SECONDHAND HOMES: HOW A PRIMARY CAVITY NESTER MAY INFLUENCE THE LOCAL AVIAN COMMUNITY

A Thesis

by

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Submitted to the Office of Graduate and Professional Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

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August 2020

Major Subject: Wildlife and Fisheries Sciences

ABSTRACT

Ecosystem engineers influence other organisms by altering and modifying the local environment. Woodpeckers act as ecosystem engineers by excavating, and then abandoning multiple cavities in dead and live trees throughout their lifetime. These cavities can be crucial to secondary cavity nesting (SCN) birds that are otherwise limited by the availability of naturally occurring cavities. Additionally, woodpeckers have been known to select sites with high resource availability. Thus, secondary cavity nesting birds that are drawn to the area due to increased cavities may reap additional benefits from higher than normal insect loads. To investigate the influence woodpeckers had on the avian assemblages, I located and monitored 55 active Golden-fronted Woodpecker nests in 2019 in south Texas and evaluated the influence of cavity characteristics on nest survival using logistic regression and model averaging. I conducted insect surveys on a subset of these nests and compared overall avian species richness and relative abundance using point counts. Within all sites I conducted nest searches for the four most common SCN species and again used model averaging to predict successful nests. The results of the insect surveys suggest that biomasses of Coleoptera, Hymenoptera, and Coleoptera were strongly correlated with woodpecker site selection and home-range size. Model averaging indicated that woodpeckers had higher nest success in trees with increased cover and lower levels of decay, while SCN birds had higher levels of nesting success in abandoned woodpecker cavities opposed to naturally occurring ones. Additionally, some species had higher success in live trees, contrary to current literature which suggests that

cavity nesting species prefer dead and decaying wood. My results suggest that SCNs may be drawn to areas with woodpecker activity due to increased cavity availability, and may reap additional benefits from higher than normal insect loads. Considering that many SCN birds are in decline, understanding the relationship between SCNs, the sources of their cavities, and potential relationships with foraging resources will be crucial to maintaining their populations.

DEDICATION

I dedicate this work to no one. For better or worse, tears, scars, and blood, it is mine.

I do however, dedicate any future work I accomplish to Karl Parker and Zach Hancock. Karl, years ago you gave me an opportunity that lead me to where I am today. By example you showed me how to care for the people I work with, hold my ground, and not take myself to seriously.

Zach, without your constant stubbornness and unyielding support throughout this academic and personal jungle, I would have never realized what I was capable of. Anything I achieve after this is because you taught me how to trust myself.

ACKNOWLEDGEMENTS

The trials of graduate school have shown me that, while we are often told otherwise, no scientist can create good work in isolation. None of the work contained in this document would have been possible without the unyielding support of many friends and colleagues within Texas A&M. Specifically, I would like to thank my committee members, Dr. Grace for her guidance with R and study design, to Dr. Cairns for his help with statistical theory, and to Dr Campbell for assisting with East Foundation logistics. Within the East Foundation, I would also like to thank Andrea Montalvo for supporting me logistically and emotionally while at SAV. Finally, Dr. Morrison, you taught me how to let things go, and that broken bones heal stronger.

For those whom this process truly would have been impossible, I would like to thank Dr. Samantha Leivers, who worked with me on every aspect of my thesis, starting with her assistance in data collection, to proof reading proposals, and to the many hours she spent explaining statistical theory and manipulating R code. You are a dear friend. I would also like to thank Emma Lehmberg for her emotional support and undying patience throughout the many successes and failures during my time at Texas A&M. Emma, I admire and respect you as a person and a scientist. I hope that someday you see yourself as I see you, the perfect blend of class, intelligence, and kindness. I would also like to thank Amanda Beckman for reminding me to be excited about science and for keeping thing in perspective.

Finally, I would like to thank the south Texas brushlands for crafting me into a stronger, more confident woman. It wasn’t easy, but we made it through.

CONTRIBUTORS AND FUNDING SOURCES

Contributors

This work was supervised by a thesis committee consisting of Professors Michael Morrison of Rangeland, Wildlife and Fisheries, Jacquelyn Grace of the Department of Ecology and Conservation Biology, Professor David Cairns of the Department of the Geography, along with Tyler Campbell of the East Foundation.

All other work conducted for the thesis was completed by the student. Field assistants Emily Green, Jake Hurd, and Dr. Samantha Leivers, assisted with some portions of the field work for this project.

Funding Sources

Graduate study was supported by a graduate research fellowship from Texas A&M University. This work was also made possible in part by the East Foundation. Its contents are solely the responsibility of the authors and do not necessarily represent the official views of the East Foundation. Additional support for graduate study was earned via multiple teaching assistantships from Texas A&M University in the Wildlife and Fisheries Sciences Department

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1. INTRODUCTION

Ecosystem engineers are defined as any organism that creates, significantly modifies, maintains or destroys the environment. Jones et al. (1994) identified two types of ecosystem engineers: allogenic and autogenic. Autogenic engineers alter the environment through their physical existence, that is their physical form may create nesting, foraging and breeding resources for other organisms. Kelp beds are crucial autogenic engineers in the waters off the western coast of North and South America (Shelamoff et al. 2019). Many organisms, such as brittle stars (Class Ophiuroidea) and many species of fish, take advantage of the protection and foraging resources the kelp fronds provide. Allogenic engineers on the other hand, control the availability of resources for other species by causing physical state changes in biotic or abiotic materials (Jones et al. 1994, Wright et al. 2002, Buse et al. 2008). Previous studies, particularly on allogenic ecosystem engineers, have shown that they can increase both general species richness and species abundance across the modified environment (Crooks 2002, Wright et al. 2002, Badano and Cavieres 2006, Byers et al. 2006, Wright and Jones 2006).

These effects have far-reaching consequences and directly impact not only ecological associations, but also the behavior of animals within an ecosystem. For example, animal movement and community composition may be altered by the changing environmental structure from ecosystem engineering activity. Lill and Marquis (2003) experimented with this idea by removing a common leaf-tying caterpillar, (*Pseudotelphusa sp*). These caterpillars build shelters that increase the structural complexity of the host plant and recruit numerous species of invertebrate herbivores within white oak trees (*Quercus alba*). In the two years following the study, the researchers observed a species richness decrease of 52% within trees where the caterpillars were removed compared to their control trees.

The most widely known allogenic ecosystem engineer is the beaver (*Castor canadensis*), which dramatically alters riparian environments through dam building. The dam, built of mud and sticks, leads to the formation of extensive wetlands capable of supporting herbaceous plants, reptiles, and fish species not found elsewhere in the riparian zone (Wright et al. 2002). For example, a before and after study on beaver-facilitated inundation of forest ponds found that both the waterbird species richness and species abundance was significantly higher during beaver activity than before (Nummi and Holopainen 2014).

Another mammal, the prairie dog (*Cynomys spp.*), acts as an environmental engineer by creating a complex system of burrows. These burrows aerate the soil, redistribute nutrients, add organic matter, and increase water filtration (Bangert and Slobodchikoff 2006). By doing so they directly and indirectly impact plants and animals within their system. The extirpation of prairie dogs has been shown to negatively influence regional and local biodiversity and positively influence invasive shrub establishment (Martínez-Estévez et al. 2013). The homogenous nature of Gunnison's prairie dog (*Cynomys gunnisoni*) mounds have been shown to facilitate darkling beetle (*Eleodes hispilabris*) movement and displacement when compared to the adjacent grasslands (Bangert and Slobodchikoff 2004). Additionally, these beetles were twice as abundant on prairie dog towns, potentially due to accumulation upon encountering this favorable environment. The result of this increased abundance in darkling beetles (and other potentially affected invertebrates) is unknown, although possible outcomes could include increased foraging opportunities for animals within higher trophic levels.

Woodpeckers are primary cavity nesting birds, meaning they excavate their own nest cavities. Woodpeckers excavate new nest cavities each year and exhibit strong selection for nest trees on the basis of diameter, height, decay characteristics, and surrounding habitat conditions, which often causes their excavations over the years to be clumped in a small area (Munnan 1977, Li and Martin 1991, Loye and Carroll 1998, Newlon 2005, Jusino et al. 2016). It is costly to excavate a new cavity every year however, previous studies have indicated that there are advantages to creating a new cavity for every brood. For example, degradation of the current nesting tree, learned predation behavior from predators, and parasite infestation, all decrease the bird’s reproductive success in cavities that are re-used (Loye and Carroll 1998, Husak and Husak 2002, Wiebe 2017). It was found that males in better body condition excavated new cavities more often than those that reused old cavities (Wiebe et al. 2007). Another study found that Black Woodpecker (*Dryocopus martius*) fledgling rates were 38% in old cavities versus 71% in new ones (Nilsson et al. 1991). The drive to create new cavities every year results in an abundance of cavities, usually centrally located in the breeding male’s territory (Husak 2000). In addition to the fully excavated cavities that woodpeckers leave behind after nesting, they also create roosting cavities used as shelter during the non-breeding season as well as “cavity starts” or partial excavations. The exact function of these cavity starts is unknown, but they may be involved in courtship activities, serve as alternative nest sites, or be used in subsequent years (Conner et al. 1994, Aubry and Raley 2002, Bull 2003).

1.1. Woodpeckers and Insects

It has been shown that woodpecker site selection and home range size are directly linked to variation in resource availability (Pechacek and d'Oleire-Oltmanns 2004). The definition of home range for my study is the area traveled by an animal in its normal activities of food gathering, mating, and caring for young (Burt 1943, Powell 2000). Site selection in the Black-backed Woodpecker (*Picoides arcticus*) has been directly linked to infestations of the mountain pine beetle (*Dendroctonus ponderosae*) (Bonnot et al. 2015). Additionally, the home range size of the Three-toed Woodpecker (*Picoides dorsalis*) was shown to decrease with an increase in potential cavity trees with an increasing DBH range in the available trees (Pechacek and d'Oleire-Oltmanns 2004). Theoretically, a bird needs to spend less energy and time defending a small home range that has the same food resources compared to a larger home range. However, no studies have looked at the impact of food resources on the site selection and home range sizes of woodpeckers, which may be indirectly impacting SCNs in the area. And while the major component of most woodpecker’s diets are species of beetles and species within the order Hymenoptera including carpenter ants (*Camponotus spp*.), most woodpeckers do eat other species of insects when the opportunity arises (Bull et al. 1992, Fay et al 2005, Powell et al. 2002). The availability of certain insect loads may be directing the site selection of woodpeckers, which in turn determine the site selection of SCNs. After all, while woodpeckers may be increasing the availability of nesting cavities for those species reliant on them, the abundance of cavities in an area does not necessarily promote high SCNs populations.

There are many factors that tie into whether or not a species will be productive and become established in an area, an important example being foraging resources (Rahman et al. 2012, Boelman et al. 2015). For instance, if a woodpecker establishes a home range within an area that has an excess of wood burrowing beetles (such as a recently burned area) that it alone can access, but low numbers of other insects, it would be unlikely that non-excavating SCN birds would become established there, regardless of cavity availability. Studies investigating the diets of woodpeckers have shown that within their insect diet, the overwhelming majority of prey consist of wood burrowing beetles (Coleoptera), and bees, wasps and ants (Hymenoptera) (Pechacek and Kristin 2004, Capernia 2009).

Many secondary cavity nesting birds such as the Ash-throated Flycatcher (*Myiarchus cinerascens*), also have Coleoptera and Hymenoptera in high proportions of their diet (Farris et al. 2002), thus areas that have foraging opportunities for woodpeckers may also be able to sustain SCNs drawn to the area by the excess cavities produced by the woodpecker. Additionally, bird species differ seasonally in their consumption of insects. Many birds that normally would be considered granivorous, such as the Chipping Sparrow (*Spizella passerine*) and the Field Sparrow (*Spizella* *pusilla*), show a marked increase in the proportion of their diet that consists of insects from April through August (Martin et al. 1961, Blancher and Robertson 1987). This increase corresponds with the breeding season and their need to supply their young with protein rich foods, even though they themselves are almost exclusively seed eaters for the non-breeding times of the year (Oliver 1998, Gómez 2018). Thus, the insect loads around areas sought out by woodpeckers may be indicative of foraging hot spots, beneficial to all bird species, not only cavity nesters.

1.2. Woodpeckers and the Avian Assemblage

In addition to selecting areas with high foraging opportunities, woodpeckers may also increase foraging opportunities for cavity and non-cavity nesting birds alike. As woodpeckers forage for food hidden within live and dead wood they directly and indirectly accelerate the decaying process for afflicted trees (Conner et al. 1994, Jackson and Jackson 2004), create openings that allow sap to flow through (Tate 1973, Williams 1990, Kitching and Tozer 2010), and create more opportunities for invertebrate communities to become established. This corresponds to more feeding opportunities for the bird community at large and may result in a more species rich and abundant assemblage.

