

MISTER PARID'S NEIGHBORHOOD - DISPERSAL BEHAVIOR AND
FLOCKING DYNAMICS OF THE SOCIAL BLACK-CRESTED
TITMOUSE (*BAEOLOPHUS ATRICRISTATUS*)

by

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TABLE OF CONTENTS

	Page
ACKNOWLEDGEMENTS.....	iv
LIST OF TABLES.....	viii
LIST OF FIGURES.....	x
ABSTRACT.....	xii
CHAPTER	
I - FOREWORD.....	1
Study Species.....	4
Thesis Objectives.....	6
II – DISPERSAL FACTORS.....	7
Methods.....	11
Results.....	17
Discussion.....	19
III – FLOCK COMPOSITION, SOCIAL INTERACTIONS AND SEASONALITY.....	24
Methods.....	27
Results.....	30
Discussion.....	31
IV - CONCLUSION.....	36
LITERATURE CITED.....	57

LIST OF TABLES

Table	Page
1. Candidate models examining the relationship between intrinsic and extrinsic factors and delayed dispersal events of black-crested titmice (<i>Baeolophus atricristatus</i>) at the Freeman Center in San Marcos, Texas, 2013 and 2014.....	39
2. Competing generalized linear mixed effects models for delayed dispersal events of black-crested titmice (<i>Baeolophus atricristatus</i>) at the Freeman Center in San Marcos, Texas, 2013 and 2014.	40
3. Candidate models examining the relationship between factors and limited dispersal events of black-crested titmice (<i>Baeolophus atricristatus</i>) at the Freeman Center in San Marcos, Texas, 2013 and 2014.	41
4. Competing generalized linear mixed effects models for limited dispersal events of black-crested titmice (<i>Baeolophus atricristatus</i>) at the Freeman Center in San Marcos, Texas, 2013 and 2014.	42
5. Fisher's Exact Test comparing the observed and expected ratios of male to female black-crested titmice (<i>Baeolophus atricristatus</i>) juveniles that limited their dispersal at the Freeman Center in San Marcos, Texas, 2013 and 2014.	43
6. Candidate models examining the relationship between factors Season/Year and flock size of black-crested titmice (<i>Baeolophus atricristatus</i>) at the Freeman Center in San Marcos, Texas, 2013 & 2014.	44

7. Top model parameter estimates, standard errors (SE), p-values, and confidence intervals of specified factors that predict flock size of black-crested titmice (<i>Baeolophus atricristatus</i>) at the Freeman Center in San Marcos, Texas, 2013 and 2014.....	45
8. Top model parameter estimates, standard errors (SE), p-values, and confidence intervals of specified factors that predict seasonality (breeding/non-breeding) of black-crested titmice (<i>Baeolophus atricristatus</i>) at the Freeman Center in San Marcos, Texas, 2013 and 2014.	46
9. Chi-squared Test of Independence comparing the observed and expected ratios of aggressive and passive interactions between related black-crested titmice (<i>Baeolophus atricristatus</i>) at the Freeman Center in San Marcos, Texas, 2013 and 2014	47

LIST OF FIGURES

Figure	Page
1. Location of the Freeman Center in Hays County, Texas, where black-crested titmice (<i>Baeolophus atricristatus</i>) were color-banded and monitored from April 2013 – September 2014.I.....	48
2. Location of black-crested titmouse (<i>Baeolophus atricristatus</i>) territories on the Freeman Center, San Marcos, Texas, 2013 and 2014.....	49
3. Habitat deliniation within occupied black-crested titmouse (<i>Baeolophus atricristatus</i>) territories on the Freeman Center, San Marcos, Texas, 2013, 2014 and 2015 (though analysis performed only on 2013 and 2014 data).	50
4. Percentage of habitat type found within black-crested titmice (<i>Baeolophus atricristatus</i>) territories ($n = 25$) on the Freeman Center in San Marcos, Texas, 2013 and 2014.	51
5. The fate of juvenile black-crested titmice (<i>Baeolophus atricristatus</i>) ($n = 123$) on the Freeman Center, San Marcos, Texas, 2013 and 2014.....	52
6. Dispersal distances and directions of five individual black-crested titmouse (<i>Baeolophus atricristatus</i>) juveniles on the Freeman Center, San Marcos, Texas, 2013 and 2014..	53
7. Weight rank as a factor for delayed dispersal in juvenile black-crested titmice (<i>Baeolophus atricristatus</i>) ($n = 123$) at the Freeman Center in San Marcos, Texas, 2013 and 2014..	54

8. Number of individual black-crested titmice (<i>Baeolophus atricristatus</i>) in a flock during different Julian calendar dates at the Freeman Center, San Marcos, Texas, 2013 and 2014..	55
9. Territory size (in hectares) between breeding (March-July) and non-breeding (August – February) seasons of black-crested titmice (<i>Baeolophus atricristatus</i>) at the Freeman Center in San Marcos, Texas, 2013 and 2014.....	56

ABSTRACT

The black-crested titmouse (*Baeolophus atricristatus*, hereafter BCTI) is a small, non-migratory passerine that has a tendency to form family flocking groups due to delayed juvenile dispersal each summer. A recently elevated species, separated from its sister-taxon, the tufted titmouse (*Baeolophus bicolor*), the BCTI is an ideal model species for studying family-flocking dynamics. The three goals of my project were to: (1) determine whether intrinsic factors, such as weight or sex, or extrinsic factors, such as territory size or habitat composition, affect the natal dispersal of the BCTI; (2) determine whether BCTI flock or territory size varied across seasons; and (3) examine the social dynamics of familial related BCTI individuals.

Between 2013-2015, 263 individual BCTI were captured and color-banded at the Freeman Center in San Marcos, Texas across a study area comprising approximately 1,400 ha where family flocks were resighted and monitored. Over 800 hours of focal observations were recorded. Using a generalized linear mixed effects model and Fisher's exact test, the intrinsic factors weight ($p < 0.01$) and sex ($p < 0.01$) of juvenile BCTI appeared to influence which individuals in a brood would delay their dispersal. Through another generalized linear mixed effects model, the predictor Julian date was found to be a significant predictor for annual flock size ($p < 0.001$), with territory size increasing an average 3.4 ha ($p < 0.01$) between the breeding season (March-July) and the non-breeding season (August – February). Juvenile BCTI that delayed their dispersal often establish territories adjacent to their parents the following year, thus creating kin-structured neighborhoods. Social interactions between related individuals on neighboring territories were almost always passive as opposed to aggressive ($p < 0.05$), potentially leading to an increase in inclusive fitness for both individuals involved.

Family flocking dynamics of the BCTI are more complicated than previously thought, and future research may yield insight into how this species evolved its current

social structure. With the ever-growing threat of habitat fragmentation, the importance of the family unit and social dynamics to the survival of the BCTI may be key for management of this species.

I - FOREWORD

Sociality, the extent to which individuals tend to interact and associate in groups, has been a growing area of research in ornithology over the last half century (Silk et al. 2014, Wey et al. 2008). Though social behaviors among birds are limited in comparison to humans and other primates, they are nevertheless receiving recognition for being more complex and diverse than previously thought (Farine and Whitehead 2015, Fisher 1954, Krebs 1974, Moller and Birkhead 1993, Wiley 1974). The studies of avian reproduction and flock formation are two areas of avian sociality research that have recently gained momentum.

The most common form of mating system among avian species is that of a pair bond, where a male and a female breed together but do not always equally partake in raising the young (Cockburn 2006). Historically, it was hypothesized that up to 92% of all bird species fell into this category (Lack 1968); however, a more recent assessment shows that only 75-81% of species display a reproductive care system involving pair-bonds (Cockburn 2006). Despite the debate, somewhere between 19-25% of avian species show different, alternative forms of breeding biology and parental care, including male-only care, female-only care, and cooperative breeding (Ekman et al. 2004). As the names imply, male-only and female-only care are found in birds where only one member of the pair is responsible for raising young (Lack 1968). The other sex either emigrates, leaving its mate and offspring to fend for themselves, or it remains in the area having very few, if any, interactions with its family (Owens 2002). This single-individual parental care strategy is more common in bird families that have precocial young that are

mobile and well camouflaged, though there are exceptions found in families that have altricial young (Cockburn 2006).

Cooperative breeding involves more than two adults caring for a single nest (Brown et al. 1978, Koenig et al. 1992). This form of parental care puzzled biologists since offspring were sometimes not direct descendants to all adults helping, implying that some form of indirect fitness benefits were necessary for this to be an evolutionary stable strategy (Emlen 1982, Hamilton 1964, Smith and Ridpath 1972). Though cooperative breeding groups are usually comprised of parents and second-year offspring, certain species recruit unrelated individuals to help on rare occasions (Dickinson et al. 1996, Riehl 2013). All cooperative group formation is initiated by individuals immigrating from one place into the family flock, or by related juveniles limiting or delaying dispersal from their natal territories (Ekman 2006).

Dispersal can happen at different life-history stages; natal dispersal, the permanent movement of an individual away from the place it was born, or breeding dispersal, where individuals of any age permanently change locations for reproductive purposes (Greenwood and Harvey 1982). Dispersal behavior may be an adaptation for avoiding inbreeding (Koenig and Haydock 2004), avoiding competition (Griesser et al. 2008, Strickland 1991), habitat saturation (Fitzpatrick and Woolfenden 1984, Greenwood et al. 1979), resource limitation (Pruett-Jones and Lewis 1990), and inherited exploratory tendencies (Dingemanse et al. 2002).

Individuals move to new locations not only for breeding purposes, but also for seasonal flock formation. Birds aggregate in groups for many reasons, including protection from predators (Roberts 1996, Thiollay and Jullien 1998), thermoregulation

(Cooper et al. 2008, Pinshow et al. 1976), and information sharing (Clark and Mangel 1984, Marzluff et al. 1996). Flocking behavior is also seen in species that migrate together, with each individual apparently becoming aerodynamically assisted by its near neighbors as the group flies in tight formation (Gill 1995). Other birds form social flocks throughout the year, often because they are related and therefore receive inclusive fitness benefits for remaining together (Ekman 2006, Sharp et al. 2011). Some of the most recognizable types of avian flocks are overwintering roosts of hundreds to thousands of individuals congregated in small areas (Russell and Gauthreaux Jr 1999).

There are various methods and technologies designed to study avian flocking, breeding and dispersal behaviors. The particular species in question and the habitat in which it resides can often limit what methodologies are appropriate. For cryptic species that inhabit relatively flat terrain, radio transmitters and PIT tags are becoming increasingly popular, giving precise locations of the individuals through radio signals to a reception tower or via hand-held antennas (Awa et al. 2009). In pelagic and far-flying species, such as the light-mantled sooty albatross (*Phoebastria palpebrata*) that is rarely seen on land except for reproductive purposes, geo locators and satellite transmitters have proven useful (Britten et al. 1999, Weimerskirch and Robertson 1994). Without this type of advanced technology, much would remain unknown for this species as well as many others with which humans infrequently come into contact (Keating et al. 1991, Phalan et al. 2007). Traditional movement and behavioral studies that are still in practice today involve color-banding individuals and gathering data through focal observations in the field (Bibby 2000, Bub 2012). Though this method is more limited in design and usually time consuming, it provides useful information on a finer scale that can often not be

achieved by more recent technologies. Focal observations also allow for examination of avian vocalizations, the actual nature of interspecific interactions, courtship behavior, and resource utilization that cannot be specifically detected by transmitters and geo-locators.

Study Species

As a resident species of Central Texas, the black-crested titmouse (*Baeolophus atricristatus*, hereafter BCTI) is an understudied non-migratory passerine in the Paridae family (Patten and Smith-Patten 2008). Both sexes display a dark gray plumage on their dorsal surface and light gray coloring on the ventral side. As its' name implies, males have a conspicuous black crest, whereas females and juveniles often display a dark grayish-black crest (Peterson 2008). A touch of rusty orange plumage runs along the axillaries and flank region close to the wings. At 15 centimeters in length, the BCTI is smaller than other members in the Family Paridae (such as the tufted titmouse, *Baeolophus bicolor*), but larger than all of the North American chickadee species (Crossley 2011, Peterson 2008).

