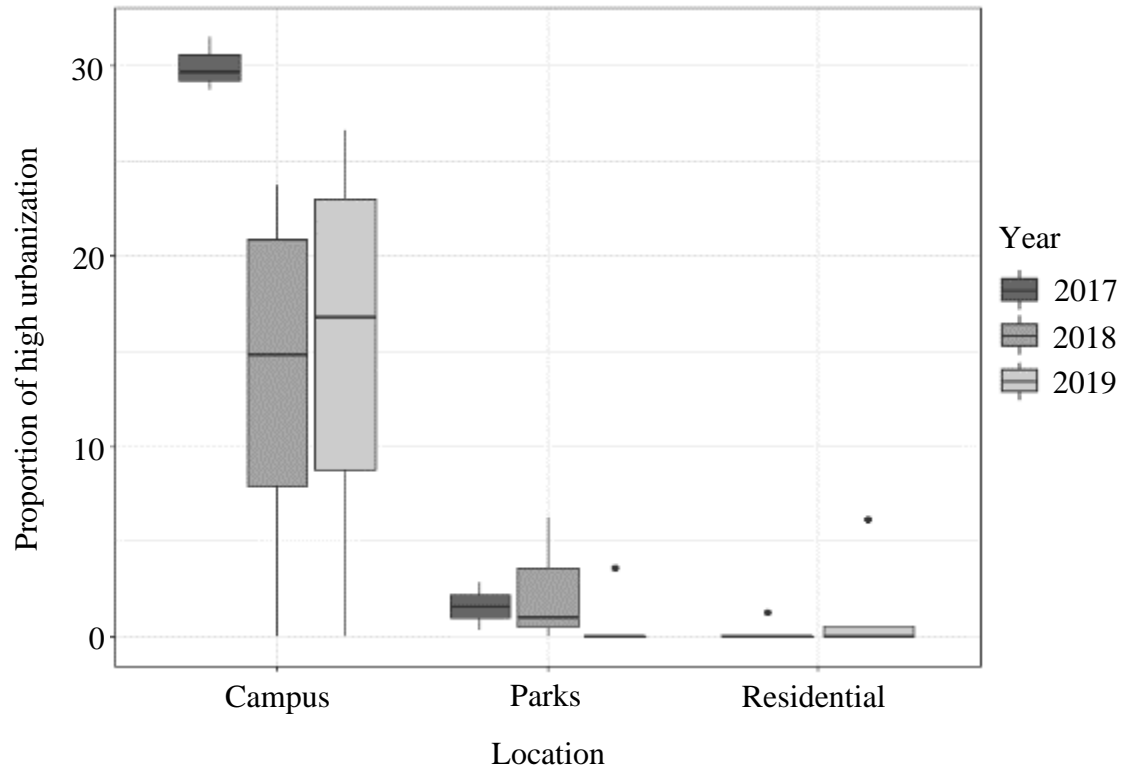
Covariates	$\beta \pm SE$	z - value	p	95% CI
(Intercept)	$0.17 \pm 0.59$	0.29	0.78	-0.97 – 1.30
Location [Freeman]	$-0.29 \pm 0.29$	-0.98	0.33	-0.85 – 0.28
Location [Parks]	$-0.20 \pm 0.39$	-0.51	0.61	-0.95 – 0.55
Location [Residential]	$-0.48 \pm 0.34$	-1.42	0.16	-1.14 – 0.17
Julian date	$0.01 \pm 0.01$	0.59	0.55	-0.01 – 0.01
Bander [RR]	$-0.24 \pm 0.24$	-1.01	0.31	-0.70 – 0.21
Year [2019]	$-0.01 \pm 0.20$	-0.05	0.96	-0.40 – 0.38
Random - Family	Variance = $1.03 \pm 1.01$ $R_c^2 = 0.56$ , $R_m^2 = 0.01$			



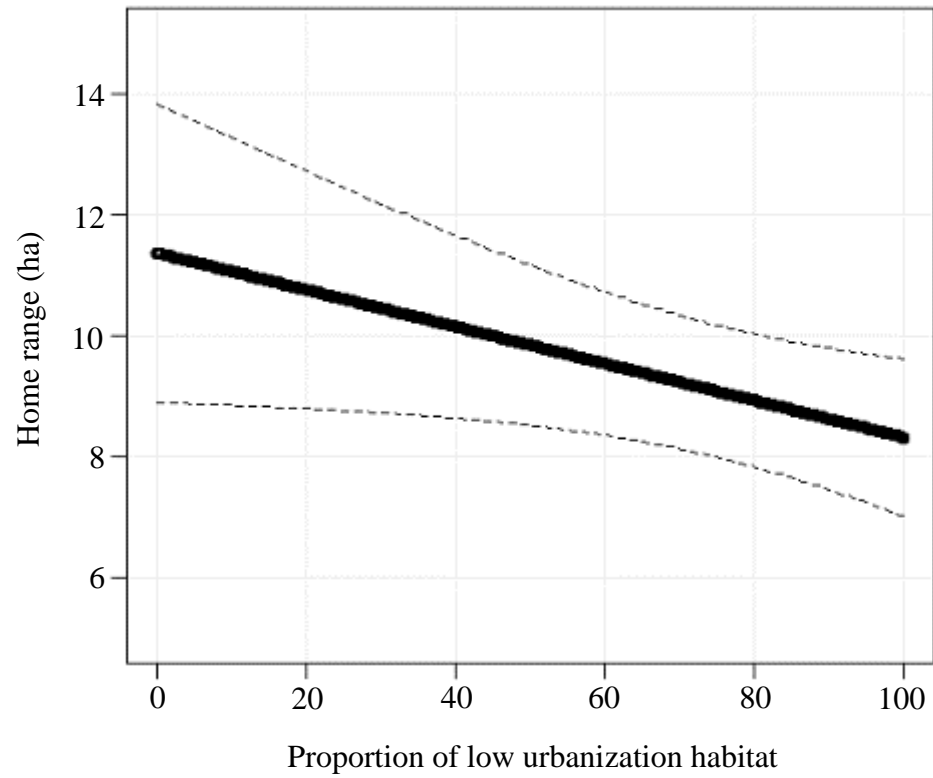
**Figure 2.1** Delineated home ranges of the black-crested titmouse (*Baeolophus atricristatus*, BCTI), 2017–2019, across an urban gradient in San Marcos, Texas. A. Home ranges separated by year, and B. Vegetation categories located within delineated BCTI home ranges.



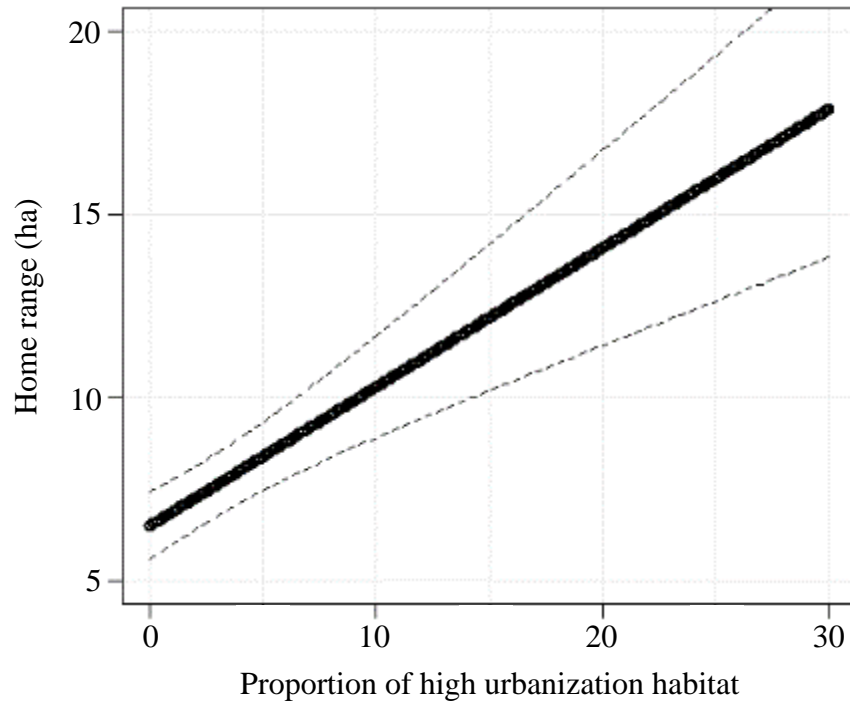
**Figure 2.2** The proportion of different vegetation categories located within black-crested titmouse (*Baeolophus atricristatus*) home ranges in San Marcos, Texas, 2017–2019.



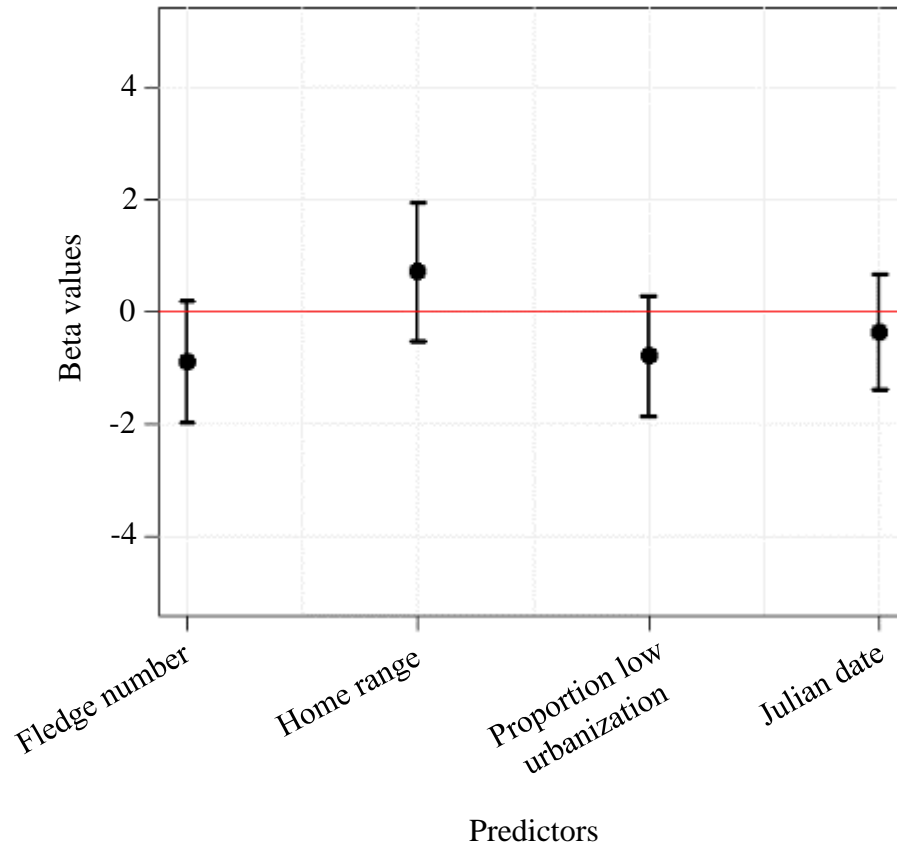
**Figure 2.3** The proportion of high urbanization habitat within black-crested titmouse (*Baeolophus atricristatus*) home ranges across Campus, Parks, and Residential locations in San Marcos, Texas, 2017–2019.



**Figure 2.4** Predictive plot of how black-crested titmouse (*Baeolophus atricristatus*) home range (ha) is influenced by the proportion of low urbanization habitat within the home range in San Marcos, Texas, 2017–2019.

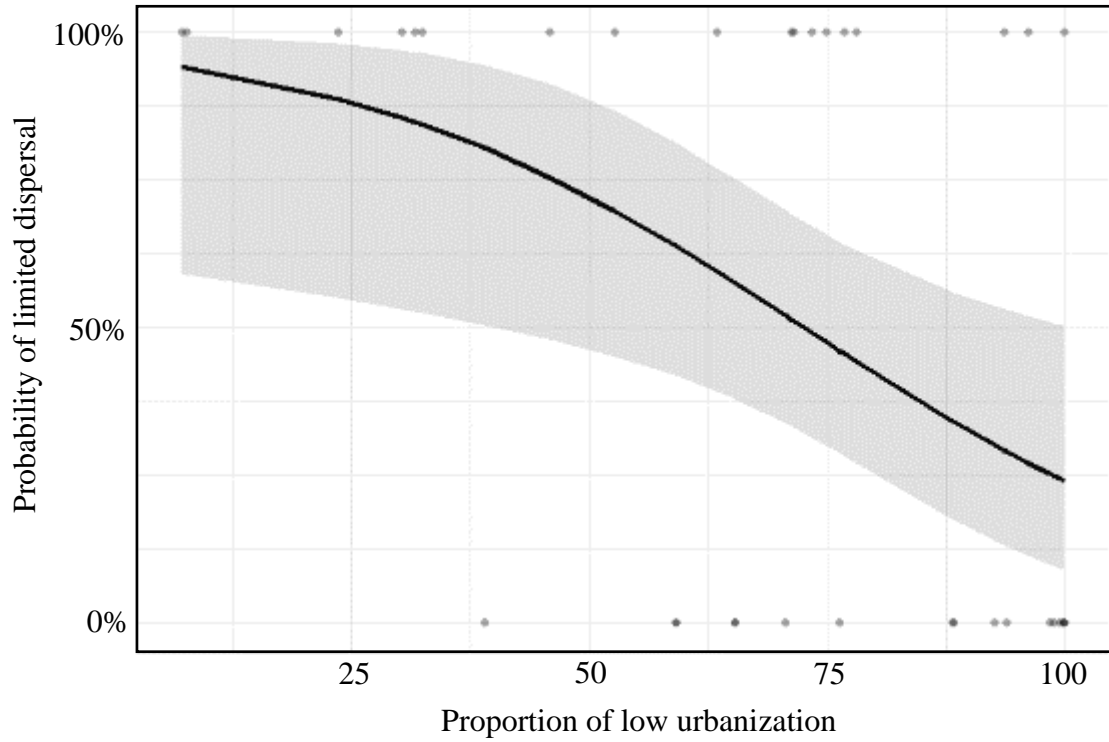


**Figure 2.5** Predictive plot of how black-crested titmouse (*Baeolophus atricristatus*) home range (ha) is influenced by the proportion of high urbanization habitat within the home range in San Marcos, Texas, 2017–2019.

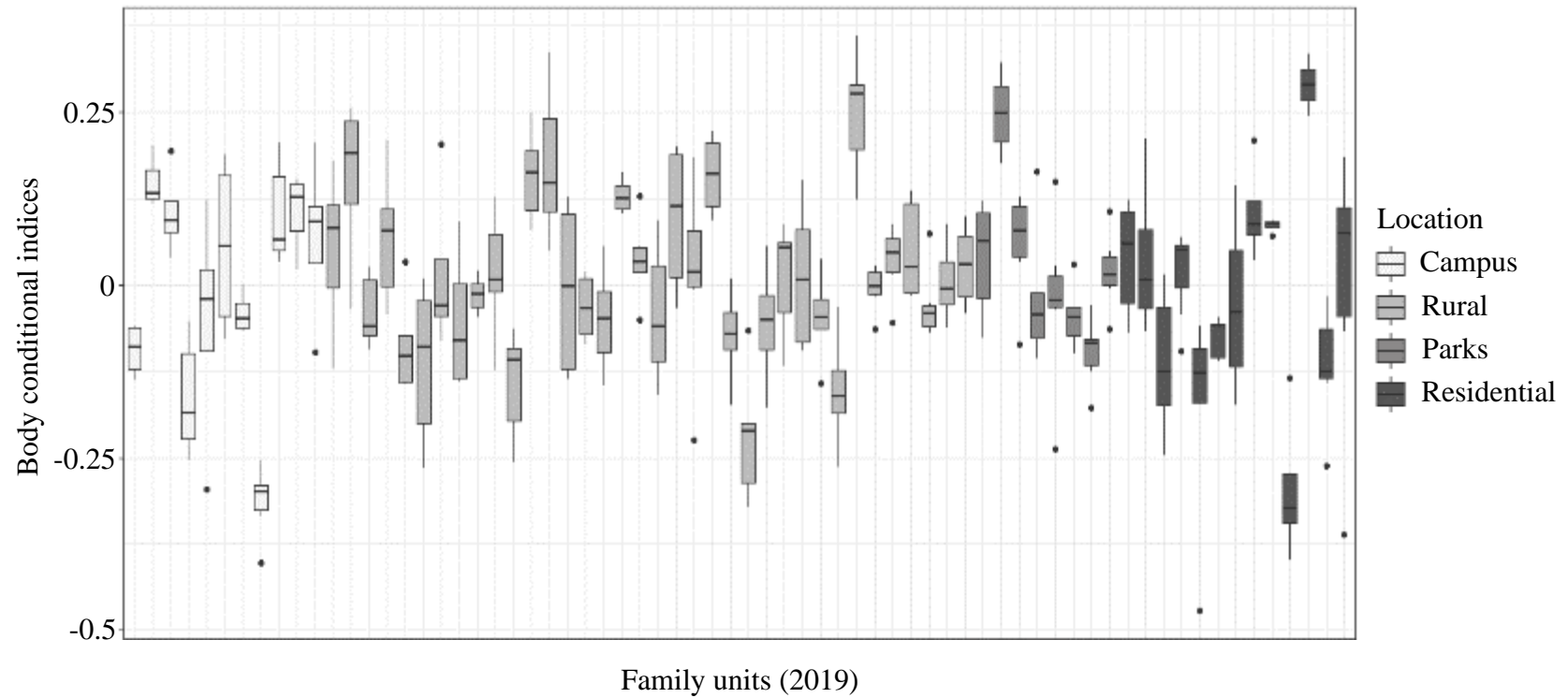


**Figure 2.6** An effect size plot demonstrating how none of the predictors in the logistic regression model influenced delayed dispersal behavior in the black-crested titmouse (*Baeolophus atricristatus*) in urban San Marcos, Texas, 2017–2019.





**Figure 2.7** The proportion of low urbanization within black-crested titmouse (*Baeolophus atricristatus*) home range in San Marcos, Texas influences the likelihood that a juvenile will limit its dispersal.



**Figure 2.8** Boxplots representing the variation of nestling body conditional indices (BCI) within and among family units of black-crested titmice (*Baeolophus atricristatus*) in San Marcos, Texas. Though black-crested titmice were captured and measured for BCI during 2018 – 2019, this graph is only depicting variation among 2019 family units.

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### III. WHETHER CITY-SLICHER OR COUNTRY-BUMPKIN, BLACK-CRESTED TITMICE ADAPT TO URBANIZATION REGARDING NESTING SUCCESS AND PRODUCTIVITY

#### Abstract

Urban environments pose novel challenges for breeding songbirds, where additional stressors in the form of phenological shifts, non-native predators, and heightened intraspecific competition can influence population persistence. However, the degree of urbanization and intensity of habitat change also influence the long-term impacts that avian species endure, especially when provisioning young. Thus, research comparing nesting parameters and productivity rates between urban and rural avian populations is indispensable when establishing management recommendations and conservation plans. To understand the impacts of varying degrees of urbanization on first clutch initiation (date first egg was laid), nesting success, nesting daily survival rates (DSR), clutch size, and productivity, I studied a banded population of black-crested titmice (*Baeolophus atricristatus*; BCTI) that utilized a series of nestboxes I installed across four various location types in San Marcos, Texas. Location types ranged from high urbanization (Texas State University campus; Campus), to low urbanization (San Marcos residential areas; Residential), to natural areas surrounded by urbanization (San Marcos public parks; Parks), to rural (1,400-ha property with native habitat and minimal human infrastructure; Freeman Center). From 2013-2021, I monitored 380 BCTI nests; 252 at the Freeman Center, 36 on Campus, 31 in Parks, and 61 in Residential areas. Rough estimates of nesting success ( $\geq 1$  successful fledgling) were greatest for Parks and Campus (83.87% and 83.33%, respectively), followed by the Freeman Center (73.02%)

and Residential areas (59.02%), with depredation being the leading cause of failure in any location. BCTI average clutch size was (mean  $\pm$  SD)  $5.99 \pm 0.90$  for all successful nests ( $n = 276$ ), and generalized linear models (GLM with Poisson distribution) revealed there were no differences in clutch size between locations or years, nor was it influenced by clutch initiation date. However, number of successful fledglings was negatively correlated with clutch initiation date ( $n = 276$ ;  $\beta = -0.004 \pm 0.001$ ;  $z\text{-value} = -3.021$ ; 95% CI =  $[-0.006 - -0.001]$ ;  $p = 0.003$ ), with fewer fledglings produced per nest later in the season. DSR of nests (estimated through program MARK) were influenced by the date in which clutches were initiated and by location, but not by habitat or weather covariates. DSR decreased as the season progressed, and nests in Residential areas had DSRs lower than all other locations. First clutch productivity (GLM with Poisson distribution) was not affected by location or year. Yet, first clutch initiation date was influenced by location (urban nests initiated  $\sim 9$  days earlier than rural nests, generalized linear mixed effects model with year as random predictor), and first clutch initiation dates between 2014–2021 at the Freeman Center were negatively influenced by February average low temperatures (GLM with Poisson distribution) ( $n = 7$ ;  $\beta = -1.94 \pm 0.42$ ;  $t\text{-value} = -4.57$ ; 95% CI =  $[-3.03 - -0.85]$ ;  $p < 0.01$ ). Overall, our results suggest that BCTI are adapting to urban environments with earlier lay dates, and that clutch sizes remain roughly the same across the urban gradient. Although productivity was similar across all locations, Residential areas had considerably higher rates of nest failure due to depredation. Thus, neighborhoods that contain a high number of cats, raccoons, and rat snakes may act as ecological traps for nesting BCTI.

## Introduction

Urbanization rapidly changes landscapes by fragmenting habitat, altering natural resources, creating microclimate shifts, and introducing novel predators and food sources into the food web (Dirzo and Raven 2003, McKee et al. 2004, Murgui and Hedblom 2017). These changes pose both opportunities and threats to avifauna worldwide, depending on the species and intensity of change (Gill and Brumm 2014, Beninde et al. 2015, Marzluff 2016). Though birds have the ability to fly and can often vacate an area more easily than other taxa, species still must either adapt to their new surroundings, suffer reproductive or fitness consequences, or permanently emigrate to a new location (Blair 1996, Mills 2013, Sol et al. 2013). However, as remaining contiguous patches of natural habitat become increasingly scarce and often more densely populated with birds (Mortburg 2001, Evans et al. 2009, Reidy et al. 2016), species that reach carrying capacity may ultimately force less-fit individuals into urbanized locations, thus creating source-sink dynamics that may or may not become stable over time (Marzluff 2005, Meffert and Dziock 2013). Thus, it is important to understand which species are urban-exploiters, urban-adaptors, or urban-avoiders when creating management plans and deciding upon which habitats to conserve (Evans et al. 2011, Farwell and Marzluff 2013).

Not all forms of urbanization are equal, and the degree to which the landscape is altered is highly variable (Fernandez-Juricic 2000, White et al. 2005). For example, residential neighborhoods that preserve large trees and purposely plan for greenspace are less intense forms of change than clear-cut practices where high-rises and shopping centers are built. The shape and size of the altered habitat also is important (Meffert and Dziock 2013, Myczko et al. 2014), as well as the surrounding habitat matrix (Mills 2013),



as many bird species will not cross large patches of bare ground or navigate through highly developed metropolitan complexes (Desrochers and Hannon 1997, Prugh et al. 2008). Additionally, the duration and time of year in which native land is urbanized also encourages or discourages species to remain or leave, with rapid habitat degradation and fragmentation during the breeding season likely being the most disruptive (Newton 1994, Vergara-Tabares et al. 2020).

Though some bird species appear common in urbanized environments, it is important to focus on their nesting behaviors and reproductive success within these altered landscapes to understand how populations are fluctuating over time (Hedblom and Soderstrom 2012, Marzluff 2016). The breeding season often is the most stressful and energetically taxing period on both males and females because food resources are shared and time for self-maintenance is divided to provide for young (Thomas et al. 2001, Liker and Szekly 2005). Subsequent stressors in the form of air, light, and sound pollution, increased predators, and, ultimately, phenological mismatch have been documented having consequences on productivity and overall nesting success of urban bird populations (Marzluff 2016, Hindmarch et al. 2017). Nonetheless, in other circumstances, reliable and abundant resources in the form of bird feeders and stable man-made nesting structures, such as nestboxes, have increased clutch size and reproductive output for some species (Purcell et al. 1997, Martin and Eadie 1999). Thus, there is an increased importance to understanding how urban and rural populations compare in breeding performance, coupled with apparent survival and recruitment, to better predict how continued urbanization will impact a species in the future (Ryder et al. 2010, Reynolds et al. 2019).

To assess if varying degrees of urbanization are impacting breeding parameters and nesting success of a species that appears stable in an urban environment, I studied the black-crested titmouse (*Baeolophus atricristatus*, hereafter BCTI), a non-migratory social member of the Paridae family (hereafter “parids”) that is fairly abundant throughout most of its range (central, south, and west Texas, into portions of southwestern Oklahoma, and into north-central portions of Mexico) (Dixon 1978, Patten and Smith-Patten 2008). Even though the BCTI is not threatened or endangered, it is unknown how urban populations compare to their rural counterparts regarding productivity, clutch size, lay date, and nesting success, among other nesting characteristics. The BCTI also makes an ideal study species because few researchers have consistently monitored BCTI nesting parameters, as current information on clutch size and breeding season duration comes from collections in the Western Foundation of Vertebrate Zoology, from observational studies with small sample sizes (Allen 1907, Bent 1946, Dixon 1955, Harrap and Quinn 1995), or are assumed to be similar to its sister-taxon, the tufted titmouse (*Baeolophus bicolor*).

To compare nesting behavior of urban and rural BCTI, I: 1) examined BCTI nesting characteristics, including initiation dates of first and second clutches, the frequency distribution of eggs, nestlings, and fledglings per nest, and factors influencing nest fate; 2) assessed BCTI annual productivity across years and locations; and 3) calculated daily survival rates (DSR) of BCTI nests. I predicted first clutch initiation dates would be earlier for urban BCTI than rural BCTI due to microclimates in urban locations causing temperatures to be slightly warmer than rural locations (Chamberlain et al. 2009), and that clutches initiated earlier in the season would be more likely to fledge young successfully because temperatures are milder and food more abundant (Gill and

Brumm 2014, Murgui and Hedblom 2017). Lastly, I predicted that urban nests would have a lower annual productivity per nesting pair and lower DSR than rural BCTI pairs due to more predators and less reliable food sources for young in urban locations (Robb et al. 2008, Marzluff 2016).

## **Methods**

### ***Study site***

Between 2013–2021, I monitored BCTI nesting behavior across four locations in San Marcos, TX, USA (29.8833° N, -97.9414° W): 1) the Freeman Center, 2) Texas State University’s main campus, 3) San Marcos public parks, and 4) residential neighborhoods in San Marcos. In all four locations, the BCTI is common, conspicuous, and readily nests in natural and man-made cavities (Rylander pers. obs.), making it an ideal species to compare nesting behavior across a variety of different landscapes through the use of nestboxes.

During November and December of 2012 and 2013, I installed 40 and 31 nestboxes, respectively, in the northern half of the Freeman Center (hereafter ‘Freeman’), a rural 1400-ha Texas State University property ~10 km northwest of downtown San Marcos. The habitat here is a mosaic of oak-juniper woodlands (*Quercus fusiformis*, *Q. buckleyi*, *Juniperus ashei*) (46%), open grassland savannahs (*Bothriochloa ischaemum*, *Schizachyrium scoparium*, *Diospyros texana*, *Forestiera pubescens*) (22%), and a mixture of grassland/woodland interface (32%). During the winter of 2017, I installed an additional 75 nestboxes at Freeman, bringing the nestbox total on property to 146 (Figure 1.2). All nestboxes were positioned ~3 m high on t-posts and were installed randomly

along roadways except for 20 that were placed in a grid arrangement (in attempts for another researcher to attract eastern bluebirds, *Sialia sialis*, Harrod et al. 2014). Due to a high number of depredation events during the spring of 2015 by raccoons (*Procyon lotor*) and Texas rat snakes (*Elaphe obsoleta lindheimeri*) that appeared to have recognized trails to nestboxes, I installed PVC-pipe style predator baffles to maintain robust sample sizes of banded BCTI for additional research projects on property.

I installed 40 nestboxes during the fall and winter of 2016 across Texas State University's campus (hereafter 'Campus'), a highly urbanized series of large multistory buildings, parking garages, dormitories, and parking lots. Additionally, I installed 34 nestboxes within public City of San Marcos parks (hereafter 'Parks') that contained > 2.5 ha of contiguous greenspace patches with old-growth trees (Dunbar, Crook's Park, Prospect, Schulle Canyon, Children's Park, and the San Marcos City Cemetery). During the winter of 2017, I installed 86 nestboxes in single-family home residential areas of San Marcos (hereafter 'Residential'), where residential lots contained mature trees and other vegetation (as opposed to housing developments located in recently clear-cut areas). Thus, in total, I installed 160 "urban" nestboxes across three sites that ranked from high to low urbanization (the amount of impervious cover) as follows: Campus > Residential > Parks (Figure 1.4). I affixed all nestboxes in urban locations with either screws or ratchet straps on various tree species > 15 cm diameter at breast height (DBH) between 2 – 4 m from the ground. Because these nestboxes were installed on trees as opposed to t-posts (as on Freeman), I was unable to install predator baffles. However, when possible, I installed nestboxes away from fences, rooftops, bird feeders, and areas with dense understory vegetation to reduce the potential of depredation of BCTI nests (Cornell Lab

of Ornithology 2021). Additionally, I installed urban nestboxes higher on trees, but still within normal BCTI nesting height, 1 – 7 m (Patten and Smith-Patten 2008), so they would be somewhat camouflaged and less likely to be tampered with by humans.

### ***Nestbox monitoring***

I monitored nestboxes 1 – 2x a week between late February – early July to identify those containing BCTI nests (comprised of moss, fur, and snakeskin; Patten and Smith-Patten 2008). Once BCTI were confirmed nesting in a particular box, I increased visits to 2 – 3x a week and documented what stage the nest was in (building, incubation, hatchlings), number of eggs, number of nestlings and their approximate age, confirmed either successful fledging or failure, and cause of failure (depredation, abandonment, infertile eggs, competition, or unknown) for each nest. I considered nests to be “successful” if  $\geq 1$  nestling fledged, and if BCTI built a nest but the female never laid eggs, I did not use it for analyses. I also calculated “clutch initiation date” for each nest as the date in which the first egg was likely laid, using prior knowledge of BCTI nesting stages and nesting cycle length as a guide (Patten and Smith-Patten 2008, Rylander 2015). BCTI typically lay one egg per day (Rylander pers. obs.), and once all eggs are laid, incubation takes ~14 days. Once eggs hatch, it takes another ~16 days for young to fledge, making the total nesting cycle from initiation date (first egg laid) to fledging roughly 32–36 days (Rylander pers. obs.). Thus, I was able to approximate clutch initiation date through backdating of known hatching date, nestling age, and/or fledging date because I did not check every nest exactly when the first egg was laid.

I monitored nestboxes on Freeman between 2013–2021, excluding 2020 due to restricted access during the COVID-19 pandemic shutdown. I monitored nestboxes on

Campus and in Parks between 2017–2021, and in Residential areas between 2018–2020. However, I was limited to only checking first clutches on Campus and in Parks (earlier in the season) during 2020 due to the COVID-19 shutdown, whereas I monitored first and second clutches in Residential locations in 2020. I did not monitor Residential nestboxes in 2021 due to time restraints.

### *Capture, banding, and resights*

To assess if the same BCTI pairs double brooded in a given year, or if second year (SY; first breeding season) birds differed in nesting success than after second year birds (ASY; birds > 2 years of age), I color banded entire family groups that used nestboxes between 2013 – 2019. When nestlings were  $\geq 5$  days old, I hand-captured adults within the nestbox when adults returned to feed their young (Rylander et. al 2020). I affixed adults with a unique combination of 1 to 3 Darvic color bands (Avinet Research Supplies, Portland, Maine) and a registered United States Geological Service (USGS) aluminum band. I sexed adults based on the presence of a brood patch (females) or cloacal protuberance (males) when possible. I color-banded nestlings with unique combinations between 10–14 days post-hatching. I did not catch both adults on the same date as to allow for one adult to continue feeding young during the banding process, and I also conducted the nestling banding ~100 m from the nestbox to prevent unnecessary stress on the tending pair.

I performed resights for previously banded BCTI during the breeding season (February – June) from 2014–2020. Once a BCTI was positively identified occupying a nestbox, I waited ~50 m from the nestbox, concealed by vegetation, until an adult appeared. If the adult was already banded, I recorded the BCTI's unique color band

combination, age, and sex (if known). Usually, I delayed resighting adult BCTI until it was apparent the nestling phase began, indicated by adults making trips to and from the nestbox with food in bill. I monitored each BCTI nestbox until both adults were either positively identified based on their bands or until captured using methods described above.

### ***Habitat composition***

To assess the influence of habitat composition on DSR of BCTI nests, I used ArcGIS Pro 2.6.1 (Environmental Systems Research Institute 2020). I created 9.07-ha circular buffers centered around each nestbox occupied by nesting BCTI based on the average home range size of BCTI (9.07 ha) in a previous study (Rylander et al. 2020). Once I constructed buffers, I used a GIS vegetation layer provided by the Texas Parks and Wildlife Department (hereafter ‘TPWD’; TPWD 2020) with a 30-m x-30-m pixel resolution to calculate the proportion of five vegetation categories within each buffer: woodland (polygons containing > 75% woodland cover), mixed shrub (polygons containing 25% – 75% woodland cover), grassland (polygons containing < 25% woodland cover), low urbanization, and high urbanization. TPWD classified low urbanization as “areas that are built-up but not entirely covered by impervious cover and includes most of the non-industrial areas within cities and towns.” TPWD defined high urbanization polygons as “built-up areas and wide transportation corridors that are dominated by impervious cover.”