The type of vegetation present within a site can be a major factor in the structure of the avian community (Ratti et al. 2001, Bock and Jones 2004.) The structural characteristics of the vegetation composition can cause drastic changes in the avian assemblages, especially as the vegetation increases in its heterogeneity. Areas with denser and more complex vegetation tend to have both higher abundances and higher species richness (Díaz 2006). This could be due in part to structural heterogeneity which can impact predation and parasitism rates along with foraging opportunities. These differences in vegetation have also been shown to influence nesting success and can alter the composition of the avian assemblage (Rotenberry 1985, Rodewald and Yahner 2001). On the broad scale, differences between avian assemblages can be detected within different ecological biomes, defined here as a regional ecological unit characterized by a dominant vegetative pattern (Woodward et al. 2004, Van Wilgen et al. 2008). Therefore, any assessment of an ecosystem engineer's impact on the surrounding avian assemblage must first be evaluated by any potential impact by the underlying vegetation characteristics to avoid biasing results.

1.3. Woodpeckers and Secondary Cavity Nesting Birds

Species that rely on cavities for nest building, but do not have the ability to excavate their own (secondary cavity nesters), are reliant on naturally occurring cavities or, if the opportunity arises, a woodpecker excavation. In this way woodpeckers act as ecosystem engineers as the resulting abundance of cavities then supports large assemblages of other organisms. For the purposes of my study, assemblage is defined as the taxonomically related group of species that occur together in space and time, such as the "avian assemblage" (Stroud et al. 2015). Other cavity nesting organisms can range from fungi, such as the red heart fungus (*Phellinus pini*), to invertebrates such as carpenter ants (*Camponotus sp*.), termites (Kalotermitidae), and paper wasps (*Polistes* *spp*.), and vertebrates such as various species of cavity nesting birds, reptiles and small mammals (Conner and Locke 1982, Mccomb and Noble 1982, Warakai et al. 2013).

Secondary cavity nesting birds are especially reliant on abandoned woodpecker cavities as they require the cavity not only as protection from the elements and predation, but to serve as a nursery for their developing eggs and chicks. Common secondary nesting bird species that often utilize abandoned woodpecker cavities include some species of flycatchers, wrens, ducks, and small owls, such as the Eastern Screech-Owl (*Megascops asio*) (Munnan 1977, Martin and Li 1992, Maziarz et al. 2017). For example, a study of the Great Spotted Woodpecker (*Dendrocopos major*) showed that the presence of this woodpecker played a more important role in the abundance of secondary cavity nesters (SCNs) than did food availability (Segura 2017). Indeed, it has been shown that SCN populations can be limited by the availability of cavities in an area (Robles et al. 2011). In forests worldwide, the population sizes of SCN birds can be reduced by 10-40% over maximum production through the availability of tree cavities (Cockle et al. 2011). However, as abandoned cavities age, their usefulness to SCN birds declines as the cavity's entrance hole expands creating higher risk of predation and the inside of the cavity begins to rot away (Pakkala et al. 2018). Therefore, fresh cavities are needed continuously within an area to continue to support SCNs. A classic example of this issue is found in the southern pine ecosystem of North America. The Red-Cockaded Woodpecker (*Leuconotopicus borealis*) is the only bird species that excavates live loblolly (*Pinus taedu*), shortleaf (*Pinus echinata*) and longleaf (*Pinus palustris*) pines (Conner et al. 1997). The resulting cavities are in high demand by approximately 24 other species of vertebrates including secondary cavity users such as fox squirrels (*Sciurus niger*), American Kestrels (*Falco sparvetius*), Wood Ducks (*Aix sponsa*), and Eastern Screech-Owls (*Otis asio*) (DeLotelle et al. 1985, Conner et al. 1997).

Given that often SCN birds are either reliant on or heavily influenced by the availability of abandoned woodpecker cavities in their local environment, understanding metrics that determine the success of woodpecker nests may also indicate which metrics determine nest success for SCN birds. Additionally, since SCN birds are reliant on pre-existing cavities, they are at risk of higher nest fatality due to less stable and irregular cavity structure from decay. Previous studies have outlined seven primary nest cavity metrics that influence the success of cavity nesting birds: (1) depth of cavity, (2) diameter of the entrance hole, (3) percent of cavity that is concealed by foliage, (4) decay state of the nesting tree, (5) height of the cavity, (6) the diameter at breast height (DBH) of the tree, and (7) the species of the nesting tree (Dobkin et al. 1995, Cockle et al. 2011, Berl et al. 2015). However, studies do not agree that all of the nest metrics affect SCN birds in the same way.

The literature is in agreement that the height of the nest, the DBH of the nesting tree and the depth of the nesting cavity are positively related to nest success, and that cavity nests have higher success rates when there is less foliage obstructing the cavity (Sedgwick and Knopf 1990, Carlson et al. 1998, Saab 2004, Combrink et al. 2017, Baroni et al. 2020). In some cases the higher the nest cavity the less likely the nest will be predated, because the main predators of cavity nests such as small mammals and tree climbing snakes would be less likely to climb long distances, and tall trees would provide the parent birds more time to detect and dislodge climbing predators (Stauffer et al. 1982, Sedgwick and Knopf 1990, Li and Martin 1991). Since the diameter of a tree is directly related to the thickness of the cavity walls, DBH can be a useful metric to estimate the insulation of a nesting cavity. Thicker walls prevent entrance from most predators and insulate the nesting chamber from fluctuating temperatures. The Eurasian Pygmy Owl (*Glaucidium passerinum*) primarily selects cavities with a thick front wall (5cm) over trees with a smaller DBH in which such a wall thickness would not be possible (Baroni et al. 2020). Combrink et al. (2017) placed dataloggers inside nesting chambers of Ground-hornbills (*Bucorvus leadbeateri*) and found that natural cavities with a thick protecting wall provided a buffer against temperature fluctuations while artificial nest boxes with thin walls provided little protection as internal temperatures often exceeded the maximum and minimum external temperatures. While these temperature fluctuations did not negatively influence the breeding success of the Ground-hornbill, they are related to decreased nesting success in other, smaller cavity nesting bird species less resistant to fluctuating temperatures (Carlson et al. 1998). Maziarz et al. (2017) found that tree cavities in thicker parts of the tree were more efficient thermal insulators, and as such were better at protecting developing eggs and chicks. Finally, Wiebe (2001) found that trees with small diameters showed extreme maximum and minimum temperatures throughout the day. Additionally, preference for deeper cavities is widespread throughout cavity nesters and increases in nesting cavity depth has been shown to be related to a decrease in predation from mustelids and woodpeckers (Berkunsky and Reboreda 2009, Fokkema et al. 2018). Lastly, while most non-cavity nesting birds rely in part on vegetation cover to conceal their nest contents from predators, cavity nesting birds show a strong deference for cavities with a low percent of cover (Cockle et al. 2011). This is likely due to high foliage cover obstructing the parent bird's view of oncoming predators, especially since the view is already obstructed by the nest being located within a cavity.

Alternatively, two of the above seven characteristics have caused some contention within the scientific literature when it comes to their relationship with cavity nesting birds; the diameter of the entrance hole and the state of decay of the nesting tree. On one hand, smaller cavity entrances have been positively related to successful nests because small cavity entrances physically prevent predators from accessing nest contents (Martin et al. 2004). In fact, the Swift Parrot (*Lathamus discolor*) has adaptively small cavity entrances that exclude native predators (Stojanovic et al. 2017), but the introduction of the sugar glider (*Petaurus breviceps*) to their breeding grounds in Tasmania has caused a dramatic decrease in population size. Over fifty percent of females nesting on the main island of Tasmania lost their nests due to sugar glider predation, and future populations are expected to decrease by 78-94% over the next few years due to this threat. Invasive Orange-winged Parrots (*Amazona amazonica*) have been observed enlarging nesting cavity holes for their own use as they are better able to defend their cavity from predators, but the enlarged cavities that they leave behind are subsequently less useful to smaller, native SCN birds (Diamond and Ross 2019).

However, the entrance hole size has also been shown to impact the internal temperature of the nesting cavity which may lead to species in different environments showing different responses. For example, the threatened SCN passerine, the South Island Saddleback (*Philesturnus carunculatus*), has smaller entrance holes that are better at maintaining internal temperatures, an important characteristic on the South Island of New Zealand where breeding season temperatures can be fairly low (Rhodes et al. 2009). Alternatively, wider entrance holes allow for more convection and facilitate cooling of the cavity and any respective nest contents (Paclík et al. 2007), which may be important for birds living in environments with extremely high temperature during the day, but this has never been directly studied.

As the entrance hole may influence the microclimate of the nesting cavity, so may the state of decay of the nesting tree; however, the literature is similarly torn on how this affects cavity nesters. Live trees tend to be denser than highly decayed or dead trees, and therefore are more efficient insulators. However, the cost involved in excavating a highly dense tree may outweigh the benefit of having a highly insulated nest and varies among species and the environment they live in (Wiebe et al. 2007). For example, excavation effort may be a critical factor in nest site selection for the Red-naped Sapsucker. Losin et al. (2006) found that this species selects nesting sites corresponding with the directional bias in heartwood rot caused by the fungus *Phellinus tremulae* which softens the dense wood of aspen (*Populus tremuloides*). Additionally, Zahner et al. (2012) found that Black Woodpeckers had a preference to initiate cavity excavation near areas of the tree subject to heart rot as these softer sections were less costly to excavate. However, Schepps et al. (1999) found that all species of cavity nesting birds included in their study had different preferences for tree hardness, and indicated that cavity nesters may be sensitive to subtle differences in wood density. Hooge et al. (1999), found that cavities in live limbs were less likely to show variance in temperature and thus provided a more stable environment for developing eggs and chicks. Wiebe (2001) found that "deader" trees were positively associated with higher internal temperatures. Given that the thickness of the walls has been shown to heavily influence the internal temperatures of nesting cavities, it would not be surprising to find that, especially in areas of extreme weather fluctuation, the rate of decay may also be a predicting factor for nest success. However, the prevalence of nests in live trees with dense hardwood may be confounded by the initial cost of excavating them.

1.4. Objectives

There have been many inferences made about how woodpeckers act as ecosystem engineers; however, no study to date has investigated the combined influence of woodpeckers creating cavities useful for SCN birds in conjunction with areas containing higher than normal insect availability (Iwata 2003, Tscharntke et al. 2008). These insect "hot spot" areas may be further inferred by increases in overall avian abundances within the areas. To investigate how woodpecker home range site selection and size may be influenced by the insect assemblages around them, and then in turn how woodpeckers may influence both the avian assemblage as a whole and the nesting success of SCN birds, I examined how insect abundances correlated with woodpecker site selection and home range sizes, and consequently, how cavity and non-cavity nesting birds correlated with woodpecker activity.

To answer these questions, I focused data collection on the little studied Golden-fronted Woodpecker (*Melanerpes aurifrons*). The Golden-fronted Woodpecker, hereafter referred to as “woodpecker”, is a medium sized bird whose range extends from Central America to Texas, occasionally reaching as far as southern Oklahoma (Sauer et al. 2013). Due to their limited range within the United States and the harsh environment they live in (ranging from dense arid scrubland to thick tropical forests) there has been little research done on this species (Husak 2000), and the literature that does exist focuses mainly on basic life history traits such as chick provisioning rates and potential hybridization with the regionally sympatric Red-bellied Woodpecker (*Melanerpes carolinus*) (Wetmore 1948, Smith 1987, Husak 1995, Styrsky and Styrsky 2003, Schroeder et al. 2013). The literature that does exist indicates that this woodpecker is a seasonally monogamous, aggressively territorial bird and that over time cavities within these fiercely defended home ranges may increase due to site fidelity (Husak 2000). Additionally, long-term population trends extracted from recent (1999-2009) Breeding Bird Surveys indicate that this species is in decline across their Texas distribution, especially in the Tamaulipan Brushlands ecoregion (Sauer et al. 2011) and is considered a species of concern in the Texas Wildlife Action Plan (Bender et al. 2006). Very little has been published on the ecology of this woodpecker (Husak and Maxwell 1998, Lowther 2001), which is a concern not only for conservation efforts of this woodpecker but also for the conservation and basic ecology of secondary cavity nesters that may rely on the cavities these birds leave behind. Considering the lack of knowledge on this charismatic bird and the prevalence of this bird in southern Texas where there are few other primary cavity nesters, I chose to investigate potential relationships between the Golden-fronted Woodpecker as ecosystem engineers and cavity and non-cavity nesting birds.