As one of twelve species of North American Paridae, the BCTI has a fairly limited distribution in comparison to its nearest relatives. Primarily stretching across most of Central Texas, its normal range extends from Mexico into South Texas up to a small portion of West Texas and southwestern Oklahoma (Dixon 1978, Dunn and Alderfer 2011). Across its range, the preferred floristic association is either a mixture of juniper/pine-oak woodlands (*Juniperus*, *Pinus* and *Quercus* spp), brushy coastal and South Texas scrub (e.g. *Prosopis* spp.), or urbanized neighborhoods and parks with a fair

amount of vegetation (Dixon 1978). BCTI will often inhabit fairly open grasslands if large trees are spaced fairly close to each other (personal observation).

The BCTI is a territorial species, with males and females pairing in February for the breeding season. Pairs have one or two broods of young, with clutch sizes between 4-6 eggs (Patten and Smith-Patten 2008). Considered a monogamous species, the BCTI pairs mate for life and show high site fidelity for territories and specific nesting cavities. Nests are constructed of twigs, moss, and grass and are placed in small cavities, though nest boxes are frequently used (Baicich and Harrison 2005). After young have fledged the nest, some juveniles remain close to their parents for several months and are even observed with their family the following year (Rylander 2002). To what extent these family groups are formed and what triggers individuals to remain in the family flock are unknown.

Until recently, the BCTI was considered a subspecies, grouped with its sister taxon, the tufted titmouse (hereafter TUTI), though genetic differentiation between BCTI and TUTI now suggests that the BCTI is a distinct species (Banks et al. 2002). Prior to the separation of BCTI and TUTI as distinct species, observational and experimental research on BCTI were lumped into studies of TUTI; therefore new research and subsequent inferences drawn from TUTI studies should not be routinely considered applicable to the BCTI (Patten and Smith-Patten 2008). Therefore the BCTI is species needing additional study in the areas of its life history, juvenile dispersal events, and family flocking dynamics.

Thesis Objectives

The goal of this study was to examine social flocking and dispersal behaviors of the black-crested titmouse in the Edwards Plateau region of Texas. Specific objectives were to: (1) determine the influence of intrinsic and extrinsic factors on limited and delayed juvenile dispersal, and document if the BCTI cooperatively breeds, (2) examine flock size, flock composition and social interactions of BCTI throughout the year and, (3) document life history traits and ecological behaviors of the BCTI that are currently unknown or that were previously lumped into the knowledge base of the TUTI.

II – DISPERSAL FACTORS

The study of social behaviors among birds is a diverse and ever-evolving field, especially in the realm of family flocking dynamics (Ekman 2006). About 9% of avian species form socially complex breeding groups, often containing a pair of adults, several of their offspring, and on occasion a couple of unrelated ‘floating’ individuals (Cockburn 2006, Condee 1970, Emlen 1995). The mechanisms in which these flocks are typically formed are by limited or delayed natal dispersal (Ekman and Griesser 2002). In limited dispersal, second-year birds remain partially in their natal territory, though they can set up their own territories that parallel or overlap with that of their parents the following year. When this occurs, aggressive encounters between the related individuals are reduced (Hatchwell et al. 2001). In delayed natal dispersal, second-year birds remain in their parents’ territory until the following breeding season begins (February-March). As their parents begin to nest, the related second-year birds either stay to assist their family in rearing young (thus becoming a ‘limited disperser’), or they disperse completely in order to find their own territory for reproductive purposes (Ekman 2006).

Both limited and delayed juvenile dispersal can lead to cooperative breeding, where more than two adults help raise the young in a single nest (Koenig et al. 1992). Usually these individuals are related, however recruitment of unrelated birds also occurs (Dickinson et al. 1996, Riehl 2013). In most socially flocking groups that exhibit cooperative breeding, grown helpers assist in a facultative manner, where the survival of the group is not completely dependent upon helpers (Cockburn 2006, Hatchwell et al. 2004). Facultative helping can occur when second-year birds experience nest failure early

in the breeding season, and thus turn to assist relatives in the rearing of their young (Dickinson 2004). Yet in certain scenarios, such as in the white-winged chough (*Corcorax melanorhamphus*), survival is pivotal on the ability of helpers, making these species obligate cooperative breeders (Brown et al. 1978).

Limited dispersal leads to the formation of kin-structured cooperative groups, where grown offspring do not necessarily help at their parents' nest, but may opportunistically provide some form of apparent altruism to the family group as a whole, such as alarm calling or resource sharing (Dickinson and Hatchwell 2004, Emlen 1995, Hatchwell 2009). In this system, all individuals have the potential to breed on their own neighboring territories, but may forgo doing so when they might accrue greater long-term benefits by helping relatives rather than risking reproduction on their own (Ekman 2006).

Many hypotheses have been proposed to explain why family flocks remain together throughout the year until the following breeding season, and what benefits are gained by doing so. Living in a group and acting in an altruistic manner towards others cannot be explained by direct fitness benefits alone (Hamilton 1964, Sherman 1977, Smith and Ridpath 1972). Therefore other indirect benefits to individuals likely play a role in the maintenance of family flocks, which include resource sharing, heightened vigilance from predators, habitat saturation, and increased indirect fitness through the survival of shared genes (Koenig et al. 1992). The prolonged brood care hypothesis proposes that both parents and juveniles benefit from remaining in a social flock, and therefore parents are less aggressive which may help in keeping juveniles near home (Dickinson et al. 2009, Ekman and Rosander 1992). In some cases, the breeding parents' fitness is decreased when their young are experimentally removed from the flock. In the

Florida scrub jay (*Aphelocoma coerulescens*), juveniles exhibit philopatry and become helpers at their parents' nest the following year. This cooperative breeding behavior has indirect fitness benefits to both the juveniles and the parents since frequencies of shared alleles are being passed to the next generation (Woolfenden 1975). In the long-tailed tit, (*Aegithalos caudatus*), both parents and offspring gain direct fitness benefits through altruistic actions such as alarm calling and resource sharing (Hatchwell et al. 2001). Whether the individuals within these groups are gaining direct or indirect benefits, their overall inclusive fitness is increased in these flocks (Ekman et al. 2001, Hamilton 1964). Therefore in many avian species that exhibit family flocking behavior, natural selection favors juveniles that delay or limit dispersal and remain in socially related groups until opportunities to directly increase their own fitness present themselves (Cockburn 2004, Ekman 2006).

However, elucidating the factors that encourage some juveniles to exhibit philopatry remains a challenge. In some species, biological factors such as sex or weight might determine if that individual will remain in the natal territory for an extended period of time (Green and Cockburn 2001, Koenig et al. 1992). In other cases, ecological factors such as habitat composition or lack of resources might influence juveniles to disperse (Pruett-Jones and Lewis 1990). For each species, it appears to be a case-by-case scenario whereby a complex mixture of biological and ecological factors accumulates and crosses some sort of threshold that precipitates a limited-dispersal or delayed-dispersal scenario.

Certain hatch-year BCTI disperse from their natal territory while others do not (Rylander 2002). Those that remain continue to flock with their parents until the following spring (Patten and Smith-Patten 2008). The second-year individuals that

completely disperse away from their natal territory shortly before the breeding season are considered ‘delayed dispersers,’ whereas those that delay and end up residing with their parents or close them to are considered ‘limited dispersers.’ It is not fully known how often juvenile BCTI exhibit limited dispersal and cooperative breeding (rather than strictly delayed dispersal). However due to the fact that the BCTI is a gregarious species, it is suspected that its social and reproductive structure is more complex than species that are less social.

The factors that influence related second-year birds to delay and/or limit dispersal is also unknown in this species. Even though, in general, male birds more often exhibit philopatry than females (Hatchwell 2009, Sharp et al. 2011), it should not be assumed that this is the case for BCTI without sound observation.

The objective of this study was to determine whether the BCTI exhibits either delayed and/or limited juvenile dispersal to form social family flocks, and what factors influence juvenile BCTI to either delay or limit their dispersal. More specifically, does the BCTI limit dispersal and thus establish cooperative breeding systems or kin-structured neighborhoods, or do they delay dispersal until the following spring and are never seen again in their natal range? Do biological factors such as sex and weight, or ecological factors such as paternal territory size, habitat composition of the territory, or brood size, influence which juveniles remain in their natal range? I hypothesize that: (1) juveniles will exhibit delayed dispersal, residing in their natal territories with their parents until the following breeding season before moving to their own territory; (2) the largest males will delay dispersal (males tend to be the non-dispersing sex in birds, and being heavier may equate to better overall body condition, thus being able to out-compete

lighter male siblings for resources (Tinbergen and Boerlijst 1990)); (3) juvenile BCTI will more likely disperse from their natal territory if the territory is smaller and contains a low percentage of woodland habitat (dispersal could be due to less resource availability, such as food and roosting sites in these areas); (4) larger broods will have more juveniles that disperse their first year.

Methods

Study Site

The Freeman Center (29°56'17.05"N, 98° 0'30.24"W), owned and operated by Texas State University, is located in Hays County, roughly 10 km northwest of San Marcos, Texas (Figure 1). It is positioned on the eastern border of the Edwards Plateau eco-region, making it a part of the Texas Hill Country that has thin clay soils covering limestone rock (Barnes et al. 2000). The majority of this 1,416 ha property is composed of mixed juniper/oak woodlands (various *Juniperus ashei*/*Quercus* spp.), as well as a variety of other habitats including grazed pastures, grasslands (*Bothriochloa ischaemum*, *Schizachyrium scoparium*), and shrublands (*Diospyros texana*, *Ilex vomitoria*, *Forestiera pubescens*) (Barnes et al. 2000). Though the Freeman Center historically was used as a cattle ranch, it is predominantly a teaching and research property that maintains some grazing (mostly cattle).

During the winter of 2012, Texas State University graduate students placed forty bluebird nest boxes throughout the Freeman Center for research purposes. An additional thirty-one boxes were added during the winter of 2013 (see Figure 1). Nearly all BCTI studied in this project were family groups that utilized these bluebird boxes between 2013-2015.

Color Banding

BCTI that occupied nest boxes at the Freeman Center were captured opportunistically during the spring and summer months of 2013, 2014 and 2015. Adults were trapped in their boxes by covering the box entry/exit hole after the individual entered to feed hatchlings. Then the side door was slightly opened, allowing the technician to slide their hand in to remove the adult for banding. Hatch-year BCTI were taken from the nest between 9 and 12 days of hatching, and were then banded and promptly returned to the nest.

Mist nets were occasionally used throughout the year to capture targeted BCTIs, though greater netting efforts were executed during the spring to establish an identifiable population of BCTI pairs and family flocks. When necessary, BCTI playback calls through speakers were used to increase chances of capturing titmice.

Registered aluminum metal bands from the USGS Bird Banding Lab and Darvic colored leg bands (Avinet Supplies Inc.) were placed on all BCTIs captured (adult and hatchlings), giving each individual a unique color combination that could be recognized through binoculars in the field. Measurements were taken at the time of capture, and included wing chord, tarsus, tail and culmen length (in mm), along with the bird's sex (if an adult), weight (using a 60-g spring scale) and location of capture. All birds were handled efficiently and quickly to minimize stress to the individual. All field methods for capturing, handling and banding BCTIs have been approved through IACUC (#0308_0406_07), USFWS permit (MB121162-0), TPWD permit (SPR-0106-005) and USGS Bird Banding Permit (#23546).