### ***Weather covariates***

To examine the relationship between weather and BCTI clutch initiation dates, I utilized data sets collected at San Marcos weather stations by the National Weather Service (NOAA 2021) for each February, 2013 – 2021, as February represents the month leading up to nesting season (Patten and Smith-Patten 2008). I calculated for each year of the study: 1) average of daily high temperatures in February (“Feb high”); 2) average of daily low temperatures in February (“Feb low”); and 3) total precipitation amounts in February (“Feb precip”). To assess if weather influenced BCTI nesting daily survival rates, I calculated the following weather covariates: 1) average daily high temperatures during incubation period for each nest (“inc high”); 2) average daily low temperatures during the incubation period for each nest (“inc low”); 3) total precipitation during the incubation period for each nest (“inc precip”); 4) average daily high temperatures during hatchling presence for each nest (“hatch high”); 5) average daily low temperatures during hatchling presence for each nest (“hatch low”); 6) total precipitation during hatchling presence for each nest (“hatch precip”); and 7) total winter precipitation (December – February) before the nesting season (“wint precip”).

I conducted all research in accordance with Institutional Animal Care and Use Committee (IACUC) (#201532811), Federal Master Banding Permit (#24108), U.S. Fish and Wildlife Permit (MB121162-2), and Texas Parks and Wildlife Collection Permit (#SPR-0417-107).



## Data Analyses

### *Nesting characteristics and parameters*

For all statistical analyses, I used software R (version 4.0.2, R Development Core Team 2020) and scaled covariates when they were continuous. I first assessed if the number of eggs, nestlings, and fledglings per successful nest were influenced by clutch initiation date, location (i.e., Freeman, Campus, Parks, Residential), and year by using three generalized linear regressions (GLM) with Poisson distributions. I included only successful nests in these specific analyses because nesting fate and annual productivity analyses included failed nests into their calculations. I also assessed if male age (SY or ASY) influenced the number of fledglings per successful nest by performing a separate Mann-Whitney U test because age was not known for all males nesting in boxes ( $n = 276$  versus  $n = 106$  with known ages). I was not able to perform the same analyses using female age as a covariate due to a low known number of SY females using nestboxes ( $n = 4$ ).

I conducted a generalized linear mixed effects model (hereafter GLMM) with a Poisson distribution to assess differences in first clutch initiation dates across the four locations (Freeman, Campus, Parks, and Residential) using year as a random factor covariate. I used only data gathered from 2018 and 2019 for this analysis, as it represented the two years when all four locations were monitored simultaneously. Additionally, I performed a Kruskal-Wallis test specifically assessing differences in first clutch initiation dates at Freeman among years (2014 – 2021). I excluded 2013 pilot data in this analysis due to small sample size ( $n = 4$ ). If results from the Kruskal-Wallis test were significant, I used a post-hoc Dunn test to assess differences among years. To

follow up, I assessed if median Freeman first clutch initiation dates correlated with weather covariates “Feb low” temperatures, “Feb high” temperatures, and “Feb precip” using a GLM. I omitted weather covariates from the same model that contained a variance inflation factor (VIF) > 3 to account for multicollinearity (Zuur 2009). Lastly, I performed a GLMM to assess if male BCTI age (SY or ASY) influenced first clutch initiation dates, with general location (rural [Freeman] versus urban [Campus, Parks, and Residential combined]) and year as random factor covariates to control for variability in clutch initiation dates between locations and years. I also only used data from 2018 and 2019 nests with known age males ( $n = 58$ ) because these were the only two years with < 1 individual from each year for each age group.

To examine if nest fate was dependent on location, clutch initiation date, or year, I used a GLM with a binomial distribution, where nests either failed ( $y = 0$ ) or succeeded ( $y = 1$ ). I included all nests from all clutches for this analysis. I also performed a GLMM assessing if nest fate was influenced by BCTI male age, blocking by general location (urban versus rural) to only examine variability due to age.

### ***Productivity***

I calculated BCTI first clutch productivity as the number of fledglings produced per BCTI pair during the early season (March – April, representing all first nests). Because of the focus of the study, I was limited to monitoring nesting activities in nestboxes and was not able to locate, observe, and keep record of second clutches in natural cavities. However, when banded BCTI did use nestboxes for both first and second clutches, I calculated overall annual productivity. For first clutch productivity, I

conducted a GLM with the number of fledglings per nest as the response variable (Poisson distribution) and location and year as fixed covariates.

### ***Daily survival rate (DSR) of nests***

I estimated DSR of BCTI nests using program MARK (White and Burnham 1999, Dinsmore et al 2002, Cooch and White 2006, Rotella 2006), implemented through the RMark package in program R (Laake 2013). To estimate DSR, I used the following data collected on all nests across the four sites: 1) first day the nest was found; 2) last day the nest was checked and eggs/chicks were alive; 3) last day the nest was checked; 4) nest fate (0 = success, 1 = failure); 5) total number of nests with the same encounter history (Dinsmore et al. 2002, Rotella 2006). From this information, I calculated clutch initiation date (date first egg was laid), nest age (approximate age from first egg laid), and nest stage (whether the nest was in incubation or nestling phase) for each nest. Additionally, I standardized all dates among years by using the first clutch initiation date for any year as the first day of the season, and the last successful fledging or failure date for any year as the last day of the season (Rotella 2006). Thus, for BCTI, I used February 28<sup>th</sup> (Julian calendar date 59) as Day 1, and July 6<sup>th</sup> (Julian calendar date 187) as Day 125, defining a 124-day nesting season in total. I followed the assumptions described in Rotella et al. 2004.

When building models, I included the following covariates: 1) DSR varies linearly over time (Time); 2) DSR remains constant over time (null); 3) DSR is influenced by location; 4) DSR varies based on the percentage of woody vegetation located near the nestbox (Wood); 5) DSR is influenced by various weather covariates (previously mentioned); 6) DSR varies by year; 7) DSR is influenced by nest stage and/or

nest age; and 8) DSR is influenced by the presence or absence of a predator baffle (Freeman 2016 – 2021). To reduce the number of models in the candidate set ( $\leq n/10$ ; Burnham and Anderson 2002), I identified the top four most influential weather covariates using a sequential-by-sub-model strategy (Morin et al. 2020) and used those when creating final candidate models. Additionally, I checked for overdispersion and failure of model convergence and removed these models from candidate sets. I also omitted variables from the same model that had a  $VIF > 3$  (Zuur 2009).

Once the candidate model set was created (26 models,  $n = 385$ , Supplementary Table 3.1), I used Akaike's Information Criterion (AIC) for small sample sizes (Akaike 1973). When the top model in the  $AIC_c$  table had a  $\Delta AIC_c$  value  $\geq 2$  units from the second top model, I selected the top model to estimate parameters. When two or more models had  $\Delta AIC_c$  values  $< 2$ , I model-averaged to obtain parameter estimates (Burnham and Anderson 2002).

## Results

I monitored 385 BCTI nests between 2013–2021 (Table 3.1), with 257 nests located at the Freeman Center and 128 across the three urban sites. I used data only from 380 nests due to 5 nests being parasitized by conspecifics at the Freeman Center (2 in 2014, 1 in 2015, and 2 in 2016), creating difficulties in estimating lay date, clutch size, and number of fledglings from attending pair. Of the failed nests ( $n = 104$ ), I determined that 73 were depredated, 26 were abandoned (causes unknown), 2 contained unviable eggs (female incubated for 30+ days), and 3 nests were outcompeted by other species building nests on top of BCTI eggs (Table 3.2). Additionally, I captured and banded 1387

BCTI in nestboxes between 2013–2019, with 918 banded at Freeman and 469 banded across the urban sites.

### *Nesting characteristics and parameters*

Of the successful BCTI nests ( $n = 276$ ), the average clutch size was (mean  $\pm$  SD)  $5.99 \pm 0.90$ , average number of nestlings was  $5.46 \pm 1.15$ , and average number of fledglings was  $5.36 \pm 1.27$ . The frequency distribution of the number of eggs, nestlings, and fledglings per nest was left skewed with six as the most common number of each (Figure 3.1). The number of eggs per nest was not influenced by clutch initiation date, year, or location. However, the number of nestlings per nest ( $n = 276$ ;  $\beta = -0.004 \pm 0.001$ ;  $z\text{-value} = -2.878$ ; 95% CI =  $[-0.006 - -0.001]$ ;  $p = 0.004$ ) and fledglings per nest ( $n = 276$ ;  $\beta = -0.004 \pm 0.001$ ;  $z\text{-value} = -3.021$ ; 95% CI =  $[-0.006 - -0.001]$ ;  $p = 0.003$ ) was influenced by clutch initiation date but not by year or location (Figure 3.2). For successful nests with tending males of known age ( $n = 106$ ), age did not influence the number of fledglings ( $W = 1043$ ,  $p = 0.59$ ).

For all nests ( $n = 380$ ), start dates displayed a bi-modal distribution with first clutch initiation ranging from March 1<sup>st</sup> to April 15<sup>th</sup> (Julian calendar dates 60 – 105) and second clutch initiation ranging from April 19<sup>th</sup> to June 5<sup>th</sup> (Julian calendar dates 109 – 156) (Figure 3.3). GLMM results estimated that during 2018 and 2019 ( $n = 114$ ), Freeman differed from the other locations in first clutch initiation date (Table 3.3, Figure 3.4). Though Campus (Julian date  $77.23 \pm 9.34$ ), Parks ( $73.92 \pm 6.26$ ), and Residential ( $73.94 \pm 7.48$ ) locations did not differ in first clutch initiation date, they all differed significantly from Freeman ( $83.43 \pm 6.57$ ). Overall, rural (Freeman) first clutch initiation

dates ( $83.43 \pm 6.57$ ) were ~9 days later than urban dates ( $74.70 \pm 7.71$ ) (Campus, Parks, and Residential data combined).

First clutch initiation dates for the Freeman Center BCTI (Kruskal-Wallis;  $n = 174$ ;  $Z = 55.3$ ;  $df = 6$ ;  $p < 0.01$ ) varied between years (Figure 3.5), with Dunn's post-hoc tests revealing 2017 initiation dates being earlier than all other years, and 2015 initiation dates being later than all other years (Table 3.4). First clutch initiation dates during 2019 were earlier than those in 2014 and 2021. Average February low temperatures each year correlated best with the median value of first clutch initiation date ( $n = 7$ ;  $\beta = -1.75 \pm 0.52$ ;  $t\text{-value} = -3.35$ ; 95% CI =  $[-3.09 - -0.41]$ ;  $p = 0.02$ ) (Figure 3.6) more so than average February high temperatures or total precipitation. As average February low temperatures increased by  $5^\circ\text{C}$ , BCTI median first clutch initiation date shifted ~9 days earlier at Freeman. Lastly, GLMM results revealed that BCTI male age did not influence first clutch initiation date ( $n = 58$ ;  $\beta = 0.02 \pm 0.03$ ;  $z\text{-value} = 0.75$ ; 95% CI =  $[-0.04 - 0.09]$ ;  $p = 0.46$ ) when general location and year were random predictors.

BCTI nest fate was influenced by clutch initiation date and location but not by year (Table 3.5). Rough estimates of nesting success rates (successful nests / total nests,  $n = 380$ ) were greatest for Parks and Campus (83.87% and 83.33% respectively), followed by the Freeman Center (73.02%) and Residential areas (59.02%). BCTI nesting in Residential locations were 1.5x more likely to fail than BCTI nesting at the Freeman Center and 2.5x more likely to fail than those at Parks or on Campus. Additionally, BCTI nests in Residential locations were more likely to fail than succeed if nest initiation date began after April 10<sup>th</sup> (Julian date 100), whereas nests at the Freeman Center and Parks were more likely to fail after May 30<sup>th</sup> (Julian date ~150) and Campus after June 20<sup>th</sup>

(Julian date 170) (Figure 3.7). GLMM results revealed that BCTI male age did not influence nest fate ( $n = 131$ ;  $\beta = 0.37 \pm 0.48$ ;  $z\text{-value} = 0.77$ ; 95% CI =  $[-0.60 - 1.30]$ ;  $p = 0.44$ ) when general location was used as a random blocking factor.

### ***Productivity***

First clutch productivity ( $n = 276$ ) for BCTI pairs across all years and all locations was  $4.33 \pm 2.54$  fledglings per pair. Site-specific productivity was greatest for Campus BCTI ( $5.20 \pm 2.24$ ), followed by Parks ( $4.56 \pm 2.59$ ), Freeman ( $4.33 \pm 2.44$ ), and Residential locations ( $3.74 \pm 2.95$ ). However, productivity did not differ across locations for first nests ( $n = 276$ ;  $\chi^2 = 6.00$ ;  $df = 3$ ;  $p = 0.11$ ) or across years ( $n = 276$ ;  $\chi^2 = 13.94$ ;  $df = 8$ ;  $p = 0.08$ ). For known banded BCTI pairs that attempted a second clutch in nestboxes ( $n = 37$ ), overall annual productivity from first and second nests combined was  $8.00 \pm 2.48$  and ranged between 4 and 13 fledglings per pair. No third clutch attempts were detected.

### ***DSR***

The top model  $S_{\text{Location} + \text{Time}}$  was used to estimate beta values (Table 3.6) and real parameter estimates (data available upon request) for BCTI nesting DSR ( $n = 385$ ), as it had a  $\Delta\text{AIC}_C > 2$  units lower than the next competing model and was heavily weighted (0.79). Weather covariates, year, nest age, nest stage, predator baffle installation, and percent woodland habitat surrounding the nestbox did not influence BCTI nesting DSR. Location was the most influential covariate for nest DSR, with Residential nests having lower DSRs than all other locations during any portion of the season (Figure 3.8). Additionally, Time influenced DSR, with nests initiated later in the season having a

lower DSR than those initiated at the beginning of the season. Estimated survival rates of nests initiated early in the season (March 3<sup>rd</sup> – April 7<sup>th</sup>) were greater than those initiated late in the season (June 1<sup>st</sup> – July 6<sup>th</sup>), and estimated survival rates of nests varied across locations (Table 3.7). Early nests on Campus were 2x as likely to survive to completion compared to late nests in the same location, whereas early nests in Residential locations were 18x more likely to survive to completion compared to late Residential nests. Early nests at Freeman, Parks, and Campus were ~1.3 – 1.4x as likely to survive to completion as Residential nests during the same time frame.

## **Discussion**

Location appears to influence BCTI nesting success and nesting DSR, with nests in Residential areas having a lower likelihood of successfully fledging young than Campus, Parks, or Freeman. Lower reproductive success of other urban parids has been linked to house sparrow (*Passer domesticus*) competition for nest sites (Goldshtein et al. 2018), a reduction of food sources, such as caterpillars, (Gladalski et al. 2017, Pollock et al. 2017), metal pollution accumulation in urban food sources (Chatelain et al. 2021), and an increase in human disturbance (Gladalski et al. 2016). Interestingly, nestboxes placed in Residential areas did not contain the proportion of highly urbanized habitat Campus nestboxes were exposed to, nor were they as rural as the boxes at the Freeman Center or in Parks. Thus, Residential BCTI nests may be more susceptible to depredation by feral cats, raccoons, rat snakes, and jays that are attracted to bird feeders, tended gardens, and numerous personal trash cans not typically found in the other three locations (Marzluff 2016). Though Campus nestboxes likely receive the highest human disturbance through foot and vehicular traffic, this constant disturbance and disruption of natural habitat also



may deter predators from taking up permanent residence in the vicinity (Segura and Reboledo 2012). Nestboxes in Parks and at Freeman are surrounded by woody vegetation that may hold enough natural prey for predators to obtain, leaving less nests disturbed per unit area (Chamberlain et al. 2009, Ryder 2010). Thus, while BCTI may be able to adapt to human-dominated landscapes, certain locations, such as residential areas, may function as an ecological trap if a high proportion of nests fail each season.

Members of the Paridae family display considerable variability in nesting behaviors across various degrees of urbanization (Mennill et al. 2007). Like the BCTI, the clutch size of coal tits (*Periparus ater*), great tits (*Parus major*), and blue tits (*Cyanistes caeruleus*) nesting in boxes on a university campus did not differ from those in nearby rural populations (Perry 2003), nor did the clutch size of mountain chickadees (*Poecile gambeli*) vary across an urban gradient (Marini et al. 2017). However, in other studies involving blue and great tits, urban clutches are smaller than their rural counterparts (Schmidt and Einloft-Achenback 1984, Vel'ky and Kanuch 2008), resulting in fewer successful fledglings per nest and an overall lower productivity per nesting pair. Smaller clutch sizes have been associated with both intrinsic and extrinsic stressors on females, with changes in diet (Ramsay and Otter 2007), ambient temperatures (Pendlebury and Bryant 2005), and female age (Winkel and Winkel 1987, Dhondt 1989) having effects on the number of eggs laid. Though results suggest BCTI have stable clutch sizes and first clutch productivity rates across locations in San Marcos, Texas, future work that focuses on female age (SY vs ASY), availability of artificial foods though bird feeders, and if different locations across the BCTI's range impact clutch sizes or productivity will assist in avian conservation.

Earlier first clutch initiation dates for urban BCTI compared to rural BCTI complement results of mountain chickadees (urban ~19 days earlier; Marini et al. 2017) and great tits (urban ~10 days earlier; Vel'ky and Kanuch 2008), among many other non-parid species (Chamberlain et al. 2009). Though this study did not focus on factors triggering egg-laying of BCTI, the difference in timing across the urbanization gradient could be attributed to temperature differences (Lack 1966, Stevenson and Bryant 2000), timing of food abundance peaks (Hajdasz et al. 2019), availability of artificial food (Nager et al. 1997, Anderies et al. 2007), or the lack of suitable nesting cavities (Newton 1994, Tomasevic and Marzluff 2017). Based on results, February temperatures, the month prior to egg laying, have some influence on BCTI rural nest initiation, which has been similarly observed in female great tits in Switzerland (Nager and van Noordwijk 1995) and gray-headed chickadees (*Poecile cincta*) in Finland (Eeva et al. 2000). Though slight differences in February microclimates between urban and rural locations may trigger female BCTI to lay earlier, observations also have been made of banded BCTI at artificial feeding stations surrounding residential nestbox locations (Rylander pers. obs.). As with great tits (Nager and van Noordwijk 1995, Seki and Takano 1998), female BCTI with access to reliable, calorie-rich diets may have more energy to invest in nest initiation compared to females that rely more on seasonal climate shifts and natural insect booms to trigger nesting behavior (Ramsay and Otter 2007, Chamberlain et al. 2009). Thus, female BCTI may have been triggered to lay earlier clutches because of the slightly warmer temperatures or food abundance in urban areas.

As in other parids, including the closely related tufted titmouse (Pogue and Carter 1995), BCTI nesting success and DSR are influenced by clutch initiation date, with

earlier clutches more likely to succeed than later clutches. Pogue and Carter (1995) attributed a high percent of late nesting failure of both tufted titmouse and Carolina chickadee (*Poecile carolinensis*) to rat snake depredation as the season progressed, an observation also made for the same species in Louisiana and Kansas (Johnston 1964, Mowbray and Goertz 1972) and appears likely for the BCTI (Rylander pers. obs.). However, Pogue and Carter (1995) also calculated tufted titmouse daily nesting success (Mayfield method) being higher during the nestling phase ( $0.933 \pm 0.03$ ) than the incubation phase ( $0.883 \pm 0.004$ ), which differs from BCTI (higher DSR during incubation). Many studies have hypothesized that DSR and nesting success is lower during the nestling phase because adults are rapidly flying into the nest to feed young, making the nest more obvious to predators (Skutch 1949, Segura and Reboreda 2021). Yet for other species, such as the northern cardinal (*Cardinalis cardinalis*), earliest clutches were more heavily depredated and overall nest survival rates improved as the season progressed (Shustack and Rodewald 2011). In other studies, DSR improves with nest age (Segura and Reboreda 2012), as adults become more invested and aggressive towards predators when feeding nestlings, as witnessed in willow tits (*Poecile montanus*) (Rytönen et al. 1990). Thus, though the tufted titmouse and BCTI are sister-taxa, they may have adapted different strategies to achieve relatively high nesting success rates.

BCTI male age did not influence first clutch initiation date, number of successful fledglings, or nest fate, indicating that male age does not equate to experience or efficiency for certain nesting behaviors. This trend was observed in mountain chickadees, where male or female age, regardless of location, did not attribute to overall nesting success (Marini et al. 2017). Additionally, Amininasab et al. (2016) assessed blue tit male

attentiveness (through feedings) to incubating females and discovered no difference between SY or ASY in this behavior. In contrast, reproductive success of great tits was correlated to male age, with sub-adult males fledging fewer chicks per nest, likely due to differences in parental care behavior and not because of infertility (Pigeault et al. 2020). However, this study also cautioned the importance of assessing the age and quality of the nesting pair because drawing conclusions from a single parent could lead to biased interpretations. Thus, future work with BCTI nesting behavior should focus on female age in combination with habitat quality and food availability, as has been done with other parids (Ramsay and Otter 2007, Amininasab et al. 2016, Marini et al. 2017). Extensive work by Dhondt (1989) on nesting blue and great tits suggests that females for both species lay earlier and increase clutch sizes after their first-year breeding (as ASYs). Once ASYs, age has no effect on lay date, clutch size, nesting success, or post-fledgling juvenile survival until females of both species were 4+ or 6+ years old for great and blue tits, respectively, after which nesting success decreased (Dhondt 1989). Contrastingly, Winkel and Winkel (1987) noted that great tit female age did not affect clutch size or number of young fledged, but that age positively influenced clutch size and fledging success in coal tits.

Other than the influence of February temperatures on BCTI first clutch initiation date, there was no indication of year-to-year fluctuation in number of eggs, nestlings, or fledglings per successful nest, nor were there differences in productivity, DSR, or nest fate. This could be an indicator that regardless of location, the San Marcos populations of BCTI have stable food availability and/or did not succumb to any extreme weather events between 2013–2021, as was documented in the bridled titmouse (*Baeolophus*

*wollweberi*) of southeastern Arizona (Christman 2002). Between back-to-back years (1998 and 1999), bridled titmice experienced a large difference in productivity caused by extreme drought (4.4 fledglings per breeding pair in 1998 compared to 0.4 in 1999), and only half of the pairs monitored during 1999 attempted to breed (compared to 100% of pairs in 1998). This could be an indicator that titmice may be able to adapt their reproductive efforts in extreme years when nesting success and overall productivity are relatively low (Christman 2002). Yet, when abrupt weather events occur during the nesting season, there is likely no option to forgo reproduction, as witnessed in 1983 when 60% of great tit nests in a German study suffered 100% mortality of first brood young due to starvation (Winkel and Winkel 1987). Additional years of data collection utilizing the nestboxes installed across San Marcos could elucidate if extreme weather fluctuations before or during breeding season influences BCTI productivity or nesting success.

BCTI using nestboxes may experience greater nesting success, lower depredation rates, and higher productivity than BCTI using natural cavities, a trend that was observed in oak titmice (*Baeolophus inornatus*) (Purcell et al. 1997) and great tits (Nilsson 1984). Similarly, BCTI that nested in abandoned woodpecker cavities with smaller openings and minimal tree decay were more likely to succeed than BCTI nesting in cavities formed by natural decay (Hardin et al. 2021). Thus, it appears nestboxes may mimic fresh cavities excavated by woodpeckers, indicating the potential importance of primary cavity-nesting species to the nesting success of BCTI and other secondary-cavity nesters (Tomasevic and Marzluff 2017). Yet, in many urban locations, woodpeckers and other excavating species are uncommon as they are more sensitive to anthropogenic disturbance (Myczko et al. 2014). Natural snags and decaying trees also are removed due to potential harm to

humans or their property (Blewett and Marzluff 2005). Therefore, the use of nestboxes for management purposes, especially in urbanized landscapes, may be assisting the persistence of BCTI populations as habitat becomes fragmented (Gladalski et al 2016). However, in residential locations where BCTI nesting success and DSR were lowest, the use of predator baffles may be necessary to prevent unintentional depredation of BCTI in nestboxes.

Overall, this work suggests that BCTI are adapting to various degrees of urbanization, a similar diagnosis made for other parids in both the New and Old World (Marini et al. 2017). Though this research did not span the number of years of other nestbox studies involving parids (14 years, Gladalski et al 2016; 18 years, Lambrechts et al. 2016), it is the first to extensively document BCTI nesting success, DSR, clutch initiation date, and productivity across an urban gradient using a consistent, large, marked population. Future work hopefully will reveal how BCTI in other portions of its range compare to central Texas BCTI regarding nesting characteristics.

**Table 3.1** Successful and failed black-crested titmouse (*Baeolophus atricristatus*) nests across four locations in San Marcos, Texas, 2013–2021. Numbers in parentheses represent the sample size used for analyses, as some nest outcomes were difficult to determine due to conspecific egg-dumping.

Year	Freeman		Campus		Parks		Residential	
	Success	Failure	Success	Failure	Success	Failure	Success	Failure
2013	3	1	---	---	---	---	---	---
2014	20 (19)	6 (5)	---	---	---	---	---	---
2015	11	11 (10)	---	---	---	---	---	---
2016	17 (15)	5	---	---	---	---	---	---
2017	18	4	3	2	3	2	---	---
2018	30	10	7	2	6	0	16	4
2019	35	15	11	0	8	1	11	11
2020	---	---	3	1	6	1	9	10
2021	52	18	5	1	3	1	---	---
<b>Total</b>	<b>187 (184)</b>	<b>70 (68)</b>	<b>30</b>	<b>6</b>	<b>26</b>	<b>5</b>	<b>36</b>	<b>25</b>
	<b>257 (252)</b>		<b>36</b>		<b>31</b>		<b>61</b>	

**Table 3.2** Failure type of black-crested titmouse (*Baeolophus atricristatus*) nests across four locations in San Marcos, Texas, 2013–2021.

<b>Failure type</b>	<b>Freeman</b>	<b>Campus</b>	<b>Parks</b>	<b>Residential</b>
Depredation	52	4	2	15
Abandonment	11	2	3	10
Infertile eggs	2	0	0	0
Competition	3	0	0	0



**Table 3.3** Generalized linear mixed-effects regression results displaying how black-crested titmouse (*Baeolophus atricristatus*) first clutch initiation dates are influenced by location during 2018–2019 in San Marcos, Texas. Year was used as a random predictor to account for variability between years. Results in bold are significant at  $\alpha = 0.05$ .

Covariate	$\beta \pm \text{SE}$	z-value	<i>p</i>	95% CI
(Intercept)	$4.34 \pm 0.04$	113.43	<0.01	4.25 – 4.43
<b>Location [Freeman]</b>	$0.08 \pm 0.03$	2.31	<b>0.02</b>	0.01 – 0.15
Location [Parks]	$-0.04 \pm 0.05$	-0.81	0.42	-0.13 – 0.05
Location –[Residential]	$-0.04 \pm 0.04$	-1.17	0.24	-0.12 – 0.03
Random - Year	Variance $0.0009 \pm 0.03$	$R_c^2 = 0.25, R_m^2 = 0.20$		

**Table 3.4** Dunn’s post-hoc test revealing the differences of black-crested titmouse (*Baeolophus atricristatus*) first brood initiation dates between years (2014–2021, excluding 2020) at the Freeman Center in San Marcos, Texas. Results in bold are significant at  $\alpha = 0.05$ .

Years	Z	p
<b>2014 – 2015</b>	<b>2.48</b>	<b>0.01</b>
2014 – 2016	-0.82	0.41
<b>2014 – 2017</b>	<b>-4.48</b>	<b>&lt;0.01</b>
2014 – 2018	-1.36	0.18
<b>2014 – 2019</b>	<b>-2.57</b>	<b>0.01</b>
2014 – 2021	-0.19	0.85
<b>2015 – 2016</b>	<b>-3.05</b>	<b>&lt;0.01</b>
<b>2015 – 2017</b>	<b>-6.66</b>	<b>&lt;0.01</b>
<b>2015 – 2018</b>	<b>-3.95</b>	<b>&lt;0.01</b>
<b>2015 – 2019</b>	<b>-5.13</b>	<b>&lt;0.01</b>
<b>2015 – 2021</b>	<b>-3.08</b>	<b>&lt;0.01</b>
<b>2016 – 2017</b>	<b>-3.33</b>	<b>&lt;0.01</b>
2016 – 2018	-0.34	0.73
2016 – 2019	-1.41	0.16
2016 – 2021	0.77	0.41
<b>2017 – 2018</b>	<b>3.53</b>	<b>&lt;0.01</b>
<b>2017 – 2019</b>	<b>2.46</b>	<b>&lt;0.01</b>
<b>2017 – 2021</b>	<b>5.04</b>	<b>&lt;0.01</b>
2018 – 2019	-1.31	0.19
2018 – 2021	1.46	0.14
<b>2019 – 2021</b>	<b>2.98</b>	<b>&lt;0.01</b>

**Table 3.5** Generalized linear regression results where covariates clutch initiation date and location influence black-crested titmouse (*Baeolophus atricristatus*) nesting fate (success or failure) in San Marcos, Texas, 2013–2021. Results in bold are significant at  $\alpha = 0.05$ .

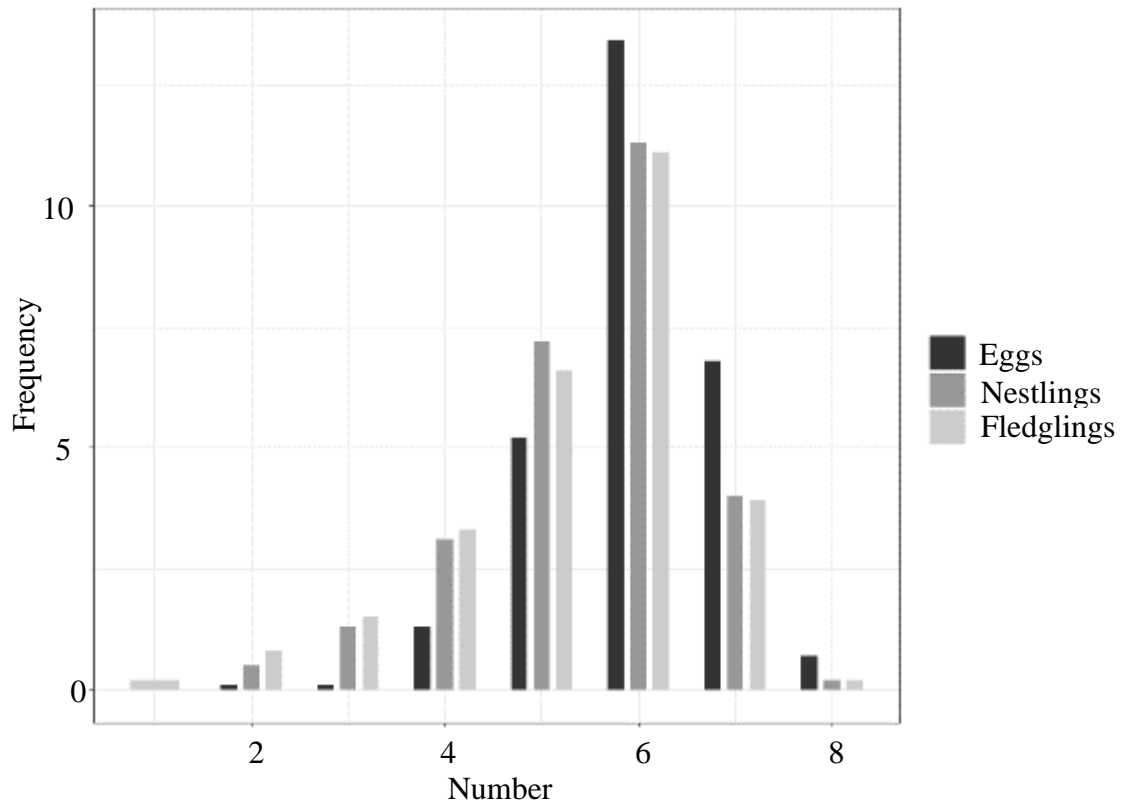
Covariate	$\beta \pm \text{SE}$	z-value	<i>p</i>	95% CI
(Intercept)	$-3.79 \pm 0.69$	-5.45	<0.01	-5.22 – -2.48
<b>Clutch initiation date</b>	$0.02 \pm 0.005$	4.40	<b>&lt;0.01</b>	0.01 – 0.03
Location [Freeman]	$0.53 \pm 0.48$	1.10	0.27	-0.36 – 1.57
Location [Parks]	$0.37 \pm 0.69$	0.54	0.59	-1.01 – 1.73
<b>Location [Residential]</b>	$1.51 \pm 0.54$	2.80	<b>&lt;0.01</b>	0.51 – 2.65

**Table 3.6** Top model  $S_{\text{Location} + \text{Time}}$  beta estimates for black-crested titmouse (*Baeolophus atricristatus*) nesting daily survival rates (DSR) in San Marcos, Texas, 2013–2021. Results in bold are significant at  $\alpha = 0.05$ .

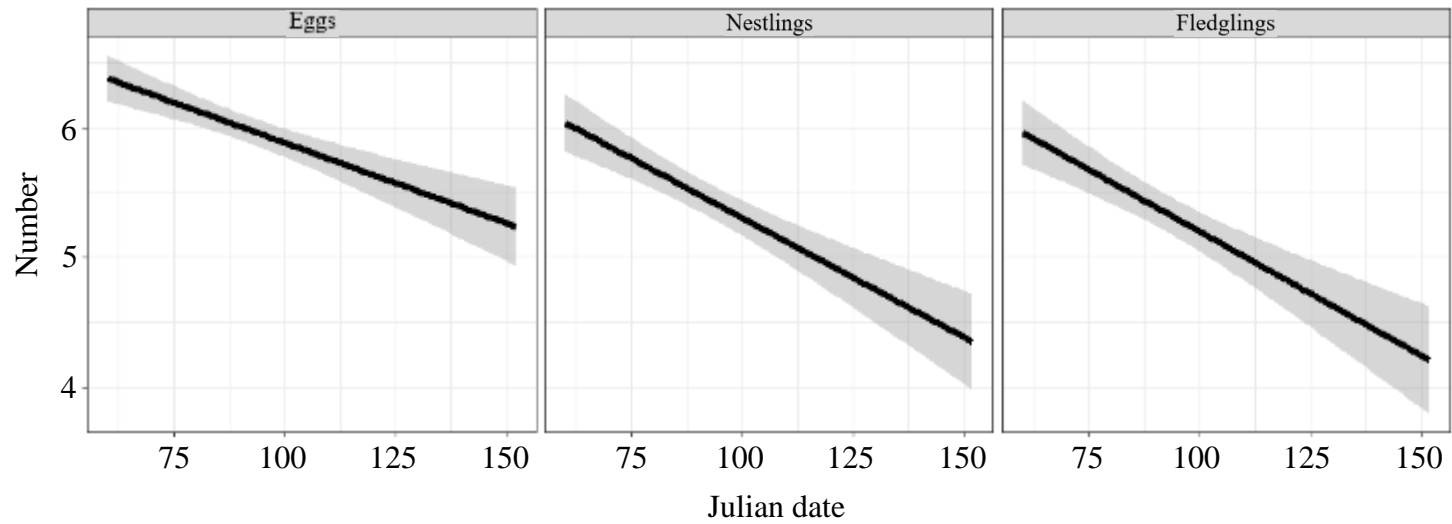
Covariate	$\beta \pm \text{SE}$	95% CI
(Intercept)	$6.43 \pm 0.49$	$5.47 - 7.39$
Location [Freeman]	$-0.47 \pm 0.43$	$-1.31 - 0.37$
Location [Parks]	$-0.37 \pm 0.62$	$-1.58 - 0.84$
<b>Location [Residential]</b>	$-1.48 \pm 0.46$	<b><math>-2.39 - -0.57</math></b>
<b>Time</b>	$-0.02 \pm 0.01$	<b><math>-0.03 - -0.02</math></b>

**Table 3.7** Calculated black-crested titmouse (*Baeolophus atricristatus*) nest survival rates (to completion) from estimated daily survival rates (DSR) based on a 36-day period, assuming 6 days for laying, 14 days for incubation, and 16 days for nestlings to fledge.