My specific objectives are as follows: My first objective (1) was to determine the potential influence of the insect assemblage on both woodpecker site selection and home range size. I hypothesized that the two orders of insects most commonly eaten by woodpeckers (Coleoptera and Hymenoptera) would be positively correlated with the presence of an active woodpecker within the site and that these two orders would have higher overall biomass near the center of an occupied site compared to the outskirts. I also hypothesized that the overall biomass of these two orders within woodpecker home ranges would be negatively correlated with the size of the home ranges. My second objective (2) was to identify any patterns in avian species richness and abundance around sites with active woodpeckers and those without, along with any differences that might be present in these numbers between biome types. I predicted that avian species richness along with overall avian abundance would be positively correlated with the presence of an active woodpecker within the site. Additionally, I expected this correlation to be significantly different between the four biome types present in the study. My third objective (3) was to investigate the following nest cavity characteristics that might predict successful woodpecker nests: diameter of the cavity opening, height of the cavity, depth of the cavity, DBH of the tree, decay class of the tree, and the percentage of the cavity that was covered by vegetation. My final objective (4) was to determine which nest characteristics best predicted the success of SCN birds common within the area. Given that SCNs can have similar nesting requirements as primary cavity nesting birds, I expected the two taxa would share predictors with the addition that SCNs would have higher nesting success in abandoned woodpecker cavities than naturally occurring ones.

Through these questions, I sought to provide information on the relationship, not only between primary and secondary cavity nesters, but between the insect assemblage, cavity nesters, and the avian community as a whole. Understanding these relationships is crucial for improving the conservation and management of both primary and secondary cavities nesting birds around the world, especially since many of these birds remain unstudied or poorly studied. Given that many primary and secondary cavity nesting birds are in decline worldwide, the information provided by this research will give managers a deeper understanding of the underlying relationships that drive these systems.

2. METHODS

2.1. Study Area

I conducted my research at the East Foundation's ~61,000 ha San Antonio Viejo Ranch (SAV) located in Jim Hogg and Starr counties, ~25 km south of Hebbronville, south Texas (14N 516336 2981647 Standard UTM). This area is representative of the Tamaulipan/Mezquital Thornscrub ecological region containing unique plants and animal communities within brush covered dunes, dense brushland, and open woods of mesquite (*Prosopsis glandulosa*). Parts of this region support grassland similar to the great plains, though the grasslands here are punctuated with clusters of trees and shrubs due to highly variable soil and moisture conditions. The scrubland of southern Texas has historically been understudied because most of the land in this area is privately owned.

The SAV is maintained as a working cattle ranch and is dedicated to managing and preserving native rangeland. Mean annual rainfall during the study year (2019) for this region was ~30 cm and the annual temperature during the breeding season (March - July) was ~27.8° C (PRISM Climate Group 2019). The annual temperature was similar to the 30 year normal for this region during those months and the mean annual rainfall was lower than average in 2019, with the 30 year normal at ~50 cm (PRISM Climate Group 2019). The SAV is home to approximately 70 residential bird species and 45 migratory species. These species include the primary cavity nester the Golden-fronted Woodpecker, and the four most common secondary-cavity nesting species, the Black-crested Titmouse (*Baeolophus atricristatus*), Ash-throated Flycatcher, Brown-crested

Flycatcher (*Myiarchus tyrannulus*), and Bewick's Wren (*Thryomanes bewickii*). Almost 80% of the bird species found on the SAV eat a diet high in insects for the majority of the year, including those species listed above.

The Golden-fronted Woodpecker is the only woodpecker commonly found year-round on the SAV ranch. Therefore, it is a pivotal excavator species as it creates nesting and roosting locations for secondary cavity nesters that are also species of concerns, such as the Black-crested titmouse (Bender et al. 2005). Additionally, it is the only organism that can excavate the dense honey mesquite (*Prosopis glandulosa*) prevalent on the ranch and contributes to the creation of future nesting and foraging locations for itself and other species.

2.2. Woodpecker Nest Location

Given that nest site characteristics of primary cavity nesters can influence the nest-site characteristics of secondary cavity nesting birds (Robles and Martin 2014), I investigated the following potential drivers of woodpecker site selection and nest success. Locating woodpecker nests within the dense vegetation present at the SAV ranch required a proactive approach to finding active nests. The East Foundation has an extensive long-term monitoring dataset on the breeding birds within their properties. This dataset was developed during the spring and summer months of 2014-2018 (and continuing) through extensive point counts taken across the ranch by technicians working on a long-term monitoring study (Baumgardt et al. 2019). The point counts consist of 25, 12-point groups established through stratified randomization by vegetation type, with some thought to accessibility to roads. The points were visited by two observers, six times each during the months of April through July. The points were 400m apart and the two observers recorded birds visually and auditorily within a 200m radius of the point. Each of the 300 points were intentionally oversampled to obtain detection probabilities as part of developing a long-term monitoring plan. The only other woodpecker present on the ranch was the Ladder-backed Woodpecker (*Dryobates scalaris*), and according to the extensive point counts taken in 2014-2018, this species is uncommon on the ranch and therefore would likely have a small impact as an ecosystem engineer compared to the Golden-fronted Woodpecker.

Using these point count data, I created abundance heat maps across the ranch to locate areas with historically high densities of active woodpeckers. These data were spatially displayed using ArcGIS version 10.3 (Environmental Systems Research Institute, Redlands, CA, USA) to map the species' densities. Using the Point Density tool in ArcGIS I took a fishnet sample with 2000 m^2 cell sizes across the SAV ranch and extracted observed woodpecker densities to the fishnet centroids. With the kriging process I interpolated density values across the ranch to create a heat map (Silverman 2018). Some areas of the ranch had a denser collection of point count locations due to a long-term study being done on the northern pastures, indicating a sample bias. To account for this, I followed the same steps listed above, but started with a fishnet sample using 500 m2 cell sizes and re-interpolated across these pastures.

Avian species richness and abundance is known to be influenced by biome type, therefore in order to understand potential ecological patterns that might have been present within the study area it was crucial to allow for underlying influences biome type may have had on the avian community (Wiebe 2011, Michon et al. 2014, Stein et al. 2014). Accounting for this, I placed my survey plots within the four biome types defined by McLendon et al. (2013): grassland, early-seral, shrubland (dominated by woody plants <3m tall), and woodland (dominated by woody plants >3m tall) (Figure 1). Early-seral vegetation was characterized by doveweed (*Croton spp*.), sandbur (*Cenchrus spp.*), and horsemint (*Monarda punctata*). Native grassland is characterized by species such as arrowfeather threeawn (*Aristida purpurascens*), and balsam scale grass (*Elyonurus tripsacoide*). While both early-seral and grassland biomes were dominated by non-woody vegetation, due to the highly variable soil and moisture conditions both were punctuated by the occasional occurrence of honey mesquite with large enough DBH to support active woodpecker nests. Shrubland regions included woody shrubs such as cat-claw (*Acacia greggii*), blackbrush (*Acacia rigidula*) and some honey mesquite. Woodlands were dominated by honey mesquite and other woody species such as whitebrush (*Aloysia lycioides*).

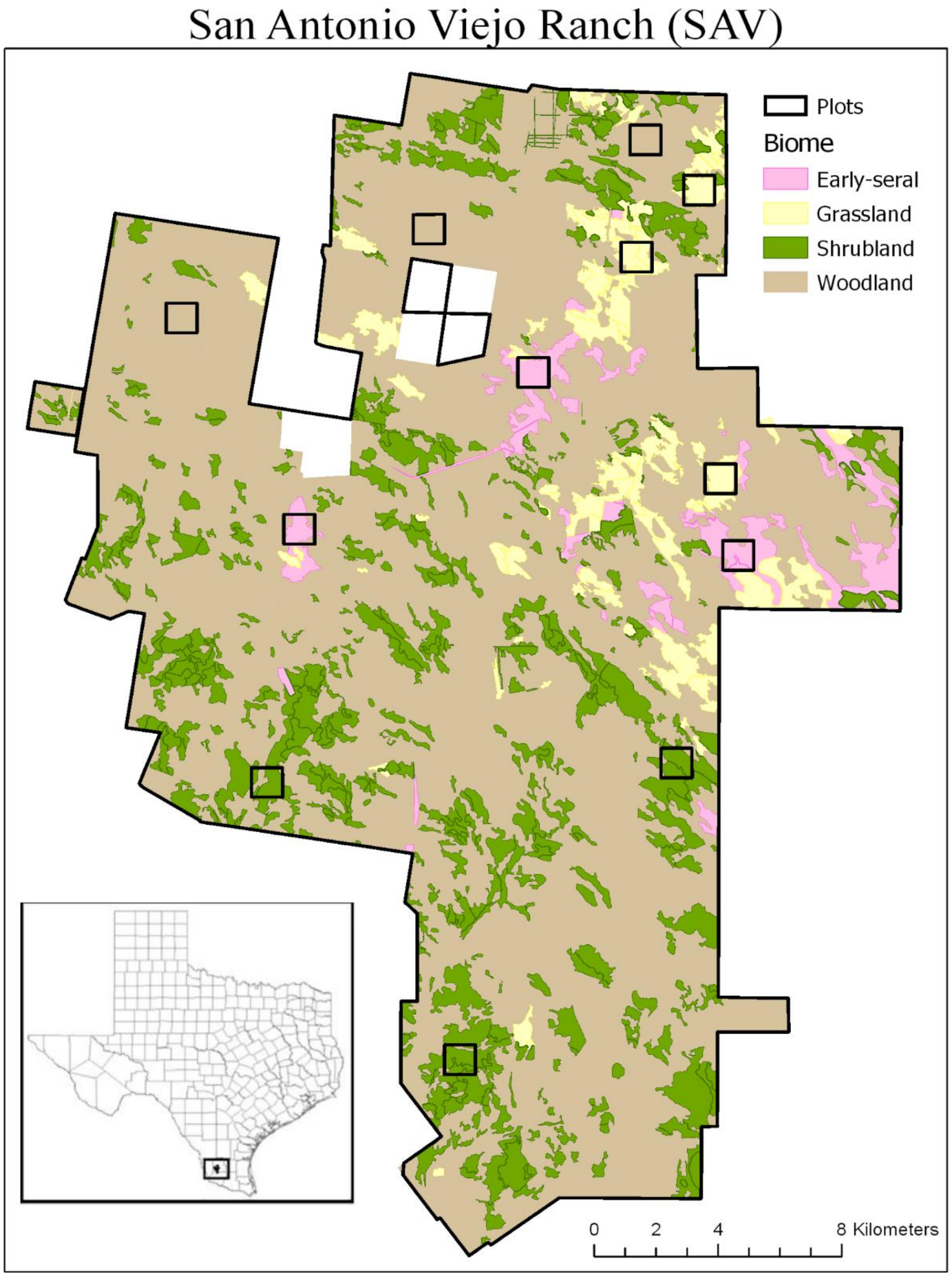

Figure 1: Map of the San Antonio Viejo Ranch, East Foundation. The four major biomes are represented in color and I placed three sites within each biome type to search for active woodpecker nests. Plots were 1 km^2.

Within the areas identified through the interpolation process to most likely to contain woodpeckers, I created 1 km^2 survey plots (3 within each of the 4 biomes) to search for active woodpecker territories using the spot-mapping technique (described below) (Svensson et al. 1970, Martin et al. 1993, Gregory et al. 2004). These plots and the biomes of the SAV ranch are shown in Figure 1.

To systematically cover each plot, I placed 3 walking transects (300 m apart) within the survey plot. All spot-mapping was conducted by myself and two technicians for 3-4 hours beginning between dawn and sunrise on each plot from mid-April till late May, 2019 and each survey plot was visited 4 times at even intervals within the breeding season. With the aid of research technicians, I walked systematically down the 1 km transects within the survey plots in a serpentine pattern and on subsequent visits we alternated the serpentine pattern so that as much of the survey plot was covered as possible (Figure 2). To ensure accurate sampling of the woodpecker I accounted for their average breeding home range area which has been estimated to be ~3.5ha (Emlen 1972) and standardized data collection by surveying each transect for 90 minutes. This excluded any potential bias due to varying vegetation density and difficulty or ease of walking (Svenson and Williamson 2009). When a woodpecker was located, I stopped the 90 minute transect search and followed that individual for a maximum of 30 minutes, or until the individual flew out of sight (Martin and Geupel 1993). I remained at least 30m away from the individual at all times to minimize any potential disturbance. To collect information on possible nesting locations through core use areas, I recorded a GPS point every one minute while observing the individual (Barg et al 2005).