Territory Mapping

After BCTIs were captured and banded, individual territories were delineated using a GPS unit (60CSx, Garmin), aerial images from Google Earth, and map and compass (Bibby 2000). Once a banded bird was located by either sight or song, it was followed from a distance (far enough so as to not influence its movements) for 30+ minutes, depending upon the bird's behavior. Throughout the observation period, specific GPS location points were taken, along with written notes on behaviors of interest, such as interactions with other conspecifics, foraging techniques and interesting song/call variations. Each individual BCTI male was observed and followed at least ten times throughout the breeding season with at least 5 days in between visits (after (Bibby 2000)).

Annual family flock home ranges were determined using similar methods. Each family group (particularly after fledgling) was monitored and mapped using GPS units and aerial imaging approximately once every two weeks for 30+ minutes per observation throughout the year. Individuals within the flocks that were not banded as part of the nuclear family group were counted and noted as either hatch-year or adult.

Dispersal Events and Measurements

Focal observations on banded family groups were conducted in the field during routine territory surveys. Through these observations, we determined when young were no longer present in their natal territories, indicating they had either dispersed or had died. Based on juvenile mortality estimates of 70-85% from studies conducted on other parid species, it is more than likely that most juveniles no longer present had not survived

(Ekman and Askenmo 1986). However without radio transmitters, it is difficult to determine the exact fate of the missing individual unless it was observed later in a different location. When banded young did move to distant locations within the Freeman Center survey boundaries, the minimum distance between their natal territory border and their newly observed location was recorded.

All BCTI offspring that remained in their natal territory with their parents for seven months post-fledging were categorized as ‘delayed dispersers.’ Offspring that either dispersed a short distance (less than 400m (Hatchwell 2009, Sharp et al. 2008)), or remained on their parents’ territory throughout the following breeding season were categorized as ‘limited dispersers.’ Individuals that actively helped their parents raise offspring the following year were categorized as ‘cooperative breeders.’

As stated earlier, all birds captured were weighed in cloth bags using a 60-g spring scale. Because all broods were not weighed at the exact same time post-hatch, all individuals within a brood were scored based on their weight rank, with 1 being the heaviest individual, and the highest number being assigned to the lightest individual. Hatchlings with tied weights were ranked with the middle of their shared ranks based on the methodology of ranking in Wilcoxon Sign Ranked Tests. By assigning ranks to individuals within a brood instead of using raw weights, all broods across families could be compared to each other during analysis.

Juveniles are not sexually dimorphic therefore the sex of each individual within a brood was not known at the time of banding. However during occasions when juveniles remained in their natal territory until the follow spring, sex was determined based on behaviors such as calling, defending nest sites, and frequent courtship displays (Patten

and Smith-Patten 2008), and previous records pertaining to such individuals were updated with sex codes retrospectively.

Geographic Information System Analysis

Once all GPS points were recorded for the various BCTI family territories and home ranges (within 3 m accuracy), ArcGIS 10.1 (ESRI, Redlands, CA) software was used to map and analyze data. Minimal convex polygons were created from GPS locations for each banded family; each family's territory was fully delineated throughout the year they were observed.

A vegetation geographic information system (GIS) layer provided by the Texas Parks and Wildlife Department was utilized to analyze habitat composition at the Freeman Center (Texas Parks and Wildlife Department 2013). Because this layer (30 m by 30 m pixels) was created with highly detailed vegetation categories, they were reclassified into three broader vegetation categories: Woodland, Grassland, and Mixed (i.e. a mix between Woodland and Grassland). Vegetation polygons containing more than 75% wooded area were considered Woodland, between 25-75% were Mixed, and less than 25% were classified as Grassland. After each territory polygon was reclassified into these three categories, the percentage of habitat type per total territory area was calculated, allowing vegetation classes to be analyzed across all territories.

There is a possibility that BCTI choose habitat based on a finer vegetation scale than presented in this study, however there is no evidence through observation or previously published studies to infer that these categories are not suitable for this type of study. Since BCTI depend upon trees for their food and roosting sites, the amount of

openness (Grassland) could negatively correlate with how many juveniles could be supported if they do not disperse. Thus a higher percentage of woodland habitat in a territory may allow more juveniles to remain in their natal territory.

Statistical Analyses

ArcMap 10.1 was also used to calculate and analyze average territory size and habitat composition, as well as movement distance of juvenile BCTI.

The programming language R (version 3.0.2) was used to analyze dispersal factors. Two generalized linear mixed effects models (glmer) were created to test whether juveniles that delayed dispersal and those that limited dispersal could be predicted by weight rank, brood size, territory size and percentage of woodland habitat as fixed factor predictors. The models were blocked by BCTI family flock (random predictor) since individual juveniles within the same family were not independent from one another. Dispersal status (binomial: dispersed versus did not disperse) was the response variable. The models are as follows:

Delayed_dispersal ~ weight_rank + woodland + territory_size + brood_size + (1/family)

Limited_dispersal ~ weight_rank + woodland + territory_size + brood_size + (1/family)

If any predictors were close to significance (p -value ≤ 0.05), additional simplified models were run using Akaike's Information Criterion (AIC) model selection. The most

parsimonious model with the lowest AIC weight was then used to generate a p -value* and gather other statistical information. In addition, 95% confidence intervals** were used to reinforce if a predictor was significant or not in the best-fit model.

A Fisher's Exact Test of Independence was used to analyze the differences between sex of the juveniles who limited their dispersal. This test was chosen due to the small sample size of banded male and female BCTI observed in their second year on their natal territories. The null hypothesis (H_0) was, "There is no difference between the number of male and female juveniles that exhibited limited dispersal."

Results

Focal observations on BCTI family flocks were recorded for a total of 805 hours during 267 visitation days at the Freeman Center. The average BCTI territory size ($n = 26$) was 7.19 ± 0.05 ha (Figure 2), with woodland habitat being the highest represented vegetation type found within territories (45%), followed by mixed (30%), and grassland (25%) (Figure 3 and Figure 4).

During the 2013 and 2014 season, 154 BCTI were captured and color banded, including 123 juveniles and 31 adults. These banded birds represented 24 family flocks that were followed throughout the entire year (from breeding season to breeding season). Of the 123 juveniles banded before fledging, 97 dispersed and were never seen in their natal territories again; note that in this study it was almost impossible to distinguish

* p -value = probability value; the probability of calculating a test statistic as extreme or more extreme by random chance alone; p -values below 0.05 will be considered significant for this project.

** 95% confidence intervals contain all plausible values for the given parameter; those that do not contain zero are interpreted that there is a true and significant difference between the mean of the sample and zero; the null hypothesis is rejected.

between dispersal and mortality since individuals were not fitted with transmitters or witnessed dying. Thus they were classified as ‘dispersed’ for this project. The other 26 juveniles remained in their natal territories for an extended period of time (at least seven months post-fledging) and were classified as ‘delayed dispersers.’ Of the 26 delayed dispersers, 15 either did not disperse at all during the next breeding season or set up their own territories within 400 m of their natal territory, and these individuals were also classified as ‘limited dispersers.’ Of the 15 limited dispersers, only 1 individual displayed true cooperative breeding behavior (fed nestlings), and was therefore classified as a ‘cooperative breeder’ (Figure 5).

Five juveniles were observed dispersing a large distance away from their natal territories and were never resighted again in that same area. Though the location in which these individuals moved to when encountered was more than likely not their final destination, the average distance moved from their natal nest box was 2050 m (range 535 m to 3164 m) (Figure 6). Sex of each of these dispersers was indeterminate from focal observation alone.

Through AIC model selection, the best-fit model for delayed BCTI dispersal was that with `weight_rank` and `year` as fixed factor predictors (`mWeight+Year`, $K = 4$, $w_i = 0.46$, $r^2 = 0.21$, Table 1). However, a second competing model with less parameters and a delta AIC value less than 2, had `weight_rank` as the only significant fixed factor predictor (`mWeight`, $K = 3$, $w_i = 0.18$, $r^2 = 0.15$). Both of these competing models were then run as mixed effects models in program R (Table 2). The model `mWeight+Year` had significant p -values for both predictors (0.004 and 0.04 respectively), but only `weight_rank` had a 95% confidence interval that did not contain zero. The model `mWeight` had a significant

p -value (0.004) and a 95% confidence interval that did not contain zero. Thus the best-fit model for the delayed dispersal data was mWeight (Figure 7). In all models run, the factors territory_size and brood_size were not significant. The model that included woodland habitat (mWeight+Year+Woodland, as seen in the AIC Table 1) appeared to be competing (Δ AIC < 2), but due to the larger number of parameters in the model ($K = 5$), it was not considered.

For limited BCTI dispersal, none of the factors used to test the model seemed to fit the data, nor have significant p -values (Table 3). AIC model selection also showed no best-fit model since four different models had Δ AIC values less than or equal to 2. When these models were analyzed in R with glmer, p -values and confidence intervals showed no significance (Table 4).

Of all the banded family groups followed ($n = 24$), 15 contained juveniles that exhibited limited dispersal. The sex of all these limited dispersers was male, with zero juvenile females observed in their natal territory the following year. A Fishers Exact Test of observed versus expected sex ratios (assuming each clutch is roughly 50% males and 50% females) resulted in a p -value of 0.002, with males observed much more than expected, and females less than expected (Table 5); the null hypothesis was therefore rejected.

Discussion

Sex and mass are important when it comes to delayed dispersal in BCTI juveniles, where the largest males tend to be those that show natal philopatry. In other parid species, males tend to be the sex that remains with their parents, often because they inherit their father's territory later in life or because they benefit through resource sharing or predator

vigilance (Grøtan et al. 2009, Kokko and Lundberg 2001). Though not directly tested in this study, I observed on several occasions juvenile males that shared a portion of their father's territory the next year, often successfully breeding and raising young. These same limited dispersers were also witnessed mobbing predators and foraging with their relatives throughout the year. Thus it is likely that limited dispersers receive multiple benefits by residing near home, though additional research needs to be done in order to understand the importance behind these benefits to fitness.

Even though it was not directly measured in this study, it is likely that the heaviest individuals of a clutch were those that hatched first since BCTI eggs hatch asynchronously (Patten and Smith-Patten 2008, Zach 1982). Heaviest individuals can have an advantage over their clutch-mates since size and age may empower one individual over the other when it comes to competition for the attention of a returning parent with food (Zach 1982). Observations on banded BCTI siblings usually showed that the heavier juveniles behaved dominantly over the others, supplanting and chasing the smaller sibling at food or water.

The single banded BCTI family that exhibited a cooperative breeding strategy in 2014 did not seem to behave or interact any differently from the other family flocks with limited dispersing juveniles, nor did they have a larger clutch or nestling survival rate. Therefore it is unknown why this group was unique, but nevertheless leads to the idea that the BCTI may be a species that can vary its reproductive strategy depending on specific location and/or resource availability (Hatchwell et al. 2004, Kraaijeveld and Dickinson 2001). Other populations of BCTI found in different regions of its range may

have higher percentages of helpers at the nest, but until further studies are performed, this conjecture remains unverified.

In my limited-dispersal model, no factors were significant, though weight rank (p -value = 0.09) was close. With a larger sample size and more years of data collection, this factor may become significant, just as it is in the delayed-dispersal model.

One shortcoming of my data collection is that I did not weigh individual hatchlings during the 2013 season. Since the 2013 season was more of a pilot study, I did not yet recognize the importance of this measurement, and thus scored all BCTI juveniles with a weight rank of '3', which is the average of the five fledglings that came from each of those three nest boxes. This in turn could be another reason why weight rank is not significant for my limited dispersal model. Lacking actual weight measurements from the 15 hatchlings from 2013 may also be why the factor 'year' was significant in my delayed-dispersal model; the small sample size is not the best representative of the actual BCTI juvenile population during that year, and thus there may not truly be significance there. However when a follow-up analysis was run excluding the 2013 data, I still did not detect any significant predictors for my limited-dispersal model. A follow-up analysis excluding the 2013 data for my delayed-dispersal model still showed weight_rank as the only significant factor for predicting which juveniles remained in their natal territory. Thus, more data must be collected to determine if there actually is year-to-year variation in both limited and/or delayed BCTI juvenile dispersers.