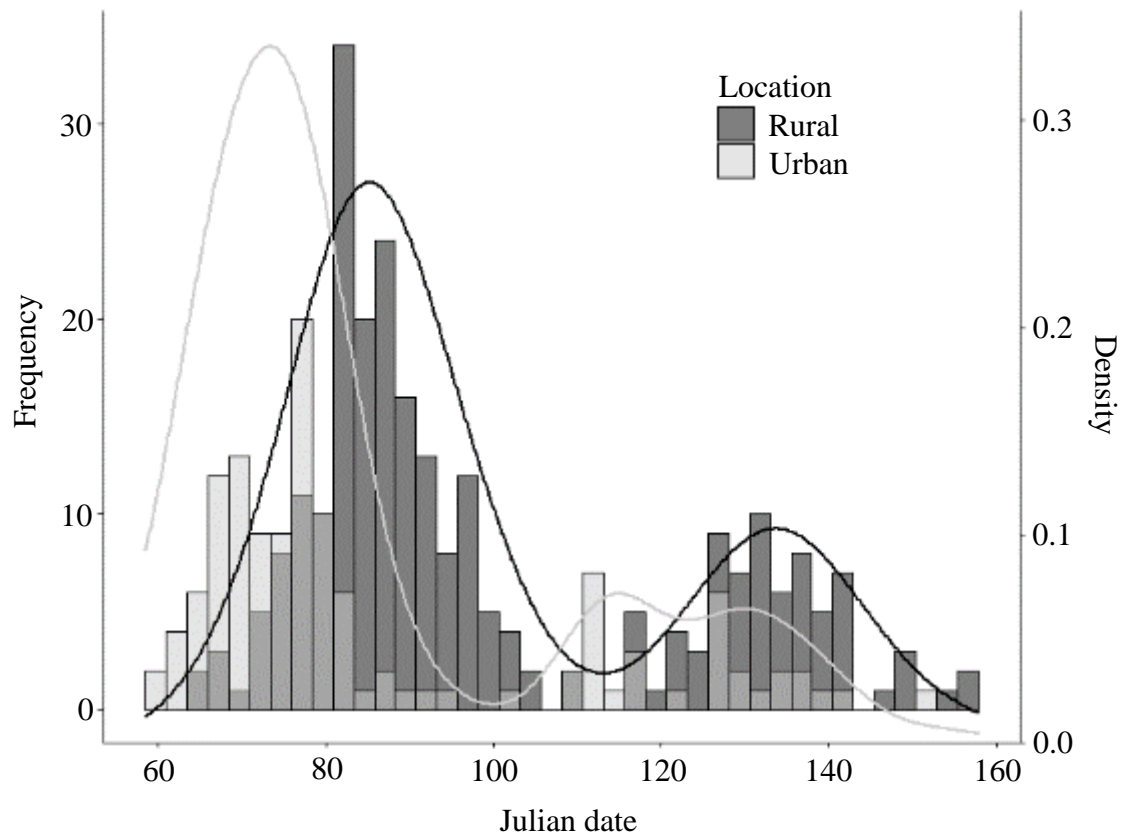
<b>Hypothetical nesting intervals</b>	<b>Freeman</b>	<b>Campus</b>	<b>Parks</b>	<b>Residential</b>
March 3 <sup>rd</sup> – April 7 <sup>th</sup>	0.86	0.91	0.88	0.67
April 1 <sup>st</sup> – May 6 <sup>th</sup>	0.74	0.83	0.76	0.45
May 1 <sup>st</sup> – June 5 <sup>th</sup>	0.54	0.68	0.57	0.19
June 1 <sup>st</sup> – July 6 <sup>th</sup>	0.29	0.45	0.32	0.04



**Figure 3.1** Frequency distribution of the number of eggs, nestlings, and fledglings found in successful nests ( $n = 276$ ) of black-crested titmice (*Baeolophus atricristatus*), 2013–2021, in San Marcos, Texas.

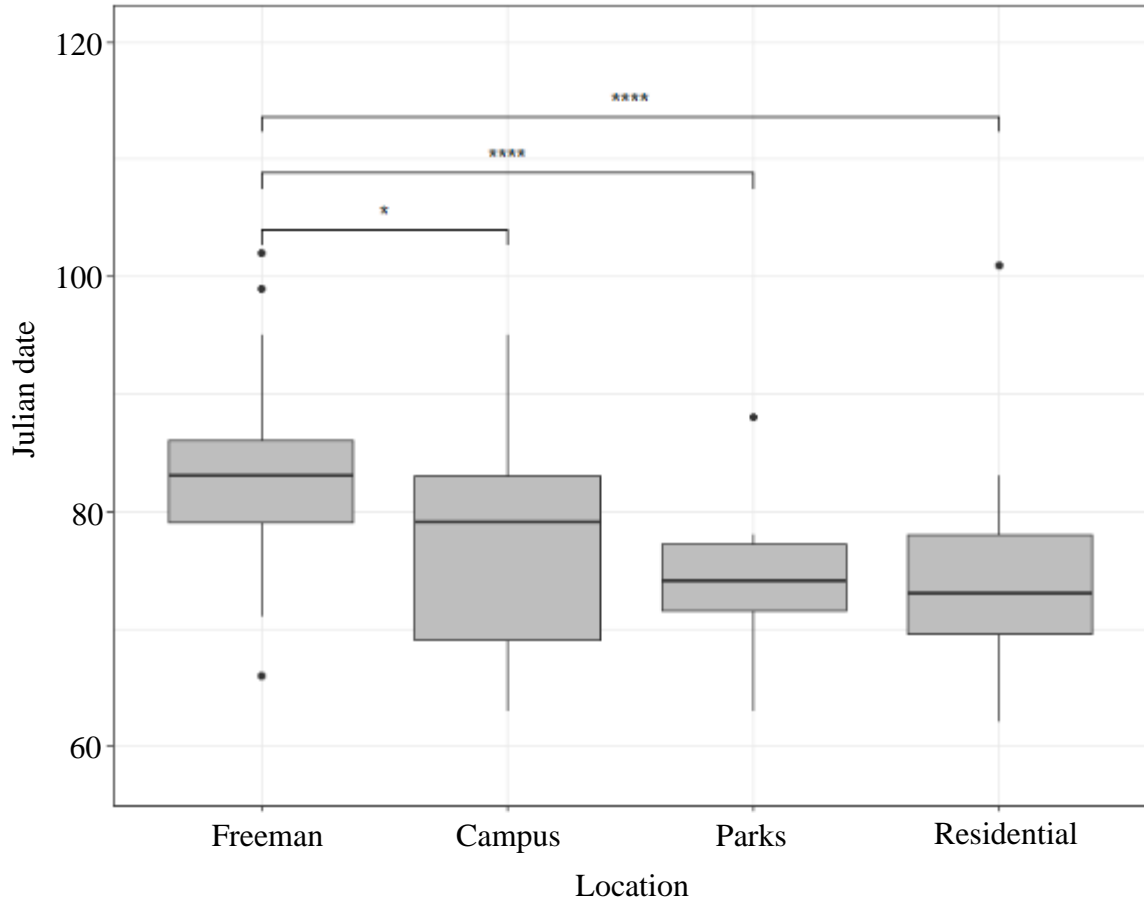


**Figure 3.2** The influence of clutch initiation date (Julian calendar) on the number of black-crested titmouse (*Baeolophus atricristatus*) eggs, nestlings, and fledglings (with 95% confidence intervals) per successful nest ( $n = 276$ ), 2013–2021, in San Marcos, Texas.

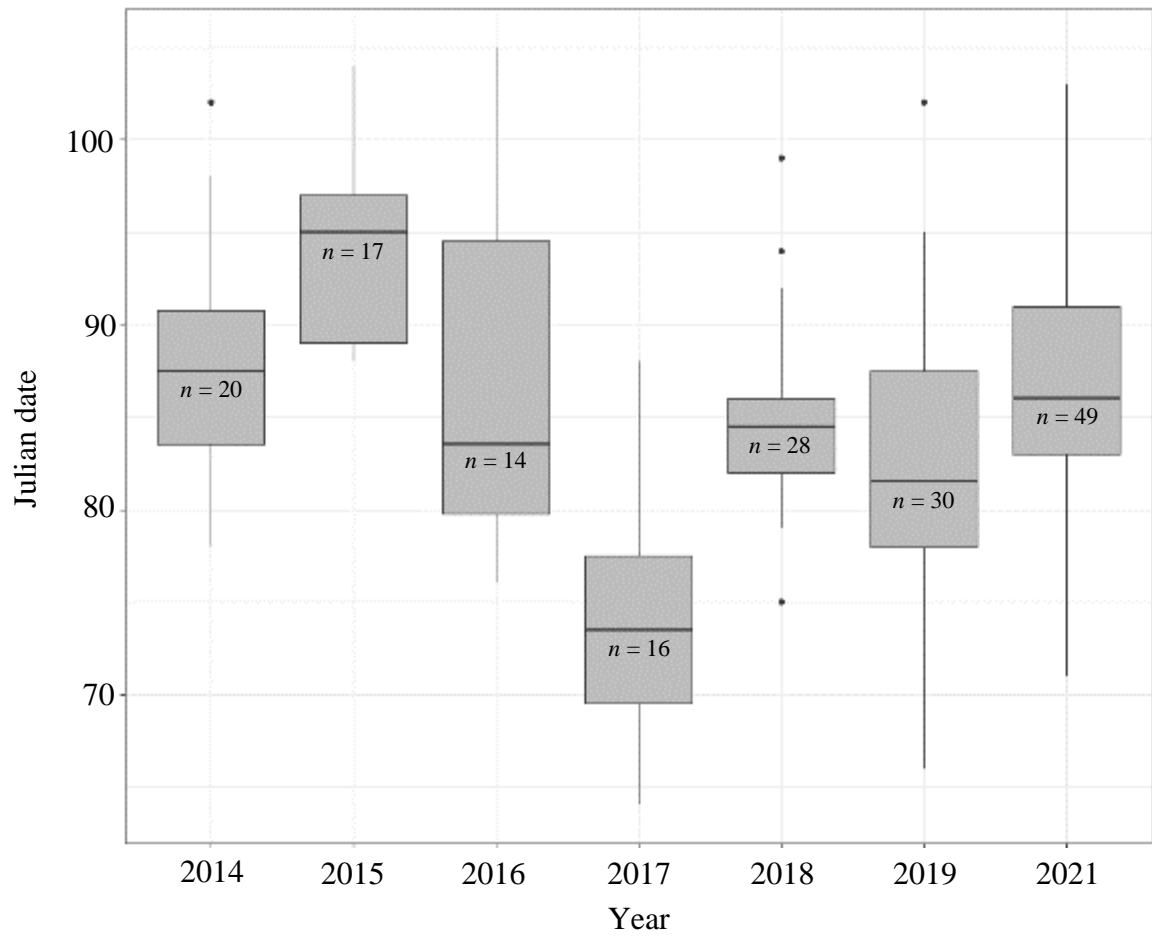


**Figure 3.3** The frequency and density distribution of clutch initiation dates of rural ( $n = 252$ ) and urban ( $n = 128$ ) populations of black-crested titmice (*Baeolophus atricristatus*) in San Marcos, Texas, 2013–2021.

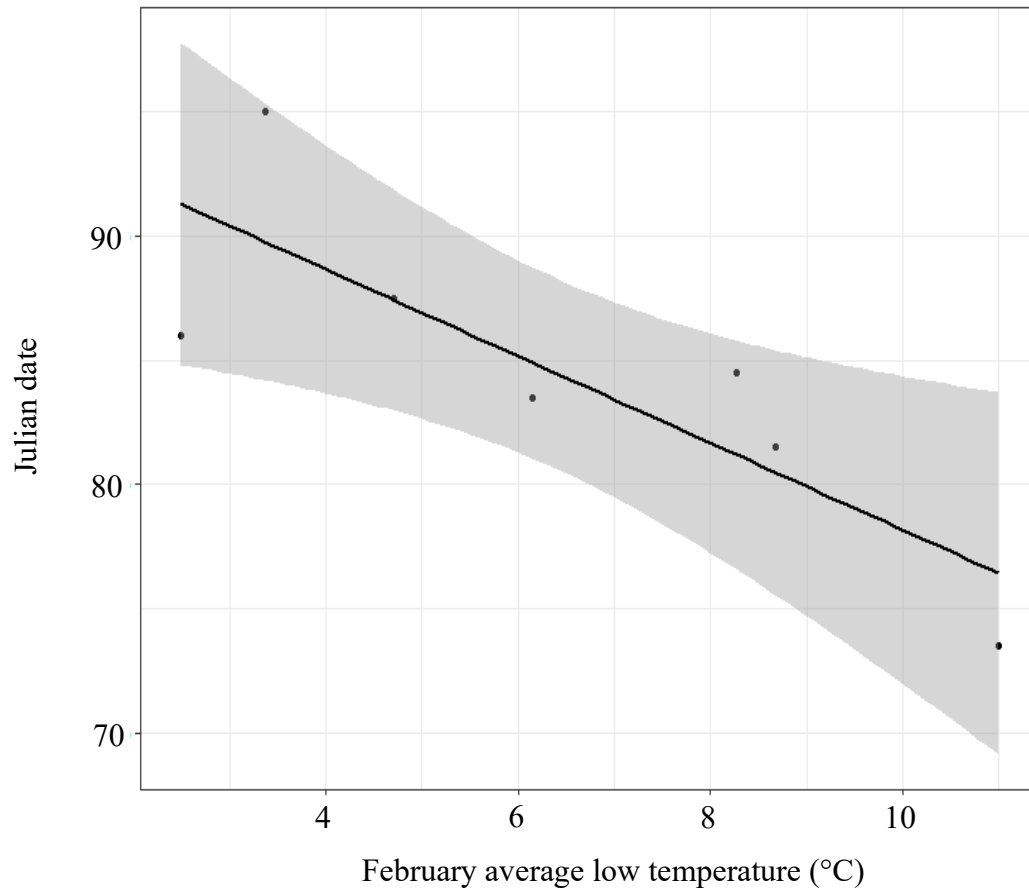




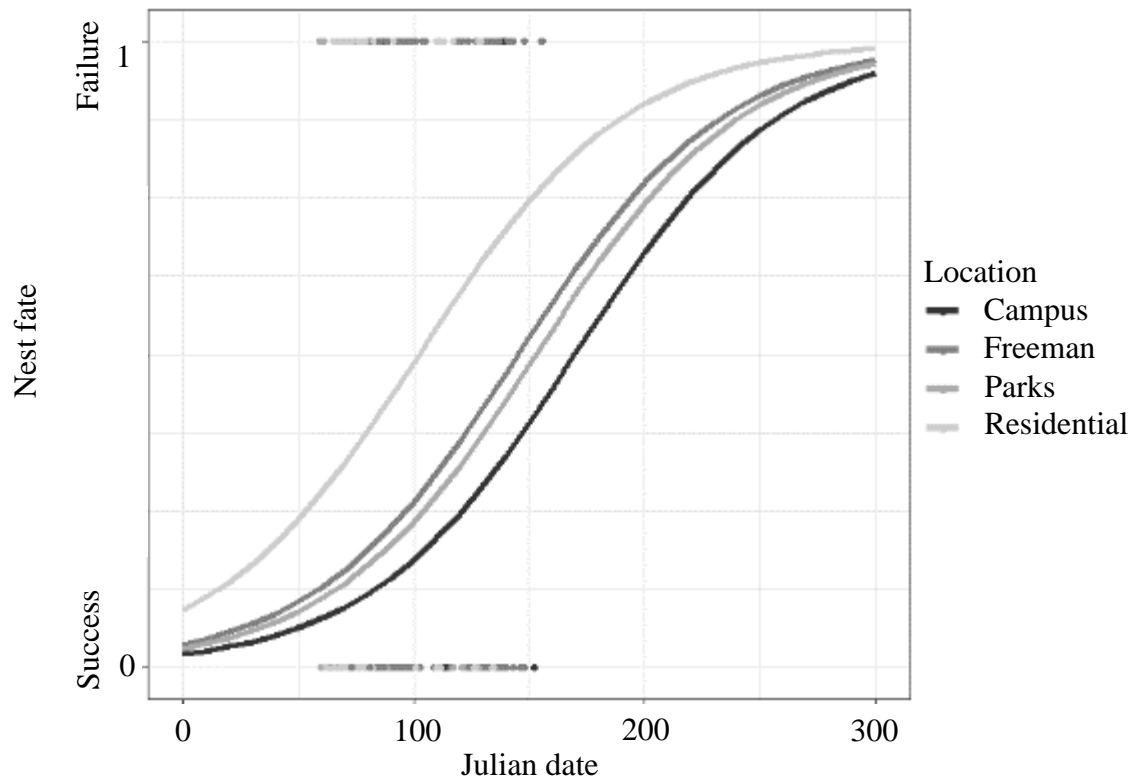
**Figure 3.4** Dunn's test comparing first clutch initiation dates of black-crested titmice (*Baeolophus atricristatus*) across four locations in San Marcos, Texas, during 2018 and 2019 ( $n = 114$ ). Significance bars reveal that initiation dates for the Freeman Center (rural) are later than all other locations.



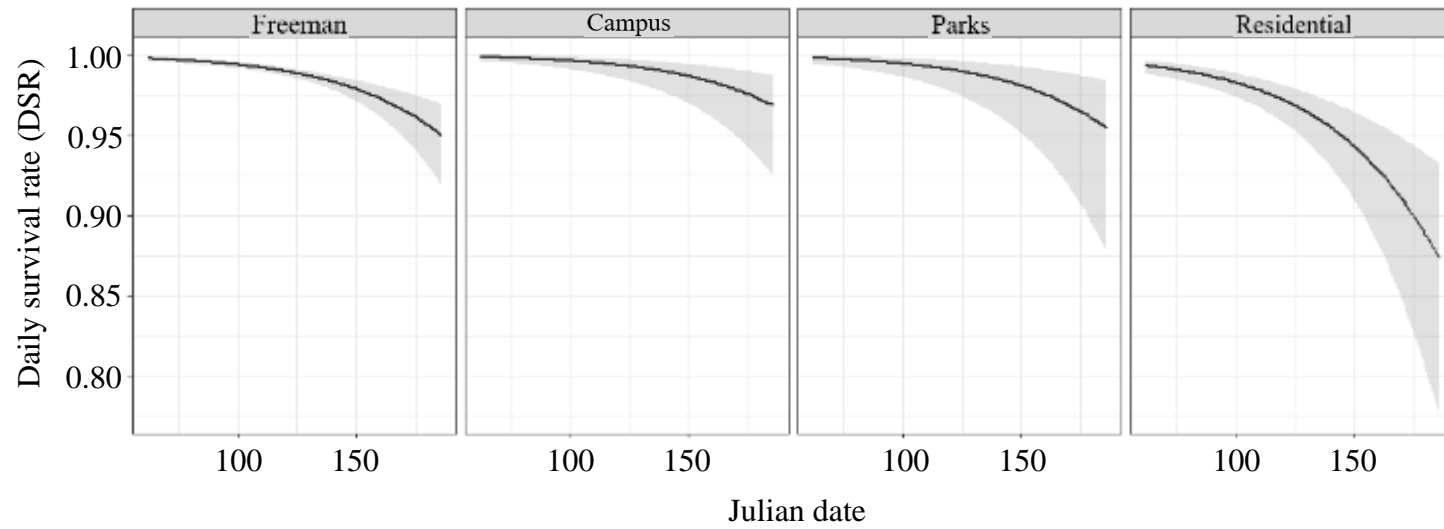
**Figure 3.5** Boxplots displaying the differences in first clutch initiation dates of black-crested titmice (*Baeolophus atricristatus*) across years 2014–2021 (2020 excluded because of COVID restrictions) at the Freeman Center in San Marcos, Texas.



**Figure 3.6** Generalized linear regression results identifying that yearly median first clutch initiation dates of the black-crested titmouse (*Baeolophus atricristatus*) correlate with that year's average February low temperatures at the Freeman Center in San Marcos, Texas, 2014–2021. The 95% confidence interval of median first clutch initiation date depicted in gray.



**Figure 3.7** Nest fate (0 = success, 1 = failure) is influenced by clutch initiation date (Julian calendar) and location for the black-crested titmouse (*Baeolophus atricristatus*) in San Marcos, Texas, 2013–2021 ( $n = 380$ ).



**Figure 3.8** Daily survival rates (DSR, with 95% confidence intervals) of nesting black-crested titmice (*Baeolophus atricristatus*) are influenced by location and clutch initiation date (Julian calendar) in San Marcos, Texas, 2013–2021 ( $n = 385$ ). DSR was not influenced by weather, habitat, year, or nest stage (incubation or nestlings).

**Supplementary Table 3.1** Table comparing competing models on which covariates best explain daily survival rates (DSR) of nesting black-crested titmice (*Baeolophus atricristatus*) in San Marcos, Texas, 2013–2021 using Akaike Information Criterion (AIC) for small sample sizes.

<b>Model</b>	<b><math>\Delta AIC_c</math></b>	<b><math>w_i</math></b>	<b><math>K_i</math></b>	<b>Dev</b>
<b>S</b> Location + Time	0.00	0.7754	5	740.20
<b>S</b> Location + Nest Age	2.60	0.2120	5	742.80
<b>S</b> Time + Predator Baffle	9.52	0.0067	3	753.72
<b>S</b> Time	12.90	0.0012	2	759.10
<b>S</b> Wood + Time	13.92	0.0007	3	758.12
<b>S</b> Time + Year	13.99	0.0007	10	744.17
<b>S</b> Nest Age	14.76	0.0005	2	760.96
<b>S</b> Wood + Nest Age	15.72	0.0003	3	759.93
<b>S</b> Nest Stage + Nest Age	16.70	0.0002	3	760.90
<b>S</b> Location + Low incubation temp	19.05	<0.0001	5	759.25
<b>S</b> Location + Low nestling temp	20.13	<0.0001	5	760.33
<b>S</b> Location + Precipitation nestling temp	22.10	<0.0001	5	762.30
<b>S</b> Location + High incubation temp	22.88	<0.0001	5	763.08
<b>S</b> Low incubation temp	26.30	<0.0001	2	772.51
<b>S</b> Precipitation nestling temp	26.73	<0.0001	2	772.93
<b>S</b> High incubation temp	30.11	<0.0001	2	776.32
<b>S</b> Low nestling temp	30.28	<0.0001	5	770.48
<b>S</b> Location + Nest Stage	30.29	<0.0001	4	772.49
<b>S</b> Location	32.13	<0.0001	2	778.33
<b>S</b> Nest Stage	37.19	<0.0001	2	783.39
<b>S</b> .	37.19	<0.0001	2	783.40
<b>S</b> Nest Stage + Predator Baffle	37.20	<0.0001	1	785.40
<b>S</b> Wood	37.28	<0.0001	3	781.48
<b>S</b> Predator Baffle	37.55	<0.0001	2	783.75
<b>S</b> Location + Year	37.99	<0.0001	12	764.16
<b>S</b> Year	42.41	<0.0001	9	774.60

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#### IV. THE BIG PICTURE: ASSESSING POPULATION DEMOGRAPHICS OF A SOCIAL-STRUCTURED PASSERINE IN RURAL AND URBAN LANDSCAPES

##### Abstract

Anthropogenic landscapes, when coupled with shifting weather patterns, alter population demographics of songbirds. Though some species evolved the ability to adjust to adverse urbanized conditions, other species suffer population declines as they are unable to rapidly adapt. To assess the influence of urbanization and weather on passerine apparent survival ( $\phi$ ), I utilized a kin-structured songbird commonly reported in cities and rural landscapes, the black-crested titmouse (*Baeolophus atricristatus*, hereafter BCTI), a species lacking  $\phi$  estimates. Between 2013 and 2020, I captured and color-banded adult and nestling BCTI using nestboxes in urban San Marcos, Texas ( $n = 469$ ) and in a nearby rural property with natural habitat ( $n = 918$ ). With the capture-mark-recapture data collected during the breeding (April – June) and non-breeding (October – December) seasons, I applied Cormack-Jolly-Seber analyses in program MARK, implemented through RMark, to estimate  $\phi$  of BCTI. I also compared  $S$  (apparent survival estimated through multistate models) between rural adult BCTI associated in kin-structured neighborhoods and adult BCTI not associated with kin. I included four weather covariates, three habitat covariates, and age and sex factors to develop candidate models that were ranked using  $AIC_C$  with a quasi-likelihood adjustment. Results revealed that rural adult males had greater  $\phi$  estimates than rural females in both summer and winter seasons (rural male summer =  $0.568 \pm 0.049$ , rural male winter =  $0.564 \pm 0.052$ , rural female summer =  $0.495 \pm 0.052$ , rural female winter =  $0.491 \pm 0.058$ ), but there was little fluctuation between summer and winter  $\phi$  for both sexes. Urban adult males also

had greater  $\phi$  estimates than urban females in both summer and winter seasons (urban male summer =  $0.677 \pm 0.093$ , urban male winter =  $0.386 \pm 0.103$ , urban female summer =  $0.455 \pm 0.095$ , urban female winter =  $0.200 \pm 0.074$ ), however estimates for both sexes were significantly lower during the winter. In contrast, juvenile BCTI had lower  $\phi$  during their first summer (directly post-fledging) compared to their first winter. Urban and rural juveniles had roughly the same  $\phi$  during the summer ( $0.067 \pm 0.020$  and  $0.078 \pm 0.010$ , respectively), but urban juveniles had a greater  $\phi$  than rural juveniles during the winter ( $0.333 \pm 0.215$  and  $0.165 \pm 0.033$ , respectively). Additionally, results from multistate models revealed that rural adult BCTI had lower  $S$  when surrounded by relatives in kin-structured neighborhoods, yet adults were 2.2 times as likely to transition into kin-structured neighborhoods (versus out of them), indicating that kin-selection still favors philopatry for the species. Overall, though  $\phi$  estimates were greater for certain urban BCTI demographics, rural  $\phi$  was more stable over time for both age classes and sexes, indicating that urban BCTI may be more susceptible to population fluctuations with inclement weather and habitat inconsistencies.

## **Introduction**

Baseline data for avian management plans stems from knowledge on population demographics (Leslie 1945, Lack 1946, Saether and Bakke 2000, Yoccoz et al. 2001), which includes vital rates, recruitment, and population growth estimates, as well as density and abundance estimates (Lancia et al. 2000, Sunderland et al. 2004). Intrinsic factors, such as sex and age, and extrinsic factors, including environmental parameters, should be considered in tandem when assessing population dynamics (Nichols and Kendall 1995, Starns et al. 2014, Fritts et al. 2018). As climate change continues to alter

precipitation patterns and temperature extremes, ecosystems are likely to shift, causing different responses across age classes and sexes (Pearce-Higgins and Green 2014). Additionally, because of shifting weather patterns, other environmental factors, such as habitat composition and structure, are likely to experience phenological deviations as well (Rottenborn 1999, Mills 2013). Over time, habitat alterations and deviating weather patterns may ultimately lead to shifting avian communities if species are not capable of adjusting to fluctuating conditions (Dirzo and Raven 2003, Chamberlain et al. 2009).

Humans are rapidly urbanizing vast areas and harvesting natural resources at an alarming rate, forcing many avian populations to either acclimate, emigrate, or perish if neither of the previous options are possible (Mills 2013). Whereas many populations persist in human-dominated landscapes, it is difficult to quantify how their demographics and dynamics are affected over time (McKee et al. 2004, Hedblom and Soderstrom 2012, Duarte et al. 2014). Natural resources, available nesting sites, and habitat structure used for shelter are likely compromised in urban areas; thus, in-depth research on populations across a gradient of urbanization intensity is beneficial to better understand the interaction between these extrinsic parameters and demographics (Murgui and Hedblom 2017).

Of special interest is the effect of extrinsic abiotic factors such as urbanization and weather patterns on demographics of social-oriented avian populations (Griesser and Lagerberg 2012, Ryder and Sillett 2016). A small percentage (roughly 9%) of bird species form extended family flocks that remain together for a prolonged period of time and benefit by cooperatively breeding and/or sharing resources and heightened predator vigilance (Ekman 2006). An even smaller percentage of species create kin-structured

neighborhoods in which generations of relatives live adjacent to each other and flock together to increase inclusive fitness (Hatchwell 2009, Rylander et al. 2020). Both natural and anthropogenic processes that disrupt the dynamics of non-social-structured avian populations have the potential to be even more pronounced in species that have evolved to better survive surrounded by family (Dickinson et al. 2009, Layton-Matthews et al. 2018).

To understand the influence of urbanization, habitat structure, and weather extremes on the demographics of a kin-structured species, I studied the black-crested titmouse (*Baeolophus atricristatus*, hereafter BCTI), a small passerine that resides in central and west Texas, southern Oklahoma, and parts of Mexico (Dixon 1978, Patten and Smith-Patten 2008). As a resident, non-migratory species, the BCTI typically forms annual family groups that result in the formation of related neighborhoods through the limited natal dispersal of juvenile males (Rylander et al. 2020). The BCTI is not a species of concern and regularly occurs in both urban and rural settings within its range, yet it is hypothesized that its complex kin-structure may make this species more sensitive to urbanization than other non-kin-structured species (Rylander pers. obs.). In addition, demographic data regarding adult and juvenile apparent survival ( $\phi$ ) have never been compiled for the BCTI (Patten and Smith-Patten 2008). These parameters are assumed to be similar to its sister-taxa, the tufted titmouse (*Baeolophus bicolor*) (Elder 1985, Karr et al. 1990, Doherty and Grubb 2002, Wolfe et al. 2013), but it is likely that there are differences given the BCTI's limited range in more arid, open habitats, as well as its smaller body size and less aggressive behavior (Dixon 1955, Grubb and Pravosudova 1994, Patten and Smith-Patten 2008).

In this study I: 1) assessed the effects of habitat composition and weather on  $\phi$  of adult and juvenile BCTI in rural and urban landscapes; and 2) examined if kin-selection influenced rural adult BCTI apparent survival ( $S$ ). I predicted that  $\phi$  would be greater in adult BCTI compared to juveniles because juveniles are less experienced locating food and evading predators (Ekman et al. 1981, Doherty and Grubb 2002). Additionally, I predicted that  $\phi$  would be greater in rural populations compared to urban populations because of patchier habitat and non-native invasive predators associated with urbanization (Wolfe et al. 2013). I also predicted that rural adult BCTI that reside near relatives in kin-structured neighborhoods would have greater  $S$  than adults not surrounded by kin because individuals surrounded by family are more likely to share resources and expend less energy in territorial defense (Ekman 2006, Layton-Matthews et al. 2018, Rylander et al. 2020).

## **Methods**

### ***Study sites***

I conducted capture-mark-recapture research in San Marcos, Texas, USA (29.8833° N, -97.9414° W), a medium-sized city (population roughly 63,000+) located within the Edwards Plateau ecoregion (DataUSA 2019). As one of the fastest growing cities in the nation per capita, San Marcos is experiencing rapid urbanization, making it an ideal location to perform research regarding wildlife response to a changing landscape (Davila 2015). The BCTI is common throughout San Marcos, both in urban and rural areas (Rylander pers. obs.), allowing for comparison between populations in different landscapes.

BCTI frequently occupy man-made nestboxes for reproductive purposes which allows for adults and nestlings to be more easily captured and marked for research purposes (Rylander 2015). Because of this, I installed 40 nestboxes across Texas State University's campus and 34 nestboxes within public City of San Marcos parks (Schulle Canyon, Crook's Park, Children's Park, Dunbar, Prospect, and the San Marcos City Cemetery) during the winter of 2016. I also installed 86 nestboxes in single-family home residential neighborhoods during the winter of 2017, for a total of 160 urban nestboxes (Figure 1.4). I positioned all urban nestboxes in locations that received foot and vehicular traffic daily and were either encompassed by or within 100 m of impervious ground cover. I installed urban nestboxes between 2.5-4 m from the ground on mature trees (diameter at breast height > 15 cm) using either decking screws or ratchet straps depending on the sensitivity of the tree species or landowner preference.