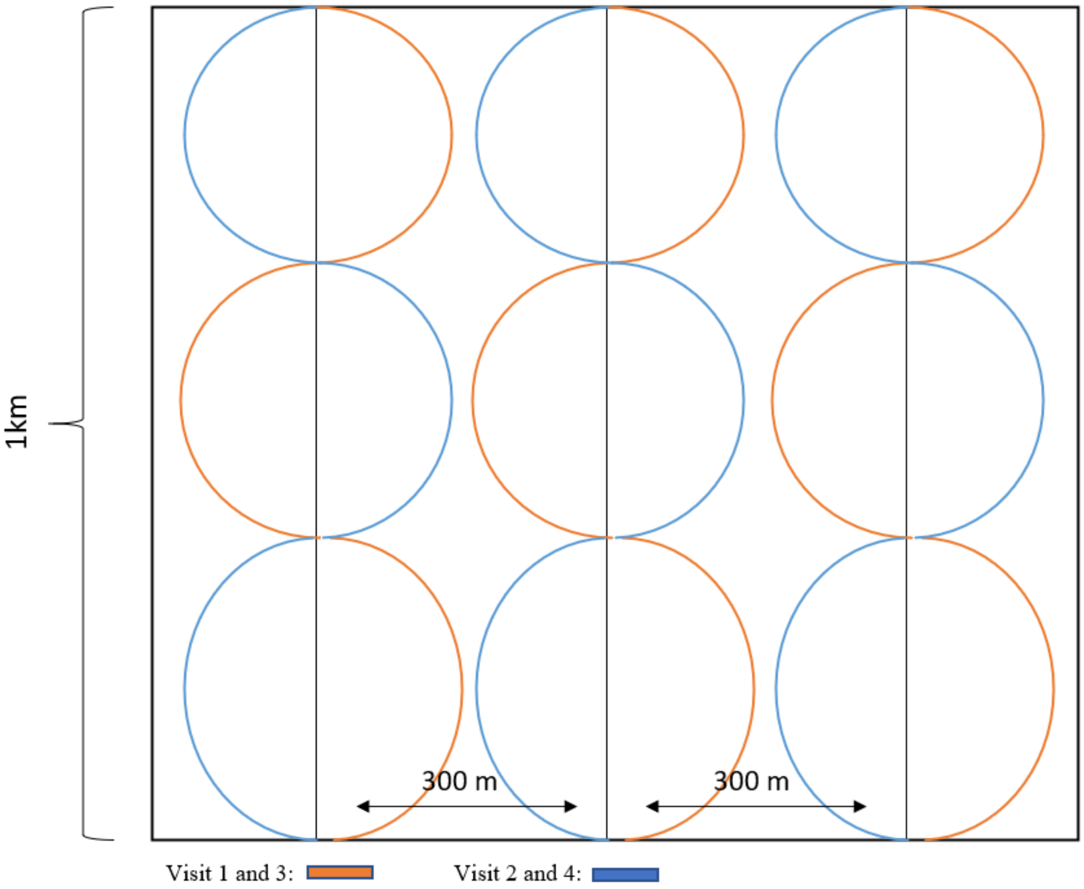

Figure 2: Visual of serpentine walking transects used to detect and locate Golden-fronted Woodpecker nests throughout the 12, 1 km plots placed within the 4 different biomes found on the ranch during spring and summer 2019. Orange path was followed during visits 1 and 3, blue path was followed for visits 2 and 4.

When monitoring I kept my eyes on the bird while a second observer recorded the individual's location using the GPS and recorded basic behaviors such as: foraging, displaying, drumming, excavating, feeding young, and removal of fecal sacs from a cavity. We recorded these behaviors solely to aid in our location of the nests. I observed no evidence that our presence disturbed individuals or forced them to move to areas they may not have otherwise. Given that the woodpecker is sexually dichromatic and extremely territorial (Husak and Maxwell, 1998), I was able to identify breeding pairs within a home range. The challenge behind most woodpecker nest studies is that any nest contents are hidden within a narrow cavity that is usually impossible to see into with the naked eye. To combat this issue, I used a lighted endoscope that wirelessly connected to a smart phone where it displayed live video (Model used: Wireless Endoscope, 5.5mm, Waterproof Inspection Camera). The stunted height (between 2.5 - 6 m) of the majority of the trees at SAV (due to limited soil nutrients and precipitation) made most cavities easily accessible from either the ground or a small climb onto a tree limb. This was advantageous as most studies on woodpeckers are limited by the accessibility of the nests located 5 m or higher in trees (Bull 1987, DeLotelle et al. 2018). For any cavities that were not accessible by foot, I climbed the tree by hand or used a small ladder to inspect the nest contents.

After locating the active woodpecker nests, I then selected sites within the 1 km^2 plots that had no observed woodpecker activity (unoccupied). It was crucial to select sites that had as similar vegetation types as possible to the areas that contained woodpecker activity, therefore I used the East Foundation's previously determined vegetation associations. These vegetation associations were created as part of a larger project by the East Foundation to classify the vegetation into a hierarchical system during the months of August-September in 2011, and April-June in 2012. On the SAV ranch three classification levels were used: biome, alliance, and association. A vegetation association was defined as the highest order sub-division of an alliance and was based on the dominant and subdominant species, with order considered. For example, an area dominated by mesquite with huisache (*Acacia farnesiana*) as the second-most abundant species would be classified as a mesquite-huisache association.

Using these associations, I randomly selected a point 300 m away from the active woodpecker cavity that had the same vegetation association, but no observed woodpecker activity (unoccupied). To select the unoccupied points, I used ArcGIS to create 300 m buffers around each active location and eliminated areas around the edge of the buffer in which woodpecker activity had been observed. Using an overlay of the vegetation associations across the ranch I paired the center of each nesting location with a randomly selected point on the buffer's edge which fell within the same vegetation association. I placed all of the unoccupied sites within the 1 km^2 survey plots to ensure that there was no influential woodpecker activity. According to the average home range size of this species during breeding season (between 3-5 hectares), and also considering that woodpeckers tend to excavate cavities and foraging holes at the center of their breeding territories, 300 m was a sufficient distance to conduct this comparison.

2.3. Insect Sampling and Analyses

2.3.1. Nest Site Selection

To further investigate any relationships between insects and woodpecker nest site choice and home-range size I collected data on the local insect assemblage around each site. Due to logistic constraints it was not possible to sample insects from all 55 occupied/non-occupied sites; therefore, I randomly selected (using a random number generator) a subset of 24 paired sites to collect data from. At each site I created an array of 11 sampling locations from the center of the site (0 m) outwards in 15 m increments to 150 m. I sampled insects at each location using the sweep-netting technique, which has been shown to be an adequate collection method to sample for insects commonly predated on by birds (Doxon et al. 2011). Given that insect communities can rapidly shift in a short period of time due to changes in precipitation, I visited each site once per week for seven weeks from late May to mid-July.

To collect samples, I used a standard 30 cm diameter canvas “American-type” sweep-net. At each sampling location within the array I swept the top 25% of the vegetation in an arc approximately 2.5 m wide in each cardinal direction (Doxon et al. 2011). To prevent the escape of collected invertebrates, after the sweep I quickly flipped the net 180° at the end of each arc and twisted the canvas material tightly from top to bottom and whipped the net back and forth to force the contents to collect at the bottom. Given the high risk of losing live flying insects while sorting I put the entire contents of each sweep net into a plastic jug containing an acetone (nail polish remover) soaked sponge. Water content in different species of insects can bias results when comparing biomass; therefore after collecting samples I placed them into a drying room consisting of an insulated shipping container supplied with a thermostat controlled heater (Model Elite Eliminator Heater) set at 55°C and air removal with a Tjernlund fan (Model V2D) so that the contents did not become humid. I periodically weighed the samples and considered them adequately dried when the mass did not decrease over three days (Pearson and Derr 1986). After drying the samples, I sorted the insects by order and collected biomass weights for each sampling location by order.

Given that woodpecker nest site selection and home-range size has been attributed to resource availability, quantifying local insects was imperative. To account for temporal bias, I summed the dried weights of the seven visits for each sampling location at each site and then took an average of all sampling distances per site. After finding that my data violated the assumptions of normality, I used a Wilcoxon signed-rank test to test for differences in the means of dried insect mass between occupied sites and unoccupied sites, and used an alpha of $P < 0.05$.

To determine if any orders of insects had has higher mass near the center of the home-ranges compared to the outskirts, I created Generalized Linear Models (GLMs) to predict each insect order's average dried weight (averaged between 7 visits) with sampling distance to the center and whether or not the site was considered occupied or unoccupied by a woodpecker (Field et al. 2012). By visualizing my data, I saw that the insect data for every order was best described by a gamma distribution (common for count data); therefore, I fitted these models with a gamma error structure and log link function (Væth and Skovlund 2004, Field et al. 2012). The log link exponentiates the linear predictors to create a natural fit for count variables. To determine if both the site type (occupied by an active woodpecker or not) and distance from the center of a home-range could be predicted with each insect order's average dried weight, I included both variables, along with an interaction term in the model. I used RStudio version 2.15.2 (R

Core Team 2012) to create the models and by looking at main effects and the interaction term between distance from the center of the site and the type of site, I determined which orders of insects increased or decreased in relation to the two woodpecker variables.

2.3.2. Home Range Size

The term home range is defined in my study as the area traversed by an individual in its normal activities of food gathering, mating, and caring for young (Worton 1989). However, resource availability has been shown to impact the home range size of woodpeckers (Pechacek and d'Oleire-Oltmanns 2004), thus within my first objective I wanted to determine if the availability of certain orders of insects were correlated with the size of woodpecker's home ranges within each site.

Due to logistic constraints on the number of sites I could conduct insect surveys on, I performed the following home range delineations on the same subset of 24 active woodpecker nests as I collected insect samples from. After finding an active nest I delineated the home ranges of each pair by constructing minimum convex polygons (MCP) that connected the outermost points of each site (Barg et al. 2004). An MCP is the smallest polygon that can be drawn that will encompass the locations of interest, and contains no internal angles greater than 180 degrees. Since comparing MCPs between studies can introduce irreconcilable and individual biases, I only used the data collected for my study to compare home ranges.

To ensure that the observed male woodpecker was indeed the parent of the active nest, I waited at the base of the active nesting tree for him to emerge from the cavity and followed him for 30 minutes taking a GPS point every one minute. I chose to follow the male woodpecker because the female sits on the brooding eggs or cares for the hatchlings during the day and only takes occasional forays outside of the nest. In contrast, the male woodpecker spends the majority of his day foraging for insects, occasionally bringing food back to the female or chicks, and defending its home range (Skutch 1969). With the help of technicians, I visited the 24 subset nets four times from 5:30 to 13:00, and collected a total of 120 observation points per male. To estimate the home ranges sizes, I read these points into ArcGIS Pro Version 1.4 (Environmental Systems Research Institute, Redlands, CA USA) and created MCPs using the minimum bounding geometry tool with convex hulls for geometry type. To avoid outlier points that likely did not fall within the individual's home range, I excluded areas where the bird only occurred 5% or less of the time. The MCP method has been criticized for being highly biased towards larger sample sizes; therefore, by standardizing the number of points taken for each pair I was able to avoid this unintentional bias. If at any point the observed male flew out of sight, I restarted my observations at the base of the tree to avoid accidentally following a different individual.

To get a measure of availability of each insect order present within the site, I took the average of the seven visits across all sampling locations within a site and then summed all 11 sampling points within an occupied or unoccupied site, resulting in a single measure of insect availability for each order per site. After checking my data for normality using the Shapiro-Wilkes test I found that the home range size data was not normally distributed; therefore, I used Spearman’s Rho, a rank-based method, to test for significant correlations between the measure of biomass for each order of insect against the size of the respective woodpecker home range (Field et al. 2012).

2.4. Avian Point Counts

Given that ecosystem engineers are known to increase species richness and abundance I investigated differences in the avian assemblages around woodpeckers, and in respect to biome type. Moving sequentially through the point counts I conducted three rounds for ten minutes at the center of each site type (occupied and unoccupied) from early May 2019 to early July 2019. To avoid temporal bias, I rotated the starting point on the second visit. Due to the fact that temperatures can easily exceed 32 °C by 10:00 AM, and the fact that the 1 km^2 plots were logistically far apart I could only survey between 6-8 points in a day. Following the standardized protocol for point counts (Barker et al. 1993, Howe et al. 1997), I began counts 30 minutes before sunrise and concluded before 10:00 AM. I recorded all species observed during the 10 minute period, along with the minute they were observed in, the type of observation (auditory or visual), and their distance from the point of observation (estimated by a range finder). To identify observations that may have been taken in less than optimal conditions such as wind over 20 mph, precipitation great enough to inhibit ability to hear bird song, and temperatures over 32°C, I recorded wind speed using the Beaufort scale and recorded cloud cover in 25% increments. I located all of the point count locations using a handheld Garmin GPS unit.

I did the following analyses to determine if there were differences in the avian assemblages between sites occupied with a woodpecker pair and those not. For each point count site, I calculated the overall observed species richness by summing the number of species encountered across the three visits per site. To determine if there was a significant difference in species richness between occupied and unoccupied sites, I performed a two-tailed t-test between site types. To determine if there was a significant difference in species richness between sites with respect to the biome type, I created a $\chi 2$ table matrix with pairwise comparisons of occupied and unoccupied sites for each biome along with each comparison's effect size calculated as the odd's ratio. As the significance test does not tell us the degree of effect, displaying effect size is helpful to show the magnitude of effect (Field et al. 2012, Kim 2017).

For each point count site, I calculated overall avian abundance by creating an index of relative abundance and then taking the highest count observed across the three visits per species. I used this index because I wanted to quantify the abundance for every species present within my sites (even those that occurred very infrequently) and methods that account for detection probabilities across species suggest using more than 40 observations per species in order to determine said probabilities (Thompson 2002, Thomas et al. 2003, Lee and Marsden 2008). Additionally, detection probability due to environmental differences was not a substantial contributor to observations across my sites. While there are minimal structural changes in vegetation across the properties, they were not enough to require adjustment for differences in detection. For example, the primary tree species across biome types was honey mesquite, and very few other tree species are present on the ranch due to the harsh and rocky soil.