Vegetation data used for this study was coarse in scale (30 m x 30 m resolution), which may not be detailed enough to capture what habitat types are actually utilized by BCTI in their territories. The TPWD vegetation layer, though still good for larger

landscape assessments, might not capture the finer resolution needed for my study. In the future, ground-truthing of vegetation patches or delineating habitat with more recent aerial photographs would give a more accurate analysis if habitat type actually factors into affecting BCTI dispersal.

The five dispersing juvenile BCTI that I resighted at the Freeman Center were, on average, 2050 m away from the boxes from which they fledged. Even though this sample size is quite small, it opens up the possibility that BCTI disperse further, on average, than other North American *Baeolophus* species (343 m) (Cicero 2000a, Cicero 2000b), but disperse shorter distances than North American *Poecile* species (8-11 km) (Mostrom et al. 2002, Weise and Meyer 1979).

There are many potential confounding factors I did not record that might play a role in BCTI fledgling dispersal. Recent studies show that temperature and rainfall can affect not only nest survival, but also recruitment and flock formation in other social parid species (Christman and Thompson III 2002, Gullett et al. 2015). Related to weather, food availability is another factor to consider when analyzing movement and dispersal. In the tufted titmouse, family flocks are hierarchically organized, and thus resources are often fought over and dominated by the territorial male (Pravosudova et al. 1999, Pravosudova et al. 2001). This can result in passive subordinates dispersing for better foraging opportunities. The density of BCTI in a given area may also have an effect on juvenile philopatry. (Emlen) (1982) describes in part of his ecological-constraints model that if suitable habitat is not available due to population saturation, then the individual might have a better chance of maintaining its alleles in the population by remaining in its natal territory the following year (Emlen 1982, Kokko and Ekman 2002).

The BCTI is a species that resides and thrives in both urban and rural areas of its range. Though the Freeman Center provided a relatively natural rural landscape for this study, it is unknown how the BCTI individuals that live in urban areas differ in behavior, particularly related to dispersal and territoriality. Habitat fragmentation may either limit movements since patch availability is scarce, or cause all individuals to leave the area due to a lack of resources, competition, or increased predation. Future studies comparing both rural and urban populations should be considered, potentially giving insight into how important family groups and kin-related neighborhoods are to the survival and longevity of individuals.

III – FLOCK COMPOSITION, SOCIAL INTERACTIONS AND SEASONALITY

A flock is a large aggregate of birds in a single place at a given time. Often flocks are comprised of a single species, though some are made up of more than one interacting species (Gill 1995, Morse 1970, Waite and Grubb Jr 1988). Size and membership of avian flocks varies depending on the species, seasonality, and location, though in all cases certain fitness benefits are likely obtained by most members of the group (Dolby and Grubb 2000, Fisher 1954). There are several proposed hypotheses to explain why birds flock together, including protection and predator vigilance (Roberts 1996), foraging opportunities (Lack 1968, Thiollay and Jullien 1998), aerodynamics during migration (Gill 1995), thermoregulation over the winter months (Cooper et al. 2008, Pinshow et al. 1976), cooperative breeding and delayed dispersal (Ekman 2006, Emlen 1995, Greenwood and Harvey 1982), temporary mating system gatherings such as lekking (Kokko et al. 1999, Wiley 1974), and communal nesting at rookeries (Buckley 1997, Krebs 1974).

Whenever birds are within a flock, there are inevitably social interactions that occur between individuals, between families, and even between the different species involved. Though many interactions are considered passive, cooperative, or benign, some can be aggressive where fighting does occur (Desrochers et al. 1988, Pravosudova et al. 2001). In many lekking species and winter roost aggregations, hierarchies may be established in order to keep aggressive interactions to a minimal. When individuals learn their rank within the flock, the group can continue to work together gathering resources, attracting mates, and watching out for predators (Ekman and Rosander 1992, Roberts

1996, Wiley 1974). For example, in long-tailed manakins (*Chiroxiphia linearis*), breeding males perform elaborate dances in acrobatic pairs or groups, even though only the dominant male usually mates with the female (Foster 1977). However in another example, black-capped chickadees (*Poecile atricapillus*) in wintering family flocks use dominance hierarchies to aggressively chase subordinate members away from food resources (Desrochers et al. 1988).

The black-crested titmouse (*Baeolophus atricristatus*, hereafter BCTI) is typically found in small family flocks throughout the year, forming when juveniles exhibit natal philopatry after fledgling (Patten and Smith-Patten 2008, Rylander 2002). Unrelated individuals can be members of these family flocks starting in the later summer and fall months, though the reasons for tolerance of these non-kin individuals remains unknown (personal observation). In other passerine species, such as the tufted titmouse (*Baeolophus bicolor*) and western bluebird (*Sialia mexicana*), unrelated individuals often join flocks and replace the breeding male or female if they should die over the winter months (Dickinson et al. 1996, Pravosudova et al. 1999).

Not only do BCTI aggregate with other conspecifics, they also form interspecific guilds during different times of the year (personal observation). In the winter months, BCTI are often accompanied by ruby-crowned kinglets (*Regulus calendula*), orange-crowned warblers (*Vermivora celata*), and blue-gray gnatcatchers (*Polioptila caerulea*). During the summer months, Carolina chickadees (*Poecile carolinensis*) and various woodpecker species (Picidae) can be found foraging in the same group as BCTI. Spring and fall migrants are also attracted to the BCTI, in theory, because the BCTI is a resident

species and therefore have information about the location of available resources (Cimprich and Grubb Jr 1994, Morse 1970).

Though the BCTI is known as a social species, flock size can vary from as few as a breeding pair up to a dozen BCTI, foraging together (Patten and Smith-Patten 2008, Rylander 2002). Reasons for extreme variation in flocking may be related to available resources, territory size and saturation, as well as successful reproduction giving way to juvenile philopatry. None of these mechanisms have been addressed in the BCTI.

As a resident species, the BCTI must shift behaviors with seasonal changes in resources (Brotons 2000). These behavioral shifts, correlated with changes in territory size and thus the amount of preferred woodland habitat, may influence the number of BCTI that are found in a social flock during different seasons. Being a species that is territorial throughout the year, the BCTI may not be able to act as aggressively towards floating, unrelated individuals during the winter months since they expend more energy towards thermoregulation and resource acquisition. Thus tolerance of unrelated members of the flock may add to the total number of individuals found in a social group.

The objective of this study is to determine if BCTI flock composition and BCTI territory size changes throughout the year, along with determining what factors might influence the size of a BCTI flock. Social interactions between family flocks are also addressed in terms of aggression and tolerance. My hypotheses predict that: (1) BCTI flock size will increase during the fall and winter months since some juveniles delay dispersal and floaters also join the group, (2) BCTI territory size will become larger during the non-breeding season and smaller in the breeding season, (3) BCTI flocks will have more members in territories that have a greater percentage of woodland habitat

available for them to use, (4) BCTI will have less aggressive encounters with related individuals that hold neighboring territories.

Methods

Flock Composition and Factors

To study which individual BCTIs made up a flock during various times of the year, all birds were color banded and focally observed according to the methods described in Chapter I. Family groups were followed at least once every two weeks across all season for at least 30 minutes per observation. These locations were marked using a GPS unit, aerial imaging and compass, giving an idea of what habitat and location flocks were utilizing (Bibby 2000). BCTI that were not color banded were included in the total flock count if they were observed passively foraging within the group for an extended period of time.

As described in Chapter I, ArcMap 10.1 was used to analyze territory size and percentage of woodland habitat (Texas Parks and Wildlife Department 2013). Calendar dates were linearized using the Julian date system, where January 1st = 1, January 2nd = 2, etc. This allowed me to analyze seasonal BCTI flock movements without being concerned with exact beginning and end dates across all groups.

Seasonality and territory size/habitat composition

To approach the question of how seasonality affects BCTI territory size and habitat use throughout the year, I used the GPS points taken during focal observations (see Chapter 1 methods) and mapped them using ArcMap 10.1, Territories for each season for each family flock were then created using minimum convex polygons, and

total area in hectares were calculated. Habitat composition of each seasonal territory was then assessed using the same methods as mentioned in Chapter 1.

Seasons were defined as (1) Breeding (March-July) and (2) Non-breeding (August – February). Though these seasons seem well defined, certain groups may have exhibited breeding behaviors before March (courtship displays, advertisement songs), and beyond July (fledgling feed, courtship display (personal observation)). However these occurrences were not common and thus the Breeding and Non-breeding cut-off dates are appropriate for this study based on the natural history of this species in central Texas. Seasons also needed to be defined for this particular analysis in order to establish any possible differences between the Breeding and Non-breeding seasons, whereas a Julian calendar system would blend the two together without a definite start or end date.

Social Interactions

Aggressive and passive social interactions between related individuals of different flocks were tallied during focal observational periods. An interaction was considered aggressive if the two either (1) chased the other away, (2) flew within several meters of each other and displayed agitated wing-quivering or supplanting at the other (personal observation), or (3) were within 20 meters of each other and made dominant, aggression noises (described as “chew” or “R2-D2” calls (personal observation, Patten and Smith-Patten 2008)). An interaction was considered passive if the two individuals either displayed tolerance of one another without any of the aggressive behaviors mentioned above. Neutral interactions, such as counter song between family groups separated by over 20 meters, were not counted as either aggressive or passive.

Only interactions between related individuals were recorded because the relatedness of unbanded birds residing in neighboring territories was unknown.

Statistical Analysis

A generalized linear mixed effects model was used to analyze if the number of BCTI in a foraging flock could be predicted by certain the factors of: seasonality (using a Julian calendar), territory size, percentage of woodland habitat in the territory, brood size, and year. I blocked by family group, as individuals within a flock can influence one another. My response variable was the number of BCTI found in a flock (following a Poisson distribution):

$$\mathbf{Flock_num} \sim \mathbf{season} + \mathbf{year} + \mathbf{woodland} + \mathbf{territory_size} + \mathbf{brood_size} + (1|\mathbf{family})$$

I also analyzed territory size and habitat composition differences during the breeding and non-breeding seasons. Season was the binomial response variable (breeding or nonbreeding), with the categorical factor year and continuous factors territory size and percent woodland habitat within the territory. I blocked by BCTI family since the breeding and non-breeding seasons for each group are not independent from one another.

$$\mathbf{Season} \sim \mathbf{terr_size} + \mathbf{year} + \mathbf{woodland} + (1|\mathbf{family})$$

Aggressive vs. passive social interactions between related BCTI family flocks were analyzed using a Chi-squared test. Here I assumed that if BCTI are not gaining any

kind of indirect fitness benefits by taking up a territory directly next to their kin, then social interactions between the two should be a 1:1 ratio of aggressive and passive interactions by chance alone. Reasoning behind this is based off of observational data that shows that BCTI are often found in passive fusion flocks throughout the year, and thus this species is not always aggressive to all outside intruding groups (personal observation). However if BCTI create kin-related neighborhoods because it is beneficial to their overall fitness, then individuals should be more passive towards relatives.

All statistical analyses were conducted using the programming language R (version 3.0.2).

Results

Complete flock composition data was collected from family groups ($n = 21$) during the 2013 and 2014 seasons. When flock size was plotted against season for each year, the data revealed a quadratic trend, and thus an additional factor, Season^2 (also centered) was placed in the full model (Table 6, Figure 8). However the linear predictor Season was not removed from the model since it was not certain if the intercept equaled zero, despite the evidence from Figure 8 that this predictor is quadratic.