For the rural site, I used the Freeman Center, a Texas State University owned property located 10 km northwest of downtown San Marcos (29.9391° N, -98.0076° W). The vegetation on the Freeman Center is typical of the Edward Plateau ecoregion – woodlands consisting of oak (*Quercus fusiformis*, *Quercus buckleyi*), juniper (*Juniperus ashei*), hackberry (*Celtis laevigata*), and cedar elm (*Ulmus crassifolia*), as well as more open grassland savannas containing honey mesquite (*Prosopis glandulosa*), agarita (*Berberis trifoliolata*), and a mixture of little bluestem (*Schizachyrium scoparium*), silver bluestem (*Bothriochloa laguroides*), and King Ranch bluestem (*Bothriochloa ischaemum*), among other grasses (Rylander pers. obs.). During the winter of 2012 and 2013, researchers installed 40 and 31 nestboxes (respectively) at the Freeman Center for eastern bluebird (*Sialia sialis*) and BCTI studies. I then installed an additional 75



nestboxes during the winter of 2017, bringing the total number of rural nestboxes at the Freeman Center to 146 (Figure 1.2). Rural nestboxes were placed along random roadways and in a single grid arrangement (initially for eastern bluebird research), with nestboxes installed ~100 m from each other (Harrod 2014, Rylander et al. 2020), and all boxes were installed on t-posts with a PVC-pipe predator baffle roughly 3 m from the ground. Other than a few caliche-based roads that transect the Freeman Center and several buildings surrounding the property's headquarters, there are no impervious surfaces or large man-made structures throughout the northern half of the property. Hereafter, the Freeman Center and the nestboxes located on the property will be referred to as the "rural" site.

#### ***Capture-mark-recapture (CMR)***

To capture and band adult and nestling BCTI, I monitored nestboxes between February and July of 2013–2019. I checked each nestbox 2 times per week for BCTI nesting substrate (fresh moss, fur, and bits of snakeskin; Patten and Smith-Patten 2008), and once confirmed, I recorded: number of eggs, number of nestlings, age of nestlings, and fledging success or failure. Once nestlings were  $\geq 5$  days old, I hand-captured adult BCTI as they entered the nestbox to feed young (Rylander et al. 2020). I affixed adults with a unique combination of 1 to 3 Darvic color leg bands (Avinet Research Supplies, Portland, Maine) and a registered United States Geological Survey (USGS) aluminum band. I determined the sex of each adult - females have brood patches whereas males usually have cloacal protuberances and no brood patch during the spring. I banded all nestlings with unique combinations of color and aluminum bands at 10-14 days post-hatching.

I performed resights on banded BCTI during the breeding (April – June) and non-breeding (October – December) seasons every year from 2013–2020. I attempted resights once every two weeks ( $\geq 5$  days between visits with positive detections, Bibby et al. 2000), recording identity, sex, age, and if the individual was potentially occupying a territory adjacent to another banded BCTI ( $< 400$  m, Sharp et al. 2008, Hatchwell 2009, Rylander et al. 2020). I searched for marked individuals near the nestbox where they were originally captured and then proceeded to spiral outward from that location (up to a  $\sim 1$ -km radius from the nestbox) until BCTI were detected. I varied times (0700 to 1800) and days of the week that I visited specific locations throughout the urban and rural sites to account for potential bias in BCTI behavior near roosting sites around dawn and dusk (Bibby et al. 2000). If known-banded individuals were not positively detected or identified while performing routing resights, I returned to the same location within 1–4 days in attempts to relocate. I performed resights throughout the entirety of the individual's presence (ranging from months to years), after which it was impossible to determine if the individual had died, dispersed from its natal home range, or emigrated beyond the search radius. I recorded all positive detections of banded individuals as 1s within CMR matrices and all non-detections as 0s. When unable to perform resights as consistently as desired, I recorded resight effort on a scale of 0 – 12. I scored each bi-monthly resight attempt between 0-2 points, totaling 4 potential points each month, and thus 12 points per breeding and non-breeding season (3-month interval). I scored a single resighting attempt as a 2 if conditions were ideal (low wind, no precipitation, low noise pollution), as a 1 if conditions were less than ideal, and as a 0 if unable to perform resights at all.

### ***Habitat composition***

To assess the influence of habitat composition on  $\phi$  of BCTI, I used ArcGIS Pro 2.6.1 (Environmental Systems Research Institute 2020) to create circular buffers that were 9.07-hectares in area and centered around each nestbox where I banded BCTI. I used 9.07-hectares as the buffer based on the average home range size of BCTI in a nearby rural population (Rylander et al. 2020). Once buffers were constructed, I used a 30-m by 30-m pixel vegetation GIS layer provided by the Texas Parks and Wildlife Department (TPWD 2020) to calculate the proportion of five broad vegetation categories within each buffer: woodland (polygons containing  $> 75\%$  woodland cover), mixed shrub (polygons containing between  $25\% - 75\%$  woodland cover), grassland (polygons containing  $< 25\%$  woodland cover), low urbanization, and high urbanization. As defined by TPWD, polygons classified as low urbanization are “areas that are built-up but not entirely covered by impervious cover and includes most of the non-industrial areas within cities and towns.” TPWD defined high urbanization polygons as “built-up areas and wide transportation corridors that are dominated by impervious cover.”

### ***Weather covariates***

To assess the influence of weather covariates on BCTI  $\phi$ , I utilized data sets collected at San Marcos weather stations by the National Weather Service (NOAA 2020) between 2013 and 2020. Each year of the study, I calculated: 1) seasonal precipitation (“precip”) as the total rainfall accumulation during the early summer (May – August) and winter (December – February) months; 2) total precipitation (“total precip”) as the total rainfall accumulation during the spring and summer (March – August) and fall and winter months (September – February); 3) seasonal temperature extremes (“temp extreme”) as

the average maximum temperature during summer months and average minimum temperatures during winter months; and 4) extreme hot and cold days (“extreme days”) which represented the number of summer days with temperatures >90<sup>th</sup> percentile, and number of winter days with temperatures <10<sup>th</sup> percentile (Fritts et al. 2018). I calculated “hot days” as any day with a recorded high temperature above 37.8° C (100° F) and “cold days” as any day with a recorded low temperature below -1.1° Celsius (30° Fahrenheit), as these represented the 90<sup>th</sup> percentile and 10<sup>th</sup> percentile of 30 years of San Marcos temperature averages (NOAA 2020). Also, I accounted for potential differences in temperature and precipitation across summer and winter seasons by including an interaction term with season. All research performed was conducted in accordance with Institutional Animal Care and Use Committee (IACUC) (#201532811), federal Master Banding Permit (#24108), U.S. Fish and Wildlife Permit (MB121162-2), and Texas Parks and Wildlife Collection Permit (#SPR-0417-107).

## **Data Analyses**

### ***Apparent survival $\phi$ and detection $p$***

I used Cormack-Jolly-Seber (CJS) (Cormack 1964, Jolly 1965, Seber 1965) model structures to estimate  $\phi$  and  $p$  using statistical software program MARK (White and Burnham 1999, Cooch and White 2006), implemented through package RMark in Program R (Laake 2013). Due to differing resight efforts between urban and rural BCTI sites across years, and because most BCTI juveniles disperse or die during their first year of life (Rylander et al. 2020), I performed four separate CJS analyses (Sandercock et al. 2000): 1) urban hatch year (HY, juvenile)  $\phi$ ; 2) urban after hatch year (AHY, adult)  $\phi$ ; 3) rural HY  $\phi$ ; and 4) rural AHY  $\phi$ . I configured the four analyses to estimate late summer

(July – September, hereafter “summer”) and late winter (January – March, hereafter “winter”)  $\phi$  during all years in which CMR occurred. For rural CJS analyses, I performed resights between 2013–2020, however, I was unable to perform resights on BCTI during the winter of 2018. Thus, in total, there were fourteen resight periods and seven capture-marking periods (always during the breeding season). For urban CJS analyses, I performed resights on BCTI between 2017–2020, totaling seven resight periods and three capture-marking periods.

For all CJS analyses, I did not include a fully time-dependent model ( $\phi_{\text{time}}, p_{\text{time}}$ ) as it failed to converge. I did include models Time ( $\phi_{\text{Time}}, p_{\text{Time}}$ ), where estimates follow a linear trend over time, and null ( $\phi_{\cdot}, p_{\cdot}$ ), where parameter estimates remained constant over time. I included weather covariates: seasonal precipitation (precip\*season), total precipitation (total precip\*season), maximum and minimum temperature (temp extreme\*season), and extreme days (extreme days\*season). I also added habitat covariates (categorized as individual covariates, Royal 2008): percent high urbanization habitat (high urb), percent low urbanization habitat (low urb), percent woodland habitat (wood), percent grassland habitat (grass), and percent mixed shrubland (mix). I scaled and centered all weather and habitat covariates. I incorporated season (summer or winter) into models as a factor covariate. I used an age-specific extension (age) for the HY  $\phi$  analyses (Pollock 1981), allowing me to account for HY birds transitioning into AHYs one year after fledging. Because I was unable to determine exact age of captured adult BCTI, I did not use age as a covariate for AHY models. I included sex as a factor variable for AHY models. For estimating  $p$ , I incorporated season, resight effort (effort), sex, time, Time, and null ( $\cdot$ ).

While building models for each of the four CJS analyses, I used a sequential-by-sub-model strategy (Morin et al. 2020) where I first focused on parameter  $p$  while maintaining constant  $\phi$  ( $\phi$  .). Once I determined which covariate(s) were influential on  $p$ , I focused on which weather and habitat covariates to include in estimating  $\phi$  in the candidate model set. By removing the least influential weather and habitat covariates first, I was able to limit the number of models built for selection ( $\leq n/10$ ; Burnham and Anderson 2002). I also removed individual models from candidate model sets if overdispersed (Fletcher's  $\hat{c} > 2$ , Fletcher 2012) or failed to converge. I omitted variables from the same model that contained a variance inflation factor ( $VIF > 3$ ) to account for multicollinearity (Zuur 2009).

After creating biologically sound candidate model sets for each CJS analysis, I used Akaike's Information Criterion (Hurvich and Tsai 1989) for small sample sizes with quasi-likelihood adjustments ( $QAIC_c$ ) which accounts for overdispersion and penalizes models with more parameters (Burnham and Anderson 2002). I implemented these adjustments using the Fletcher's  $\hat{c}$  value from the most parameterized model in the candidate set (Cooch and White 2006, Fletcher 2012). If the top model in the  $QAIC_c$  table was  $< 2 \Delta QAIC_c$  units less than the second model, I used the top model to estimate parameters. If two or more models had  $\Delta QAIC_c$  values  $< 2$ , I either 1) model averaged to obtain parameter estimates if the difference in the number of parameters in each model was  $\leq 1$ , or 2) selected the most parsimonious model if the top models differed by  $\geq 2$  parameters and beta estimates of those additional parameters were not significant (Burnham and Anderson 2002). Once real parameter estimates for  $\phi$  and  $p$  were obtained,

I used Program CONTRAST to test for significant differences between sexes, age groups, seasons, and between urban and rural locations (Sauer and Williams 1989).

I assessed twelve candidate models for rural AHY BCTI  $\phi$  ( $n = 174$ , Supplementary Table 4.1), and adjusted for overdispersion using Fletcher's  $\hat{c} = 1.13$  ( $\phi_{\text{sex} + \text{season}, p_{\text{season}}}$ ). I created eleven candidate models to estimate  $\phi$  for rural HY BCTI ( $n = 731$ , Supplementary Table 4.2). Because Fletcher's  $\hat{c}$  was  $\approx 1$  ( $\phi_{\text{age} + \text{precip} * \text{season}, p_{\text{effort}}}$ ), I did not perform a quasi-likelihood adjustment. I examined ten candidate models to assess urban AHY BCTI  $\phi$  ( $n = 97$ , Fletcher's  $\hat{c} = 1.07$  ( $\phi_{\text{sex} + \text{season} + \text{high urb}, p_{\text{effort}}}$ ), Supplementary Table 4.3), and fifteen candidate models for urban HY BCTI  $\phi$  ( $n = 334$ , Fletcher's  $\hat{c} = 1.16$  ( $\phi_{\text{age} + \text{wood} + \text{season}, p_{\text{effort}}}$ ), Supplementary Table 4.4).

### ***Apparent survival $S$ and state transition $\Psi$***

To assess if  $S$  is influenced by residing near kin, I used a multistate (MS) model analysis (Nichols and Kendall 1995) in program MARK, implemented through RMark. I performed the MS analysis only on the rural AHY BCTI data set, as the urban and HY data was too sparse for MS parameter estimation, particularly for parameter  $\Psi$ . I used the CMR matrices created for rural AHY CJS analyses (2013 – 2020), but instead of assigning 1s as positive detections within the CMR matrices, I assigned positive detections as two distinctive states – an adult residing near kin (F) or not residing near kin (A). Adults could transition between states from one season to another. Because I banded full family groups and had information of kin-structured neighborhoods at the rural site (Rylander et al. 2020), I could determine if an adult was in state F or A during the summer or winter seasons.

I created thirteen MS candidate models ( $n = 174$ , Fletcher's  $\hat{c} = 1.03(S_{\text{stratum} + \text{sex} + \text{season}, p_{\text{effort}}, \Psi^{-1} + \text{stratum:tostratum})$ , Supplementary Table 4.5) using the following covariates to estimate  $S$ ,  $\Psi$ , and  $p$ : stratum (the state the adult was in during that season), season, sex, Time, and null (.). I included the covariate effort in models estimating  $p$ , and covariate stratum:tostratum in models estimating  $\Psi$ . I used QAIC<sub>c</sub> model selection as described above for CJS analyses to obtain parameter estimates, and Program CONTRAST to compare  $S$  estimates between sexes and states.

## Results

### *CMR*

Between 2013 and 2020, I captured and banded 1387 BCTI (Table 4.1). I was unable to perform resights on all 1387 BCTI due to: 1) banded nestlings being depredated before fledging; 2) individuals or family groups moving to inaccessible private properties after banding; and 3) certain urban locations undergoing massive construction projects that likely forced BCTI to emigrate far distances. I was unable to resight the majority (>80%) of HYs after their first season due to dispersal out of resight zones or due to mortality. However, I was able to record multiple years of resights on many individuals, including four rural males being sighted ~ 5 years, and four urban AHYs being resighted ~ 4 years.

### *CJS: Rural AHY $\phi$*

For rural AHY BCTI ( $n = 174$ ), there were three models with a  $\Delta\text{QAIC}_c < 2$ , therefore I model averaged to estimate parameters (Supplemental Table 4.6). There were no differences in  $\phi$  between males and females ( $\chi^2 = 1.908$ ;  $\text{df} = 1$ ;  $p = 0.167$ ) in both



summer and winter seasons (rural male summer =  $0.568 \pm 0.049$ , rural male winter =  $0.564 \pm 0.052$ , rural female summer =  $0.495 \pm 0.052$ , rural female winter =  $0.491 \pm 0.058$ ) (Figure 4.1). Season influenced  $p$  ( $\chi^2 = 10.804$ ;  $df = 1$ ;  $p < 0.001$ ) with summer detection estimates being 1.3x greater ((mean  $\pm$  SE)  $0.877 \pm 0.040$ ; 95% CI = [0.774 – 0.934]) than winter estimates ( $0.687 \pm 0.041$ ; 95% CI = [0.600 – 0.762]).

### ***CJS: Rural HY $\phi$***

The top model  $\phi_{\text{age} + \text{precip} * \text{season}}, p_{\text{effort}}$  was used to estimate  $\beta$  values (Table 4.2) and real parameter estimates for rural HY BCTI ( $n = 731$ ) (Supplemental Table 4.7). Age had the greatest effect ( $\beta = 2.04 \pm 0.27$ ; 95% CI = [1.52 – 2.57]), with real estimates indicating that HYs had a significantly lower  $\phi$  than AHYs during both summer and winter seasons ( $\chi^2 = 302.35$ ;  $df = 3$ ;  $p < 0.001$ ) (Figure 4.2). Additionally, HY  $\phi$  was significantly lower during summer months compared to winter months ( $\chi^2 = 23.613$ ;  $df = 1$ ;  $p < 0.001$ ), even though HY  $\phi$  was lower during the winter of 2016. The amount of winter precipitation also influenced HY  $\phi$  ( $\beta = -1.39 \pm 0.51$ ; 95% CI = [-2.29 – -0.39]) but summer precipitation did not (Figure 4.3). As total seasonal precipitation increased, HY  $\phi$  decreased during winter and slightly increased during summer. Covariate effort had a significant effect on  $p$  ( $\beta = 0.51 \pm 0.26$ ; 95% CI = [0.01 – 1.01]), with positive resight detections ranging from 0.765 – 0.913 depending on effort.

Though model  $\phi_{\text{age} + \text{season}}, p_{\text{effort}}$  was ranked second in the AIC<sub>C</sub> table for rural HY BCTIs, I used real parameter estimates calculated from this model for direct comparison with urban HY estimates (Supplemental Table 4.8, Figure 4.1), as this model provided a single mean estimate for both age groups during each season.

### ***CJS: Urban AHY $\phi$***

The top model for urban AHY  $\phi$  used for parameter estimates was  $\phi_{\text{sex} + \text{season} + \text{high urb}, p_{\text{effort}}}$  ( $n = 97$ ) (Table 4.3, Supplemental Table 4.9, Figure 4.1). Season had the greatest effect on  $\phi$  ( $\beta = -1.20 \pm 0.55$ ; 95% CI = [-2.28 – -0.13]), with summer  $\phi$  estimates significantly greater than winter estimates for both urban males and females ( $\chi^2 = 8.831$ ;  $df = 1$ ;  $p = 0.003$ ). Sex had the second highest influence on  $\phi$  ( $\beta = 0.92 \pm 0.43$ ; 95% CI = [0.07 – 1.77]), with males having between 1.75 – 2.25x greater  $\phi$  than females depending on season ( $\chi^2 = 4.931$ ;  $df = 1$ ;  $p = 0.026$ ). Percent high urbanization within a BCTI home range also influenced  $\phi$  ( $\beta = 0.50 \pm 0.21$ ; 95% CI = [0.09 – 0.91]); male and female  $\phi$  increased as the percentage of high urbanization increased (Figure 4.4). Effort affected  $p$  ( $\beta = 0.28 \pm 0.14$ ; 95% CI = [0.01 – 0.56]), with positive resight detections ranging from 0.511 – 0.915 depending on effort.

### ***CJS: Urban HY $\phi$***

Top model  $\phi_{\text{age} + \text{low urb} + \text{season}, p_{\text{season}}}$  was used to calculate urban HY  $\phi$  parameter estimates ( $n = 334$ ) (Table 4.4, Supplemental Table 4.10, Figure 4.1). Season and age were the most influential covariates affecting  $\phi$  (season:  $\beta = 1.94 \pm 1.10$ ; 95% CI = [-0.21 – 4.10]; age:  $\beta = 1.42 \pm 0.78$ ; 95% CI = [-0.12 – 2.96]). HY  $\phi$  during summer and winter seasons did not differ ( $\chi^2 = 1.518$ ;  $df = 1$ ;  $p = 0.218$ ), nor were there differences between age groups during either season ( $\chi^2 = 2.537$ ;  $df = 1$ ;  $p = 0.111$ ). Interestingly, the 95% CIs of real estimates were large for all groups except for urban HY summer  $\phi$ , indicating some variability surrounding the estimates. Additionally, the percentage of low urbanization habitat within a BCTIs home range significantly

influenced HY and AHY  $\phi$  ( $\beta = -0.67 \pm 0.18$ ; 95% CI = [-1.02 – -0.32], Figure 4.5), with  $\phi$  decreasing as the percent of low urbanization habitat increases. Covariate season significantly affected  $p$  ( $\beta = 1.31 \pm 0.50$ ; 95% CI = [0.32 – 2.30]), with summer having greater detection estimates than winter ( $\chi^2 = 6.895$ ; df = 1;  $p = 0.009$ ).

### ***MS: Rural AHY S & $\Psi$***

The top MS model  $S_{\text{stratum} + \text{sex}, p_{\text{season}}, \Psi_{-1 + \text{stratum:tostratum}}$  was used to calculate beta and real parameter estimates ( $n = 174$ ) (Supplemental Table 4.11, Figure 4.6). Sex had the greatest influence on  $S$  ( $\beta = 0.63 \pm 0.25$ ; 95% CI = [0.15 – 1.11]) followed by stratum ( $\beta = -0.57 \pm 0.28$ ; 95% CI = [-1.12 – -0.03]) (Table 4.5). Both males and females had greater  $S$  when in state A (adults not near kin) compared to state F (adults with kin nearby) ( $\chi^2 = 6.808$ ; df = 1;  $p = 0.009$ ), and males had greater  $S$  in both states compared to females ( $\chi^2 = 8.254$ ; df = 1;  $p = 0.004$ ). Males in state A had an  $S$  29.1% greater than females in state F, whereas males in state F only had an  $S$  1.4% greater than females in state A. For parameter  $\Psi$ , adults transitioned from state A to state F ( $\beta = 0.57 \pm 0.20$ ; 95% CI = [0.19 – 0.96]) at a significantly greater rate ( $0.639 \pm 0.046$ ; 95% CI = [0.546 – 0.723]) than adults transitioning from state F to state A ( $\beta = -0.91 \pm 0.21$ ; 95% CI = [-1.33 – -0.50]) ( $0.287 \pm 0.043$ ; 95% CI = [0.210 – 0.378]) ( $\chi^2 = 31.249$ ; df = 1;  $p < 0.001$ ). Thus, adults were more likely to transition into kin-structured neighborhoods and remain there compared to transitioning out of kin-structured neighborhoods. Season influenced  $p$  ( $\beta = -1.79 \pm 0.52$ ; 95% CI = [-2.81 – -0.77]), with adults more likely to be detected during the summer than winter ( $\chi^2 = 20.692$ ; df = 1;  $p < 0.001$ ).

### ***Comparing Urban and Rural CJS $\phi$ Results***

Overall, urban and rural male  $\phi$  estimates did not differ during summer ( $\chi^2 = 1.075$ ;  $df = 1$ ;  $P = 0.300$ ) or winter ( $\chi^2 = 2.380$ ;  $df = 1$ ;  $P = 0.123$ ), and urban and rural female  $\phi$  estimates did not differ during summer ( $\chi^2 = 0.136$ ;  $df = 1$ ;  $P = 0.712$ ). However,  $\phi$  estimates differed during winter ( $\chi^2 = 9.579$ ;  $df = 1$ ;  $P = 0.002$ ), with urban females having lower  $\phi$  than rural females. Additionally, urban and rural HY  $\phi$  estimates did not differ during either summer ( $\chi^2 = 0.242$ ;  $df = 1$ ;  $P = 0.623$ ) or winter ( $\chi^2 = 0.597$ ;  $df = 1$ ;  $P = 0.440$ ).

### **Discussion**

This study is the first of its kind using CMR techniques to calculate and compare  $\phi$  estimates between rural and urban populations, between sexes, and across age classes of any New World parid (genera *Baeolophus* and *Poecile*). Other studies have estimated  $\phi$  for New World parids, but few have used a species-specific approach on a large population of color-banded individuals (tufted titmouse, Elder 1985; black-capped chickadee (*Poecile atricapillus*), Loery et al. 1997; tufted titmouse and Carolina chickadee, Doherty and Grubb 2002; black-capped chickadee, Schubert et al. 2008). Most  $\phi$  estimates for New World parids have been calculated from opportunistic banding station data and/or from small sample sizes (oak titmouse, Dixon 1956; tufted titmouse, Karr et al. 1990; Carolina chickadee and tufted titmouse, DeSante et al. 1998; bridled titmouse (*Baeolophus wollweberi*) Christman 2002). Additionally, this BCTI study incorporated the use of nestboxes, allowing for entire family groups to be uniquely marked and monitored which enabled the calculation of  $S$  for rural adults based on their spatial nearness to kin. Schubert et al. (2008) performed a detailed CMR multistate study

assessing how social rank influences  $S$  in the black-capped chickadee, yet no other multistate analysis has been performed on New World parids examining  $S$  based on family orientation.

Adult BCTI  $\phi$  estimates were more consistent and stable across seasons and between sexes in rural populations than urban populations, which is contradictory to other studies that hypothesize that urban environments provide more stability in predictable food sources and less intense weather extremes than nearby rural landscapes (Chamberlain et al. 2009, Lowry et al. 2013). Direct human disturbance in urban locations, such as noise pollution and increasing the abundance of non-native predators (Balogh et al. 2011, Murgui and Hedblom 2017), may counteract the seeming stability of urban environments. Recent work published by Phillips et al. (2018) estimated that although male white-crowned sparrows (*Zonotrichia leucophrys*) had greater  $\phi$  in urban locations, increased noise pollution negatively affected body conditions. More work is needed assessing urban BCTI  $\phi$  estimates and how sensitivity to direct human disturbance may be more influential than weather patterns or fragmented habitat.

As observed in other species, the degree of urbanization influences the survival of BCTI differently across age classes and between sexes. Adult BCTI have a greater  $\phi$  as the proportion of highly urbanized habitat increases within the home range, which is contradictory to other studies that indicate highly fragmented, less suitable habitat likely decreases  $\phi$  (Doherty and Grubb 2002, Lampila et al. 2006, Layton-Matthews et al. 2018). Yet, BCTI males (and their accompanying females) occupying sparse, patchy territories within urban landscapes may experience increased  $\phi$  based on their ability to display heightened aggression towards subordinate competitors, as did urban great tits

(*Parus major*) over rural conspecifics in an experimental study (Hardman and Dalesman 2018). However, urban females, particularly during the winter, had lower  $\phi$  estimates than rural females, which suggests the sexes are likely not influenced by the same weather and habitat variables. Additionally, juvenile BCTI have lower  $\phi$  estimates as the proportion of low urbanized habitat increases within the home range, possibly because young are more susceptible to window collisions and predation by feral cats and hawks that target birds visiting supplemental feeders (Dunn 1993, Balogh et al. 2011, Murgui and Hedblom 2017). Juvenile BCTI also may quickly disperse away from areas that contain a high proportion of low urbanized habitat, such as residential areas, because of an increased level of aggression in adult male conspecifics as they defend supplemental feeders and tended yards (Ydenberg 1984, Galbraith et al. 2017, Hardman and Dalesman 2018), resulting in low-biased estimates of  $\phi$ .

Adult male BCTI have consistently greater  $\phi$  estimates when compared to females in both urban and rural locations, which is consistent with other studies (Ekman 1990, Payevsky 2020). Though male BCTI consistently defend year-round territories and assist with feeding young in and out of the nest (Patten and Smith-Patten 2008), females overall may expend more energy building nests, incubating eggs, and feeding and corralling young fledglings, leading to lower survival rates (Liker and Szekly 2005, Harrison et al. 2013). Yet, studies by Clobert et al. (1988) and Hobek and Lebreton (1998) on great tits both consistently calculated greater  $\phi$  rates for females. In addition, it was hypothesized by Ekman and Askenmo (1986) that their observed low  $\phi$  estimate of adult male willow tits (*Poecile montanus*) was linked to the amount of energy and time

devoted to territorial defense. More research is needed on energy expenditure and individual fitness of BCTI adults during summer and winter seasons.

As in other passerines, in BCTI adult  $\phi$  is greater than juvenile  $\phi$  in both urban and rural locations. Juveniles generally have lower survival rates than adults (Ekman 1990, Koivula 1996, Marzluff et al. 2016, Cirule et al. 2017), although differences in  $\phi$  could be attributed to age-specific dispersal patterns (Loery et al. 1997, Pradel 1997). Most juvenile BCTI disperse from their natal home range before their first winter (Rylander et al. 2020) and subsequently are not detected near their home range during surveys, possibly leading to low-biased  $\phi$  estimates due to heterogeneity in detection rates (Szep 1999, Crespín et al. 2008, Chambert 2012, Roche et al. 2013). Regardless of detection bias, juvenile BCTI typically experienced the lowest  $\phi$  estimates directly after fledging (summer months), greater  $\phi$  into their first winter, and even greater  $\phi$  as they transitioned into AHYs. This is consistent with results calculated from other parids, such as the great tit and willow tit, where mortality is highest during the first year of life (Ekman 1984, Payevsky 2006).

Many studies have examined how kin-selection often increases survival through inclusive fitness benefits (Sklepko et al. 1997, Layton-Matthews et al. 2018). This study estimated a lower  $S$  for rural adult BCTI that reside near kin versus individuals not surrounded by kin, although closer examination of BCTI and how they form kin-structured neighborhoods illuminates these seemingly contradictory estimates. Once established, pairs of BCTI often remain in the same territory year after year, and male offspring frequently limit their dispersal to establish territories adjacent to their parents (Rylander et al. 2020). Because dominant adults eventually transition into a state where

they are surrounded by kin, they typically remain in kin-structured neighborhoods until death (Rylander pers. obs.). Once multiple generations of related BCTI reside near one another, it is unlikely that dominant adults emigrate to a new territory and transition out of kin-structured neighborhoods ( $\Psi$  from F to A:  $\beta = -0.91 \pm 0.21$ ). Therefore, adult BCTI that have reached a state surrounded by kin are likely benefiting through kin-selection (Ekman 2006, Layton-Matthews et al. 2018) or social rank (Hogstad 1987, Schubert et al. 2018), males more so than females due to male-biased philopatry, even if it is not reflected in  $S$  estimates.

Weather affects urban and rural BCTI  $\phi$  during winter more than summer, a pattern also observed in other parid species (Ekman 1984, Cirule et al. 2017). Tufted titmice in small woodland plots in Ohio have lower survival rates during winters with longer periods of snow cover, regardless if they have access to supplemental food (Doherty and Grubb 2002). Similarly, willow tits in Finland are less likely to survive long-lasting colder than average temperatures during the winter, yet survival increases among juveniles and adult males when presented with supplemental feeders during extreme weather (Lahti et al. 1998). Though snowfall is rare in central Texas, sleet and freezing rain occur regularly, which may lead to lower survival of rural juvenile BCTI that are not as efficient as adults in locating shelter. Dispersal, emigration, and transitory behavior triggered by extreme weather patterns, such as an increase in precipitation during winter months, may be low-biasing  $\phi$  estimates of rural juvenile BCTI that have left the area in search of resources instead of dying (Mortberg 2001, Coetzee et al. 2018). In contrast, urban BCTI that locate a steady food source may move less to forage during inclement weather during the winter (Roth and Vetter 2008), likely saving energy leading



to an increase in  $\phi$  estimations (Marzluff et al. 2016). Pakanen et al (2018) witnessed that during winter months, great tits had a greater site fidelity at feeding stations during colder intervals and less site fidelity during warmer intervals, particularly for juveniles. Thus, urban BCTI may ultimately have an advantage over rural BCTI during winter weather extremes if supplemental food is available (Grubb and Cimprich 1990, Chamberlain et al. 2009).

Overall, estimates for adult BCTI annual  $\phi$  (summer  $\phi$  \* winter  $\phi$ ) are lower than those calculated for other adult New World parids (Table 4.6). These lower estimates may be linked to the project's use of nestboxes (over mist nets and cage-traps at feeders) as well as calculating seasonal  $\phi$  and then deriving annual  $\phi$ . Confining capture efforts to BCTI that utilize nestboxes in the spring could lead to data loss on marked individuals that use natural cavities the following breeding season. Though efforts were made to resight all banded birds in known locations, it was easier to relocate individuals if they occupied nestboxes. Other studies have considered the physical act of capturing and handling birds to trigger emigration out of a study area, particularly for younger birds (Galbraith et al. 2017). Doherty and Grubb (2002) hypothesized that capturing juvenile Carolina chickadees using cage traps at feeders may have influenced emigration away from their study plot. Because young BCTI were banded as nestlings, his study likely did not influence pre-mature natal dispersal as most juveniles instinctively disperse out of their parents' territory during the first couple of months post-fledging (Rylander et al. 2020). In concordance, many adult BCTI consecutively nested in the same nestbox for many years, indicating that capture and banding adults as they fed nestlings did not negatively affect reuse of boxes.

This study elucidates how urban and rural environments influence BCTI  $\phi$  among different age classes and sexes during different seasons, which is important step in determining how survival, when coupled with productivity and recruitment, influences BCTI population growth and persistence. Research conducted on willow tits in Finland detected that whereas adult  $\phi$  was stable, local recruitment and immigration rates were not consistent and were responding to the different environmental covariates, meaning overall population growth was likely to decline (Lampila et al. 2006). A meta-analysis conducted by Chamberlain et al. (2009) on several avian species reflected the trends in Lampila et al. (2006). Given the relatively high mortality rates of juvenile BCTI, it is likely that adult  $\phi$  estimates need to remain high for populations to stabilize (Saether and Bakke 2000, Caswell 2006) since immigration into new populations by BCTI adults is not probable due to documented high annual site-fidelity (Rylander et al. 2020). I recommend that future studies on population demographics of BCTI focus on reproductive success, fecundity, and nesting success rates among urban and rural environments.

**Table 4.1** The number of black-crested titmouse (*Baeolophus atricristatus*) adults and nestlings that were banded across four locations in San Marcos, Texas, 2013–2019. Locations spanned from rural habitat (Freeman) to varying degrees of urbanization (Parks < Residential < Campus).

<b>Year</b>	<b>Rural</b>		<b>Urban</b>					
	<b>Freeman</b>		<b>Campus</b>		<b>Parks</b>		<b>Residential</b>	
	<u>Nestlings</u>	<u>Adults</u>	<u>Nestlings</u>	<u>Adults</u>	<u>Nestlings</u>	<u>Adults</u>	<u>Nestlings</u>	<u>Adults</u>
<b>2013</b>	16	6	---	---	---	---	---	---
<b>2014</b>	111	21	---	---	---	---	---	---
<b>2015</b>	87	22	---	---	---	---	---	---
<b>2016</b>	89	17	---	---	---	---	---	---
<b>2017</b>	89	9	23	7	23	9	---	---
<b>2018</b>	163	51	47	5	37	7	90	28
<b>2019</b>	205	32	49	6	45	8	70	15
<b>Total</b>	744	174	119	18	105	24	160	43
<b>Total Rural = 918</b>			<b>Total Urban = 469</b>			<b>Grand Total = 1387</b>		

**Table 4.2** Beta estimates ( $\beta \pm \text{SE}$ ) and 95% confidence intervals (CI) from top model  $\phi_{\text{age} + \text{precip} * \text{season}}$ ,  $p_{\text{effort}}$  for rural hatch year (HY) and after hatch year (AHY) black-crested titmice ( $n = 731$ ) (*Baeolophus atricristatus*) in San Marcos, Texas, 2013–2020. Estimated parameters are  $\phi$  = apparent survival and  $p$  = detection.