To determine if there was a significant difference in relative abundance for all species combined between occupied and unoccupied sites, I performed a two-tailed t-test between site types. Again, to determine if biome had any influence on the relationship between woodpecker presence and overall avian abundance, I created a $\chi2$ table matrix with pairwise comparisons of relative abundance across biomes, along with their respective odds ratios. Given that some of the finer resolution may have been lost by combining all species into one dataset, I divided my dataset into non-cavity nesting birds and secondary cavity nesting birds using their life history traits and compared abundances of each independently between occupied and unoccupied sites using a two-tailed t-test followed by a $\chi2$ matrix by biome for both cavity and non-cavity nesting species.

2.5. Cavity Nesting Success

2.5.1. Primary Cavity Nesters

Understanding the nesting parameters that influence the success or failure of a woodpecker nest can provide insight into the factors that may be affecting SCN birds, especially considering that many SCN birds rely on the cavities woodpeckers leave behind. In conjunction with my third objective, I investigated which factors contributed to the success or failure of the Golden-fronted Woodpecker nests. For all woodpecker nests found on the ranch, I monitored nest contents every 2-3 days with the endoscoping camera, recording the number of eggs, chicks, or the loss of eggs or chicks, respectively.

Having observed either a nest success (at least one fledgling was observed outside of the nest) or a nest failure (all eggs/chicks died) I took the following measurements of nest metrics shown *a priori* to be predictors of cavity nesting success: the height of the nest measured from the center of the cavity opening to the base of the tree in meters, the diameter at breast height of the tree (DBH) in centimeters, diameter of the cavity opening in centimeters, the depth of the cavity measured in millimeters, and decay class: (1) live, wet inner bark, sap and foliage present; (2) dying, dry stem and bark, fine branches present, attached bark; (3) dead, fine branches gone, main branches present, bark variable: (4) few or no branches, softening stem, variable bark; (5) no branches, stem soft, bark mostly gone, (6) no branches, stem soft, no bark, top intact, (7) no branches, soft stem, no bark, broken top. (Dobkin et al. 1995, Bonar 2001, Cockle et al. 2011, Berl et al. 2015). Previous studies have shown that nest cover may be a determining factor for both primary and secondary cavity nesting birds (Schaaf 2020). To account for this, I collected nest cover estimates by placing the middle of a 0.5 x 0.5 m^2 cover board consisting of 25 squares in front of the cavity opening (Nudds 1997). At a distance of 5m, I estimated the percentage of the board obscured by vegetation in the four cardinal directions and averaged it for the site (Chotprasertkoon et al. 2017).

To model nesting success of the woodpecker, I used RStudio version 2.15.2 (R Core Team 2012) to create logistic regression model averages (Field et al 2012). Knowing that bias can enter models through collinearity of the variables, I checked for statistically significant correlations between dependent variables using variance inflation factors (VIFs) with the R package *cars*. I considered VIF values >5 to be significantly correlated (O'Brien, 2007). I z-scaled all continuous variables as several of my nest metrics were measured using different metrics (cm vs m vs mm). To evaluate effects of the aforementioned parameters on the nest success (0 = fail, 1 = success). I used the *MuMIn* package in R which generates a model selection table with all possible parameter combinations (Burnham and Anderson 2002, Field et al. 2012), and evaluated model fit using AIC adjusted for small sample sizes (AICc) (Burnham and Anderson 2002). Models that had ≥10% of the weight of the top model were considered candidate models for model averaging (Burnham and Anderson 2004, Mazerolle 2006). Using the R package *modave* I estimated the parameter coefficients through model averaging and determined which parameters were significant using $P = 0.05$ and its corresponding confidence intervals.

2.5.2. Secondary Cavity Nesting Success

Knowing where primary cavity nesters are establishing home ranges and creating nesting cavities can inform researchers on potential predictors for secondary cavity nesting birds. As stated in my fourth objective, I hypothesized that both primary and secondary cavity nesters would share the same nest success predictors. Additionally, I expected individuals that nested in abandoned woodpecker cavities to have higher success than those that nested in naturally occurring cavities.

I developed the following nest searching techniques and implemented this for all sites formerly determined through the woodpecker nest searches, and their paired unoccupied sites. Using the center of each site (n = 110, occupied = 55, unoccupied = 55) I created a 150 m square grid with transects spaced 20 m apart and trimmed it to fit within the 150 m squared point count detection circle. Given that no woodpecker home range within the study was larger than 150 m squared this was an adequate area in which to search for secondary cavity nests that might be influenced by being within an active woodpecker home range (Rodewald 2004). I systematically searched along the transects for nests across each study site every 3-5 days between April and July 2019. On all cavities present within the site, I used a handheld GPS unit to check on every return visit with the endoscoping camera. I also found nests opportunistically during routine checks of other nests. Once a nest was located, I recorded the species and number of eggs or nestlings present and monitored nests every 2-5 days to determine nest success or failure, being careful not to approach the nest from the same direction each time to avoid alerting potential predators to the nest's location (Rodewald 2004). After confirming nest fate, I recorded nest site metrics along with the additional metric of whether the nest was in a naturally occurring cavity or an abandoned woodpecker cavity. Excavated woodpecker cavities were easily identified by their symmetrical cavity entrance.

Cavity availability has been shown to be a limiting resource for SCN birds in environments with limited number of cavities, as species may compete for nesting space. In addition to monitoring active nests I also monitored every cavity present within the 150 m radius to consistently check for new nesting birds. In this way I was able to monitor the cavity availability of each area to determine if the availability of the cavities might have been a factor in SCN bird nesting choices. I recorded the number of existing cavities, whether they were an abandoned woodpecker cavity or a naturally occurring one, whether there was a nesting attempt at some point throughout the season, and what biome type it was located in.

I developed logistic regression model averages for the four most commonly found secondary cavity nesters within my study site (Nemes et al. 2009, Field et al. 2019): the Bewick's Wren (BEWR), the Ash-throated Flycatcher, the Brown-crested Flycatcher, and the Black-crested Titmouse (BCTI). The Ash-throated and Brown-crested Flycatchers overlap extensively in breeding and winter distributions, migration patterns, and habitat. The only reliable identification features are their songs (Cardiff and Dittmann 2000). Given the similarity of their body metrics and life history traits I combined data on these two species, ATBC. This was particularly important for the Brown-crested Flycatcher for which I only collected 23 nesting observations, and analyses on a sample size this low could create statistical issues.

As with the woodpecker, I used the same logistic regression and model averaging process to predict whether a nest would succeed or failed for SCN birds, the only difference being the addition of the type of cavity (natural or abandoned woodpecker cavity) as a predictor. For each species I checked for multicollinearity among predictors and z-scaled the continuous nest metric variables. Again, I used the *MuMIn* package in R to evaluate candidate models for each secondary cavity nesting bird species using AICc (Burnham and Anderson 2002) and used the *modavg* package in R to estimated model averaged parameter coefficients per SCN bird species.

3. RESULTS

3.1. Woodpecker and their Food

3.1.1. *Nest Placement*

Between March and July 2019 my technicians and I spent 560 hours observing, following, and recording the activities of the woodpecker. I found 55 active woodpecker territories within the four different biomes. Of these 55 nests, 9 were in early-seral, 12 were in grassland, 12 were in shrubland, and 22 were in woodland biomes. My first objective was to determine if there were any significant relationships between woodpecker site selection and the local insect assemblages. After locating these nests, I spent an additional 220 hours collecting insect samples across the 48 subset sites (24 occupied, 24 unoccupied). After drying and weighing these samples I collected the following means for each order of insect per site: Coleoptera, 0.22 ± 0.04 grams; Orthoptera 0.48 ± 0.11 grams; Diptera, 0.11 ± 0.04 grams; Hymenoptera, 0.06 ± 0.01 grams; Hemiptera, 0.08 ± 0.01 grams; Matodea, 0.52 ± 0.05 grams; and Phasmatodea, 0.14 ± 0.02 grams.

Because both Coleoptera and Hymenoptera are common dietary items for woodpeckers, my first objective predicted that biomass of both of these orders would be positively correlated with the presence of an active woodpecker within the site. After sorting and drying the insects I found that Coleoptera, Orthoptera, and Hymenoptera had higher mass on sites occupied by a woodpecker that those without (Spearman's signed rank test, Coleoptera: $W = 19$, $P < 2.2e-16$, Hymenoptera: $W = 186$, $P < 0.03551$, Orthoptera: W = 13, P = 2.313e-11). Coleoptera and Orthoptera had large effect sizes (0.801 and 0.818 respectively), and Hymenoptera had a moderate effect size (0.304) indicating that Coleoptera and Orthoptera had a larger magnitude of difference between site types than did Hymenoptera. The dried insect mass of Diptera (W = 219, P= 0.159); Hemiptera (W = 357, P = 0.247), Mantodea (W = 274, P = 0.782); and Phasmatodea (W = 285, P = 0.9593), were not significantly different (P > 0.05) between occupied and unoccupied sites. After data visualization, some orders of insects seemed to have a higher mass on occupied sites and within those occupied sites they had higher masses near the centers of the site (see Figure 3).

As mentioned in the second hypothesis of my first objective, I expected the insect orders Coleoptera and Hymenoptera to have higher mass near the center of the nesting site than away from it, given that most woodpecker species tend to localize their nests around abundant food resources for ease of foraging. I did not, however, expect any other insect orders to show this relationship given their low prevalence in woodpecker’s diets.

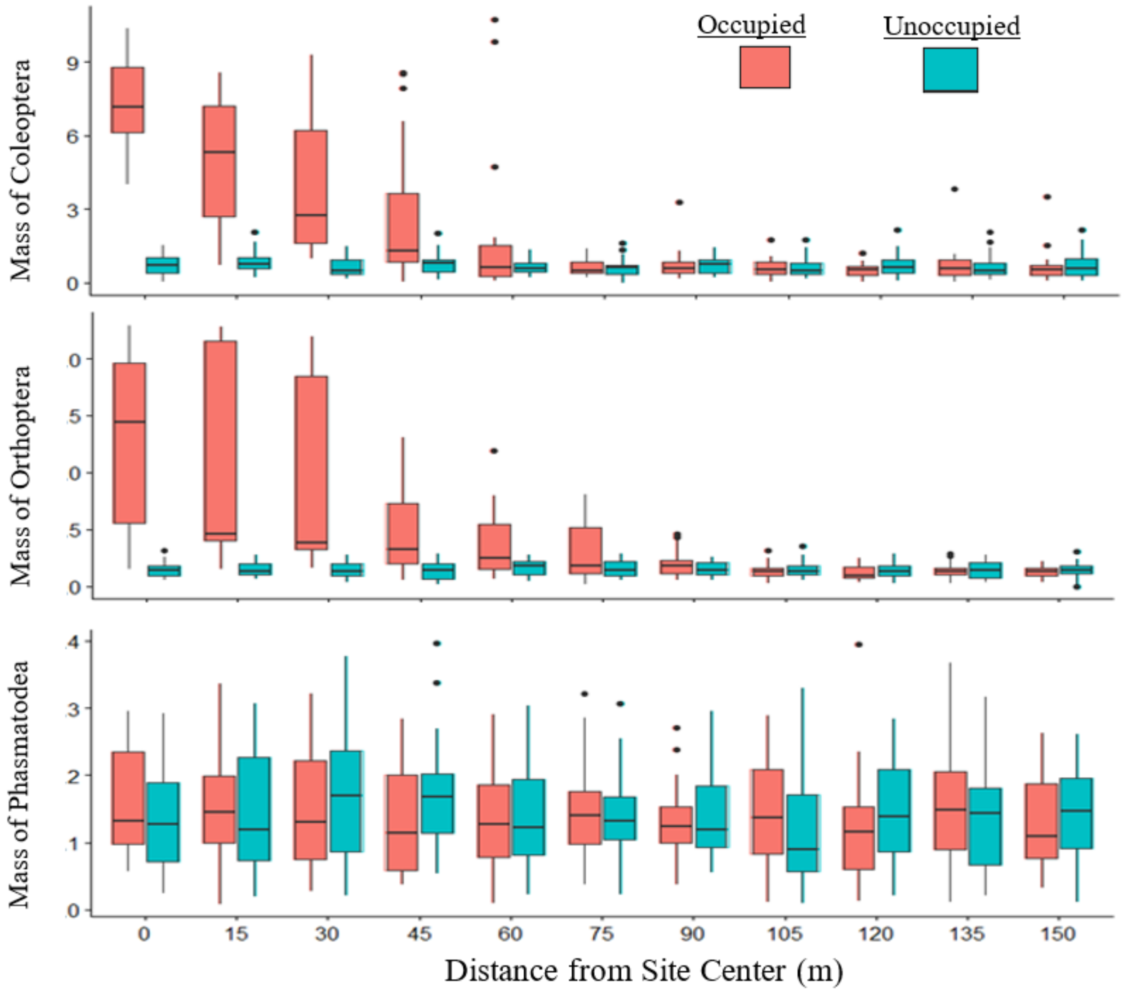

Figure 3: Data visualization for 3 of 7 orders of insects collected (averaged over 7 visits) by sweep net across sites occupied by an active woodpecker (occupied = red) and those without (unoccupied = blue). Total occupied sites = 24, total unoccupied sites = 24. Within each site samples were collected at 11 locations from the center of the site outwards to 150 m. Insects were dried and weighed per sampling location within each site. Total number of averaged samples per order = 528. Boxes indicate the first and third quartile, central lines depict the mean. Dots are averaged samples that lie outside the 1st and 3rd quartile.