The best-fit model for predicting flock size was $m\text{Season} + \text{Season}^2 + \text{Year}$, with the lowest AIC value and highest Akaike weight (0.84). Both Season^2 and Year had significant p -values (<0.0001 and 0.002 respectively), and confidence intervals that did not cross zero (Table 7).

The average territory size during the breeding season was 3.2 ± 0.3 ha, and 6.6 ± 0.6 ha for the non-breeding season (Figure 9). Territory size (p -value < 0.01 , confidence interval not crossing zero) changed from season to season (Table 8). All other factors in

the model did not show a significant difference between breeding and non-breeding seasons.

A total of 40 different social interactions were observed between related family flocks of BCTI. Of these interactions 31 were passive and 9 were aggressive. There were more passive interactions observed between related flock members than predicted by chance alone ($X^2 = 5.41$, $df=1$, p -value = 0.02, Table 9).

Discussion

BCTI flocks with relatives throughout the non-breeding season, unlike many other Parid species that do not form related social groups throughout the year (Brotons 2000, Condee 1970). BCTI also stay in related flocks when their reproductive strategy is not typically cooperative. Most cooperatively breeding species remain in related territorial flocks throughout the year, almost as a precursor for preparing juvenile helpers that limit or delay their dispersal (Ekman 2006). Thus whether the BCTI remains in these flocks during the fall and winter for protection against predation, for resource or information sharing, or for other reasons still remains unknown.

BCTI flock size fluctuated throughout the year, and Julian date was a good predictor for number of flock members at a given time. This apparent shift in group size makes sense, given that post-fledgling, several juveniles may limit their dispersal and remain with their parents instead of emigrating to new areas. This increase in flock membership occurs around May-June. However once breeding season nears (February the following year), juveniles either set up territories adjacent to their parents, or emigrate presumably in search for a mate/better habitat (personal observation); thus membership numbers drop, and the fluctuation continues.

There was no correlation between flock size and territory size or habitat composition. The lack of relationship between flock size and woodland habitat does supports my previous results that flock size (often containing many of the juveniles that do not disperse) does not necessarily depend on such ecological factors. BCTI are habitat generalists, known to utilize a variety of habitats (Patten and Smith-Patten 2008), and this generalist behavior appears to hold true for flock composition as well; territories comprised of all habitat types and sizes were equally as likely to support flocks with many members.

Unrelated BCTI individuals that joined family flocks after the breeding season were not directly addressed in this study, but are nevertheless important since their numbers added to total flock membership. These recruited BCTI of each flock were counted during focal observation, though the reason for their tolerance among the related group was not investigated. In other species, such as the western bluebird, related individuals were often recruited into larger family flocks in theory to either inherit their father's territory, or to increase their own fitness through indirect means (Dickinson et al. 2009). Though juveniles definitely display limited dispersal for similar reasons, this still does not explain unrelated floaters and their role in BCTI social flocks. It is of interest whether the majority of these floaters are male or female; one would speculate that due to the fact that females are the more dispersing sex of this species, they might comprise the majority of the unrelated floaters counted within flocks. In the willow tit (*Parus montanus*) and crested tit (*Parus cristatus*), research has shown that unrelated individuals are usually females that join in a 1:1 ratio with the number of unpaired males in the flock (Ekman 1979). Whether this is the case for the BCTI, it is still unknown, though there is

evidence that similar flock recruitment of unrelated females may hold true (personal observation).

There are several other factors that may affect flock membership that were not addressed in my study. Recent investigation shows that seasonal temperatures can influence recruitment on certain flocking parid species, as well as affect the abundance of food availability for the survival of those recruited into unrelated groups (Grøtan et al. 2009, Gullett et al. 2015). Future studies analyzing BCTI flock dynamics should include similar abiotic factors since they might further explain membership numbers across and between recorded seasons.

Density of conspecifics in a given area may have also influenced the number of individual BCTI found in a social flock. Habitat saturation can lead greater juvenile philopatry (Kokko and Lundberg 2001), or can increase aggressive interactions between individuals, which force dispersal, and emigration (Pravosudova et al. 1999). I did not conduct surveys for estimation of BCTI density during this study however, so it is unclear if habitat saturation is occurring at the Freeman Center.

Though human disturbance was low at the Freeman Center when compared to nearby urban landscapes, it could have been an influential predictor on BCTI flock size. On several occasions while making focal observations, I was interrupted by passing vehicles, riding lawn mowers, or educational classes that were co-using the same location as my banded birds. The negative impacts on BCTI from these human disturbances are more than likely minimal, but could potentially be quantified in future studies to see if there is any correlation.

Territory size during the breeding season and the non-breeding season differed greatly for the Freeman Center population of BCTI, with a significant increase in size during the non-breeding season. In all cases, both breeding and non-breeding territories overlapped to a large extent, meaning that territories did not shift in location during the different seasons, just expanded and contracted. This trend is not uncommon for residential species living in areas of mild and moderate temperatures extremes across all seasons (Kraaijeveld and Dickinson 2001). At latitudes where winters are harsh, annual territories may shift in location as well as size since resources are scarce and have to be sought out (Salomonson and Balda 1977). Thus with the BCTI residing in an area of Texas with relatively mild winters, resources are probably available to a certain extent to where large movements between the seasons is unnecessary.

As discussed in Chapter I, a shortcoming of this study was the lack of fine-scaled habitat assessment. The TPWD 30 m x 30 m resolution vegetation layer provided a convenient and quick way to add a habitat component to my research, yet the coarse scale in which this layer was made may not provide enough detail to capture if habitat shifts are made during different seasons of the year for the BCTI. It has been discovered that other species shift their wintering territories where resources are more available (Kraaijeveld and Dickinson 2001), and this could still be the case with the BCTI, yet the coarse scale resolution of my vegetation layer was not able to detect this shift. By ground-truthing the different habitats out at the Freeman Center, or delineating my own habitat polygons from aerial imaging could possibly provide a better assessment to this question.

There were more passive than aggressive interactions between related family groups. BCTI do create kin-structured neighborhoods (personal observation), so there are likely indirect benefits in behaving passively towards relatives, such as resource sharing and an increase in predator vigilance.

One occurrence of cooperative breeding was observed during the spring of 2014. A second year male did not disperse and joined his parents in the rearing of their new brood. There were never aggressive interactions observed between the parents and this son, nor the new fledglings and their brother. This behavior presumably increased the fitness to all parties due to the passive nature of social interactions between related BCTI.

Since banding all individuals within a given area is very difficult, not all individuals observed were uniquely marked. This is unfortunate as I was unable to tell if interactions between banded and unbanded flocks were between related or unrelated individuals. Many interactions that I witnessed and documented may have been between related neighbors, though there is no way to ascertain. Hopefully as this study continues, a larger population of identifiable, banded individuals will provide a larger sample size for comparing interactions between related BCTI at the Freeman Center.

Flock membership, seasonal territoriality and passive (and even beneficial) interactions between related individuals had never been thoroughly observed and analyzed for the BCTI prior to this study. Though there is still much to be discovered, this study should hopefully provide baseline ecological and behavioral information on the BCTI that will be pertinent to future research.

IV - CONCLUSION

There is compelling evidence that social interactions and behaviors among birds are more detailed and complicated than previously thought. Break-through research continues to be made across the globe on avian species that are abundant and widely studied (Dhondt 1989, Gullett et al. 2015), as well as on birds that are rarely seen in exotic locations (Awa et al. 2009, Weimerskirch and Robertson 1994). Each study, no matter the location or species, gives a glimpse into a greater picture of how far our knowledge has come, and yet how much still remains unknown.

With ever-evolving technology being designed and produced, it is of great interest what questions will be answered in the near future in regards to avian movement and dispersal and the importance these behaviors have on a local and global scale. Satellite transmitters and geolocators are already producing results showing how climate change is affecting migration routes and migration departure times (Fox et al. 2003, Hooijmeijer et al. 2014). Radio-telemetry is revealing how deforestation and habitat fragmentation disrupts the connectivity of populations (Hansbauer et al. 2008). Though these discoveries are nothing less than impressive, smaller and simpler movement and dispersal studies should never go unappreciated since they often lay the groundwork for furthering the knowledge about a species as a whole.

As biological indicators for healthy ecosystems, the study of birds and the habitats they occupy can give clues as to how robust and stable a particular location is. Though certain species are residential and may not occupy large ranges, they still fill an ecological niche that affects other biotic and abiotic systems. Thus an abnormal fluctuation in abundance or a shift in behavior should be closely monitored since it could

have greater implications. Documenting dispersal and flocking movements can lead to the discovery of ecological sources, sinks or traps. Observing social dynamics may deepen our understanding of the role that particular species plays in its community. For example, Carolina chickadees and tufted titmice are often considered the ‘police officers’ of the forest since other avian and mammal species react to their alarm calls, knowing to take shelter or help mob a predator (Bartmess-LeVasseur et al. 2010, Nolen and Lucas 2009). Thus these two birds serve a greater purpose for this particular ecosystem, and a shift in the abundance of either of these species could lead to detrimental changes for others.

The Black-crested Titmouse of the Edwards Plateau of Texas is common yet understudied, which is one main reason why I choose to do my research on it. Before this project started, it was unknown that the BCTI creates kin-structured neighborhoods through limited dispersal of the heaviest juvenile males. Though this gives way to many questions as to how such a complex community system evolved, the main interest should be the importance behind these related neighborhoods in regards to BCTI population dynamics.

Since the BCTI can have either a cooperative (rare) or non-cooperative breeding strategy, it may thrive in a variety of habitats and surroundings more so than species that strictly breed in a non-cooperative manner. However like western bluebirds in California, the BCTI may shift its reproductive strategies towards more cooperative or non-cooperative means depending on the specific location, habitat type, or density of other conspecifics (Kraaijeveld and Dickinson 2001). Thus further banding and monitoring

studies of BCTI should be made throughout its' range in order to get a better grasp as to how prevalent these two mating systems are.

By examining this species' basic ecology, we may be able to manage for the BCTI in the future if its' status ever becomes threatened or endangered. Understanding natal dispersal and flock movements gives way to identifying connectivity among local populations, which then can lead to larger concerns with the species' survivability and gene flow. Though the BCTI seems to thrive in both rural and urban communities, it is unpredictable how urbanization will eventually affect this bird's abundance. Therefore having a solid foundation of the BCTI's basic behaviors and interactions may prove important for the future.

Table 1. Candidate models examining the relationship between intrinsic and extrinsic factors and delayed dispersal events of black-crested titmice (*Baeolophus atricristatus*) at the Freeman Center in San Marcos, Texas, 2013 and 2014.

Model	K^1	AIC ²	Δ^3	Log-likelihood	w_i^4	r^2^5
mNull	7	126.81	5.29	0.07	0.03	0.22
mWeight	3	123.34	1.82	0.40	0.18	0.15
mWeight+Year	4	121.52	0.00	1.00	0.46	0.21
mWeight+Year+Woodland	5	122.97	1.45	0.48	0.22	0.22
mWeight+Woodland	4	124.59	3.07	0.22	0.1	0.16
mYear+Woodland	4	131.4	9.88	0.01	0.00	0.04

¹ K = the number of parameters estimated in the given model.

² AIC = Akaike's Information Criterion.

³ Δ = the difference in AIC values between the model in question and the model with the lowest AIC value.

⁴ w_i = the Akaike weight that shows relative model support.

⁵ r^2 = how well the model fits the data. Conditional and marginal r^2 values are equal to each other in these models and are therefore reported as just r^2 .

*Boldface values indicate top completing models.

Table 2. Competing generalized linear mixed effects models for delayed dispersal events of black-crested titmice (*Baeolophus atricristatus*) at the Freeman Center in San Marcos, Texas, 2013 and 2014.