Parameter	Covariate	$\beta \pm \text{SE}$	95% CI
$\phi$	(Intercept)	$-2.50 \pm 0.14$	$-2.78 - -2.22$
	Age [AHY]	$2.04 \pm 0.27$	$1.52 - 2.57$
	Precip	$0.13 \pm 0.11$	$-0.07 - 0.34$
	Season[Winter]	$0.68 \pm 0.31$	$0.08 - 1.28$
	Precip:Season[Winter]	$-1.39 \pm 0.51$	$-2.39 - -0.39$
$p$	(Intercept)	$1.96 \pm 0.27$	$1.43 - 2.49$
	Effort	$0.51 \pm 0.26$	$0.01 - 1.01$

**Table 4.3** Beta estimates ( $\beta \pm \text{SE}$ ) and 95% confidence intervals (CI) from top model  $\phi_{\text{sex} + \text{season} + \text{high urb.}}$ ,  $p_{\text{effort}}$  for urban after hatch year (AHY) black-crested titmice (*Baeolophus atricristatus*) in San Marcos, Texas, 2017–2020 ( $n = 97$ ). Estimated parameters are  $\phi$  = apparent survival and  $p$  = detection.

Parameter	Covariate	$\beta \pm \text{SE}$	95% CI
$\phi$	(Intercept)	$-0.18 \pm 0.39$	$-0.94 - 0.57$
	Sex [Male]	$0.92 \pm 0.43$	$0.07 - 1.77$
	% High Urban	$0.50 \pm 0.21$	$0.09 - 0.91$
	Season [Winter]	$-1.20 \pm 0.55$	$-2.28 - -0.13$
$p$	(Intercept)	$-0.54 \pm 1.05$	$-2.59 - 1.52$
	Effort	$0.28 \pm 0.14$	$0.01 - 0.56$

**Table 4.4** Beta estimates ( $\beta \pm \text{SE}$ ) and 95% confidence intervals (CI) from top model  $\phi_{\text{age} + \text{season} + \text{low urb.}}$ ,  $p_{\text{season}}$  for urban hatch year (HY) and after hatch year AHY black-crested titmice (*Baeolophus atricristatus*) in San Marcos, Texas, 2017 – 2020 ( $n = 334$ ). Estimated parameters are  $\phi$  = apparent survival and  $p$  = detection.

Parameter	Covariate	$\beta \pm \text{SE}$	95% CI
$\phi$	(Intercept)	$-2.64 \pm 0.32$	$-3.26 - -2.01$
	Age [AHY]	$1.42 \pm 0.78$	$-0.12 - 2.96$
	% Low Urban	$-0.67 \pm 0.18$	$-1.02 - -0.32$
	Season [Winter]	$1.94 \pm 1.10$	$-0.21 - 4.10$
$p$	(Intercept)	$-0.72 \pm 0.41$	$-1.51 - 0.08$
	Season [Winter]	$1.31 \pm 0.50$	$0.32 - 2.30$

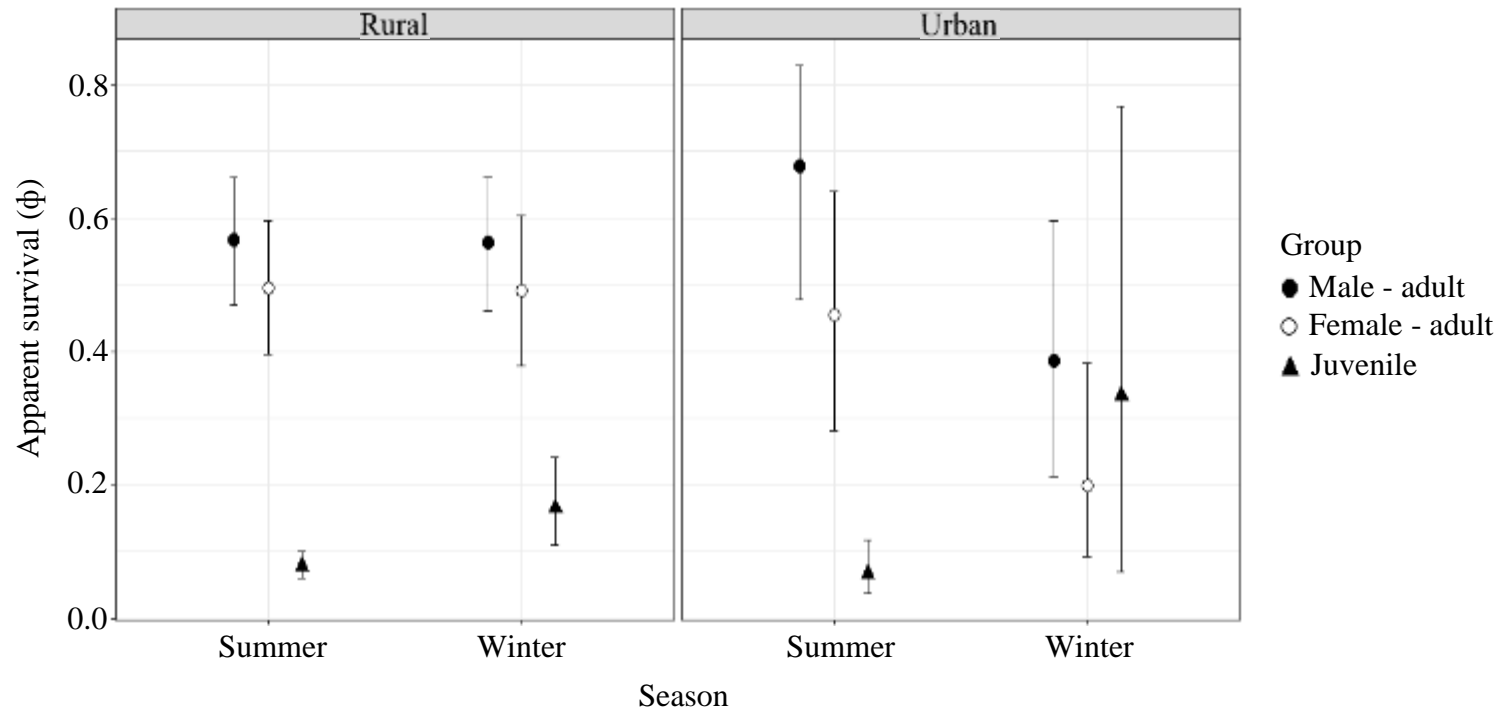
**Table 4.5** Beta estimates ( $\beta \pm \text{SE}$ ) and 95% confidence intervals (CI) from top model  $S_{\text{stratum} + \text{sex}}, p_{\text{season}}, \Psi_{-1 + \text{stratum:tostratum}}$  for rural after hatch year AHY black-crested titmice (*Baeolophus atricristatus*) in San Marcos, Texas, 2017–2020 ( $n = 174$ ). Estimated parameters are  $S$  = apparent survival,  $p$  = detection, and  $\Psi$  = state transition rate. Stratum F indicates adults occupying territories near kin (< 400 m) and stratum A indicates adults occupying territories not near kin (>400 m).

Parameter	Covariate	$\beta \pm \text{SE}$	95% CI
$S$	(Intercept)	$0.02 \pm 0.20$	$-0.38 - 0.42$
	Sex [Male]	$0.63 \pm 0.25$	$0.15 - 1.11$
	Stratum [F]	$-0.57 \pm 0.28$	$-1.12 - -0.03$
$p$	(Intercept)	$2.85 \pm 0.50$	$1.87 - 3.83$
	Season [Winter]	$-1.79 \pm 0.52$	$-2.81 - -0.77$
$\Psi$	Stratum F to A	$-0.91 \pm 0.21$	$-1.33 - -0.50$
	Stratum A to F	$0.57 \pm 0.20$	$0.19 - 0.96$

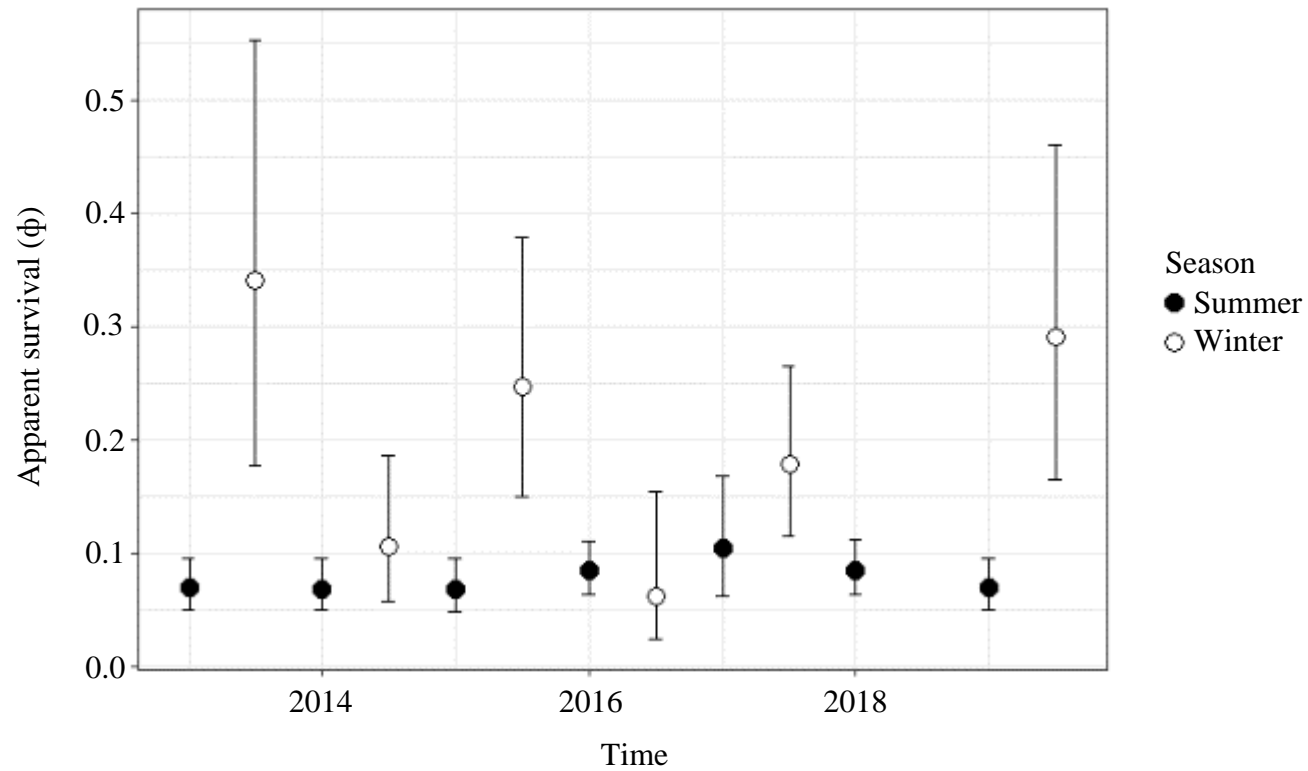
**Table 4.6** Summary table of  $\phi$  estimates from various capture-mark-recapture studies on New World members of the Paridae family.

Species	Study	$\phi$ Estimate
Tufted titmouse	Nichols et al. 1981	0.53
	Elder 1985	0.62
	Karr et al. 1990	0.54
	DeSante et al. 1998	0.55 – 0.74
	Doherty and Grubb 2002	0.32
	Wolfe et a 2013	0.45
Oak titmouse	Dixon 1956	0.76
Carolina chickadee	Dixon 1963	0.56
	Karr et al. 1990	0.60
	DeSante et al. 1998	0.43 – 0.50
Black-crested titmouse	Rylander 2021	0.09 – 0.32

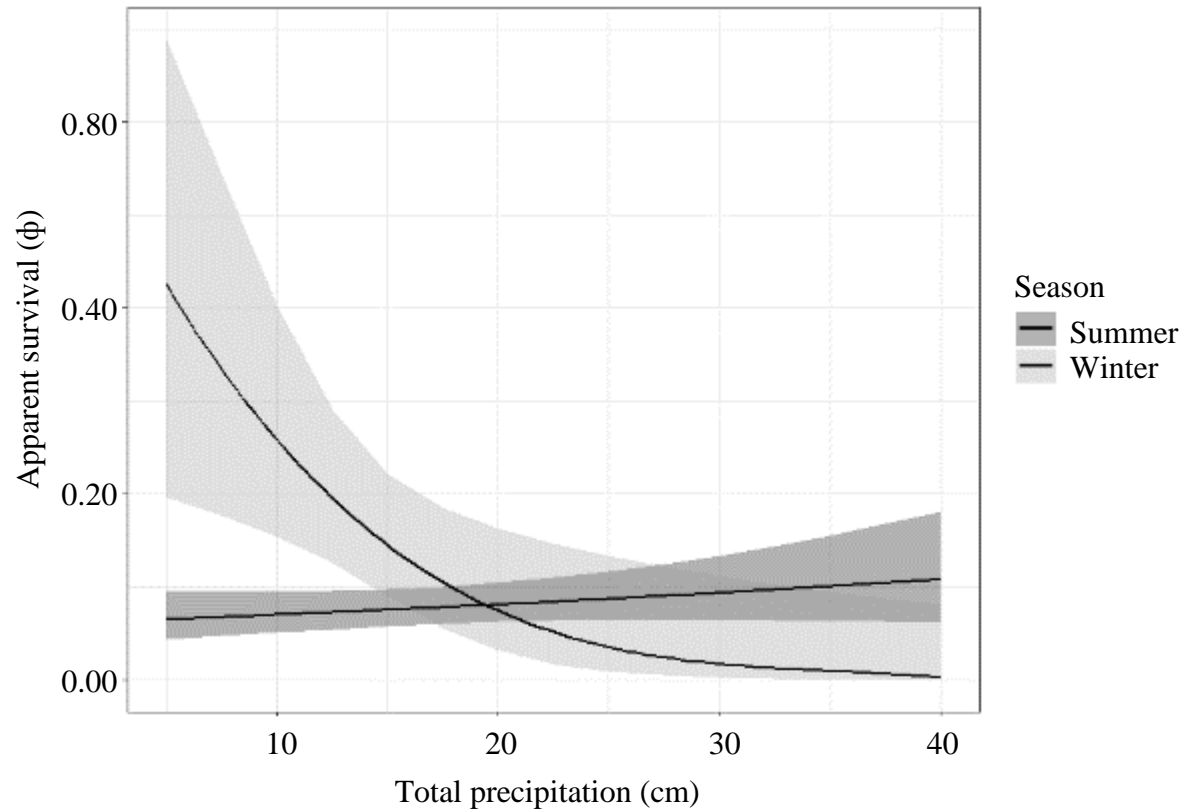




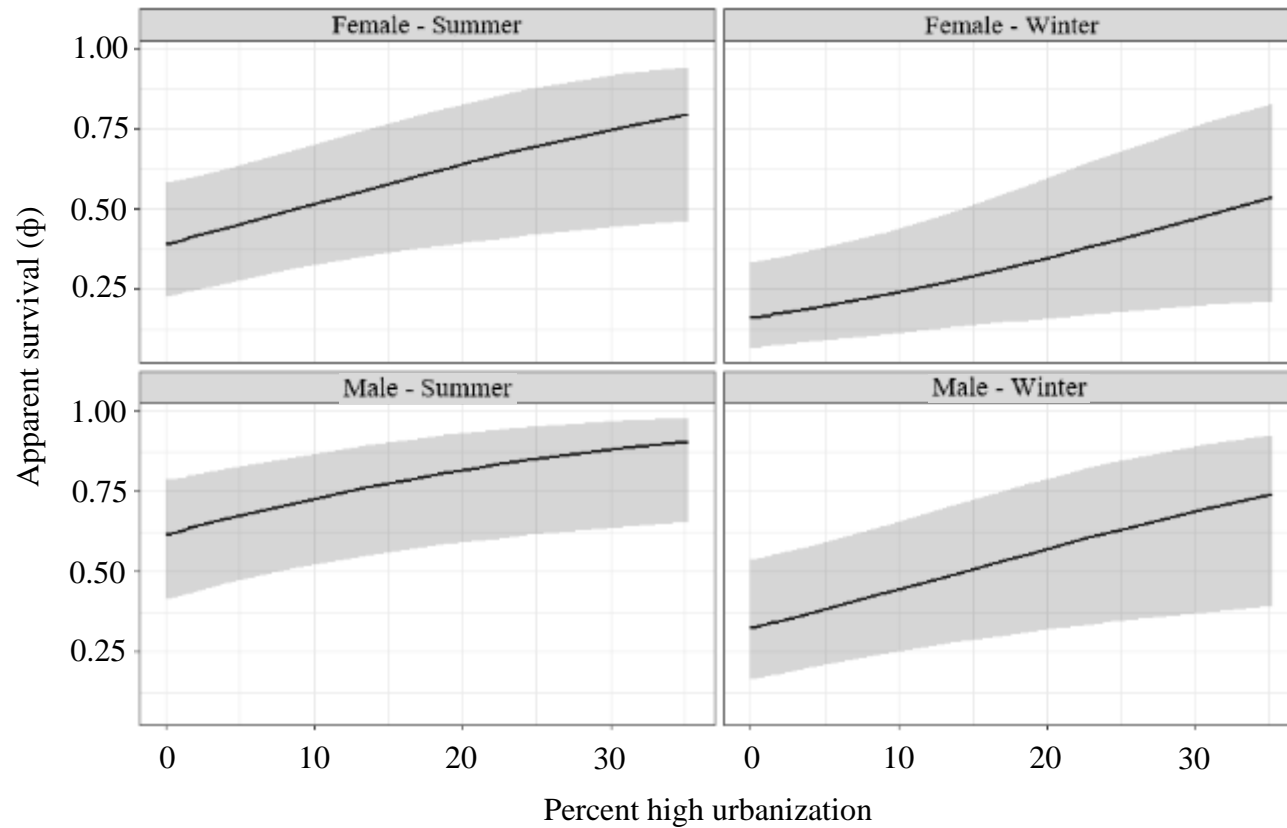
**Figure 4.1** Apparent survival ( $\phi$ ) estimates (with 95% confidence intervals) for the black-crested titmouse (*Baeolophus atricristatus*) ( $n = 1336$ ) in San Marcos, Texas, 2013–2020. Estimates are categorized into season (Summer/Winter), location (Rural/Urban), sex, and age group (adult/juvenile).



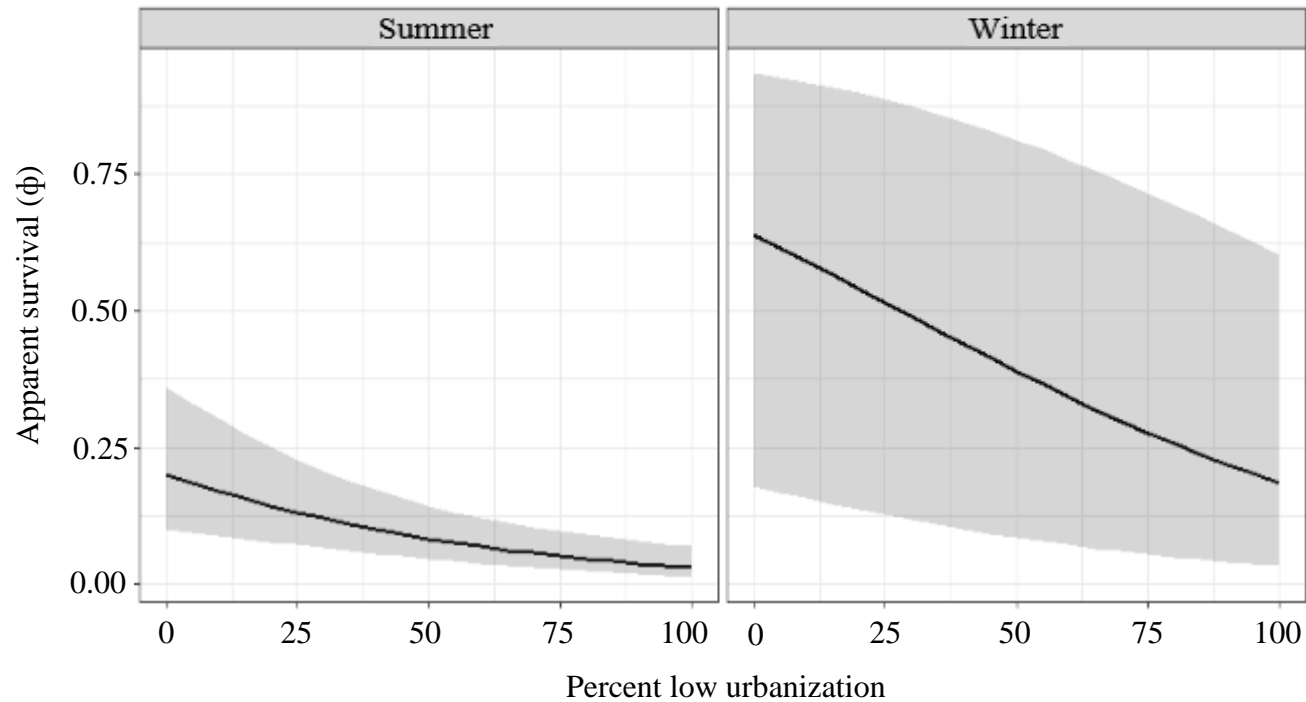
**Figure 4.2** Rural hatch year (HY) black-crested titmouse (*Baeolophus atricristatus*) apparent survival ( $\phi$ ) estimates (with 95% confidence intervals) as calculated using top  $\phi_{\text{age} + \text{precip} * \text{season}, p_{\text{effort}}}$  for the individuals ( $n = 731$ ) sampled in San Marcos, Texas, 2013–2020.



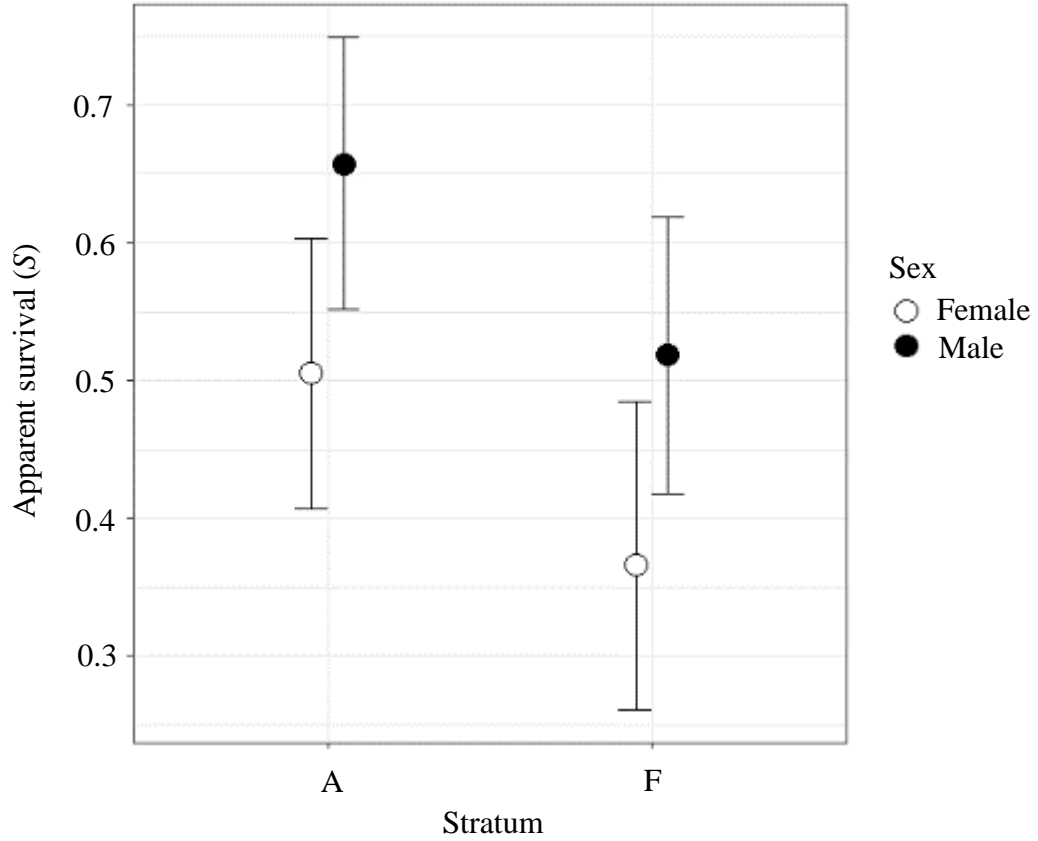
**Figure 4.3** Rural hatch year (HY) black-crested titmouse (*Baeolophus atricristatus*) apparent survival ( $\phi$ ) estimates (with shaded 95% confidence intervals) as influenced by seasonal precipitation totals (cm). Apparent survival estimates were calculated using top  $\phi$  age + precip\*season,  $p$  effort for the individuals sampled ( $n = 334$ ) in San Marcos, Texas between 2013 – 2020.



**Figure 4.4** Urban after hatch year (AHY) apparent survival ( $\phi$ ) estimates (with shaded 95% confidence intervals) as influenced by season (Summer/Winter), sex, and the percentage of high urbanization habitat located within black-crested titmouse (*Baeolophus atricristatus*) home ranges. Apparent survival estimates were calculated using top model  $\phi_{\text{sex} + \text{season} + \text{high urb.}} p_{\text{effort}}$  for the individuals sampled ( $n = 97$ ) in San Marcos, Texas between 2017 – 2020.



**Figure 4.5** Urban hatch year (HY) apparent survival ( $\phi$ ) estimates (with shaded 95% confidence intervals) as influenced by season (Summer/Winter) and the percentage of low urbanization habitat located within black-crested titmouse (*Baeolophus atricristatus*) home ranges. Apparent survival estimates were calculated using top model  $\phi_{\text{age} + \text{season} + \text{low urb}}, p_{\text{season}}$  for the individuals sampled ( $n = 334$ ) in San Marcos, Texas between 2017 – 2020.



**Figure 4.6** Multistate apparent survival ( $S$ ) estimates and their 95% confidence intervals calculated using top model  $S_{\text{stratum} + \text{sex}}, p_{\text{season}}, \Psi_{-1} + \text{stratum:tostratum}$  for rural male and female after hatch year (AHY) black-crested titmice (*Baeolophus atricristatus*) in San Marcos, Texas, 2013–2020 ( $n = 174$ ). Stratum F indicates adults occupying territories near kin ( $< 400$  m) and Stratum A indicates adults occupying territories not near kin ( $> 400$  m).

**Supplementary Table 4.1** QAIC<sub>c</sub> table comparing candidate models estimating rural after hatch year (AHY) apparent survival ( $\phi$ ) and detection ( $p$ ) of the black-crested titmouse (*Baeolophus atricristatus*) in San Marcos, Texas (2013 – 2020) ( $n = 174$ ).

Model	$\Delta$ QAIC <sub>c</sub>	$w_i$	$K_i$	QDev
$\phi_{\text{sex}, p_{\text{season}}}$	0.00	0.3358	4	230.82
$\phi_{\cdot, p_{\text{season}}}$	0.82	0.2229	3	233.68
$\phi_{\text{sex} + \text{season}, p_{\text{season}}}$	1.99	0.1244	5	230.75
$\phi_{\text{wood} + \text{sex}, p_{\text{season}}}$	2.05	0.1205	5	659.91
$\phi_{\text{wood}, p_{\text{season}}}$	2.86	0.0804	4	662.77
$\phi_{\text{sex} + \text{extreme days} * \text{season}, p_{\text{season}}}$	4.38	0.0376	7	229.01
$\phi_{\text{sex} + \text{precip} * \text{season}, p_{\text{season}}}$	4.89	0.0291	7	229.52
$\phi_{\text{extreme days} * \text{season}, p_{\text{season}}}$	5.15	0.0256	6	231.85
$\phi_{\text{precip} * \text{season}, p_{\text{season}}}$	5.73	0.0191	6	232.44
$\phi_{\cdot, p_{\cdot}}$	10.02	0.0022	2	244.91
$\phi_{\text{sex}, p_{\text{effort}}}$	10.39	0.0019	4	241.20
$\phi_{\text{Time}, p_{\text{Time}}}$	13.02	0.0005	4	243.84

**Supplementary Table 4.2** AIC<sub>C</sub> table comparing candidate models estimating rural hatch year (HY) and after hatch year (AHY) apparent survival ( $\phi$ ) and detection ( $p$ ) of the black-crested titmouse (*Baeolophus atricristatus*) in San Marcos, Texas (2013 – 2020) ( $n = 731$ ).

Model	$\Delta$ AIC <sub>C</sub>	$w_i$	$K_i$	Dev
$\phi$ age + precip*season, $p$ effort	0.00	0.8681	7	126.77
$\phi$ age + season, $p$ effort	4.32	0.0999	5	135.15
$\phi$ age + total precip*season, $p$ effort	6.89	0.0277	7	133.66
$\phi$ age, $p$ effort	11.27	0.0031	4	144.11
$\phi$ age + wood, $p$ effort	13.09	0.0012	5	1195.84
$\phi$ precip*season, $p$ season	56.83	0.0000	6	185.63
$\phi$ season, $p$ effort	59.74	0.0000	4	192.59
$\phi$ total precip*season, $p$ season	64.12	0.0000	6	192.92
$\Phi$ Time, $p$ Time	73.20	0.0000	4	206.04
$\phi$ ., $p$ .	74.49	0.0000	2	211.37
$\phi$ wood, $p$ effort	74.87	0.0000	4	1259.64



**Supplementary Table 4.3** AIC<sub>C</sub> table comparing candidate models estimating urban after hatch year (AHY) apparent survival ( $\phi$ ) and detection ( $p$ ) of the black-crested titmouse (*Baeolophus atricristatus*) in San Marcos, Texas (2017 – 2020) ( $n = 97$ ).

Model	$\Delta \text{QAIC}_C$	$w_i$	$K_i$	QDev
$\phi$ sex + season + high urb, $p$ effort	0.00	0.3675	6	287.94
$\phi$ sex + extreme days*season + high urb, $p$ effort	0.10	0.3503	8	283.72
$\phi$ sex + precip lag*season + high urb, $p$ effort	1.20	0.2013	8	284.83
$\phi$ high urb, $p$ effort	5.01	0.0301	4	297.17
$\phi$ season, $p$ effort	6.63	0.0133	4	52.12
$\phi$ sex, $p$ effort	6.68	0.0130	4	52.17
$\phi$ precip lag*season, $p$ effort	6.84	0.0120	6	48.11
$\phi$ Time, $p$ Time	8.30	0.0058	4	53.79
$\phi$ extreme days*season, $p$ effort	8.64	0.0049	6	49.90
$\phi$ ., $p$ .	10.59	0.0018	2	60.22

**Supplementary Table 4.4** QAIC<sub>C</sub> table comparing candidate models estimating urban hatch year (HY) and after hatch year (AHY) apparent survival ( $\phi$ ) and detection ( $p$ ) of the black-crested titmouse (*Baeolophus atricristatus*) in San Marcos, Texas (2017 – 2020) ( $n = 334$ ).

Model	$\Delta$ QAIC <sub>C</sub>	$w_i$	$K_i$	QDev
$\phi$ age + low urb + season, $p$ season	0.00	0.6659	6	450.70
$\phi$ age + low urb + precip*season, $p$ season	3.42	0.1202	8	449.97
$\phi$ age + low urb, $p$ effort	3.49	0.1161	5	456.25
$\phi$ age + wood + season, $p$ effort	6.01	0.0330	6	456.71
$\phi$ age + low urb + total precip*season, $p$ effort	6.79	0.0223	8	453.35
$\phi$ wood, $p$ season	6.89	0.0212	4	461.70
$\phi$ low urb, $p$ effort	7.10	0.0191	4	461.91
$\phi$ age, $p$ season	12.71	0.0012	4	32.26
$\phi$ age + precip*season, $p$ season	14.39	0.0005	7	27.76
$\phi$ age + total precip*season, $p$ effort	16.51	0.0002	7	29.88
$\phi$ precip*season, $p$ season	16.61	0.0002	6	32.05
$\phi$ total precip*season, $p$ season	16.63	0.0002	6	32.07
$\phi$ ., $p$ .	19.37	0.0000	2	42.98
$\phi$ season, $p$ effort	20.68	0.0000	4	40.23
$\phi$ Time, $p$ Time	23.38	0.0000	4	42.93

**Supplementary Table 4.5** QAIC<sub>C</sub> table comparing candidate models estimating rural after hatch year (AHY) apparent survival ( $S$ ), state transition rate ( $\Psi$ ), and detection ( $p$ ) of the black-crested titmouse (*Baeolophus atricristatus*) in San Marcos, Texas (2013 – 2020) ( $n = 174$ ).

Model	$\Delta \text{QAIC}_C$	$w_i$	$K_i$	QDev
$S_{\text{stratum} + \text{sex}, p_{\text{season}}, \Psi_{-1 + \text{stratum:tostratum}}}$	0.00	0.7321	7	468.05
$S_{\text{stratum} + \text{sex} + \text{season}, p_{\text{season}}, \Psi_{-1 + \text{stratum:tostratum}}}$	2.03	0.2654	8	468.00
$S_{\text{stratum} + \text{sex} + \text{season}, p_{\text{effort}}, \Psi_{-1 + \text{stratum:tostratum}}}$	11.61	0.0022	8	477.58
$S_{\text{stratum} + \text{season}, p_{\text{effort}}, \Psi_{-1 + \text{stratum:tostratum}}}$	15.48	0.0003	7	483.53
$S_{\text{stratum} + \text{season}, p_{\text{season}}, \Psi_{\text{sex} + \text{season}}}$	30.79	0.0000	8	496.76
$S_{\text{stratum} + \text{sex} + \text{season}, p_{\text{effort}}, \Psi_{\text{season}}}$	34.50	0.0000	8	500.47
$S_{\text{stratum} + \text{sex} + \text{season}, p_{\text{effort}}, \Psi_{\text{sex} + \text{season}}}$	36.11	0.0000	9	499.99
$S_{\text{season}, p_{\text{effort}}, \Psi_{\text{season}}}$	39.35	0.0000	6	509.47
$S_{\text{stratum}, p_{\cdot}, \Psi_{\text{season}}}$	42.84	0.0000	5	515.02
$S_{\text{sex}, p_{\text{effort}}, \Psi_{\text{sex}}}$	43.69	0.0000	6	513.81
$S_{\cdot, p_{\text{effort}}, \Psi_{\cdot}}$	44.94	0.0000	4	519.17
$S_{\text{sex} + \text{stratum}, p_{\cdot}, \Psi_{\text{sex}}}$	47.68	0.0000	6	517.80
$S_{\cdot, p_{\cdot}, \Psi_{\cdot}}$	49.20	0.0000	3	525.46

**Supplemental Table 4.6** Model averaged real parameter estimates ( $\phi$  apparent survival and  $p$  detection) for rural after hatch year (AHY) black-crested titmice (*Baeolophus atricristatus*) in San Marcos, Texas (2013 – 2020) ( $n = 174$ ).