The results of the GLM for each insect order are shown in Table 1, along with their corresponding main effect and interaction term values. The following insect orders showed a significant relationship with both the main effects of site type (occupied or unoccupied) and the interaction term of distance from the center of the site and the site type: Coleoptera ($P < 2e-16$), Orthoptera ($P < 2e-16$), Diptera ($P = 0.02$), Hymenoptera ($P < 0.00224$), and Hemiptera ($P = 0.000118$). The only two orders that were not significant were Phasmatodea and Mantodea. No orders showed significant relationships with the main effect distance from center.

To determine the biological effect of both main effects and the interaction term, we turn to the coefficient estimates (β). For the main effect of Site Type I found that all significant orders, Coleoptera ($\beta = 2.0218$), Orthoptera ($\beta = 2.151$), Diptera ($\beta = 0.759$), Hymenoptera ($\beta = 0.5022$), and Hemiptera ($\beta = 0.2338$) had β values higher than 0.01, indicating that the increase seen in sites occupied by a woodpecker would likely impact the insect assemblage and nesting birds foraging behaviors. However, when looking at the interaction term, not all significant orders had realistic biological impacts. The small coefficient estimates for Diptera ($\beta = -0.00536$) and Hemiptera ($\beta = -0.00393$) indicate that though they may be statistically significant, the actual increase in biological mass would not be enough to impact the insect community or the foraging habits of local nesting birds.

Table 1: List of Gamma GML models. Insect samples collected in an array from the center of the site to 150m (Sampling Distance), and on sites occupied and unoccupied by a woodpecker. Significant parameters in bold. (*) indicates interaction term.

	Model Values		Interaction Values			
Insect Order	χ2	chisq *P*	β	SE	z-value	*P*
Coleoptera**	365.97	1.25E-08				
Sampling Distance			-0.00055	0.00107	-0.508	0.611
Site Type			**2.0218**	**0.1346**	**15.019**	**2.00E-16**
Sampling Distance*Site Type			**-0.168**	**0.0015**	**-11.083**	**2E-16**
Orthoptera**	371.17	0.000247				
Sampling Distance			0.00004	0.001	0.045	0.964
Site Type			**2.151**	**0.098**	**21.867**	**2E-16**
Sampling Distance*Site Type			**-0.177**	**0.001**	**-15.965**	**2E-16**
Diptera**	35.12	1.16E-07				
Sampling Distance			0.000528	0.0017	0.317	0.75102
Site Type			**0.759**	**0.209**	**3.631**	**0.00031**
Sampling Distance*Site Type			**-0.00536**	**0.00236**	**-2.274**	**0.02336**
Mantodea	0.126	0.99				
Sampling Distance			-0.00013	0.000639	-0.21	834
Site Type			0.0333	0.0802	0.415	0.678
Sampling Distance*Site Type			-0.00012	0.000905	-0.134	0.893
Hymenoptera**	22.304	0.000056				
Sampling Distance			-0.00079	0.00089	-0.89	0.374
Site Type			**0.5022**	**0.1125**	**4.464**	**9.80E-06**
Sampling Distance*Site Type			**-0.037**	**0.0013**	**-2.926**	**0.00358**
Phasmatodea	0.72	0.8685				
Sampling Distance			-6.90E-04	0.0007	-0.966	0.334
Site Type			-0.0072	0.0903	-0.08	0.936
Sampling Distance*Site Type			-0.00011	0.00102	-0.112	0.911
Hemiptera**	6.239	0.01005				
Sampling Distance			0.00104	0.00074	1.42	0.1561
Site Type			**0.2338**	**0.09225**	**2.534**	**0.0116**
Sampling Distance*Site Type			**-0.00393**	**0.00104**	**-3.776**	**0.000178**

** significant value with alpha = 0.05

3.1.2. *Woodpecker Home Range Size*

My technicians and I collectively spent 2,880 hours observing individual males within their home ranges during the summer of 2019. To estimate individual home ranges, I created the MCPs in ArcPro, and found that the average home range size within my study was 2.67 ± 0.35 hectares. In objective 1, I hypothesized that the insect orders Coleoptera and Hymenoptera would be negatively correlated with the size of the woodpecker home range associated with them, due to woodpeckers reducing their home range size when abundant resources are available. The insect order Coleoptera (P = 0.0000659, rho = -0.74, n = 24), had the strongest biological relationship as home ranges of the woodpecker increased with a decrease in overall Coleoptera mass. Hymenoptera (P = 0.0093, rho = -0.53, n = 24), and Orthoptera (P = 0.0065, rho = -0.55, n = 24) has slightly less strong correlations, but again, woodpecker home ranges increased with a decrease in both order’s masses (see Figure 3).

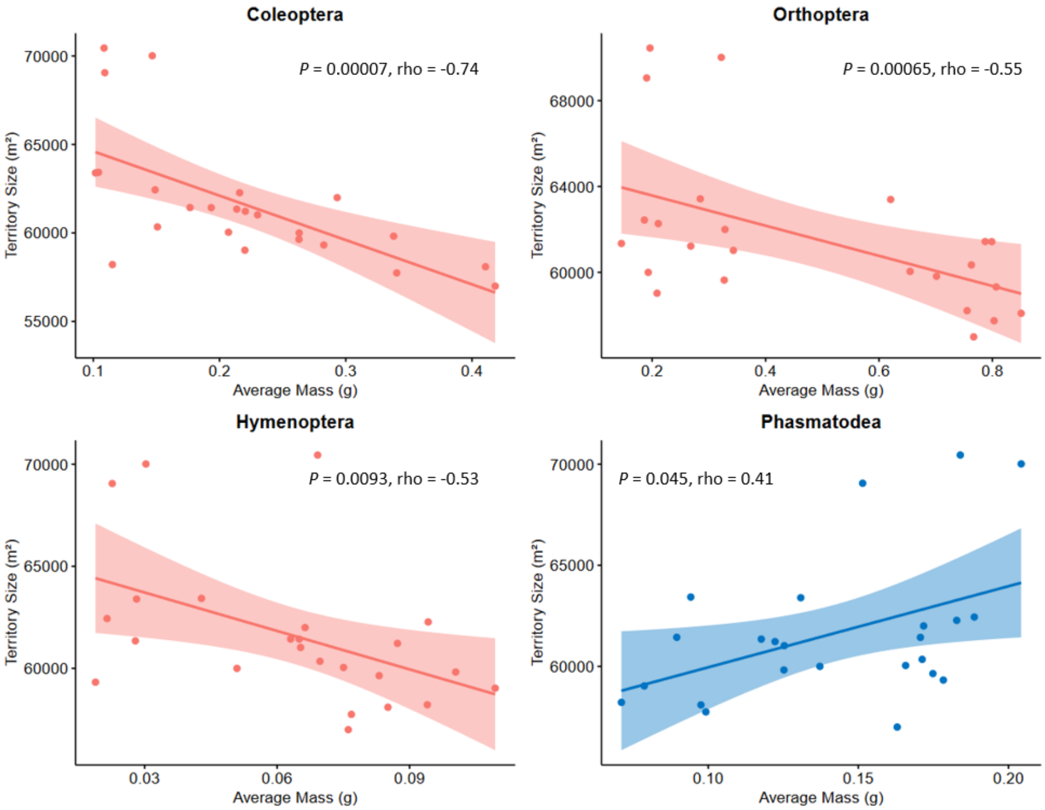

Figure 4: Scatter plots of woodpecker home range size correlated with average mass (g) of significant insect orders. Increases in Coleoptera, Orthoptera, Hymenoptera were negatively correlated with home range size and Phasmatodea was positively correlated. Mantodea, Diptera, and Hemiptera were not significantly correlated. Red indicates negative correlations, blue positive.

The overall mass of Phasmatodea increased in association with an increase in woodpecker home range size (P = 0.045, rho = 0.41). Hemiptera, Diptera, and Mantodea were not significantly correlated with home range size.

3.2. Avian Assemblage

Identifying patterns of avian species richness and abundance within site types (occupied by a woodpecker and unoccupied) gave additional information into relationships the woodpecker had with the avian community as a whole, not just SCN birds. Within my tsecond objective, I hypothesized that avian species richness and abundance would be higher in areas occupied by woodpeckers and that this increase would be apparent in biomes with few suitable nesting trees (grassland and/or early-seral) but not apparent in biomes with abundant suitable trees (scrubland and/or woodland). Across all point counts within my sites, I observed a total of 69 species between the months of May and July 2019. A full index of the species observed between occupied and unoccupied sites can be found in Appendix A. Species richness differed between site types; occupied sites had significantly higher species richness than unoccupied sites ($t = 5.9$, $df = 85$, $P = 5.14e\text{-}08$). There were no significant differences in species richness between biome types (Table 2).

Table 2: χ2 matrix of the four biome types present on the SAV property comparing species richness, and relative abundances of both non-cavity and cavity nesting birds between occupied and unoccupied sites. Left side of matrix indicates the significance value, the right side indicates the corresponding odds ratio. Significant values indicated in bold. Grassland and early-seral biomes have limited numbers of suitable nesting trees (diameter > 20cm), scrubland and woodland have abundant suitable nesting trees.

Species Richness				
	E	G	S	W
E		0.99	0.79	0.90
G	0.99		0.79	1.11
S	0.51	0.48		0.89
W	0.73	0.72	0.69	
Non-cavity Nesters				
	E	G	S	W
E		0.68	1.00	1.22
G	0.07		0.91	0.91
S	1.00	0.42		0.82
W	0.11	0.39	0.07	
Cavity Nesting Birds				
	E	G	S	W
E		0.68	0.45	0.51
G	0.07		0.31	2.99
S	0.00834*	0.000163*		0.91
W	0.01*	0.000195*	0.67	

E = Early-Seral, G = Grassland, S = Scrubland, W = Woodland

* significant value with alpha = 0.05

The index for avian abundance detected through the point counts across site types can also be seen in Appendix A. Occupied sites had significantly higher avian abundance than unoccupied sites (t = 10.80, df = 87, P < 2.2e-16) with a sample mean of 33 birds for occupied sites and a sample mean of 22 birds for unoccupied sites. There were no significant differences in avian abundance between biomes. Within non-cavity nesting species, abundance between site types was significantly higher in occupied sites compared to unoccupied (t = 7.2, df = 88.9, P < 1.56e-10) with a sample mean of 25 birds for occupied sites and a sample mean of 19 birds for unoccupied sites. However, non-cavity nesting bird abundance between occupied and unoccupied sites was not influenced by biome type (see Table 2).

Alternatively, secondary cavity nesters had significantly higher abundances within occupied sites compared to unoccupied sites ($t= 11.092$, $df = 102.56$, $P < 2.2e-16$), and biomes with fewer suitable trees had increased numbers of SCNs when occupied by a woodpecker, while biomes with ample trees did not show a significant difference between sites. The following biomes had significantly different numbers of secondary cavity nesting birds between site types: shrubland and early-seral, shrubland and grassland, woodland and early-seral, and woodland and grassland, seen in Table 2 along with their corresponding effect sizes as an odds ratio.

3.3. Woodpecker Nest Success

The factors that influence how woodpeckers excavate their nesting cavities and influence the success or failure of their chicks may play an important role in the nest choice and success of SCN birds within the area. The average height for a woodpecker nest within my study was 2.3 m ± 0.26, the average DBH of the nesting tree was 52 cm ± 6.2, the average diameter of the cavity opening was 9 cm ± 0.8, the average depth of the cavity was 7 cm ± .7, and the average percent cover was 43% ± 6.3. The count and percent of woodpecker nests in each decay class is shown in Table 3.

Table 3: Nesting tree decay class rank for each cavity nesting bird found within the study. Count and percent of that species within the decay class are shown for each species of secondary cavity nesting bird, along with the primary cavity nesting bird, the woodpecker. The data on the Ash-throated and Brown-crested Flycatchers were combined due to similar life history traits between species.