Model	Coef. Est. ¹	SE ²	z-value ³	p-value	C.I. lb ⁴	C.I. ub
mWeight						
family (intercept)	-0.17	0.52	-0.33	0.74	-1.20	0.86
weight_rank	0.52	0.18	2.89	0.004	0.18	0.89
mWeight+Year						
family (intercept)	-1.33	0.79	-1.67	0.09	-2.93	0.22
weight_rank	0.58	0.20	2.91	0.004	0.21	1.00
year	1.21	0.60	2.01	0.04	-0.004	2.38

¹ Coef. Est. = the coefficient estimate of the given parameter in the model.

² SE = the standard error of the parameter in the given model

³ z-value = the given test statistic for each parameter in the given model

⁴ The 95% lower bound (lb) and upper bound (ub) confidence intervals for each of the parameter estimates in the given model.

*Note: p-values and confidence intervals in boldface are statistically significant.

Table 3. Candidate models examining the relationship between factors and limited dispersal events of black-crested titmice (*Baeolophus atricristatus*) at the Freeman Center in San Marcos, Texas, 2013 and 2014.

Model	K¹	AIC ²	Δ ³	Log-likelihood	w_i ⁴	r^2 ⁵
m2Null	7	99.11	5.82	0.05	0.02	0.00
m2Weight	3	94.27	0.98	0.61	0.22	0.00
m2Weight+Year	4	93.29	0.00	1.00	0.35	0.00
m2Weight+Year+Woodland	5	95.15	1.86	0.39	0.14	0.00
m2Weight+Woodland	4	96.20	2.91	0.23	0.08	0.00
m2Year	3	94.49	1.20	0.55	0.19	0.00

¹ K = the number of parameters estimated in the given model.

² AIC = Akaike's Information Criterion.

³ Δ = the difference in AIC values between the model in question and the model with the lowest AIC value.

⁴ w_i = the Akaike weight that shows relative model support.

⁵ r^2 = how well the model fits the data. Conditional and marginal r^2 values are equal to each other in these models and are therefore reported as just r^2 .

* Note: there are no competing models.

Table 4. Competing generalized linear mixed effects models for limited dispersal events of black-crested titmice (*Baeolophus atricristatus*) at the Freeman Center in San Marcos, Texas, 2013 and 2014.

Model	Coef. Est. ¹	SE ²	z-value ³	p-value	C.I. lb* ⁴	C.I. ub*
m2Weight						
family (intercept)	0.97	0.62	1.56	0.12	-0.22	2.25
weight_rank	0.35	0.21	1.66	0.10	-0.05	0.79
m2Weight+Year						
family (intercept)	-0.18	0.92	-0.20	0.84	-2.03	1.62
weight_rank	0.40	0.23	1.70	0.09	-0.04	0.90
year	1.24	0.68	1.83	0.07	-0.18	2.54

¹ Coef. Est. = the coefficient estimate of the given parameter in the model.

² SE = the standard error of the parameter in the given model.

³ z-value = the given test statistic for each parameter in the given model.

⁴ The 95% lower bound (lb) and upper bound (ub) confidence intervals for each of the parameter estimates in the given model.

*Note: there are no significant p-values or 95% confidence intervals.

Table 5. Fisher's Exact Test comparing the observed and expected ratios of male to female black-crested titmice (*Baeolophus atricristatus*) juveniles that limited their dispersal at the Freeman Center in San Marcos, Texas, 2013 and 2014.

Sex	Observed	Expected¹
Female	0	7
Male	15	8

* p -value = 0.002; 95% confidence interval = (2.6, inf), and thus does not cross zero.

¹ This test was run using data $n = 15$ limited dispersers, and therefore the expected value of 7.5 for both male and female juveniles represents the scenario that limited dispersal occurs equally among sexes. Because Fisher's Exact Test will not calculate statistics from decimals estimates, a conservative 8 was placed in 'male – expected' cell, and 7 in the 'female – expected' cell.

Table 6. Candidate models examining the relationship between factors Season/Year and flock size of black-crested titmice (*Baeolophus atricristatus*) at the Freeman Center in San Marcos, Texas, 2013 & 2014.

Model	K^1	AIC ²	Δ^3	Log-likelihood	w_i^4	Marg. r^2 ⁵	Cond. r^2 ⁶
m3Null	8	1145.71	4.08	0.13	0.11	0.16	0.16
m3Season+Season²+Year	5	1141.63	0.00	1.00	0.84	0.16	0.16
m3Year	3	1178.72	37.09	<0.01	<0.01	0.02	0.03
m3Season+Season ²	4	1147.39	5.76	0.06	0.05	0.13	0.15

¹ K = the number of parameters estimated in the given model.

² AIC = Akaike's Information Criterion.

³ Δ = the difference in AIC values between the model in question and the model with the lowest AIC value.

⁴ w_i = the Akaike weight that shows relative model support.

⁵ Marginal r^2 = proportion of variance explained by the fixed predictors.

⁶ Conditional r^2 = proportion of variance explained by the model.

*Note: the model in boldface is the top competing model.

Table 7. Top model parameter estimates, standard errors (SE), *p*-values, and confidence intervals of specified factors that predict flock size of black-crested titmice (*Baeolophus atricristatus*) at the Freeman Center in San Marcos, Texas, 2013 and 2014

Model	Coef. Est. ¹	SE ²	z-value ³	<i>p</i>-value	C.I. lb ⁴	C.I. ub
m3Season+Season²+Year						
family (intercept)	1.94	0.07	27.04	<0.01	1.79	2.08
Season	-0.06	0.03	-1.92	>0.05	-0.12	>0.01
Season ²	-0.18	0.03	-6.23	<0.01	-0.23	-0.12
Year	-0.22	0.07	-3.05	<0.01	-0.36	-0.07

¹ Coef. Est. = the coefficient estimate of the given parameter in the model.

² SE = the standard error of the parameter in the given model.

³ z-value = the given test statistic for each parameter in the given model.

⁴ The 95% lower bound (lb) and upper bound (ub) confidence intervals for each of the parameter estimates in the given model.

*Note: *p*-values and confidence intervals in boldface are significant.

Table 8. Top model parameter estimates, standard errors (SE), *p*-values, and confidence intervals of specified factors that predict seasonality (breeding/non-breeding) of black-crested titmice (*Baeolophus atricristatus*) at the Freeman Center in San Marcos, Texas, 2013 and 2014.

Model	Coef. Est. ¹	SE ²	z-value ³	<i>p</i> -value	C.I. lb ⁴	C.I. ub
m4Full						
family (intercept)	-5.35	2.10	-2.54	0.01	-7.29	-0.63
Terr_size	1.23	0.43	2.87	< 0.01	0.36	1.47
Year	-0.09	1.19	-0.07	0.94	-2.21	2.30
Wood	< -0.01	0.01	-0.15	0.88	-0.02	0.02

¹ Coef. Est. = the coefficient estimate of the given parameter in the model.

² SE = the standard error of the parameter in the given model.

³ z-value = the given test statistic for each parameter in the given model.

⁴ The 95% lower bound (lb) and upper bound (ub) confidence intervals for each of the parameter estimates in the given model.

*Note: the *p*-value and confidence intervals in boldface are statistically significant.

Table 9. Chi-squared Test of Independence comparing the observed and expected ratios of aggressive and passive interactions between related black-crested titmice (*Baeolophus atricristatus*) at the Freeman Center in San Marcos, Texas, 2013 and 2014.

Interaction	Observed	Expected¹
Aggressive	9	20
Passive	31	20

* Note: $X^2 = 5.41$, $df=1$, p -value = 0.02.

¹ This test was run using data from $n = 40$ BCTI interactions between related individuals. The expected value of 20 for both types of interactions is based on the assumption that each are equally likely to occur between individuals if there is no benefit for passive or aggressive behavior toward family.

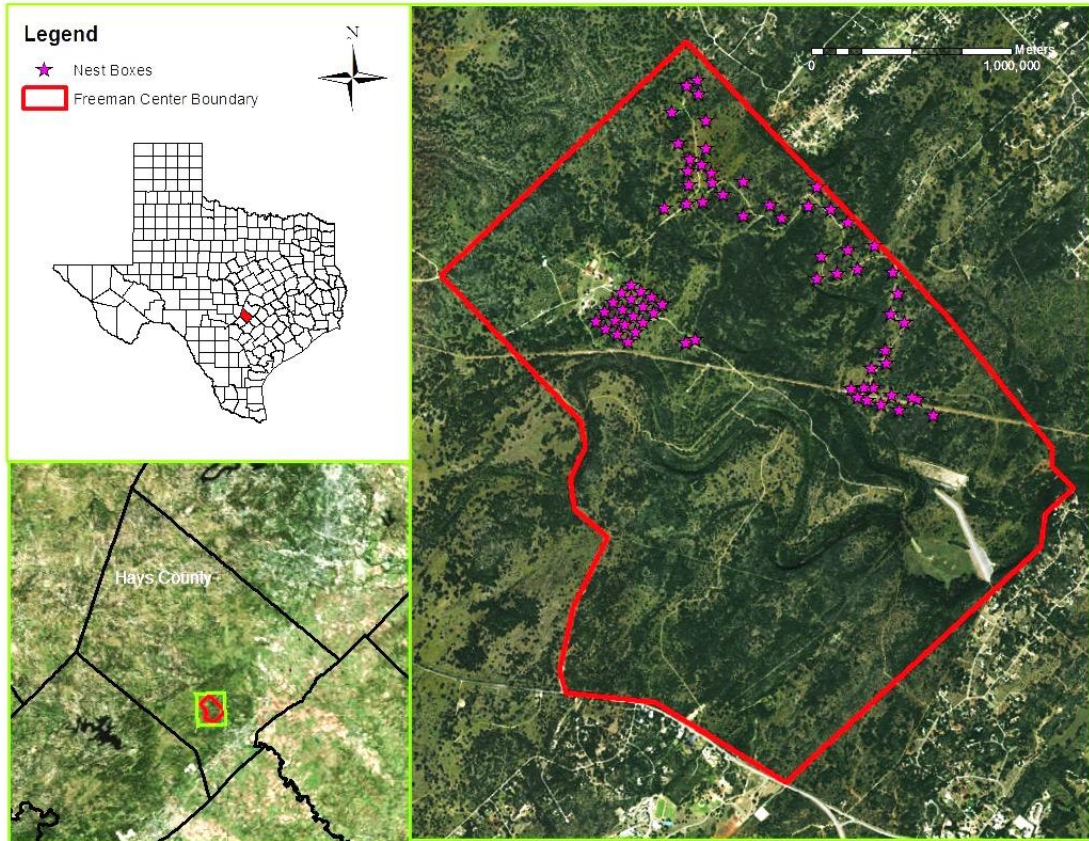


Figure 1. Location of the Freeman Center in Hays County, Texas, where black-crested titmice (*Baeolophus atricristatus*) were color-banded and monitored from April 2013 – September 2014. All nest boxes at the Freeman Center are shown, though not all were occupied by BCTI.