$\phi$ Male			$\phi$ Female		$p$ (all)	
Season	Estimate $\pm$ SE	95% CI	Estimate $\pm$ SE	95% CI	Estimate $\pm$ SE	95% CI
Summer	0.568 $\pm$ 0.049	0.470 – 0.660	0.495 $\pm$ 0.052	0.395 – 0.596	0.873 $\pm$ 0.039	0.775 – 0.932
Winter	0.564 $\pm$ 0.052	0.460 – 0.661	0.491 $\pm$ 0.058	0.379 – 0.604	0.687 $\pm$ 0.041	0.602 – 0.761

**Supplemental Table 4.7** Real parameter estimates ( $\phi$  apparent survival and  $p$  detection) using top model  $\phi_{\text{age} + \text{precip} * \text{season}}, p_{\text{effort}}$  for rural hatch year (HY) and after hatch year (AHY) black-crested titmice (*Baeolophus atricristatus*) in San Marcos, Texas (2013 – 2020) ( $n = 731$ ).

Covariates			$\phi$ HY		$\phi$ AHY		$p$ (all)	
Time	Precip*Season ( $\phi$ )	Effort ( $p$ )	Estimate $\pm$ SE	95% CI	Estimate $\pm$ SE	95% CI	Estimate $\pm$ SE	95% CI
2013	97.54	12	0.070 $\pm$ 0.011	(0.051 – 0.096)	---	---	0.920 $\pm$ 0.032	(0.832 – 0.964)
2013.5	74.93	11	0.341 $\pm$ 0.100	(0.178 – 0.553)	---	---	0.909 $\pm$ 0.031	(0.827 – 0.955)
2014	91.44	8	0.069 $\pm$ 0.012	(0.050 – 0.096)	0.365 $\pm$ 0.064	(0.251 – 0.496)	0.870 $\pm$ 0.030	(0.800 – 0.918)
2014.5	176.02	6	0.106 $\pm$ 0.032	(0.058 – 0.187)	0.479 $\pm$ 0.094	(0.305 – 0.658)	0.836 $\pm$ 0.035	(0.755 – 0.894)
2015	83.31	4	0.068 $\pm$ 0.012	(0.049 – 0.096)	0.362 $\pm$ 0.064	(0.247 – 0.495)	0.795 $\pm$ 0.052	(0.676 – 0.879)
2015.5	106.43	3	0.246 $\pm$ 0.059	(0.150 – 0.378)	0.716 $\pm$ 0.075	(0.550 – 0.839)	0.773 $\pm$ 0.064	(0.625 – 0.874)
2016	230.63	---	0.085 $\pm$ 0.012	(0.064 – 0.111)	0.416 $\pm$ 0.061	(0.303 – 0.539)	---	---
2016.5	216.41	---	0.062 $\pm$ 0.030	(0.024 – 0.154)	0.338 $\pm$ 0.120	(0.151 – 0.594)	---	---
2017	328.27	---	0.105 $\pm$ 0.026	(0.063 – 0.169)	0.474 $\pm$ 0.085	(0.316 – 0.638)	---	---
2017.5	134.62	---	0.178 $\pm$ 0.038	(0.116 – 0.265)	0.626 $\pm$ 0.075	(0.473 – 0.758)	---	---
2018	238.25	---	0.085 $\pm$ 0.012	(0.064 – 0.113)	0.419 $\pm$ 0.062	(0.305 – 0.543)	---	---
2019	97.79	---	0.070 $\pm$ 0.011	(0.051 – 0.096)	0.367 $\pm$ 0.063	(0.254 – 0.497)	---	---
2019.5	90.93	---	0.291 $\pm$ 0.077	(0.165 – 0.460)	0.760 $\pm$ 0.077	(0.579 – 0.879)	---	---
2020	146.56	---	---	---	---	---	---	---

**Supplemental Table 4.8** Real parameter estimates ( $\phi$  apparent survival) using the second top model  $\phi_{\text{age} + \text{season}, p_{\text{effort}}}$  for rural hatch year (HY) and after hatch year (AHY) black-crested titmice (*Baeolophus atricristatus*) in San Marcos, Texas (2013 – 2020) ( $n = 731$ ). The second top model was used to calculate simplified  $\phi$  estimates that could be directly compared to urban HY  $\phi$  estimates.

Age ( $\phi$ )	Season ( $\phi$ )	Estimate $\pm$ SE	95% CI
HY	Summer	$0.078 \pm 0.010$	$0.060 - 0.100$
	Winter	$0.165 \pm 0.033$	$0.109 - 0.241$
AHY	Summer	$0.400 \pm 0.058$	$0.292 - 0.517$
	Winter	$0.608 \pm 0.072$	$0.462 - 0.737$

**Supplemental Table 4.9** Real parameter estimates ( $\phi$  apparent survival and  $p$  detection) using top model  $\phi_{\text{sex} + \text{season} + \text{high urb.}}$ ,  $p_{\text{effort}}$  for urban after hatch year (AHY) black-crested titmice (*Baeolophus atricristatus*) in San Marcos, Texas (2017 – 2020) ( $n = 97$ ). Percentage high urbanization not shown in the table because it's an individual-level covariate.

Covariate		Male $\phi$		Female $\phi$		$p$ (all)	
Season ( $\phi$ )	Effort ( $p$ )	Estimate $\pm$ SE	95% CI	Estimate $\pm$ SE	95% CI	Estimate $\pm$ SE	95% CI
Summer	10	0.677 $\pm$ 0.093	0.477 – 0.829	0.455 $\pm$ 0.095	0.282 – 0.639	0.907 $\pm$ 0.045	0.774 – 0.965
Winter	6	0.386 $\pm$ 0.103	0.212 – 0.596	0.200 $\pm$ 0.074	0.092 – 0.382	0.848 $\pm$ 0.045	0.738 – 0.917
---	6	---	---	---	---	0.760 $\pm$ 0.063	0.617 – 0.862
---	4	---	---	---	---	0.644 $\pm$ 0.122	0.389 – 0.837

**Supplemental Table 4.10** Real parameter estimates ( $\phi$  apparent survival and  $p$  detection) using top model  $\phi_{\text{age} + \text{low urb} + \text{season}}$ ,  $p_{\text{season}}$  for urban hatch year (HY) and after hatch year (AHY) black-crested titmice (*Baeolophus atricristatus*) in San Marcos, Texas (2017 – 2020) ( $n = 334$ ). Percentage low urbanization not shown in the table because it’s an individual-level covariate.

Covariates		$\phi$		$p$ (all)	
Age ( $\phi$ )	Season ( $\phi$ & $p$ )	Estimate $\pm$ SE	95% CI	Estimate $\pm$ SE	95% CI
HY	Summer	0.067 $\pm$ 0.020	0.037 – 0.118	0.644 $\pm$ 0.081	0.475 – 0.783
	Winter	0.333 $\pm$ 0.215	0.070 – 0.768	0.328 $\pm$ 0.089	0.180 – 0.519
AHY	Summer	0.229 $\pm$ 0.140	0.059 – 0.585	---	---
	Winter	0.674 $\pm$ 0.183	0.288 – 0.913	---	---



**Supplemental Table 4.11** Real parameter estimates ( $S$  apparent survival,  $\Psi$  state transition rate, and  $p$  detection) from top model  $S$  stratum + sex,  $p$  season,  $\Psi$  -1 + stratum:tostratum for rural after hatch year (AHY) black-crested titmice (*Baeolophus atricristatus*) in San Marcos, Texas (2013 – 2020) ( $n = 174$ ).

Covariates				$S$		$p$		$\Psi$	
Sex ( $S$ )	Stratum ( $S$ )	Season ( $p$ )	Stratum to stratum ( $\Psi$ )	Estimate $\pm$ SE	95% CI	Estimate $\pm$ SE	95% CI	Estimate $\pm$ SE	95% CI
Male	A	Summer	A to F	0.657 $\pm$ 0.051	0.552 – 0.749	0.945 $\pm$ 0.026	0.867 – 0.979	0.639 $\pm$ 0.046	0.546 – 0.723
	F	Winter	F to A	0.519 $\pm$ 0.052	0.418 – 0.619	0.743 $\pm$ 0.036	0.666 – 0.807	0.287 $\pm$ 0.043	0.210 – 0.378
Female	A	---	---	0.505 $\pm$ 0.051	0.407 – 0.603	---	---	---	---
	F	---	---	0.366 $\pm$ 0.058	0.261 – 0.485	---	---	---	---

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**V. LIVING AT HOME: ASSESSING INCLUSIVE FITNESS BENEFITS  
ASSOCIATED WITH RESOURCE SHARING IN A FAMILIAL FLOCKING  
SONGBIRD**

**Abstract**

Kin-selection theory proposes that the survival of related family members increases indirect fitness of individuals through the passing of shared genes to future generations, even at the cost of decreasing their own personal survival. However, in social avian populations that often congregate with extended relatives, there is debate as to how far kin-selection is favored when the proportion of shared genes decreases. Thus, the ability to study an avian population of both closely and distantly related individuals could elucidate what inclusive fitness benefits are gained by individuals participating in various social flocks. To understand the benefits (or lack thereof) for members that engage in social flocks with relatives, particularly regarding resource sharing, I studied a passive integrated transponder (PIT) tagged population of black-crested titmice (*Baeolophus atricristatus*, BCTI), a kin-structured songbird observed to frequently interact with close (~50% shared genes) and extended (<50% shared genes) relatives. I captured and PIT-tagged BCTI at the Freeman Center in San Marcos, Texas, during the spring of 2018 and 2019, and I installed and deployed 12 radio frequency identification (RFID) feeder stations between January 2019–April 2020. Of the 451 PIT-tagged BCTI, only 61 individuals were recorded at feeding stations, with these individuals comprising 24 distinct family groups (male, female, and offspring) and 16 lineages (extended relatives). Among the 61 tagged BCTI, there were 26,428 reads recorded during 9,684 unique feeding bouts. The observed proportion of feeding bouts where extended family

shared resources was lower than the expected proportion of feeding bouts based on the number of related members present at a feeder ( $n = 1,344$ ;  $\chi^2 = 76.69$ ;  $df = 1$ ;  $p < 0.01$ ). However, the duration of feeding bouts when extended kin were present was significantly longer than feeding bouts when unrelated individuals were present ( $n = 1,298$ ;  $\beta = -0.02 \pm 0.01$ ;  $t = -2.25$ ; 95% CI =  $[-0.04, -0.01]$ ;  $p = 0.02$ ). Moreover, the observed proportion of nepotistic feeding bouts (father or mother with an offspring, close relatives) was not different than the expected proportion of nepotistic feeding bouts ( $n = 775$ ;  $\chi^2 = 0.01$ ;  $df = 1$ ;  $p < 0.95$ ). Yet, the duration of nepotistic feeding bouts trended positively, with feeding bouts of nepotistic pairs lasting longer than those between unrelated individuals ( $n = 472$ ;  $\beta = -0.04 \pm 0.02$ ;  $t = -1.79$ ; 95% CI =  $[-0.09, -0.01]$ ;  $p = 0.07$ ). Therefore, results from this study suggest “quality over quantity” (time over frequency) when sharing resources may increase inclusive fitness of individuals participating in foraging bouts together.

## Introduction

Social flocking is a common behavior of avifauna, where flock membership can vary between several individuals to hundreds of thousands of birds per group depending on time of year, biotic and abiotic factors, and species (Pulliam 1973, Wey et al. 2008, Silk et al. 2014). Large social flocks are common during migration and at wintering roosts (Russell and Gauthaux 1999), whereas smaller social flocks typically are associated with resource acquisition, mate attraction through lekking, and predator mobbing (Gill 2007). While it may be difficult to decipher the potential fitness benefits for each individual participating in flocking behavior, it is of interest to understand the



function of the flock as a whole and why natural selection favors group formation (Lima 1995, Marzluff et al. 1996, Napper and Hatchwell 2016).

A specific field of study on bird sociality involves kin-structured flocking dynamics, which involves a male and female accompanied by offspring for an extended period after the breeding season (Condee 1970, Cockburn 2006). Juveniles in this situation either: 1) delay their dispersal and provide no alloparental care to the family group; 2) delay their dispersal and participate in cooperative breeding; or 3) limit their dispersal and establish a territory adjacent to their parents, ultimately forming kin-structured neighborhoods (Ekman 2006, Hatchwell 2009, Rylander et al. 2020).

Depending upon the species, the fate of retained offspring may be obligate or facultative in nature, where environmental or social factors influence the family flocking structure the following year (Emlen 1995, Cockburn 2006). When resources are scarce or when the surrounding habitat matrix is saturated with dominant conspecifics, juveniles may alter their dispersal behavior until an opportunity to become independent arises (Komdeur 1992, Emlen 1995).

Species that form kin-structured flocks exhibit behaviors that can increase an individual's inclusive fitness (Koenig et al. 1992, Kokko and Ekman 2002). One of the direct benefits of juveniles remaining with familial flocks is enhanced access to food (Sklepkovych 1997, Chiarati et al. 2011). The prolonged brood care hypothesis proposes that parents display nepotism by sharing resources with their offspring, even at the cost of decreasing their own intake, in return for offspring to increase their fitness through food energy (Ekman and Rosander 1992, Dickinson et al. 2014). When unrelated individuals attempt to share food with family groups, elder members often aggressively defend the

resource and tolerate only their young in the vicinity, which in turn defend the resource for their parents (Pravosudova et al. 1999, Ekman et al. 2001). More distant relatives residing in nearby territories also may receive direct benefits by obtaining access to reliable food resources through more tolerant interactions (Griesser et al. 2015, Rylander et al. 2020). Therefore, allocating energy reserves to only those of close relatedness is likely an evolved behavior due to kin-selection in kin-based avian species, and the behavior of tolerant resource sharing among relatives inadvertently increases indirect fitness benefits of individuals, as shared genes among the family are passed on to future generations (Ekman 2006, Hatchwell 2009).

Resource sharing has been thoroughly documented as a common avian behavior between related individuals, with certain biotic factors (such as sex and age) and abiotic factors (such as season and habitat) influencing foraging behavior of individuals within social groups (Nystrand 2007, Lajoie et al. 2019, Madsen et al. 2021). In most bird species, males are dominant over females and adults are dominant over juveniles (Waite 1987, Krams et al. 2020), but when groups are comprised of extended kin, parents and offspring, or even mated pairs, the foraging hierarchy can become more complicated (Farine et al. 2012, Hogstad 2015). Moreover, resource sharing and foraging behavior can vary during certain times of the year, as breeding and non-breeding season stressors also vary across time (Pravosudova et al. 1999, Davis 2002), and in landscapes experiencing fragmentation or urbanization, birds may be less likely to share scarce food resources with relatives if they are critical to an individual's survival (Griesser and Lagerberg 2012, Krams et al 2020).

There are many ways to study foraging dynamics of avifauna (Bibby et al. 2000, Bub 2012), but the use of passive integrated transponder (PIT) tags recently has become a wildly available technology to researchers and is an affordable alternative to GPS or satellite transmitters (Bridge et al. 2019). PIT tags can be externally attached to or surgically implanted in the individual, and each tag is calibrated with its own radio frequency identification (RFID) signal that can be detected by an antenna and receiver (Bridge and Bonter 2011, Sokolov 2011). Thus, if programmed data loggers are connected to a stationary antenna at a feeding port, PIT-tagged individuals can be detected and their information recorded in real time across a spatiotemporal scale (Hou et al. 2015, Bridge et al. 2019). This allows researchers to examine social flocking behaviors involving resource sharing without being physically present (Bridge and Bonter 2011, Smith et al. 2020). Hence, complex interactions between immediate and extended family members that may be overlooked by focal observation alone can be easily recorded through RFID technology.

I studied a PIT-tagged population of black-crested titmice (*Baeolophus atricristatus*, hereafter BCTI), a gregarious member of the Paridae family (hereafter “parid”) commonly observed throughout most of its range (north-central Mexico to southwestern Oklahoma, and portions of west Texas) (Dixon 1978, Patten and Smith-Patten 2008), to examine if relations at the direct family level and extended kin level impact resource sharing. The BCTI is an ideal model species to examine resource sharing behaviors among kin of both direct and distant relation, as well as between individuals and flocks that are unrelated. Previous research on the BCTI revealed that heavy male offspring often limit their natal dispersal and establish territories adjacent to their father’s

the following year, creating kin-structured neighborhoods (Rylander et al. 2020).

Additionally, the same study observed that interactions between two BCTI extended kin groups were less aggressive than when two unrelated flocks interacted.

In this study, I: 1) documented if there were differences in feeding behaviors among age groups, between sexes, and across seasons at reliable food sources; 2) examined if kin-selection favors resource sharing between two separate, but related, family groups (“extended kin”) compared to two unrelated family groups; 3) assessed if parents display nepotistic behaviors towards retained juveniles in relation to resource allocation; and 4) determined if mated pairs visit a common food resource more often in the presence or absence of the other. For this study, I defined a “family” as the male, female, and their juvenile offspring, and a “lineage” as all BCTI members that shared genes with a common ancestor (including extended family and juveniles from previous seasons). For example, if two male siblings establish territories adjacent to their father and to one another the following spring, and all three of these males reproduce and have families of their own, all three of these distinct families belong to the same lineage and are therefore “extended kin.”

I predicted that adult male BCTI would visit feeding stations more frequently and for longer durations than females or juveniles because males are more dominant and likely to defend resources from other conspecifics (Dickinson 1997, Krams et al. 2020). Resources can be scarce during certain times of the year, so I predicted that BCTI would frequent feeding stations more often in the winter when natural food sources become depleted (Bonter et al. 2013). I predicted that because of inclusive fitness benefits, separate BCTI families stemming from the same lineage (compared to unrelated BCTI

families from different lineages) would more likely share resources, as sharing increases the likelihood that common genes are passed on to future generations (Ekman and Rosander 1992, Dickinson et al. 2009). Likewise, I predicted that retained BCTI juveniles would frequently accompany parents on feeding bouts, as juveniles would gain access to food resources on their parents' defended territory through nepotism (Pravosudova et al. 2001, Ekman and Griesser 2002). Lastly, I predicted that female BCTI would more frequently visit a food source if the male was present, particularly during the spring, because males typically provide additional protection for their mates (Kokko and Morrell 2005, Hansen et al. 2009).

## **Methods**

### ***Study site***

Between January 2019–April 2020, I assessed BCTI resource sharing behaviors in the northern half of the Freeman Center (29°56'17.05"N, 98° 0'30.24"W), a 1400-ha property owned by Texas State University located ~10 km northwest of San Marcos, Texas. The habitat at the Freeman Center is typical of the Edwards Plateau ecoregion, with a mosaic of juniper/oak woodlands (*Juniperus ashei*, *Quercus fusiformis*, *Quercus buckleyi*) (46%), grassland savannahs (*Bothriochloa ischaemum*, *Schizachyrium scoparium*) (22%), and a mixture of woodland/grassland interface (*Diospyros texana*, *Ilex vomitoria*, *Forestiera pubescens*) (32%) covering the majority of the property (Barnes et al. 2000). Thus, the Freeman Center is ideal habitat for the BCTI which is commonly observed in flocks of 2 – 4 individuals year-round throughout the property (Rylander 2015, Rylander et al. 2020).

### *Capture and banding*

To capture family groups of BCTI, I installed 146 nestboxes throughout the northern half of the Freeman Center — 40 during the winter of 2012, 31 in the fall of 2013, and 75 during the fall of 2017 (Figure 1.2). I affixed all nestboxes 2–3 m high on t-posts with PVC pipe predator baffles to discourage northern raccoon (*Procyon lotor*) and Texas rat snake (*Elaphe obsoleta*) predation. During each breeding season (late February – early July, 2018 & 2019), I checked nestboxes 1–2x a week for signs of BCTI nests (moss, animal fur, and snake skin (Patten and Smith-Patten 2008, Rylander pers. obs.), and once confirmed, monitored nests until completion. I hand-captured adults within the nestbox when they entered to feed young that were  $\geq 5$  days post-hatching (Rylander et al. 2020). I aged and sexed adults (Pyle 1997), as well as fitted individuals with a registered United States Geological Service (USGS) aluminum band and 0–2 Darvic color bands (Avinet Research Supplies, Portland, Maine) on their legs for resight purposes. Additionally, I affixed a preconstructed plastic colored leg band with inserted PIT tag (8 mm tall, 2.6 mm in diameter, 20 mg in weight; IB Technology, Aylesbury, U.K.) on the opposite leg of the aluminum band, ensuring the total weight of the bands and PIT tag were  $< 1\%$  of the BCTI's body weight (USGS Bird Banding Laboratory). Each PIT tag was pre-programmed by IB Technology to emit an individualized radio frequency signal that could be read by a stationary antenna attached to a data logger (Bridge and Bonter 2011). Once nestlings were 10–14 days post-hatching, I fitted all individuals with unique combinations of color bands, PIT tag, and aluminum band. I was not able to sex nestlings at the time of banding but was able to sex some individuals

retrospectively based on territorial behaviors once they became reproductively active the following year (Rylander et al. 2020).

Though I was unable to perform genetic analyses on PIT-tagged BCTI families, I was able to determine familial relationships based on banding the male, female, and young at the same nestbox. Additionally, I conducted repetitive and detailed focal monitoring observations at nestboxes during the entirety of the nesting cycle, recording the same adults entering to feed young, as well as the same adults feeding banded offspring outside of the nest once they fledged. Genetic paternity for these family groups is unknown, but I assume BCTI experience low rates of extra-pair copulations (ECPs), similar to its closely related sister taxon, the tufted titmouse (*Baeolophus bicolor*), with an ECP rate of 8.8% (Pravosudova et al. 2002).

### ***Radio frequency identification feeding stations***

To record feeding behaviors of PIT-tagged BCTI, I constructed 12 RFID feeder stations custom designed for the study (F01 – F12, Figure 5.1). I manipulated a plastic tube bird feeder so that only a single circular perch opening was available for seed dispensing for each station (Queller and Murphy 2017). I affixed a 125-kHz, 51.5 mm copper loop antenna (QKits Electronics, Kingston, Ontario) to the circular perch using zip ties and placed the antenna wires into a waterproof container mounted to the bottom of the tube feeder (Figure 5.2). Inside the waterproof container, I secured the antenna wires to a pre-constructed RFID reader circuit board that was developed by the University of Oklahoma (Bridges et al. 2019) for avian research purposes. RFID readers were pre-programmed using software Arduino (Arduino LLC, Scarmagno, Italy) so that when a PIT-tagged BCTI landed on the antenna, it would record the time, date, and the

identity of the individual (hereafter a “read”) on a removable 32-MB SD card. Because the leg-mounted PIT tags only emitted a signal that could be read by the antenna ~1 cm away from the tag, I was able to prevent false reads and only record BCTI that perched on the antenna to obtain a seed. To provide continuous power to the RFID reader throughout the season, I used a 12V battery housed in a waterproof box with a solar panel attachment for recharging (HME product). I configured a 12V to 5V step-down power supply module (Knacro product) between the battery and RFID reader because the reader circuit board could not handle 12V (Figure 5.3).

To allow BCTI access to the RFID feeding stations while also preventing other wildlife from tampering with equipment or depleting seed (raccoons, fox squirrels (*Sciurus niger*), mourning doves (*Zenaida macroura*)), I suspended tube feeders in a 92 x 68 x 68 cm wire mesh cage (3.81 x 3.81 cm mesh size), held together by zip ties or hog rings. Inside the mesh cage, I included 1–2 natural perches ~10 cm from the antenna, as to increase accessibility to the feeding port for banded BCTI but far enough away to where the individual had to jump on the antenna to obtain a seed. I then used baling wire to mount the entire cage setup on top of a 1.5 m tripod stand (Guide Gear Portable Game Hanger) to prevent cattle and wild hogs (*Sus scrofa*) from damaging the feeding station and electronics. I secured each tripod leg to the ground by tethering it with baling wire and zip ties to steel rebar that I drove into the ground. I also increased the stability of the entire feeding station by anchoring opposite sides of the mesh cage to shepherds hooks that also were driven into the ground (Figure 5.4).

To ensure that PIT-tagged BCTI had access to RFID feeding stations, I strategically deployed feeders in locations at the Freeman Center in the vicinity of



nestboxes where I had banded entire family groups with PIT tags during the spring of 2018 and 2019 (Figure 5.1). I also placed feeding stations based on previous knowledge of banded BCTI genealogy at the Freeman Center from 2013 – 2017 (Rylander 2015, Rylander et. al 2020). I positioned RFID feeder systems within mapped home ranges of PIT-tagged family groups that shared at least one home range boundary with another PIT-tagged family group and > 50 m from nestboxes previously occupied by BCTI families to prevent heightened defense behavior that can sometimes occur directly next to nesting cavities (Slagsvold 1993, Slagsvold and Wiebe 2021, Rylander pers. obs.). I installed feeding stations in relatively open savannah habitat on the edge of woodland patches (> 10 m from any trees > 5 m in height), so that feeding stations were easily detected by all BCTI in the vicinity. I also installed feeding stations ~3 m from 1–2 shorter shrubs or small trees (< 3 m in height), giving BCTI a place to perch next to feeders because BCTI often are hesitant making long flights across open habitat to examine novel structures (Rylander pers. obs.). I performed routine feeder station checks once every two weeks between January 2019–April 2020, where I replenished seed, changed out batteries and SD cards, and fixed any broken equipment.

### ***Lineages, families, and nepotistic feeding bouts***

Because BCTI family groups have been banded and monitored at the Freeman Center from 2013–2020 (Rylander 2015, Rylander et al. 2020), I was able to determine extended relationships between kin and assign individuals into family groups and lineages during feeding bouts. For this study, I defined a single “feeding bout” as any reads < 5 minutes from each other (Rylander pers. obs.). Thus, based on recorded RFID feeding station reads, I defined “extended kin bouts” (hereafter EKB) when  $\geq 2$  families

were present that belonged to the same lineage during a feeding bout. Furthermore, I defined a “nepotistic” relationship feeding bout as one where either male or female were accompanied by  $\geq 1$  of their offspring.

I conducted all research in accordance with the Institutional Animal Care and Use Committee (IACUC) (#201532811), federal Master Banding Permit (#24108), U.S. Fish and Wildlife Permit (MB121162-2), and Texas Parks and Wildlife Collection Permit (#SPR-0417-107). I handled all birds as advised by the Ornithological Council's Guidelines for wild avifauna in research

## **Data Analyses**

### ***Feeding bouts by season, age, and sex***

I used a generalized linear mixed effects model (GLMM, Zurr et al. 2009) with gamma distribution (with log-link function) and feeder as the random effect to assess if the duration of BCTI feeding bout was influenced by season or the number of reads per feeding bout. I did not include single-read feeding bouts for this analysis and did not remove putative outliers as I was interested in the recorded differences in duration for each season. Single reads are created when a lone PIT-tagged BCTI takes a single seed and leaves, providing no data. I used statistical software program R (version 4.0.2, R Development Core Team 2020) for all analyses in this study.

I used a GLMM with a gamma distribution to assess differences in the duration of feeding bouts between BCTI sexes and ages when only one individual is present (“single individual,” not referring to paired versus unpaired status). I set sex (male or female), age (adult or juvenile), and season (spring, summer, fall, winter) as fixed effects and feeder as

the random effect. I only used feeding bouts where a single individual was present at the feeder and removed feeding bouts of individuals when sex was unknown. I classified adults as individuals  $\geq 1$  year of age and juveniles as those who had not entered their first breeding season ( $< 1$  year old). Additionally, I removed single reads from this analysis, as they have a duration of zero and cannot be computed with a gamma distribution. I removed outlier feeding bouts from this analysis that contained durations  $< 1.5$ x the interquartile range from the lower boundary or  $> 1.5$ x the interquartile range from the upper boundary.

To assess differences in the total number of reads from a single individual BCTI based on sex, age, or season, I used a GLMM with Poisson distribution, with number of reads as the response variable. I used sex, age, and season as fixed covariates and feeder as the random effect. For this analysis, I included feeding bouts that contained single reads and multiple reads from a single individual and removed outliers as noted above.

### ***Extended kin bouts (EKB)***

I used a chi-squared goodness-of-fit test (Pearson 1900), comparing the proportion of observed versus expected number of EKB (out of total feeding bouts), to assess if extended kin influenced BCTI flock membership at a reliable food resource. I calculated the expected number of EKB by calculating the total number of possible PIT-tagged BCTI groups at a feeder, then tallying how many of those groups contained  $\geq 1$  member from  $\geq 2$  related families. For example, if four PIT-tagged BCTI are in an area near a feeder, groups of 1, 2, 3, or all 4 individuals could visit the feeder together, meaning 15 hypothetical unique groups ( $2^n - 1$ , for  $n = 4$  individuals) could be possible

in a given feeding bout. However, because resource sharing requires  $>1$  individual in a bout, I removed feeding bouts containing only 1 individual from both the observed and expected calculations. Additionally, because of the low frequency of feeding bouts with  $\geq 5$  individuals present ( $\sim 1.9\%$ , 190/9684), I calculated only hypothetical groups of BCTI between 2–4, as this represented realistic foraging flock size for the species (Patten and Smith-Patten 2008, Rylander 2015). When calculating the proportion of observed EKB, I used data collected between June 2019 – February 2020 because reads during the spring were possibly confounded by heightened defensive behavior of adult BCTI during the nesting season (March – May) (Landys et al. 2010, Ritchison et al. 2020). I conducted separate chi-squared analyses for each feeder as well as a pooled chi-squared analysis to assess potential differences between feeders, as the combination of related individuals varied greatly between feeders.

I used a generalized linear model (GLM) with feeding bout duration as the response variable (gamma distribution) and “extended kin present” (binary Yes or No), season (only summer, fall, winter), and feeder as fixed covariates to assess if extended kin influenced the duration of feeding bouts. I pooled feeders for this analysis instead of setting it as a random effect because only three feeders had enough data collected on EKBs for analysis. I used the duration of feeding bouts recorded between June 2019 – February 2020 that had groups of 2 – 4 BCTI. Additionally, I removed outlier feeding bouts from the analysis as noted above.

### *Nepotism*

As with assessing EKBs, I used a chi-squared test of independence to assess if there were differences between the proportion of observed versus expected feeding bouts

(out of total feeding bouts) where nepotism occurred. For this analysis, I only examined groups containing two individuals in a feeding bout, as I wanted to remove potential confounding flocking behavior influenced by additional BCTI (whether related or not). I calculated the expected number of nepotistic feeding bouts as the total number of combinations where male + offspring or female + offspring could occur out of all possible combinations of groups of two. I limited the number of feeding bouts for this analysis to summer and fall (June – November 2019), as many offspring disperse during the fall and are no longer present in the winter (Rylander et al. 2020). I conducted a separate chi-squared analysis for each feeder and a pooled chi-squared analysis to determine if there were differences among feeders.

When comparing feeding bout duration between nepotistic and non-nepotistic groups of BCTI, I used a GLMM with gamma distribution for the response variable duration. I used covariates season (summer, fall) and “nepotistic relationship present” (binary Yes or No) as the fixed effects, and feeder as the random effect. For this analysis, I did not pool feeders because there were differences in the number of potential nepotistic groups between feeders that I wanted to control for. I removed outliers using the methods described above.

### ***Mated pairs***

To assess if the male or female in a mated pair are more likely present at a feeder if the other is present (hereafter “together bout”), I used a Friedman’s test, as individuals in a mated pair are not independent from another and calculated proportions did not follow a normal distribution (Friedman 1937). I blocked calculated proportions by season because mated pairs behave differently towards one another during the breeding versus

non-breeding season, even though they can remain paired for several years (Rylander et al. 2020). For each mated pair, I calculated the number of together bouts and divided that by the total number of feeding bouts where the male or female were present (together bouts / (together bouts + bouts with just male or just female)). Thus, I compared these proportions to assess if one of the sexes was more dependent on the other regarding feeding bouts during each season. I further assessed if there were differences between sexes of a mated pair regarding the proportion of feeding bouts where the other mate was not present (hereafter “without bout”), out of the total number feeding bouts when male, female, or both were present. For this analysis, I used an additional Friedman’s test and blocked by season. For both together and without bout analyses, I used data collected from mated pairs between dates where I knew both individuals were alive and present in the area (Rylander pers. obs.).

## **Results**

### ***Banding and feeder stations***

During the spring of 2018 and 2019, I PIT-tagged 214 and 237 BCTI, respectively. Of those 451 tagged BCTI, 61 individuals (18 adult males, 12 adult females, and 31 juveniles) were detected through RFID reads at feeding stations. These 61 individuals represented 24 families and 16 lineages, although no more than 6 families and 4 lineages were ever recorded at a single feeding station (Table 5.1). Ages of PIT-tagged BCTI ranged from hatch-year (HY) juveniles that had recently fledged to two adult males and one adult female that were  $\geq 6$  years old during the spring of 2020. At two feeders (F03 and F04), four generations of related individuals were recorded over the duration of their deployment, often with individuals from three generations feeding in the same bouts

(F03, F04, F10 and F12). On three occasions, seven individuals from the same lineage were recorded at the same feeding bout.

Across all feeding stations between January 2019–April 2020, 26,428 reads were recorded during 9,684 unique feeding bouts (Figure 5.5). Adult females were present 27.1% of the time (2,621 bouts), whereas 46.4% of the total feeding bouts were comprised of single reads (4,493 bouts). The number of feeding bouts and recorded reads were not evenly distributed across feeders, as some feeders were deployed and functioning sooner than others (Table 5.1). Certain feeders became “hot spots,” whereas others were rarely visited by PIT-tagged BCTI, even though BCTI family groups were captured and PIT-tagged near all RFID stations. Additionally, adult females were not detected at four of the feeders (F05, F06, F07, and F08) and were rarely detected at two other feeders (9 bouts at F02 and 2 bouts at F11), even though adult females were banded at the same nests as males and offspring that frequented these feeders.