Biome	Natural		Woodpecker		Total
	Empty (%)	Occupied (%)	Empty (%)	Occupied (%)	
Early-seral	161 (91.5)	15 (8.5)	12 (31.6)	26 (68.4)	214
Grassland	149 (85.6)	25 (14.4)	12 (27.9)	31 (72.1)	217
Shrubland	275 (88.4)	36 (11.6)	12 (19.4)	50 (80.6)	373
Woodland	443 (91.5)	41 (8.5)	33 (33.3)	66 (66.7)	583

The candidate model selection processes for the woodpecker nesting success is shown in Appendix B, and the model averaging results are shown in Table 4. Model averaging for the woodpecker suggested that the decay state of the tree and the percent of nest cover were significant predictors for a successful nest. The corresponding beta estimates (β) indicate that with every unit increase in decay the nest was less likely to be successful ($\beta = -0.9086$), and that with every unit increase in vegetation covering the cavity entrance, the more likely that nest was to succeed ($\beta = 0.0992$).

Table 4: Model average estimates with 95% confidence intervals (CIs) for variables retained in the candidate model sets predicting cavity nesting bird nesting success. Data was collected across the SAV Ranch, East Foundation during 2019. Decay state of the nesting tree = Decay, amount of cavity covered by vegetation = Nest Cover, whether the nest was located in an abandoned woodpecker cavity or a naturally occurring one = Nest Type, the height of the cavity = Height, the diameter of the nesting tree at breast height = DBH, the diameter of cavity entrance hole = Hole, the depth of cavity = Depth.

				95% CI	
	Model averaged β	SE	p	Lower	Upper
BEWR					
Nest Cover	**0.0585**	**0.0195**	**0.0017**	**0.0203**	**0.0968**
Nest Type	**1.9166**	**0.9505**	**0.0232**	**0.0536**	**3.7795**
DBH	0.6256	0.4927	0.1035	-0.34	1.5913
Hole	-0.0424	0.181	0.4077	-0.3971	0.3123
Decay	-0.0275	0.1368	0.4206	-0.2955	0.2405
Height	0.0084	0.1711	0.4804	-0.3438	0.327
Depth	3.10E-08	0.1721	0.4999	-0.3374	0.3373
ATBC					
Decay	**-0.4009**	**0.1893**	**0.0183**	**-0.7719**	**-0.0299**
Nest Type	**3.5382**	**0.7737**	**2.10E-05**	**2.0217**	**5.0547**
Hole	-0.6276	0.3916	0.0561	-1.3952	0.14
Depth	-0.05	0.1747	0.3877	-0.3925	0.2925
Nest Cover	0.0018	0.0061	0.3829	-0.0101	0.0137
Height	0.0557	0.1908	0.3854	-0.3183	0.4298
DBH	0.0007	0.1393	0.4981	-0.2724	0.2737
GFWO					
Decay	**-0.9086**	**0.411**	**0.0147**	**-1.7141**	**-0.1031**
Nest Cover	**0.0992**	**0.0511**	**0.0275**	**-0.001**	**0.1994**
DBH	0.1071	0.3015	0.3616	-0.4839	0.6981
Hole	0.0455	0.3275	0.4449	-0.5963	0.6874
Height	0.0199	0.277	0.4715	-0.5231	0.5628
Depth	0.0182	0.1792	0.4596	-0.3331	0.3696
BCTI					
Decay	**-1.0188**	**0.4137**	**0.0077**	**-1.8297**	**-0.208**
Nest Cover	0.0266	0.0288	0.1795	-0.0299	0.0831
Nest Type	**2.5338**	**1.2761**	**0.0249**	**0.0326**	**5.035**
Height	-0.0524	0.2932	0.4292	-0.627	0.5222
DBH	0.0703	0.2857	0.403	-0.4896	0.6302
Hole	0.0213	0.2104	0.4598	-0.3911	0.4336
Depth	-0.0018	0.2139	0.4967	-0.421	0.4174

Note: Candidate models were chosen if they had an AICc weight ≥10% of the AICc weight of the top model. Also included is the *SE* = standard error of β, p = p value (alpha = 0.05).

3.4 Secondary Cavity Success

Given that the success of SCN birds may be reliant on the metrics of the pre-existing cavities they require for nesting, I hypothesized that model averaging would result in predictor variables similar to the woodpecker, given that over half of the cavities used by secondary cavity nesters were abandoned woodpecker cavities. As stated in my fourth objective, I not only expected the SCN birds to share predictor variables, I also expected SCN birds to have higher nesting success when nesting inside an abandoned woodpecker cavity than when nesting in a naturally occurring one (nest type). This was mainly due to abandoned woodpecker nests being more uniform in shape and, within my study sites, tended to be in trees with lower rates of decay than trees that had naturally occurring cavities.

On average woodpecker cavities were higher (2.0 m ± 0.17) than natural cavities (1.3 m ± 0.15), were located within less decayed trees (2 decay rate ± 0.3) than natural cavities (4 decay rate ± 0.3) with larger DBHs (71 cm ± 8.2) than natural cavities (63 cm ± 4.9). The woodpecker cavities also had more nest cover (46% ± 4.1) than natural cavities (41% ± 5.7), smaller entrance holes (9 cm ± 0.5) than natural cavities (10 cm ± 0.7), and deeper cavity depths (4 cm ± 0.5) than natural cavities (4 cm ± 0.5) but these results were not significant. Additionally, the number of available cavities increased within biomes of increasing woody cover, with early-seral and grassland biomes having the fewest cavities, and shrubland and woodland biomes having the most. Abandoned woodpecker cavities were more likely to have a nesting attempt than a natural cavity in all biomes (see Table 4).

Table 5: Secondary cavity nesting bird's success in relation to whether they were built in an abandoned woodpecker cavity (Woodpecker) or a naturally occurring one (Natural) and their relative percent values. Data on the Ash-throated and Brown-crested Flycatchers were combined due to similar life history traits between the two species. All species had higher success rates when nesting in abandoned woodpecker cavities than in natural cavities.

	Decay class						
Species	1 (%)	2 (%)	3 (%)	4 (%)	5 (%)	6 (%)	7 (%)
Ash-throated/Brown-crested Flycatcher	14 (13.7)	11 (10.8)	16 (15.7)	23 (22.5)	19 (18.6)	16 (15.7)	3 (2.9)
Black-crested Titmouse	7 (17.9)	5 (12.8)	5 (12.8)	3 (7.7)	10 (25.6)	6 (15.4)	3 (7.7)
Bewick's Wren	16 (20.3)	10 (12.7)	13 (16.5)	15 (19)	14 (17.8)	11 (13.9)	0 (0)
Golden-fronted Woodpecker	14 (25.5)	8 (14.5)	7 (12.7)	4 (7.3)	7 (12.7)	9 (16.4)	6 (10.9)

Several nesting characteristics have been shown to influence cavity nesting success; therefore, my fourth objective investigated which factors were most important to my study system in south Texas. Between biomes there were progressively more available cavities in biomes that had more tree coverage, and though there were more natural cavities available within the study sites, a higher percentage of the abandoned woodpecker cavities were occupied than the natural (see Table 3). All species of SCNs had higher success rates in woodpecker cavities than in naturally existing ones (Table 5).

The candidate model selection processes for SCN bird success is shown in Appendix B, and the model averaging results are shown in Table 4. Model averaging for the BEWR suggested that the percent of nest cover and the nest type were significant predictors for a successful nest. The corresponding beta estimates (β) indicate that with every unit increase in nest coverage the nest was more likely to be successful (β = 0.0585), and that when the nest was placed in an abandoned woodpecker cavity it had higher chance of succeeding (β = 1.9166). For the flycatchers (ATBC), model averaging suggested that the decay of the nesting tree and the cavity type were significant predictors for nests. The β values indicate that with every unit increase in decay the nest was less likely to be successful (β = -0.4009), while nests placed in abandoned woodpecker cavities were more likely to succeed (β = 3.5382). Similarly, the BCTI model averaging suggested that the decay of the nesting tree and the cavity type were significant predictors for nests. The β values indicate that with every unit increase in decay the nest was less likely to be successful (β = -1.0188), while nests placed in abandoned woodpecker cavities were more likely to succeed (β = 2.5338). Note that all SCN birds had higher nest success when in an abandoned woodpecker cavity than in a naturally occurring one. Additionally, the magnitude of these coefficients indicate that cavity type was a stronger predictor than either decay or nest cover for every species of SCN bird, and that the flycatchers and the titmouse had higher β values for nest type than did the BEWR. For both the titmouse and the flycatchers, decay of the tree negatively impacted nesting success, but the BEWR was not impacted by decay, only nest type. The BEWR is a habitat generalist and often makes nests in metal pipes and mailboxes and may not be influenced by the decay state of a nesting tree.

4. DISCUSSION

4.1. Overview

Overall, the only insect orders that are known to be heavily predated on by woodpeckers were positively correlated with woodpecker presence, with the addition of orthopterans also being highly correlated. Similarly, woodpecker home range size decreased with an increase in food availability. Likewise, the avian assemblage mirrored this trend as both species richness and abundance was significantly higher in areas with woodpeckers than those without. All SCN birds had higher rates of success in abandoned woodpecker cavities than natural ones, and both the woodpecker and secondary cavity nesting birds had higher rates of success in trees with either high coverage or low decay. These results suggest a potential ecosystem engineering effect from the woodpecker as it creates multiple cavities in areas with higher than average food availability, thus encouraging SCN birds to establish nests in their stable cavities, in areas of abundant food resources.

4.2. Insect Trends

Overall, the only insect orders that are known to be heavily predated on by woodpeckers were positively correlated with woodpecker presence, with the addition of orthopterans also being highly correlated. Similarly, woodpecker home range size decreased with an increase in food availability. Likewise, the avian assemblage mirrored this trend as both species richness and abundance was significantly higher in areas with

woodpeckers than those without. Both primary and secondary cavity nesting birds had higher rates of success when in a live tree compared to those with varying rates of decay, and all SCN birds had higher rates of success in abandoned woodpecker cavities than natural ones. These results suggest a potential ecosystem engineering effect from the woodpecker as it creates multiple cavities in areas with higher than average food availability, thus encouraging SCN birds to establish nests in their stable cavities, in areas of abundant food resources.

Based on previous literature, I expected insects within the order Coleoptera to be positively correlated with woodpecker presence given that Coleoptera are proportionally high in their diets, followed by Hymenoptera (Beckwith and Bull 1985, Hess and James 1998, Fayt et al. 2005, Pechacek and Kristin 2010). Within my first objective, I hypothesized that these insect orders would be significantly correlated both with the presence of an active woodpecker and the size of the woodpecker's home range. However, I did expect Coleoptera to have a stronger effect size than Hymenoptera due to previous literature that has highlighted the importance of beetles in woodpecker diets (Murphy and Lehnhausen 1998, Fayt 2005, Kelly 2019). The Golden-fronted Woodpecker, along with the life-history and interspecies interactions of southern Texas birds, has historically been understudied. This is due in part to the majority of the land being privately owned, the ruralness of the area, and the dense vegetation which consists of thorny shrubs including catclaw and blackbrush (*Coleogyne ramosissima*). Additionally, the Golden-fronted Woodpecker is known to be a diet generalist in that they not only glean from dead and decaying trees, but have been seen eating and feeding their young a wide variety of food types (Schroeder et al. 2013). Thus, my first objective presented a unique opportunity to investigate factors that influenced where the woodpecker chose to build their nests and establish territories based on insect availability, gleaned not only from observations of insects within the order Coleoptera (and to a lesser degree Hymenoptera), but from several insect orders commonly eaten by birds.

All recorded orders of insects collected within my study were found at all occupied and unoccupied site types, though not every insect order was found at each sweep netting location within the sites. Surprisingly, the presence or absence of a woodpecker within a site was not only positively correlated with the insect orders Coleoptera and Hymenoptera (as shown in previous studies), but Orthoptera as well, a trend that has never been reported within woodpecker diet studies. This suggests that the woodpeckers may be seeking out areas that have high availability of not only beetles and hymenopterans, but orthopterans as well. This trend continued with the same three orders of insects showing a biologically significant interaction term between the occupied and unoccupied sites type and the distance from the center of the site, along with significant main effects for site type. This indicates that the woodpeckers were seeking out areas that had higher masses of insects than would be expected by chance, and that the woodpecker chose these areas to establish its nest and the center of its home range. This insect concentration could be due to fine scale differences in vegetation and water availability (Huang et al. 2015).

In addition, the delineated home-range sizes of the woodpecker were only significantly correlated with the same three orders of insects, with the Orthopterans having the highest correlation coefficient. In general, these results coincided with results from the past, in that as resources (in this case food) increased within a site, the size of the woodpecker home range decreased. Studies have previously shown that woodpeckers reduce their defended areas when resources are abundant (Pasinelli 2000, Tingley et al. 2014). However, these studies have all been focused on potential woodpecker nesting habitat such as snag basal area and have not investigated the influence of food availability on the home range sizes of woodpeckers. I also highlight the importance of orthopterans in the Golden-fronted woodpecker's diet. In addition to the strong trends seen between orthopterans and both presence and home range size of the woodpecker, I observed the woodpecker and several species of SCN birds eating grasshoppers and locusts. During observations, I frequently observed a woodpecker fly from a perch on the side of a tree to catch a grasshopper or locust mid-air, from the grass, or glean it from a cactus or bush. These woodpeckers frequently fed their young orthopterans, and on several occasions, I saw a woodpecker cache a decapitated grasshopper or locust in the crook of a tree along with pieces of prickly-pear fruit (Opuntia).