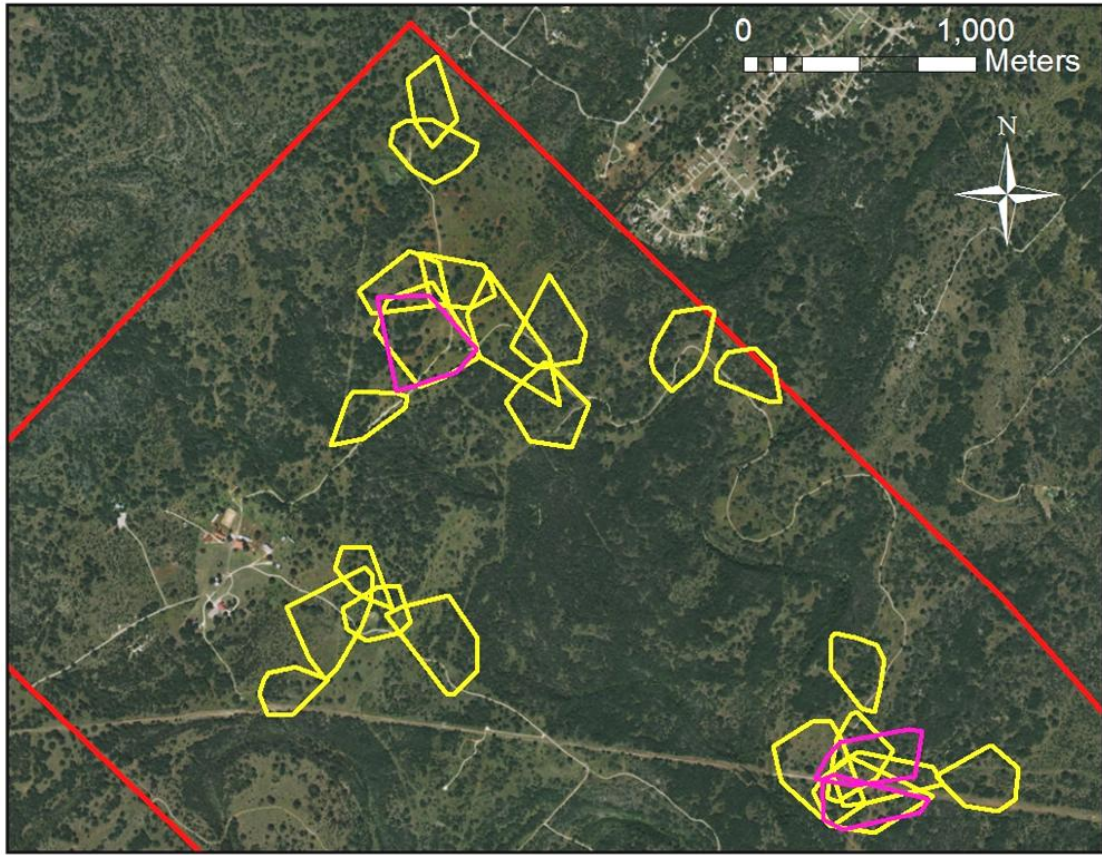


Figure 2. Location of black-crested titmouse (*Baeolophus atricristatus*) territories on the Freeman Center, San Marcos, Texas, 2013 and 2014. Those outlined in pink are from 2013 ($n = 3$), and those outlined in yellow are from 2014 ($n = 22$). Note the frequent overlap in territories during the same year.

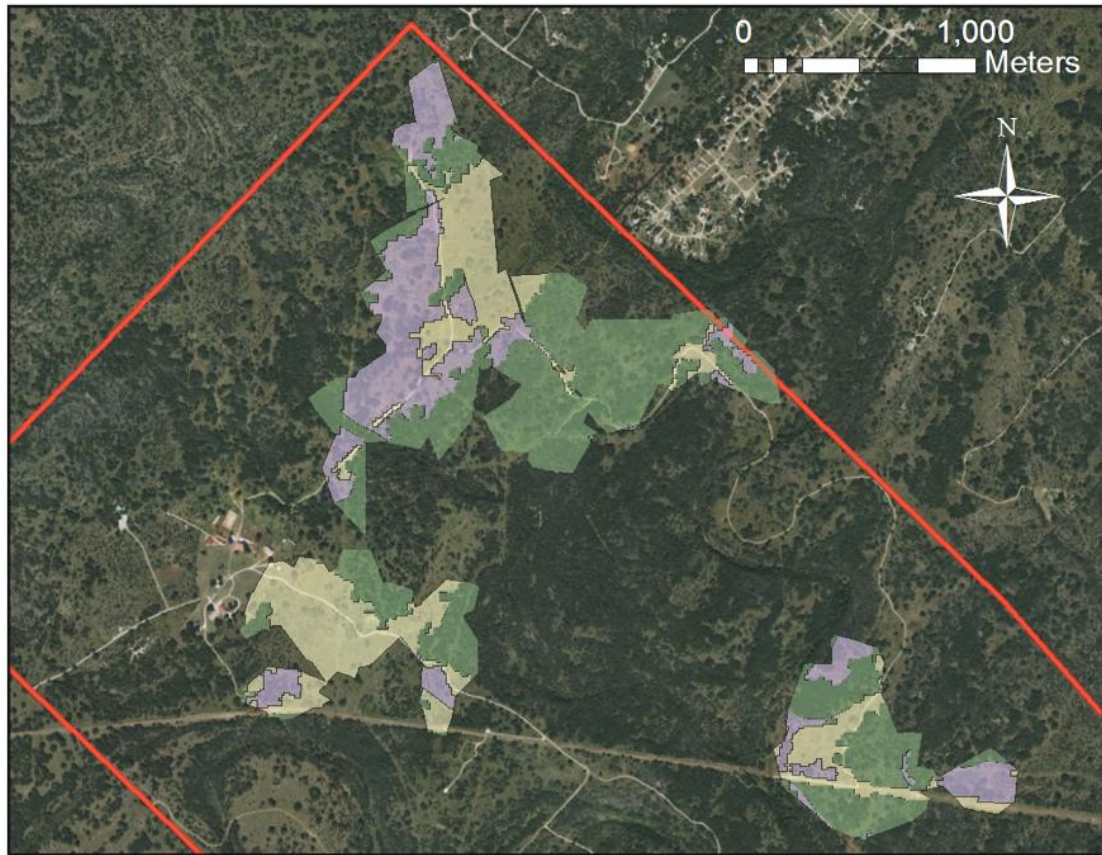


Figure 3. Habitat delimitation within occupied black-crested titmouse (*Baeolophus atricristatus*) territories on the Freeman Center, San Marcos, Texas, 2013, 2014 and 2015 (though analysis performed only on 2013 and 2014 data). Vegetation layers seen above represent woodland (green), grassland (yellow), and mixed woodland and grassland (purple) habitat.

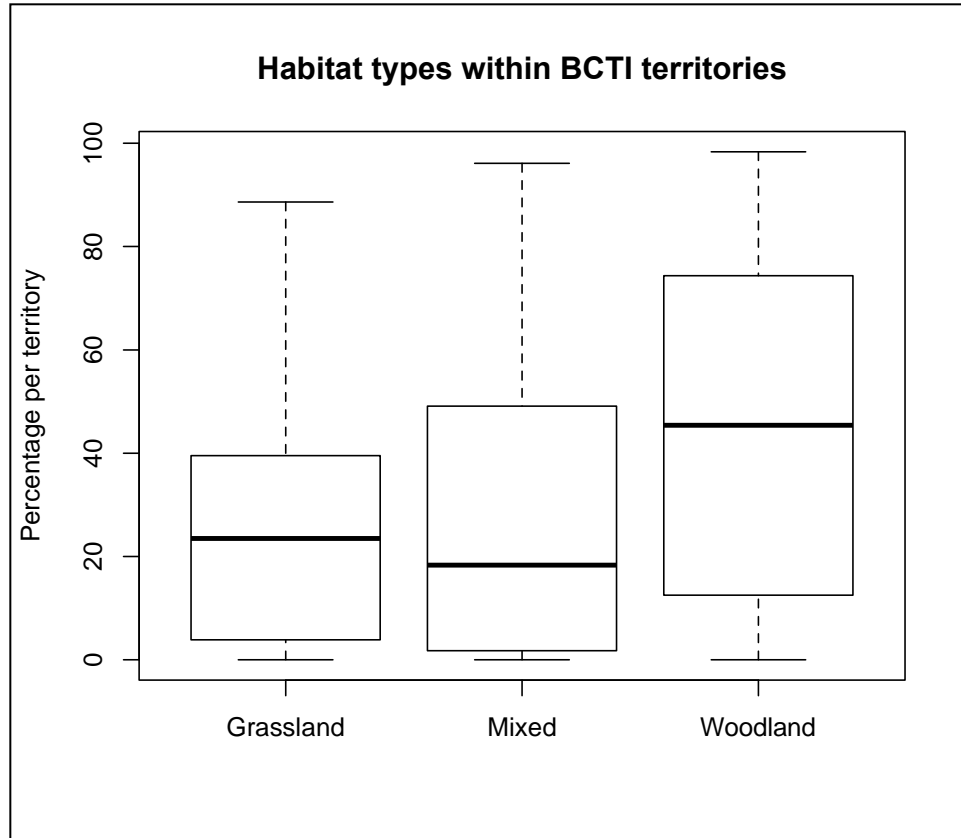


Figure 4. Percentage of habitat type found within black-crested titmice (*Baeolophus atricristatus*) territories ($n = 25$) on the Freeman Center in San Marcos, Texas, 2013 and 2014.

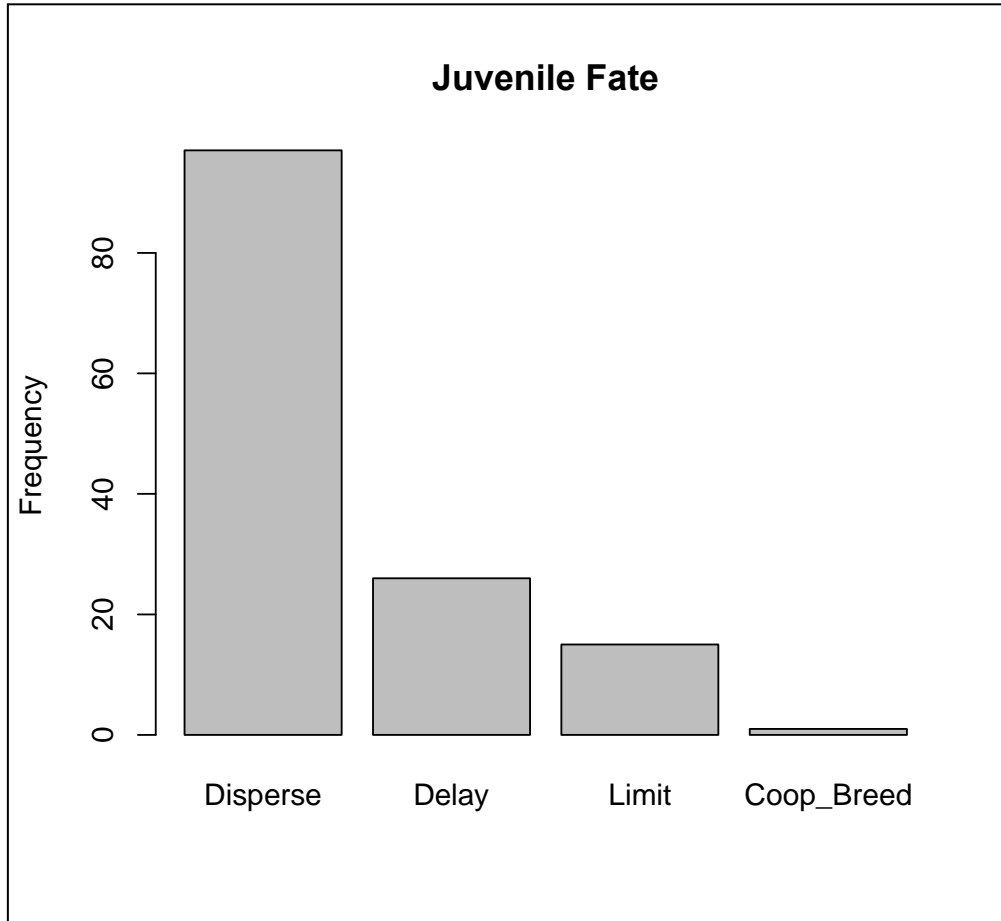


Figure 5. The fate of juvenile black-crested titmice (*Baeolophus atricristatus*) ($n = 123$) on the Freeman Center, San Marcos, Texas, 2013 and 2014. Most individuals dispersed and were never resighted again, though several either delayed or limited their dispersal. Cooperative breeding was observed on one occasion.