Four feeders (F01, F03, F04, and F12) recorded > 1,000 reads for six individuals (2 juveniles of unknown sex and 4 males), with one 3-year-old male accumulating 3,787 reads (1,614 feeding bouts) between feeders F03 and F04. Most (66%) PIT-tagged BCTI were only detected at one feeding station, although a juvenile of unknown sex was detected at 5 stations (F02, F06, F07, F08, and F12, with F08 being the “home” station), covering an area of ~46 ha, potentially representing territory scouting or erratic dispersal behavior. On two occasions, juveniles entering their first breeding season were recorded consistently in the spring of 2020 at feeding stations ~1.47 km and ~2.5 km from the nestboxes they fledged from in 2019, potentially indicating dispersal and territory establishment. Moreover, during the summer and fall, HY juveniles ranked second in the

number of reads per bout, averaging 2.38 and 2.11 reads per bout, respectively, which was only lower than the average number of reads per bout by adult males  $\geq 3$  years of age. In the winter, juveniles averaged the greatest reads per bout at 2.53.

### ***Feeding bouts by season, age, and sex***

The duration of a feeding bout was influenced by season and the number of reads per feeding bout ( $n = 5,191$ ) (Table 5.2, Figure 5.6). Duration was the longest during the fall (mean  $\pm$  SD) ( $5.14 \pm 5.97$  mins), followed by the summer ( $4.91 \pm 5.38$  mins), winter ( $4.57 \pm 4.80$  mins), and spring ( $2.74 \pm 2.29$  mins). Additionally, as the number of reads per feeding bout increased by 1, the duration of the feeding bout increased by  $\sim 1 - 2$  mins. Once feeding bouts exceeded 19 reads, the average duration of feeding bouts ranged from 25.6 – 55.37 min., with 42 min. being the maximum number of reads in a bout. The feeding bout with the longest duration (55.37 min.) recorded 37 reads and comprised of a father ( $\geq 5$  years old) and son (3 years old) at feeder F03 during the fall.

Due to the low number of feeding bouts of known sexes at feeders F02 and F07, I omitted these feeders from further analyses regarding sex. Season influenced the duration of feeding bouts by single individuals ( $n = 1,523$ , 69 outliers removed) (Table 5.3), as displayed with violin plots in Figure 5.7. I used violin plots because they display the distribution and density of data points more informatively than basic boxplots for these analyses. Spring feeding bouts ( $1.85 \pm 1.31$  mins) were shorter than summer ( $2.39 \pm 1.83$  mins), fall ( $2.46 \pm 1.90$  mins), or winter ( $2.31 \pm 1.62$  mins). Including outliers, feeding bouts made by single females ranged from 0.03 – 12.42 mins, whereas feeding bouts by single males ranged from 0.07 – 29.93 mins. Age did not influence the duration of a feeding bout made by a single individual.



Season and sex influenced the number of reads per feeding bout by a single individual ( $n = 4,411$ , 47 outliers removed), with males averaging  $1.67 \pm 1.06$  reads per bout while females averaged  $1.25 \pm 0.64$  reads per bout (Table 5.4, Figure 5.8). There also were significantly more reads per bout during the spring ( $1.88 \pm 1.13$ ) and significantly less reads in the winter ( $1.50 \pm 0.91$ ) than in the summer ( $1.65 \pm 1.06$ ) or fall ( $1.63 \pm 1.08$ ). Age did not influence the duration or number of reads per feeding bout. Including outliers, the number of reads from single males during a feeding bout ranged from 2 – 23, while females ranged from 2 – 7 per feeding bout.

### ***Kin-selection***

Only five feeding stations had sufficient extended family structure for analyses regarding kin-selection: F03, F04, F09, F10, and F12. However, I omitted feeders F03 and F09 from these analyses because they contained most of the same families and individuals that were recorded at stations F04 and F10, respectively. Thus, I chose the feeder that contained the most reads of the two (F04 and F10), along with F12, for kin-structured analyses.

Based on chi-squared analyses, there were differences between the proportion of observed vs expected number of EKB, with the proportion of observed bouts being lower than expected at all three feeders (**F04**: 36% compared to 45%, respectively;  $n = 1,114$ ;  $\chi^2 = 36.91$ ;  $df = 1$ ;  $p < 0.01$ ; **F10**: 53% compared to 84%, respectively;  $n = 116$ ;  $\chi^2 = 24.29$ ;  $df = 1$ ;  $p < 0.01$ ; **F12**: 39% compared to 82%, respectively;  $n = 114$ ;  $\chi^2 = 35.95$ ;  $df = 1$ ;  $p < 0.01$ ) (Table 5.5). A chi-squared analysis with data pooled from all three feeders

also resulted in a lower proportion of observed EKB than expected (38% compared to 51%, respectively); ( $n = 1,344$ ;  $\chi^2 = 76.69$ ;  $df = 1$ ;  $p < 0.01$ ).

The duration of feeding bouts was influenced by the presence of extended kin ( $n = 1298$  (46 outliers removed);  $\beta = -0.02 \pm 0.01$ ;  $t = -2.25$ ; 95% CI =  $[-0.04, -0.01]$ ;  $p = 0.02$ ), with feeding bouts being longer if extended kin were present ( $4.29 \pm 2.82$  mins) compared to unrelated family groups ( $3.93 \pm 2.81$  mins) (Figure 5.9). The covariates season and feeder were not influential.

### *Nepotism*

Though seven feeding stations had sufficient data for analyses regarding nepotism (F03, F04, F05, F08, F09, F10, and F12), I used only five feeders in the analysis and omitted feeders F03 and F09 because they contained repeated visits from the same individuals from F04 and F10, respectively. Chi-squared analyses indicated that there were no differences between the proportion of observed and expected number of nepotistic feeding bouts at four of the five feeders (**F04**: 22% compared to 23%, respectively;  $n = 594$ ;  $\chi^2 = 0.24$ ;  $df = 1$ ;  $p = 0.62$ ; **F05**: 59% compared to 41%, respectively;  $n = 17$ ;  $\chi^2 = 1.06$ ;  $df = 1$ ;  $p = 0.30$ ; **F08**: 65% compared to 55%, respectively;  $n = 49$ ;  $\chi^2 = 1.06$ ;  $df = 1$ ;  $p = 0.30$ ; **F10**: 51% compared to 62%, respectively;  $n = 79$ ;  $\chi^2 = 2.08$ ;  $df = 1$ ;  $p = 0.15$ ). However, at feeder F12, there was a significantly greater proportion of observed occurrences of nepotism than expected (92% compared to 64%, respectively); (**F12**:  $n = 36$ ;  $\chi^2 = 8.04$ ;  $df = 1$ ;  $p < 0.01$ ) (Table 5.6). The pooled chi-squared analysis revealed overall that there was no difference between the

proportion of observed and expected nepotistic feeding bouts (32% compared to 31%, respectively); ( $n = 775$ ;  $\chi^2 = 0.01$ ;  $df = 1$ ;  $p = 0.95$ ).

When groups of two BCTI were at a feeder, the difference in feeding bout duration was longer if a nepotistic group was present or absent ( $n = 472$  (18 outliers removed);  $\beta = -0.04 \pm 0.02$ ;  $t = -1.79$ ; 95% CI =  $[-0.09 - 0.01]$ ;  $p = 0.07$ ). The covariates season and feeder were not influential. Nepotistic feeding bouts averaged  $3.23 \pm 2.16$  mins ( $n = 125$ ), and non-nepotistic bouts averaged  $2.84 \pm 2.07$  mins ( $n = 347$ ) (Figure 5.10). Additionally, the duration of a nepotistic feeding bout when a male was present with an offspring was  $4.20 \pm 4.15$  mins ( $n = 99$ ), which was  $\sim 1.5$  times longer than a nepotistic bout when a female was present with an offspring ( $2.90 \pm 2.36$  mins ( $n = 26$ )).

### ***Mated pairs***

Proportion of together bouts differed between sexes ( $n = 1,316$ ;  $\chi^2 = 4$ ;  $df = 1$ ;  $p = 0.05$ ), with females having a greater proportion of together bouts than males (Figure 5.11). On average, when females of a mated pair were present at a feeding bout, 51% of those were together bouts with their mate, compared to 27% being together bouts for males. Differences existed in the proportion of without bouts for males compared to females (58% and 20%, respectively) ( $n = 1,316$ ;  $\chi^2 = 4$ ;  $df = 1$ ;  $p = 0.04$ ). Both males and females had a greater proportion of together bouts during the spring (41% and 81%, respectively) compared to any other season, and both sexes had a lower proportion of without bouts during the spring (53% and 9%, respectively) compared to any other season.

## Discussion

Groups of closely and distantly related BCTI shared food resources in a “quality over quantity” manner, with kin foraging bouts lasting longer but occurring less frequently than expected. The longer duration of foraging bouts is likely due to individuals being more tolerant towards relatives (Sklepko 1997, Baglione et al. 2006, Rylander et al. 2020), therefore leaving more energy to forage than fight (Mathot and Giraldeau 2010, Chiarati et al. 2011). By reducing aggressive interactions, related BCTI may be able to watch for and deter predators more efficiently, as has been documented in the Siberian jay (*Perisoreus infaustus*), in which juveniles actively mob predator models more often when they are with kin than with unrelated groups (Griesser and Suzuki 2016). Even if related BCTI forage together longer, it could come at the cost of one of the families leaving their territory unattended, potentially explaining the infrequent foraging bouts by extended kin. Established BCTI adults maintain and defend year-round territories, aggressively confront unrelated conspecifics, and are typically not observed far from their home ranges (Rylander 2015, Rylander et al. 2020). Thus, kin-selection may favor infrequent, lengthier, foraging bouts between extended BCTI relatives as they provide safety and quality access to resources for all individuals, which in turn increases inclusive fitness (Hamilton 1964, Sherman 1977, Emlen 1995, Nowak 2006). Alternatively, natural selection may drive BCTI to maintain vigilance on defended territories where adults increase their direct fitness (Price 1998, Gill 2007, Hatchwell 2009). Regardless, though BCTI share resources with kin from time to time, it is unlikely that this behavior is a strongly kin-selected trait (Parker et al. 1994).

Results from the mated pair analyses suggest that male BCTI are mate guarding females during the spring breeding season (Dickinson 1997, Kokko and Morrell 2005), as noted by the high proportion of together bouts when the female is present and the low proportion of without bouts by the female alone, an observation similarly made in willow tits (*Poecile montanus*, Hogstad 2015). During other seasons, BCTI females are accompanied less frequently by males, indicating that the pair bond is present all year, but to a lesser extent when compared to the breeding season (Kempnaers et al. 1995, Davis 2002). Though BCTI likely are not promiscuous to a high degree (Pravosudova et al. 2002), male BCTI may engage in intense mate guarding during the spring to prevent ECPs, as has been witnessed in many other species, including blue tits (*Cyanistes caeruleus*, Kempnaers et al. 1995), black-throated blue warblers (*Setophaga caerulescens*, Chuang-Dobbs et al. 2001), and great tits (*Parus major*, Hansen et al. 2009). In an experimental study, Dickinson (1997) captured and temporarily held breeding male western bluebirds (*Sialia mexicana*), known to mate-guard, and discovered that unattended females of the captured male were pursued and often copulated with by other males within 15 minutes, although the female did not always accept these ECPs, instead being selective and further confirming that female choice is a strong part of sexual selection (Fisher 1930, Jones and Ratterman 2009). Furthermore, research by Kempnaers et al. (1995) on blue tits discussed that females may benefit from mate guarding because it decreases harassment by neighboring males, allowing females to forage quickly and return to the nest more efficiently. This idea is supported by BCTI males and females both averaging more reads per feeding bout in the spring, even though feeding bout duration was shortest in the spring. More research is needed on the BCTI

regarding potential mate guarding and ECPs as a possible explanation for the high proportion of together bouts for mated pairs foraging during the spring.

Previous work on limited dispersal behavior of juvenile male BCTI hypothesized that offspring likely gain access to resources and adjacent territory openings through nepotism of tolerant parents (Rylander et al. 2020). This current study does not suggest that BCTI juveniles accompany parents during foraging bouts more often than expected, thus complicating the discussion of resource sharing as a large driver to remaining with kin. Thorough work conducted on the kin-structured Siberian jay suggests that even though retained juveniles were not necessarily accompanied by parents more often than expected at artificial feeding stations, retained juveniles had greater load sizes (for potential hoarding) and greater foraging rates when parents were present (Sklepkovych 1997). Therefore, retained BCTI juveniles may still accrue fitness benefits through shared foraging bouts in the same manner as Siberian jays, but they also may gain access to future territories, as witnessed in other species (Pakanen et al. 2016). In the willow tit, it is hypothesized that philopatric juvenile males have a higher survival rate compared to dispersing juvenile males because of increased site familiarity and knowledge of winter food resources (Pakanen et al. 2016). Additionally, in the Seychelles warbler (*Acrocephalus sechellensis*) experiment by Komdeur (1992), young birds that remained on high-quality territories of their parents often gained access to breed there, overall increasing their lifetime inclusive fitness. Further investigation is needed to better understand reasons juvenile BCTI limit dispersal, as it could disentangle the mechanisms for maintaining kin-selection in the species.

Differences in BCTI foraging behaviors between the sexes complement research performed on other members of the parid family (Brawn and Samson 1983). Feeder studies assessing seed consumption rate of male and female blue tit, great tit, willow tit, and crested tit (*Lophophanes cristatus*), demonstrated that males visit feeders more often than females in all species (Crates et al. 2016, Krams et al. 2020), which was observed in BCTI. Female BCTI were banded with PIT tags in the same manner and time frame as their mates, most (62.5%) were never detected at RFID stations where their mates were detected, a pattern that could, in part, be due to lower survival rates of female BCTI (see Chapter IV), yet there were many instances when these females were known to be alive and present near the feeder but did not visit it (Rylander pers. obs.). This cross-species pattern could be because: 1) females wait for more dominant males to finish feeding (Pravosudova et al. 2001, Ritchison et al. 2020) but never make it to the feeder because the foraging flock is disrupted; 2) females tend to forage in protected areas or are more hesitant to approach a feeder (Nystrand 2007, Tryjanowski et al. 2017); 3) females have heightened aggression toward other females (Slagsvold 1993, Dickinson et al. 2009), preventing them from engaging in larger groups in general; or 4) females allocate more time for incubation, feeding young inside and outside of the nest, and scouting for potential nest sites (Harrap and Quinn 1995, Fogg et al. 2013).

Results from this study relating to juvenile BCTI foraging behavior support, as well as conflict with, other work published on similar social flocking species (Waite and Grubb 1987). When alone, juvenile BCTI are similar to adults regarding feeder foraging behavior, which complements work published on tufted titmice (Waite 1987) and black-capped chickadees (*Poecile atricapillus*) comparing foraging rates between the age

classes (Brittingham and Temple 1992). In other studies, juveniles had a higher foraging rate than adults (blue tits, great tits, and Siberian jays) and even thrived when other individuals were present (Sklepkovych 1997, Crates et al. 2016). When all foraging bouts were compiled from this BCTI study, regardless of group size, juveniles ranked higher in the average number of reads per feeding bout over all age classes during the winter, and second highest in the summer and fall only to adult males  $\geq 3$  years of age. Thus, juveniles may display hesitancy or are less efficient foraging alone, as witnessed in pale chanting goshawks (*Melierax canorus*, Malan 1998) and snow buntings (*Plectrophenax nivalis*, Smith and Metcalfe 1994), which could be due to inexperience handling or locating new food sources on their own (Cadieu and Cadieu 2004, Midford et al. 2000). Once in the company of other conspecifics, regardless of relation (Sklepkovych 1997), BCTI juveniles may let their guard down (Waite and Grubb 1987) and forage more rapidly in a shorter period of time compared to adults that maintain vigilance.

It is unclear why almost half (46%) of the foraging bouts of BCTI in this study were comprised of single reads, but literature points to possible explanations for this behavior. In other parids, including the tufted titmouse, individuals visiting feeders often take a single seed and fly off with it, either to shuck the hull and eat it from a safer, sturdier location or to cache the seed during the fall and winter months (Petit et al. 1989, Sherry 1989). There is no literature on the caching behavior of BCTI, but observations have been made on this species hiding black oil sunflower seeds, acorns, and peanuts among vegetative substrate from time to time (Rylander pers. obs.). The extent to which BCTI cache food may be less than tufted titmice due to the differences in climate, where most tufted titmice experience harsher, longer winters at higher latitudes than BCTI



(Ritchison et al. 2020). Moreover, BCTI are incredibly social and usually observed in pairs or groups (Rylander 2015); thus, BCTI foraging alone may take advantage of a quick meal at a feeder but feel susceptible to predation and therefore not linger.

There is debate as to whether conclusions can be made regarding studies using artificial feeding stations as well as RFID technology, as both have strengths and weaknesses. Established feeding stations allow researchers to make more detailed observations on subjects that may be difficult to follow and monitor in a natural setting (Jokinen and Suhonen 1995, Hou et al. 2015). Certain variables can be controlled for at feeding stations that otherwise cannot be accounted for as easily in the natural environment, such as type and amount of food presented to subjects (Richardson et al. 2013, Johansen et al. 2014), or how individuals or groups respond to predators while foraging (Sklepkovych 1997, Freeberg et al. 2016). Nevertheless, artificial feeding stations may shift avian population dynamics by increasing survival during harsh seasons because of the additional caloric intake (Grubb and Cimprich 1990, Lahti et al. 1998, Chamberlain et al. 2009), decreasing survival if birds transmit diseases through close contact at feeding stations or are depredated more easily by hawks and domestic cats (Balogh et al. 2011, Murgui and Hedblom 2017), or altering behaviors that may lead to a change in fitness (Baglione et al. 2006, Saggese et al. 2011). And although RFID technology enables researchers to collect massive amounts of data while decreasing field hours, it is inevitable that technology can fail or lead to misinterpretation of results (Prorakis et al. 2015, Iserbyt et al. 2018). It would be beneficial in the future for work to use video recordings alongside RFID feeding stations to assess quality control and accuracy of reads (Iserbyt et al. 2018).

Overall, this study expands on previous knowledge regarding the social intricacies of the BCTI, specifically addressing the hypothesis that resource sharing may be a kin-selected behavior for the species to continue establishing kin-structured neighborhoods through the limited dispersal of juvenile males (Rylander et al. 2020). Results display that individuals participating in kin social groups likely increase inclusive fitness through “quality over quantity” foraging bouts from time to time, but there are likely additional kin-selected drivers at work among BCTI populations. Future research should focus on disentangling additional proximate behavioral mechanisms that may maintain family structure in the common but understudied BCTI.

**Table 5.1** Summary statistics for radio frequency identification (RFID) feeding stations at the Freeman Center in San Marcos, Texas, for social behavior studies of the black-crested titmouse (*Baeolophus atricristatus*). For each feeder, information is given on deployment duration, the total number of reads recorded (Tot. reads), the total number of feeding bouts recorded (Tot. bouts), the number of feeding bouts where a female was present (Fem. bouts), the number of feeding bouts consisting of a single read (Sing. bout), and the number of individuals (# indiv.), families (# fam.), and lineages (# lin.) recorded throughout the deployment of the feeders.

Feeder	Deployment dates	Tot. reads	Tot. bouts	Fem. bouts	Sing. bouts	# indiv.	# fam.	# lin.
<b>F01</b>	1/26/19 - 3/25/20	4243	1435	616	650	6	5	5
<b>F02</b>	12/30/19 - 3/25/20	154	100	9	71	3	2	1
<b>F03</b>	1/17/19 - 3/20/20	5740	1597	796	553	13	6	4
<b>F04</b>	1/17/19 - 4/1/20	9289	3146	757	1312	21	6	3
<b>F05</b>	8/21/19 - 3/28/20	573	411	0	326	7	3	3
<b>F06</b>	1/8/20 - 3/31/20	892	350	0	137	4	2	2
<b>F07</b>	10/10/19 - 3/24/20	530	238	0	118	4	4	4
<b>F08</b>	10/31/19 - 4/1/20	1039	346	167	119	8	3	2
<b>F09</b>	8/30/19 - 3/26/20	435	291	39	207	8	3	2
<b>F10</b>	8/28/19 - 3/27/20	1168	612	235	359	7	2	1
<b>F11</b>	10/4/19 - 3/16/20	621	344	2	204	5	2	1
<b>F12</b>	9/2/19 - 3/30/20	1744	814	0	437	6	4	2

**Table 5.2** Results from a generalized linear mixed effects model ( $n = 5,191$ ) where covariates season and number of reads per bout significantly influenced the duration of a feeding bout made by groups of 1–10 black-crested titmice (*Baeolophus atricristatus*) at the Freeman Center in San Marcos, Texas, January 2019–April 2020. Random effect Feeder was used to account for variation in the amount of time each feeding station was deployed.

Covariate	Estimate $\pm$ SE	t-value	<i>p</i>	95% CI
<b>(Intercept)</b>	0.49 $\pm$ 0.03	18.40	<b>&lt;0.01</b>	0.44 – 0.54
<b>Number of reads per bout</b>	0.20 $\pm$ 0.01	50.52	<b>&lt;0.01</b>	0.19 – 0.20
<b>Season [Spring]</b>	-0.32 $\pm$ 0.04	-8.30	<b>&lt;0.01</b>	-0.39 – -0.24
Season [Summer]	0.03 $\pm$ 0.03	0.79	0.43	-0.04 – 0.09
Season [Winter]	-0.01 $\pm$ 0.02	-0.11	0.91	-0.05 – 0.05
Random - Feeder	Variance 0.00002 $\pm$ 0.005		$R_c^2 = 0.56$ , $R_m^2 = 0.56$	

**Table 5.3** Using a generalized linear mixed effects model ( $n = 1,532$ ), covariate season significantly influenced the duration of a feeding bout made by individual (foraging alone) black-crested titmice (*Baeolophus atricristatus*) at the Freeman Center in San Marcos, Texas, January 2019–April 2020. To account for variation in the amount of time different feeders were deployed, I set Feeder as a random effect. Single-read feeding bouts were removed from this analysis.

Covariate	Estimate $\pm$ SE	t-value	<i>p</i>	95% CI
<b>(Intercept)</b>	0.42 $\pm$ 0.02	19.80	<b>&lt;0.01</b>	0.37 – 0.46
<b>Season [Spring]</b>	0.12 $\pm$ 0.04	3.42	<b>&lt;0.01</b>	0.05 – 0.20
Season [Summer]	0.02 $\pm$ 0.03	0.03	0.45	-0.03 – 0.07
Season [Winter]	0.02 $\pm$ 0.02	0.02	0.50	-0.03 – 0.06
Random - Feeder	Variance 0.0004 $\pm$ 0.02		$R_c^2 = 0.01$ , $R_m^2 = 0.01$	

**Table 5.4** A generalized linear mixed effects model assessing how sex and season significantly influenced the number of reads per bout when an individual black-crested titmouse (*Baeolophus articularis*) is alone at a feeder ( $n = 4,411$ ) on the Freeman Center in San Marcos, Texas, January 2019–April 2020. Random effect Feeder was used to account for variation among deployment time of each feeder station. Single-read feeding bouts were used in this analysis, along with multiple-read bouts.

<b>Covariate</b>	<b>Estimate <math>\pm</math> SE</b>	<b>t-value</b>	<b><i>p</i></b>	<b>95% CI</b>
(Intercept)	0.42 $\pm$ 0.07	1.94	0.05	-0.01 – 0.27
<b>Sex [Male]</b>	0.31 $\pm$ 0.04	7.78	<b>&lt;0.01</b>	0.23 – 0.38
<b>Season [Spring]</b>	0.20 $\pm$ 0.05	4.43	<b>&lt;0.01</b>	0.11 – 0.29
<b>Season [Summer]</b>	-0.07 $\pm$ 0.04	-1.20	<b>0.05</b>	-0.14 – -0.01
<b>Season [Winter]</b>	-0.08 $\pm$ 0.03	-2.44	<b>0.01</b>	-0.14 – -0.01
Random - Feeder	Variance 0.03 $\pm$ 0.17		$R_c^2 = 0.03$ , $R_m^2 = 0.07$	

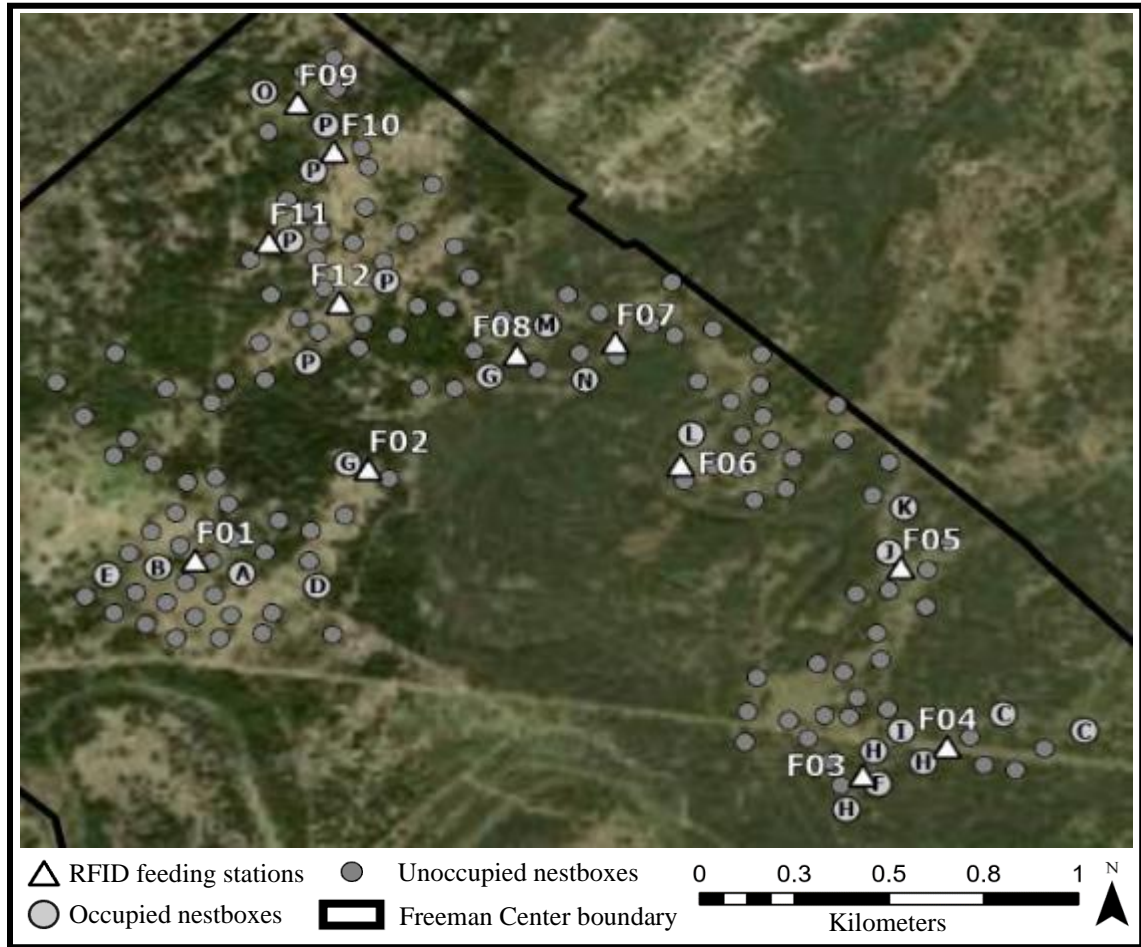
**Table 5.5** Results from a chi-squared test of independence comparing the number of observed versus expected (Obs/Exp) feeding bouts of black-crested titmice (*Baeolophus atricristatus*) when extended kin (Ext. kin) were present during the same feeding bout. “Extended kin” was counted when  $\geq 1$  individual from two separate family groups from the same lineage were detected at feeders together. This study was conducted at deployed feeding stations between January 2019 – April 2020 at the Freeman Center in San Marcos, Texas.

<b>Feeder</b>	<b>Obs/Exp</b>	<b>Ext. kin bouts</b>	<b>Total bouts</b>	<b><math>\chi^2</math></b>	<b><i>p</i></b>
<b>F04</b>	Observed	402	1,114	36.91	<b>&lt;0.01</b>
	Expected	498	1,114		
<b>F10</b>	Observed	62	116	24.49	<b>&lt;0.01</b>
	Expected	97	116		
<b>F12</b>	Observed	45	114	35.97	<b>&lt;0.01</b>
	Expected	93	114		
<b>Pooled</b>	Observed	509	1,344	76.69	<b>&lt;0.01</b>
	Expected	688	1,344		

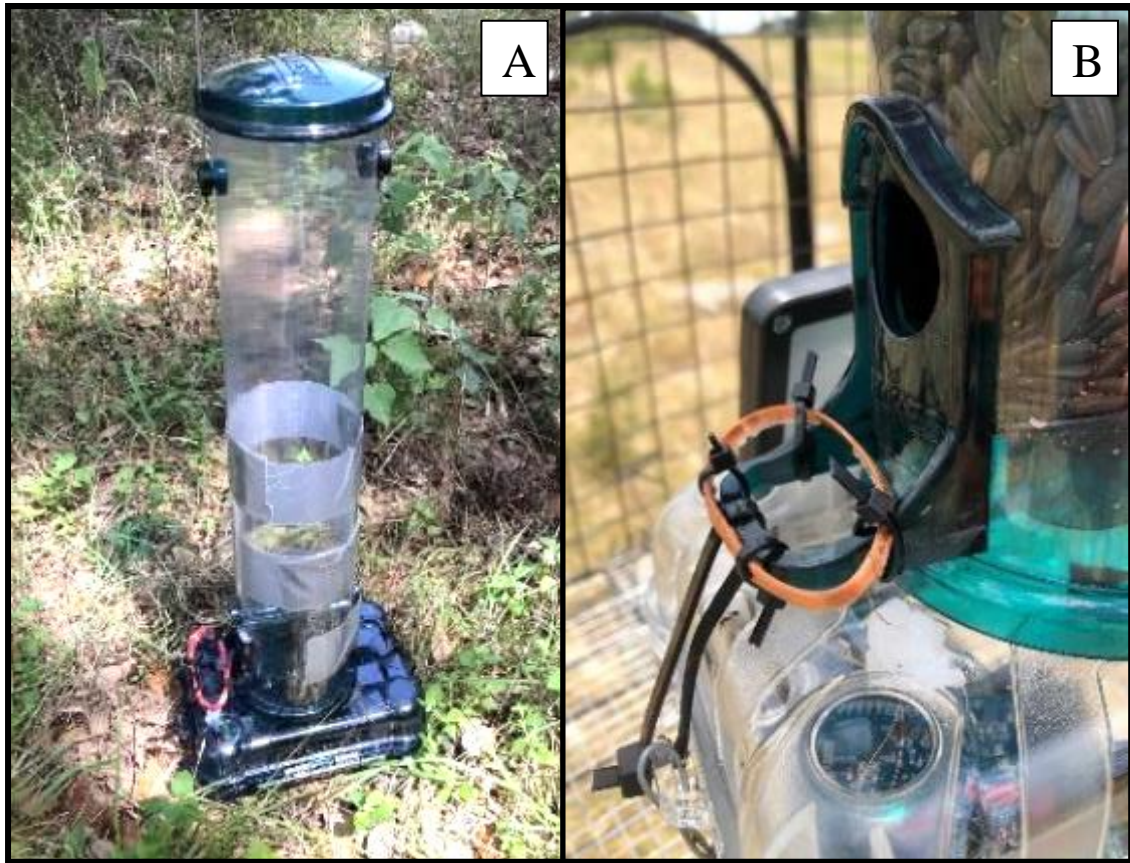
**Table 5.6** A chi-squared test of independence was used to compare the number of observed versus expected (Obs/Exp) feeding bouts when two black-crested titmice (*Baeolophus atricristatus*) in a nepotistic relationship (Nepo. Bouts) were present during the same feeding bout. A “nepotistic relationship” was considered when a father or mother were accompanied with one of their offspring. This study was conducted at the Freeman Center in San Marcos, Texas at deployed feeding stations between January 2019 – April 2020.

<b>Feeder</b>	<b>Obs/Exp</b>	<b>Nepo. bouts</b>	<b>Total bouts</b>	<b><math>\chi^2</math></b>	<b><i>p</i></b>
F04	Observed	128	594	0.24	0.62
	Expected	135	594		
F05	Observed	10	17	1.06	0.30
	Expected	7	17		
F08	Observed	32	49	1.06	0.30
	Expected	27	49		
F10	Observed	40	79	2.08	0.15
	Expected	49	79		
<b>F12</b>	Observed	33	36	8.04	<b>&lt;0.01</b>
	Expected	23	36		
Pooled	Observed	243	775	0.01	0.95
	Expected	241	775		

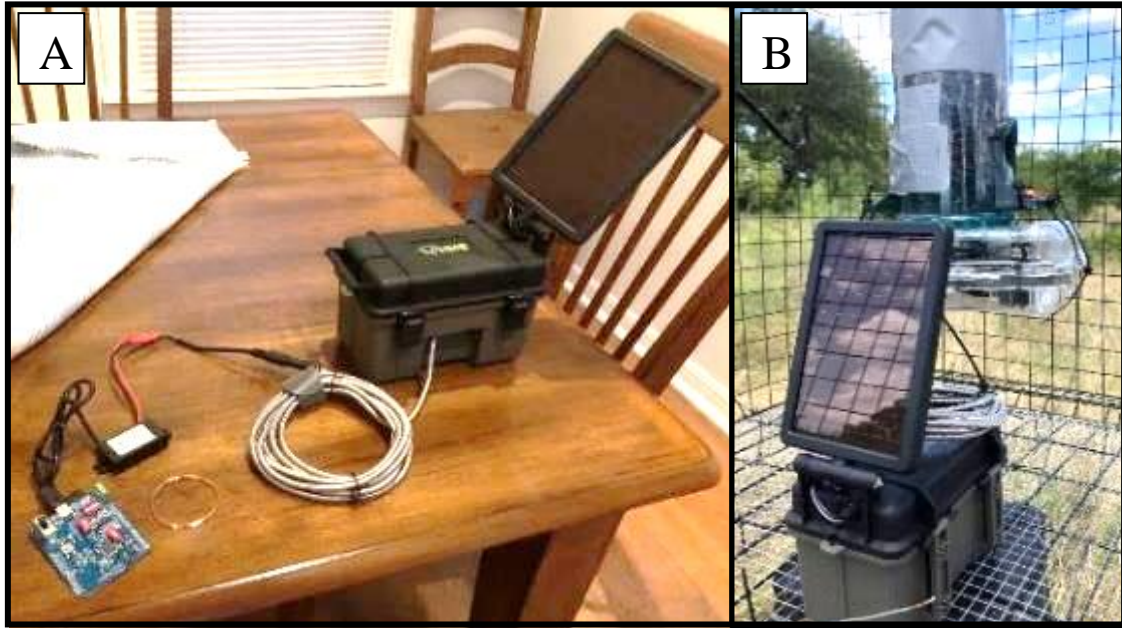




**Figure 5.1** Placement of nestboxes and radio frequency identification (RFID) feeding stations on the Freeman Center in San Marcos, Texas for resource sharing behavioral studies of the black-crested titmouse (*Baeolophus atricristatus*, BCTI), January 2019–April 2020. Occupied nestboxes represent those used for nesting during the spring of 2019 by tagged and detected BCTI at feeding stations. Letters on occupied nestbox markers indicate the lineage (shared genes) in which each family group belongs to.