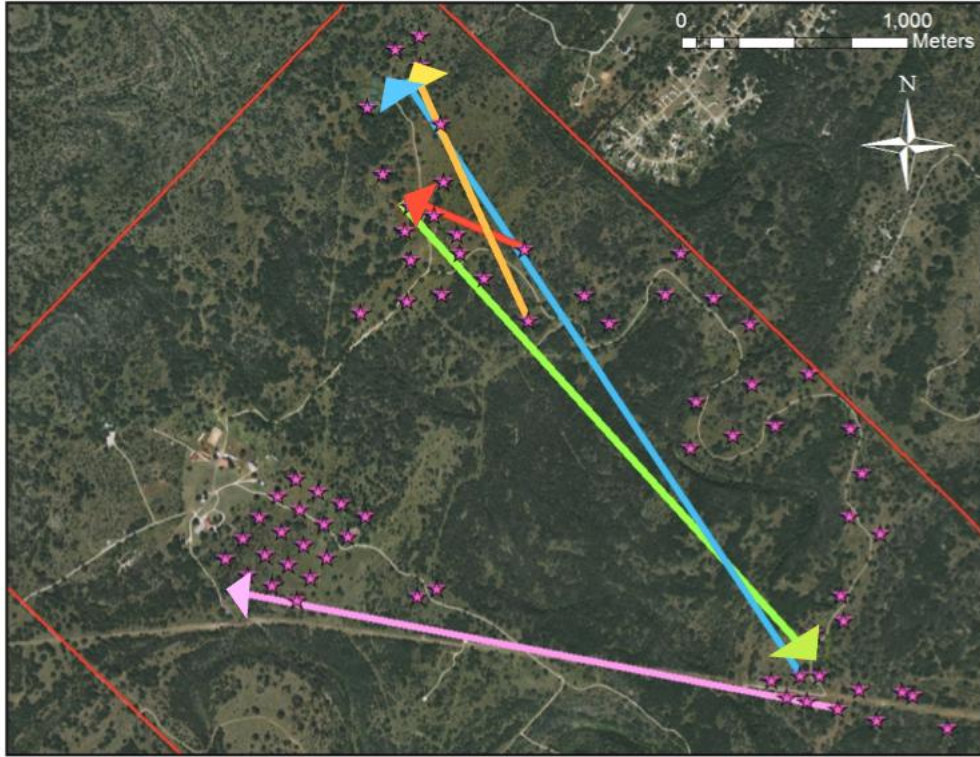


Figure 6. Dispersal distances and directions of five individual black-crested titmouse (*Baeolophus atricristatus*) juveniles on the Freeman Center, San Marcos, Texas, 2013 and 2014. Each different colored line represents a unique individual, and direction of movement is given with small arrowheads at the end of the lines.

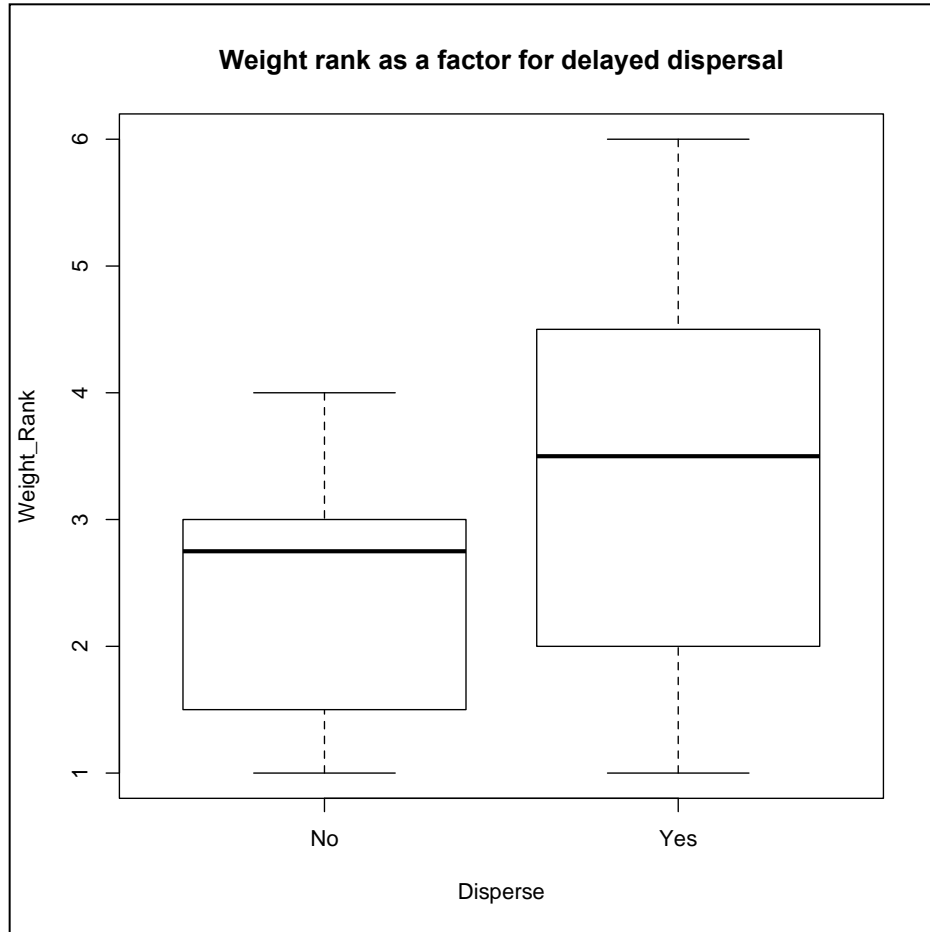


Figure 7. Weight rank as a factor for delayed dispersal in juvenile black-crested titmice (*Baeolophus atricristatus*) ($n = 123$) at the Freeman Center in San Marcos, Texas, 2013 and 2014. Individuals that did not disperse were typically the heavier of the clutch (p -value = 0.004*).

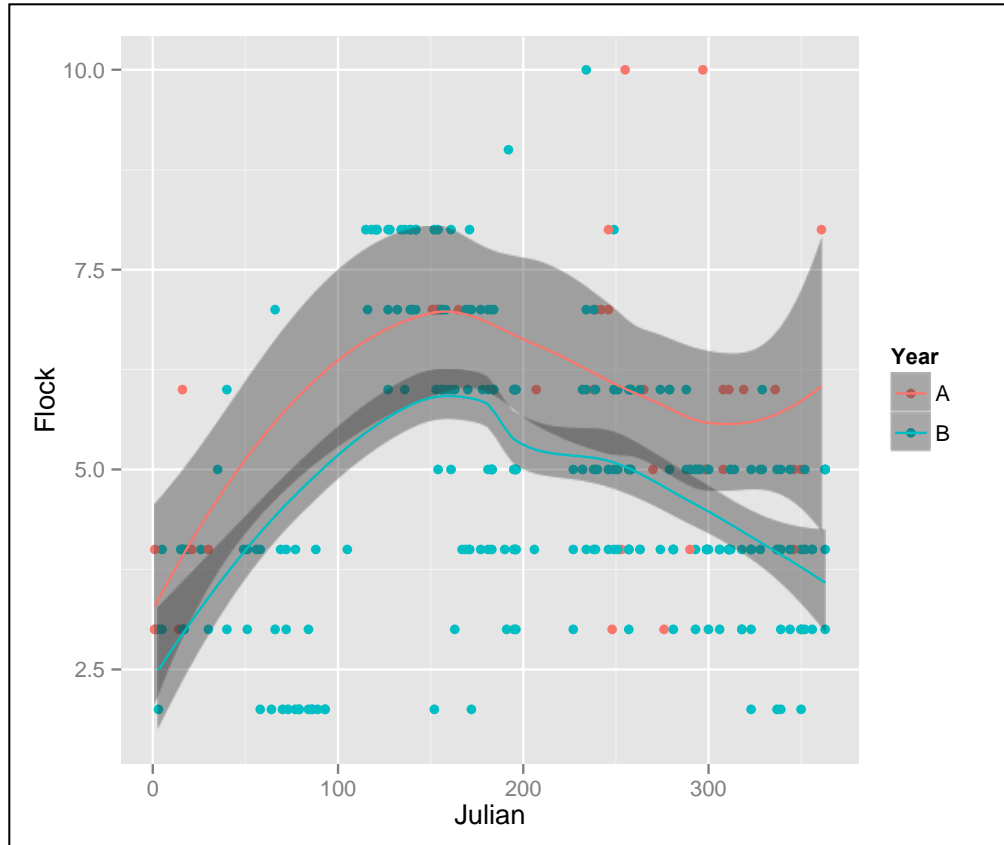


Figure 8. Number of individual black-crested titmice (*Baeolophus atricristatus*) in a flock during different Julian calendar dates at the Freeman Center, San Marcos, Texas, 2013 and 2014. Season (Julian date), as a quadratic factor, predicts flock size in my generalized linear mixed effects model (p -value $< 0.001^*$). Predictor Year also has an effect on flock size (p -value $< 0.01^*$).

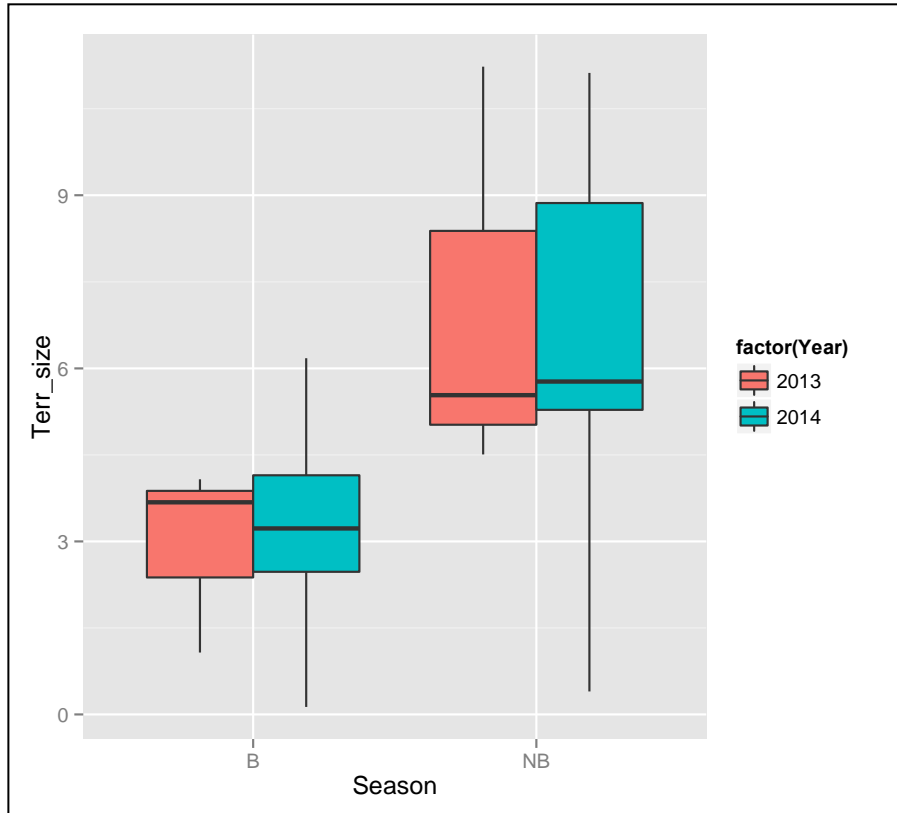


Figure 9. Territory size (in hectares) between breeding (March-July) and non-breeding (August – February) seasons of black-crested titmice (*Baeolophus atricristatus*) at the Freeman Center in San Marcos, Texas, 2013 and 2014. Significant differences are seen between breeding and non-breeding territory size (p -value < 0.01*).

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