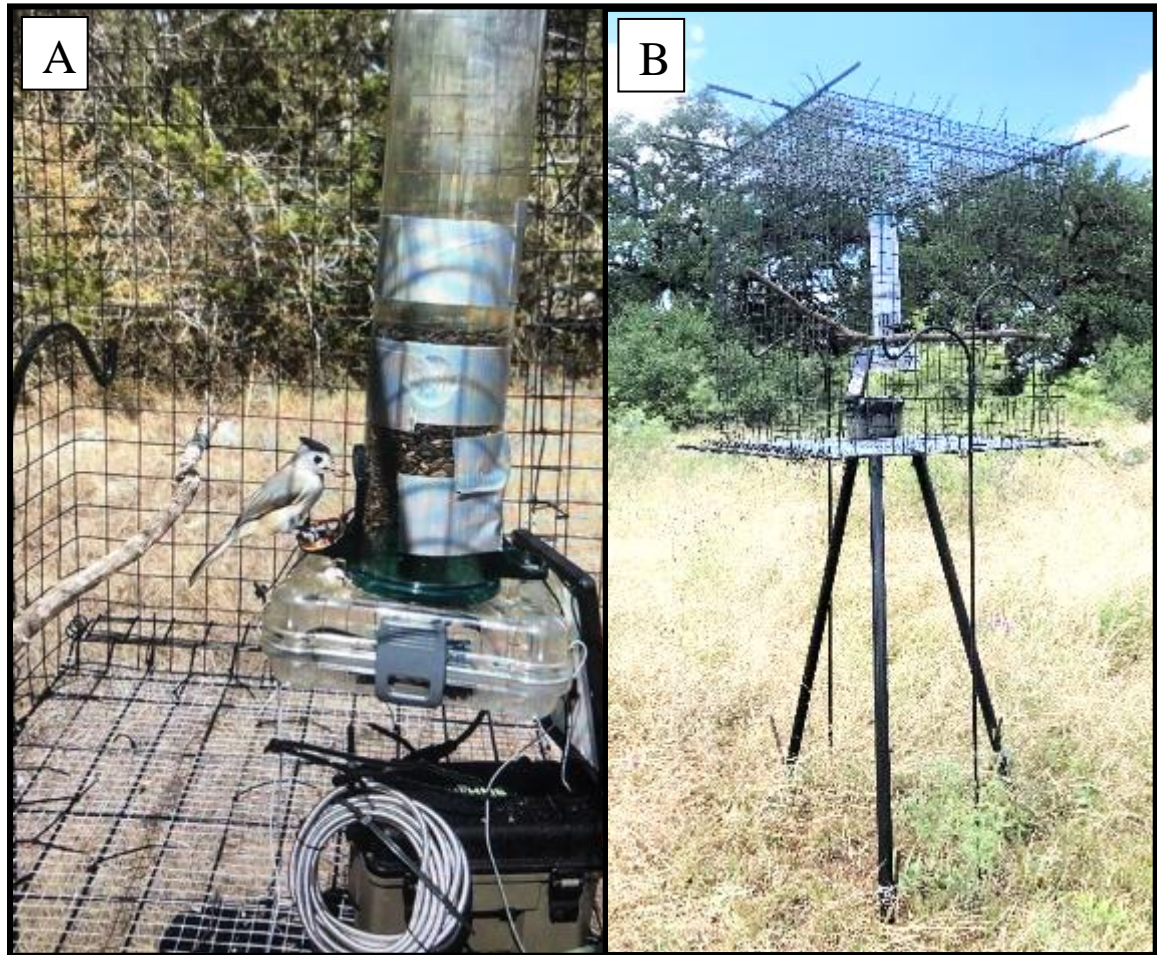


**Figure 5.2** A modified bird feeder used for resource sharing studies of the black-crested titmouse (*Baeolophus atricristatus*, BCTI) at the Freeman Center in San Marcos, Texas, January 2019–April 2020. A. Seed can only be obtained through a single feeding port because other openings were intentionally sealed. B. A circular copper antenna affixed to the single available feeding port to pick up signals from BCTI with passive integrated transponder (PIT) tags.

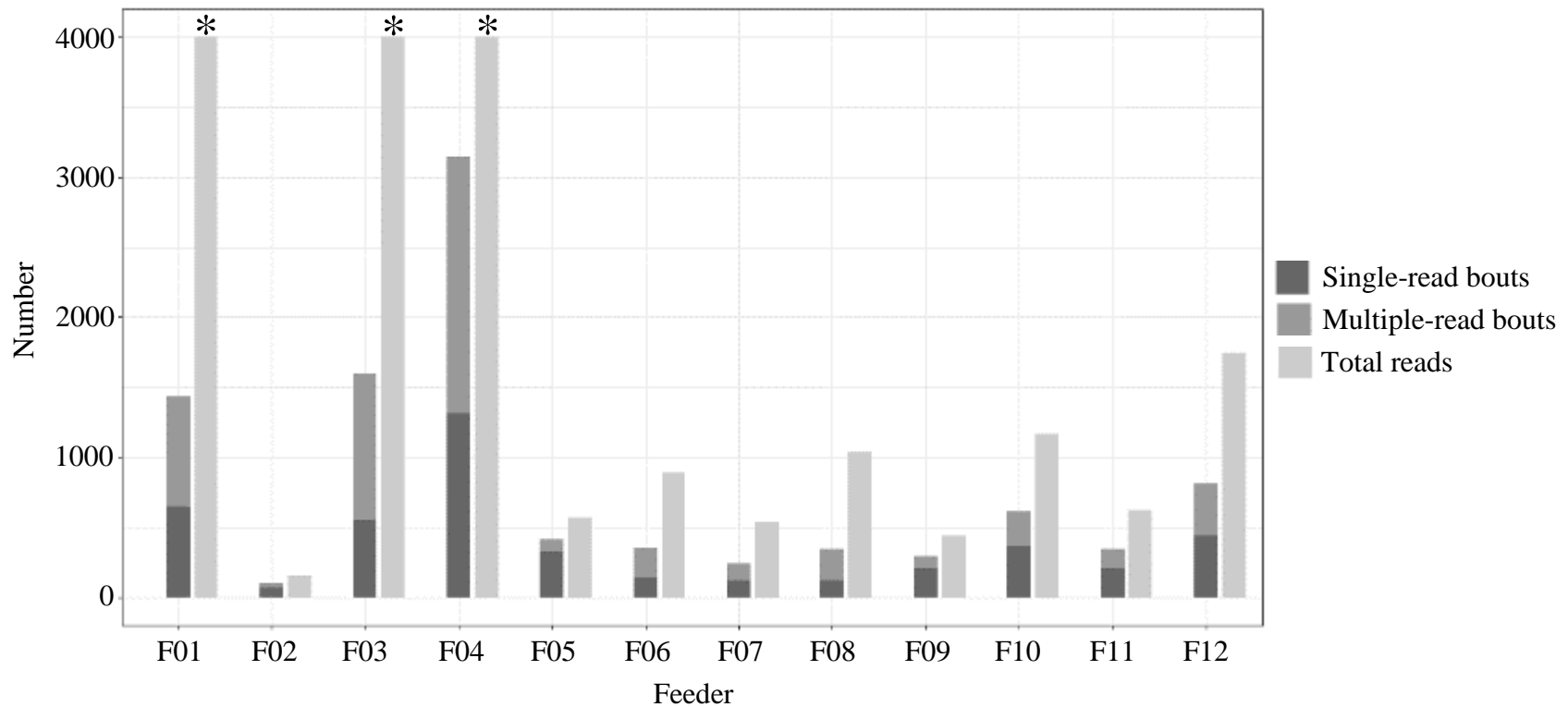


**Figure 5.3** Materials used at radio frequency identification (RFID) feeding stations installed at the Freeman Center in San Marcos, Texas, January 2019–April 2020, for resource sharing behavioral studies of the black-crested titmouse (*Baeolophus atricristatus*, BCTI). A. The pre-constructed RFID circuit board received and logged passive integrated transponder (PIT) tag signals from BCTI that landed on the copper wire antenna during foraging bouts. The 12V solar charged battery provided power to the circuit board but was configured with a 12V to 5V step-down power supply module, as the circuit board could not handle 12Vs. B. The solar power battery and circuit board set-up at the feeding station.

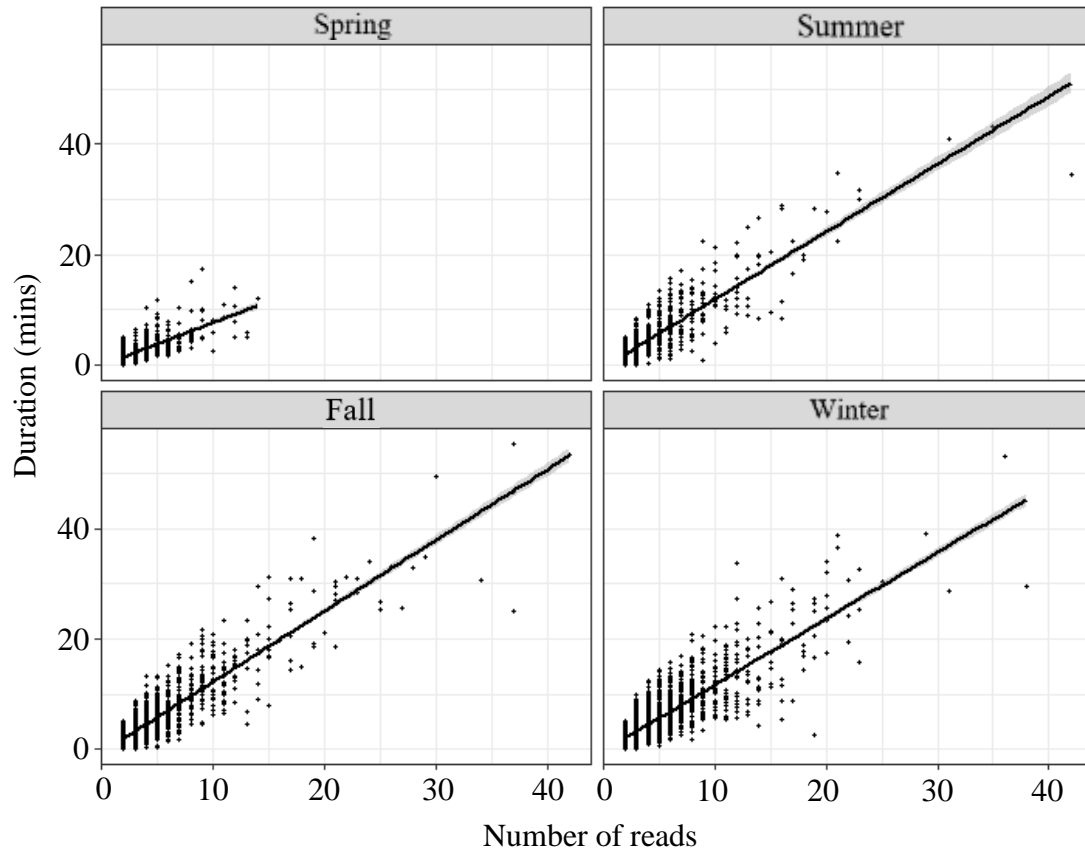




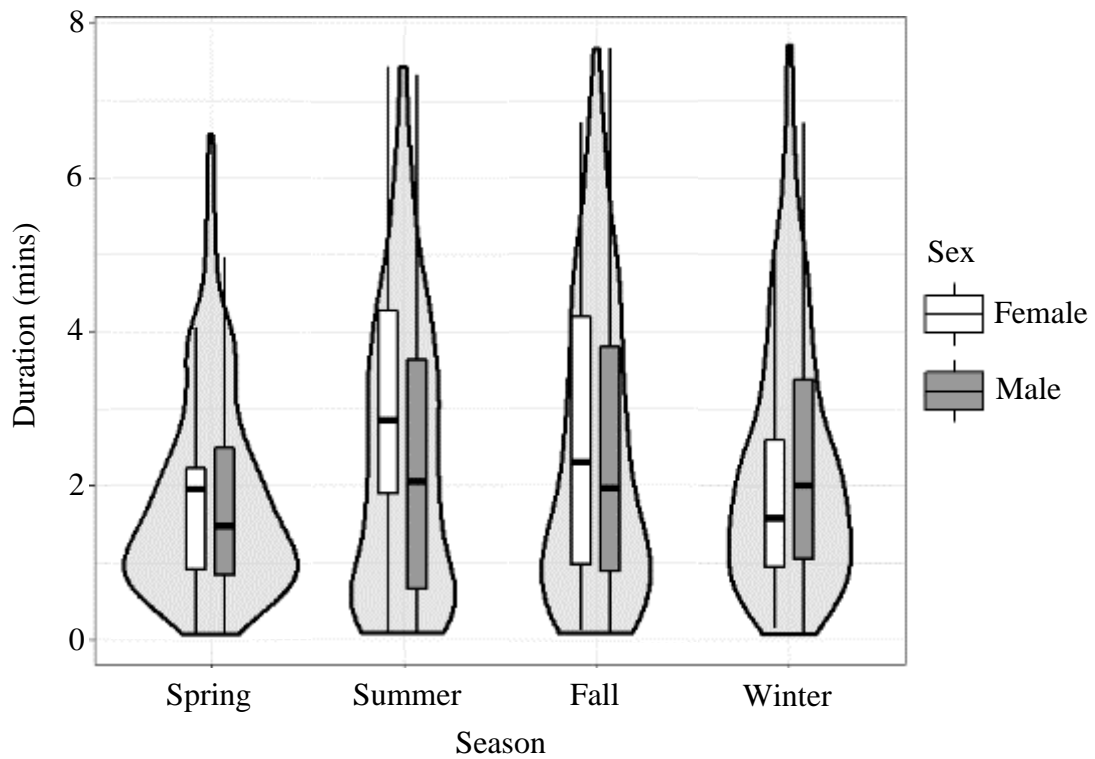
**Figure 5.4** Cage construction and configuration to protect radio frequency identification (RFID) feeder equipment used in behavioral studies of foraging black-crested titmice (*Baeolophus atricristatus*, BCTI) at the Freeman Center in San Marcos, Texas, January 2019–April 2020. A. Wire cages were constructed to allow BCTI into the enclosure but prevent raccoons, squirrels, and other animals from tampering with equipment. Natural perches were installed to provide foraging BCTI with places to land in between obtaining seeds. B. Cages with RFID feeders were mounted ~1.5 m high on a tripod stand to prevent cattle and wild hogs from damaging equipment. Shepherd’s hooks and hardware cloth along the top and bottom of the cage increased cage stability.



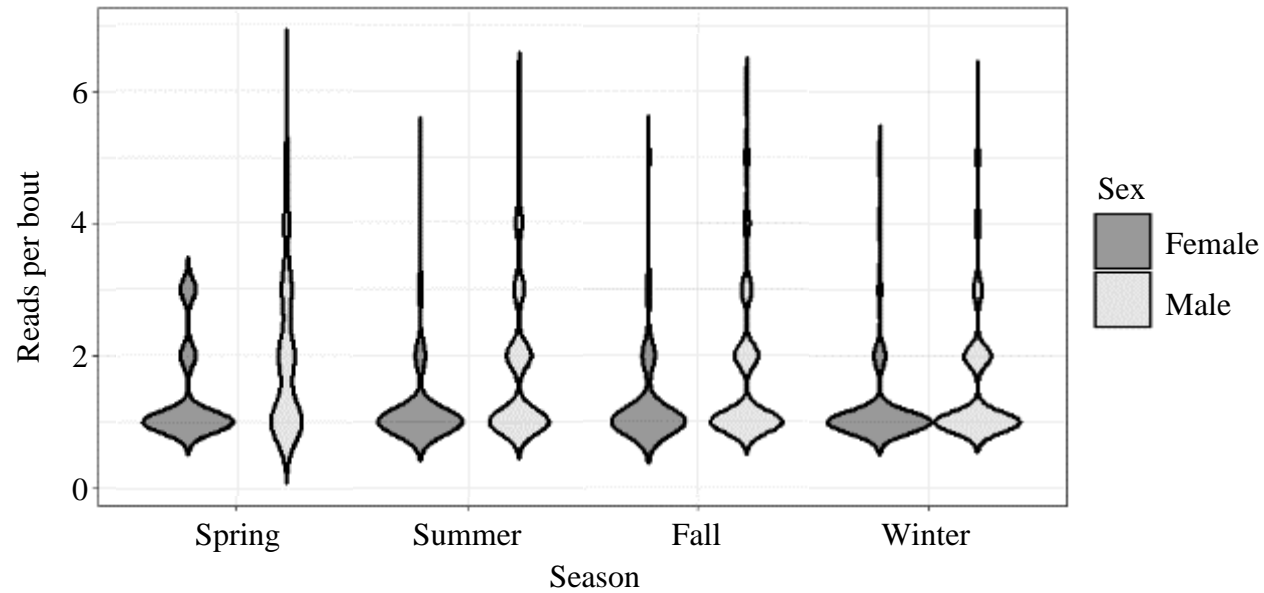
**Figure 5.5** Summary statistics displaying the number of total reads and total feeding bouts (single and multiple read bouts) at each radio frequency identification (RFID) feeding station deployed at the Freeman Center in San Marcos, Texas. Feeders were deployed between January 2019 – April 2020 for foraging behavioral studies of the black-crested titmouse (*Baeolophus atricristatus*). The \* symbol at feeders F01, F03, and F04 indicate that the number of reads exceeded 4,000 (F01 = 4,243, F03 = 5,740, F04 = 9,289).



**Figure 5.6** At twelve established radio frequency identification (RFID) feeding stations at the Freeman Center in San Marcos, Texas, season and the number of reads in a feeding bout ( $n = 5,191$ ) influenced the duration of the feeding bout. Reads were recorded from black-crested titmice (*Baeolophus atricristatus*) that were banded with passive integrated transponder (PIT) tags between January 2019 – April 2020 for foraging behavioral studies.

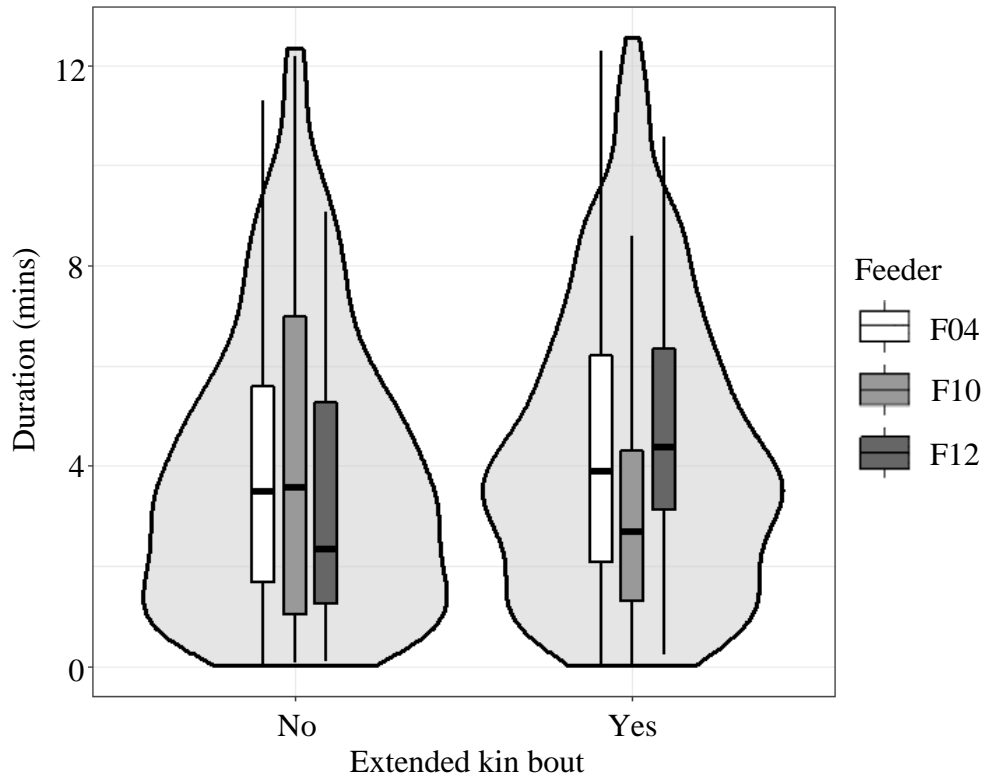


**Figure 5.7** For individual black-crested titmice (*Baeolophus atricristatus*) foraging alone, the duration of recorded feeding bouts ( $n = 1,523$ ) at radio frequency identification (RFID) feeding stations deployed at the Freeman Center in San Marcos, Texas, January 2019–April 2020, was influenced by season. There were no significant differences between the sexes, and single-read feeding bouts were not included in this analysis.

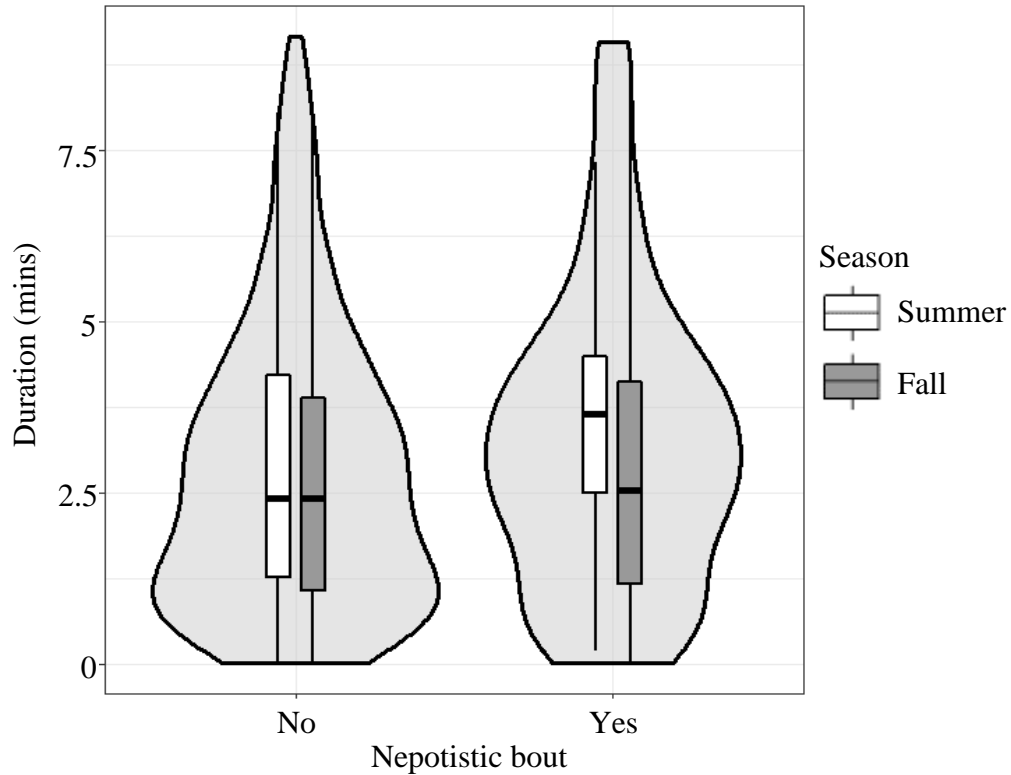


**Figure 5.8** For individual black-crested titmice (*Baeolophus atricristatus*) foraging alone, the number of reads recorded per feeding bout ( $n = 4,411$ ) at radio frequency identification (RFID) feeding stations deployed at the Freeman Center in San Marcos, Texas, January 2019–April 2020, was influenced by season and sex. Single-read feeding bouts were included in this analysis.

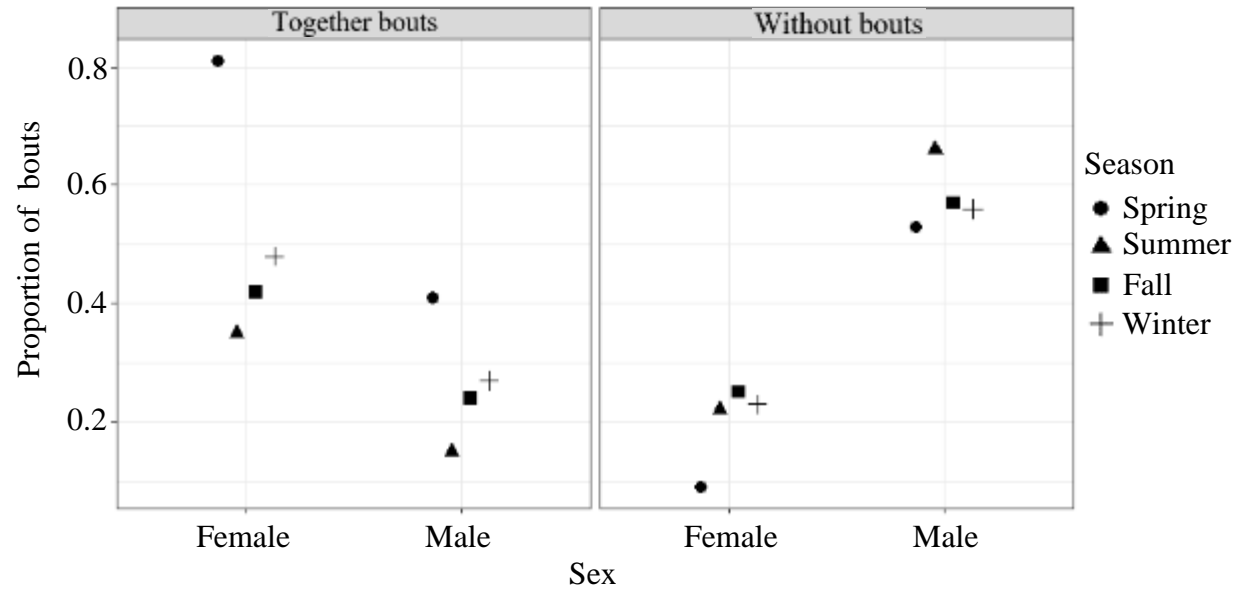




**Figure 5.9** When groups of black-crested titmice (*Baeolophus atricristatus*) were comprised of extended kin (“Yes”), the duration of feeding bouts were longer than when groups were not comprised of extended kin (“No”). Feeding bouts ( $n = 1,298$ ) were recorded at radio frequency identification (RFID) feeding stations deployed at the Freeman Center in San Marcos, Texas between January 2019 – April 2020 for behavioral studies. Only three feeders (F04, F10, F12) recorded adequate data for extended kin analyses.



**Figure 5.10** When groups of two black-crested titmice (*Baeolophus atricristatus*) were considered nepotistic (father or mother with an offspring, “Yes”), the duration of feeding bouts were longer than when groups of two were not comprised of parent and offspring (“No”). Feeding bouts ( $n = 374$ ) were recorded at radio frequency identification (RFID) feeding stations deployed at the Freeman Center in San Marcos, Texas between January 2019 – April 2020 for behavioral studies. Only three feeders (F04, F10, F12) recorded adequate data for extended kin analyses.



**Figure 5.11** For mated pairs of black-crested titmice (*Baeolophus atricristatus*), the proportion of feeding bouts where both male and female were present (Together bouts) out of the total number of bouts each individual made (with or without their mate) was significantly different for males and females, especially during the spring. Additionally, the proportion of feeding bouts an individual in a mated pair made without the other (Without bouts) out of the total number of bouts was significantly greater for males than for females for all seasons. Feeding bouts ( $n = 1,316$ ) were recorded at radio frequency identification (RFID) feeding stations deployed at the Freeman Center in San Marcos, Texas between January 2019 – April 2020 for behavioral studies.

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## VI. CONCLUSIONS

Through four interwoven chapters, this dissertation focused on a kin-structured songbird, the black-crested titmouse (*Baeolophus atricristatus*, BCTI) and how urbanization and weather variability influenced limited dispersal behavior, home range size, body condition, nesting success, productivity, and apparent survival, among other behaviors and social parameters (Chapters II, III, and IV). This dissertation also addressed if resource sharing was a strong kin-selected trait for the BCTI to maintain extended kin relationships (Chapter V). Additionally, throughout all four chapters, I addressed many knowledge gaps pertaining to life history and natural history characteristics of the BCTI that previously had not been studied through scientific methods. Thus, this research is foundational for the species and should provide biologists with a sound framework when designing future projects revolving around the BCTI and possibly other members of the Paridae family.

Overall, populations of BCTI residing in urban locations are likely incurring lower reproductive success and apparent survival rates due to threats and stressors that are not as common in rural settings. Urban environments likely provide less suitable, contiguous habitat for BCTI, therefore reducing the likelihood that juvenile BCTI are able to limit their dispersal and establish kin-structured neighborhoods. Though results from Chapter II demonstrate that urban BCTI retain kin-structure from time to time, the inability to fully associate with kin may be lowering survival rates (Chapter IV) and causing pairs to produce fewer offspring per nest (Chapter III). Moreover, BCTI residing in urbanized locations may be exposed to light and noise pollution, non-native predators, window and vehicle collisions, among a handful of other stressors that are known to

affect other urban avifauna. Therefore, future work should focus on determining if differences in apparent survival and nesting success are due to the lack of kin-structure or from other urban factors.

Interestingly, results from Chapters II – IV present the idea that urban environments are not equal and influence populations of BCTI in different ways. Both Campus and Park BCTI populations are similar to Freeman (rural) regarding most nesting parameters, including nesting success. Yet, BCTI nesting in Residential locations succumb to higher rates of failure, especially as the breeding season progresses. Though I was unable to test this hypothesis directly, I think that the presence of outdoor cats, along with artificial bird feeders that attract rats, racoons, and other predators, influenced the reproductive output of Residential BCTI. In all locations across the study, there were depredation events, revealing that predators were present and frequented nestboxes during the breeding season. However, the concentration of available food that accumulates near and around bird feeders, garbage cans, and in gardens likely increases the density of predators in residential neighborhoods. Thus, people wishing to install nestboxes for BCTI and other songbirds should use caution and make educated decisions on where to install nestboxes and how to deter predators. Else, residential locations may act as an “ecological trap” that leads to population sink dynamics for the BCTI.

Similar to nesting success, urban BCTI are likely experiencing more pronounced stochastic events that lead to unstable apparent survival estimates. Male BCTI may experience higher survival rates compared to rural males during the summer, possibly due to predictable water and food resources that can become scarce in drought years for rural BCTI. However, during the winter months, urban males may experience higher

mortality if patchy vegetation provides less protection from extreme temperatures (Chapters II and IV). Males may have to use more energy defending larger territories in search for resources during inclement weather. Additionally, urban BCTI females had the lowest apparent survival estimates of adult BCTI, and I hypothesize that the stress on females, particularly during the breeding season, is so great that it has carry-over effects on their survival into the harsh winter months, a hypothesis that has been tested in Old World parid species. Even though results from Chapter II revealed that there were no differences in body conditional indices (BCI) between urban and rural BCTI adults or juveniles, I suggest future researchers use additional methodologies designed to examine body condition and health, as I believe there are differences between the populations that I was unable to detect through BCIs.

Arguments associated with the costs and benefits of artificial feeders on wild bird populations appear to be consistent with results from all chapters. I did not examine bird feeder location or intensity of use during my urban BCTI studies, but BCTI were frequently observed at feeders in Residential neighborhoods every year of the study. Artificial feeders can promote early nesting (Chapter III), can reduce home range size (Chapter II), and even influence survival in juveniles and adults (Chapter IV). Additionally, though to a small extent, feeders can provide opportunities for extended BCTI kin to forage together (Chapter V) and may encourage juveniles to limit their dispersal if resources are abundant. I highly encourage future studies to assess how feeders in urban environments alter the dynamics of kin-structure compared to other urban locations where feeders are not present. I hypothesize that although artificial feeders likely attribute to higher survival, I also believe that feeders may falsely influence

juveniles to linger with adults on natal territories for longer periods of time. This could become problematic if neighboring habitat is not suitable or large enough for juveniles to establish kin-structured territories the following spring. Thus, juveniles may be forced to disperse later than expected which could result in lower survival or fewer BCTI locating mates during their first breeding season.

Though this study revealed some interesting behaviors of the BCTI that were previously undescribed, there is always room to expand. This study focused only on BCTI in the central Texas portion of its range, and therefore it would be interesting to compare results from this dissertation to similar studies performed on BCTI located in west Texas (possibly the Davis Mountains or Chisos Basin in Big Bend National Park), north Texas and Oklahoma, and BCTI residing near the border in the south Texas Tamaulipan thornscrub. BCTI in these ecoregions likely have different selective pressures due to dissimilar habitat and climate, which in turn should influence survival, reproductive success, and kin-structure formation. Thus, comparing populations of BCTI throughout their range may further elucidate the importance (or unimportance) of maintaining extended family relationships for the species as a whole.

All in all, this dissertation presented a reliable and cost-efficient way to examine population dynamics and social structure of an understudied songbird. I was able to provide detailed examination of undescribed behaviors of the BCTI through strategic placement of nestboxes, self-constructed RFID feeding stations, and dedicated focal monitoring. I am hopeful that this research will inspire others to examine additional common, but overlooked, species with a more critical eye. Though it is uncertain how the BCTI will respond to climate change and further destruction of natural habitat, I truly

believe that my research will assist in formulating a management plan should BCTI populations begin to sharply decline. I am proud to think that my work may assist in proactive conservation of the BCTI and similar species in the future.