The high correlation of orthopterans with woodpecker presence is consistent with another study done on the woodpecker's nestling provisioning rates (Schroeder et al. 2013), but are not consistent with studies done on other woodpecker species at higher latitudes. These findings could suggest that Orthoptera are a larger component of the Golden-fronted Woodpecker's diet than other woodpeckers. Considering that the vast majority of woody trees within the Tamaulipan thornscrub ecoregion are mesquite and have an extremely dense wood (and thus are harder to excavate for Hymenoptera and beetles), it is not surprising that woodpeckers in these regions have more diverse diets. Indeed, this could be part of the reason why the Golden-fronted Woodpecker is known to forage on the ground, eat and feed prickly pear fruit to its young (Kujawa 1984, Schroeder et al. 2013).

4.3. Avian Assemblage

While it was surprising to find a larger than expected array of insect orders correlating with the woodpecker's presence and home-range size, SCN birds (and indeed the avian assemblages as a whole) may have been impacted by the increased insect masses and the presence of the woodpecker within these sites. Within objective 2, I predicted that avian species richness and abundance would be correlated with the presence or absence of an active woodpecker within the site. Given that Coleoptera, Orthoptera, and Hymenoptera are also orders of insects that are in high proportion of non-excavating birds diets, the excavations left behind by the woodpecker may be attracting SCN birds to areas that already have high insect loads. Additionally, while the orders Hemiptera and Diptera had small effect sizes within the interaction term of site type and distance from the center of the site (example: dc), small increases in insect loads across a large area may have a direct impact on birds searching for food during the breeding season.

While the impacts for SCN birds were fairly clear, the influence of the woodpecker presence on the avian assemblage as a whole was more nuanced. Both avian species richness and abundance was significantly correlated with the presence of an active woodpecker. This trend was true for both SCN birds and non-cavity nesting bird species. While avian species abundance and richness was higher in sites with woodpeckers, it is less clear what may be causing this trend. On one hand, the avian community may be responding directly to the presence of an active woodpecker within the site. Previous studies have shown that as woodpeckers forage for food on dead and decaying trees they loosen the bark, create small holes in the wood and speed up the overall decay of the tree being foraged on (Lawton and Jones 1995, Cockle et al. 2011, Jusino et al. 2015). The result is that insects, such as wood burrowing beetles that were not accessible to non-excavating birds can now be eaten. Also, the increase in the attacked tree’s rate of decay results in an increase in heterogeneity as the cavities and foraging holes increase surface area, providing shelter and access points for insects. This increase in heterogeneity is also directly related to increases in both insect abundance and species richness (Dennis et al. 1998, Brown 2003).

Therefore, it is possible that the presence of a woodpecker in an area may directly influence foraging availability for other bird species and thus impact the composition of the avian assemblage. However, my study did not investigate this question directly and it is not possible to distinguish if the resulting differences in assemblage are due to the presence of the woodpecker correlating with higher masses of desirable insects, or due to some unknown factor such as fine scale differences in vegetation structure. Regardless, the types of insects available may influence the success of any nests established within the area. All SCN bird species sampled within my study were insectivorous and had some overlap in diet items with the woodpecker. However, many of the non-cavity nesting birds studied are granivorous for the majority of the year. Furthermore, most of these granivorous birds increase the amount of insects in their diet during the breeding season in addition to feeding their young high protein loads (Capernia 2009). Not only are woodpeckers reliant on some species of Coleoptera for population growth and nesting success (Rota et al. 2015), but many other bird species rely on the high amount of protein attainable by eating insects during the breeding season.

Within my second objective I hypothesized that within biomes with limited suitable nesting trees the addition of a woodpecker would significantly increase richness and abundance, whereas in biomes with abundant suitable trees the influence of a woodpecker would not impact local avian richness or abundance. In fact, biome type did not seem to affect species richness, the overall relative abundances, or specifically the non-cavity nesting birds. Only within the secondary cavity nesting birds did biome have an effect and only in biome types on opposite ends of the spectrum. For instance, early-seral had proportionally higher abundances of SCN birds in occupied than unoccupied sites when compared to occupied and unoccupied abundances in the shrubland biome. The same was found for early-seral compared to woodland, grassland compared to shrubland, and grassland compared to woodland. Both early-seral and grassland biomes were characterized by lower numbers of woody trees, and larger gaps between mottes of trees.

The establishment of a woodpecker into an area with a limited number of naturally occurring cavities (early-seral or grassland) may have a larger impact than in biomes already containing substantial amounts of naturally occurring cavities such as shrubland and woodland biomes. Indeed, studies of woodpeckers in heavily wooded areas have shown that the exclusion of a woodpecker from such an area does not have a direct impact on the secondary-cavity nesting organisms present (e.g., Weibe 2011). However, the inclusion of a woodpecker in areas with a lower number of suitable trees has a direct relationship with the persistence of SCN bird populations (Cockle et al. 2010). As described by Cockle et al. (2010) the nesting density of SCN birds increased in proportion to the increase of trees with a DBH >100cm.

My findings support the results of Weibe (2011) who found that cavity availability was not a limiting factor for SCN bird populations in mature forests. The significant difference (Table 5) between only biomes of substantially different proportions of available trees further validates previous studies that have at once heralded the importance of woodpeckers as ecosystem engineers and also indicated that in some ecosystems there is little reliance of SCNs on primary cavity excavators.

4.4. Woodpecker Nest Success

The majority of previous studies that have been done on North American woodpeckers have been conducted in the west (Siegel et al. 2016, Tingley et al. 2020), the east coast (FitzGerald et al. 2018), the northern United States and Canada (Frei et al. 2015, Blanc and Martin 2012) with the exception of some species-specific studies such as the work done on the Red-cockaded Woodpecker in the southern states (Shaw and Long 2007, Kesler and Walters 2012). This may in part be due to the accessibility of the land and the abundance of woodpecker species present in the regions. For example, previous studies in northern latitudes focus on the diversity of woodpeckers (4-6 species), the cavity networks they create (Straus et al. 2011, Ouellet-Lapointe et al. 2012), and thus how they collectively may influence secondary cavity nesters. However, this study provided a unique opportunity to investigate an understudied system which has only one strong primary excavator, the other being the weaker and much less common Ladder-backed Woodpecker. Additionally, I had the unique opportunity to study a large tract of moderately undisturbed land in a southern latitude within the Tamaulipan thornscrub region of southern Texas. This region has high biodiversity and unique species not found elsewhere in the continental United States, but research in this area has been stifled due to the majority of the area being privately owned (>95%) and inaccessible.

As for the parameters that determined the nesting success of both the woodpecker and secondary cavity nesting birds, several trends became apparent. Firstly, all nests were located within honey mesquite trees. Other woody species exist on the property, such as Texas persimmon (*Diospyros texana*) and Sweet acacia (*Vachellia farnesiana*), but none of these species found within the study plots had a DBH larger enough to sustain an active cavity (>20 cm) (Cockle et al. 2010). Secondly, both coverage of the nesting cavity and the percent coverage of the cavity opening were significant predictors of a successful woodpecker nest, but the decay rate of the tree indicated an opposite relationship as has been previously been discussed in the literature (Conner et al. 1976, Cockle et al. 2011, Blanc and Martin 2012). Such studies have indicated that woodpeckers seek out trees, or even portions of trees that show increased heart rot decay. Blanc and Martin (2012) found that multiple woodpecker species in British Columbia were selecting trees that were unhealthy or completely dead. In western North America, the Black-backed Woodpecker preferred heavily decayed dead and dying trees (Raphael and White 1984, Bull et al. 1986). However, Seavy et al. (2012) found that Black-backed Woodpeckers may have preferred completely dead trees, but that the preferred decay state was lower than previously indicated. They also found a higher proportion of Black-backed Woodpecker nests than they expected in live trees based on the availability.

Given the location of my study site in southern Texas, I was able to study a woodpecker in an arid location where temperature can exceed 46 ºC during the breeding season which may introduce a unique stress on developing eggs and chicks. Woodpecker species and other cavity nesting birds in more northern areas of North America do not contend with extreme heat during their breeding season. Though they may occasionally contend with below freezing temperatures in the early breeding season, this is easily rectified by direct incubation, which may limit their ability to forage but is not energy costly as no movement is necessary. The Golden-fronted Woodpecker in southern Texas, however, must find a way to keep their developing eggs and chicks cool during the heat of the day. One speculation for how birds in hot environments keep their eggs cool is by shading them (Ward 1990, Downs and Ward 1997), where the bird spreads its wing above the nest and lifts its brood patch off of the eggs to allow airflow to cool the egg surface area. However, the only accounts of this behavior are in ground or cup nesting birds. There is currently no information on how cavity nesting birds may regulate the temperature of their eggs in a hot or arid environment. There are reports of the adults clinging to the sides of the cavity once the chicks have hatched (Skutch 1969), which could be an attempt to reduce body contact and thus heat transfer with the chicks.

Therefore, the extreme heat of the breeding season in south Texas may explain the Golden-fronted Woodpeckers willingness to expend additional energy to build cavities within live trees, in contrast to woodpeckers from more northern areas. Within my study, 52.7% of woodpeckers built nests in trees with decay rates between 1-3 with the highest proportion of nests (25.5%) in live trees with no signs of illness (n = 55). While highly decayed trees and sections of trees are easier to excavate than dense live wood, the water contained in live wood acts as an excellent incubator and can protect nest contents from drastic heat spikes during the day (Whittow and Tazawa 1991, Lamprecht and Schmolz 2004). This was further supported through my study as one unit change in decay class decreased the log odds of the nests success by 0.895, see Table 4. Additionally, live trees with denser wood provide better protection from predators. Minks, raccoons, squirrels and raptors have all been observed destroying soft wood to access bird eggs (Purcell and Verner 1999, Fisher and Wiebe 2006). In addition, I observed a vulture ripping apart a highly decayed snag to eat the woodpecker eggs within.

While half of the woodpeckers chose to put their nests in trees with low decay rates, about half chose trees with decay rates >3 (see Table 2). While this is much higher than other studies on most woodpecker species (with the exception of specialists like the Red-cockaded woodpecker), this suggests that other factors may be in play here. Excavating a cavity in a live tree may be safer for the chicks, but there is a trade-off for the amount of energy expended. The percent cover of the tree cavity was also a significant predictor of nest success with each unit increase in nest cover increasing the log odds of a successful woodpecker by 0.1 (see Table 4). This contrasts with previous studies that have suggested lower cavity cover increases nest survival due to increased visibility by the parents (Cockle et al. 2011, Schaaf 2020). While this trend was significant within my models, it should be noted that the average percent nest cover was 43%, indicating that neither complete nest exposure nor coverage was preferred. However, given the extreme heat of the region, shaded cavities may have lower internal temperatures than those exposed to the elements, though cavity temperature was not measured. Additionally, the main predators of nesting birds in this region are snakes (Davis, 2017), and snakes are often deterred by obstructions on the tree trunk or to the cavity in a way that small and large mammals are not due to their dexterity (Rudolph et al. 1990, Neal et al. 1998, Wetherhead and Blouin-Demers 2004).

4.5. Secondary Cavity Success

Many SCN birds rely on pre-existing cavities to build their nests, and the presence of a woodpecker within an area may increase the availability of stable cavities. Within my study the Ash-throated/Brown-crested Flycatchers and the Black-crested titmouse showed a decrease in nest success with increasing tree decay as did the woodpeckers, indicating that other species of cavity nesting birds may rely on the stability produced by cavities in live trees. However, the proportion of nests for both species suggested that, similar to the woodpecker, other factors may be important as only 40.2% and 43.5% of each species respectively were in nests with decay rates ≤3 (see Table 2). Within my study, the log odds of the Black-tufted Titmouse (-0.041) and the Ash-throated/Brown-crested Flycatcher (-0.4) decreased with every increase in decay rate, indicating that while both species may be subject to the same temperature and stability pressures as the woodpecker, the Black-crested Titmouse had little biological impact with such a low decrease in the log odds (see Table 4). Alternatively, the Bewick's Wren did not appear to be influenced by the decay rate of the cavity tree. This may be explained by the fact that Bewick's Wrens are extremely opportunistic and have been observed building their nests in outbuildings, abandoned automobiles, and brush piles (Kennedy and White 2013). I observed successful Bewick's Wren nests built in metal pipes on the ranch roads (outside of my transects), indicating that while temperature may be a determining factor for the other species of cavity nesting birds, it is not the case for this specific nesting generalist.

Across all SCN birds, one trend remained consistent: all species had a higher likelihood of nest success when in an abandoned woodpecker cavity compared to a naturally occurring one. The type of cavity had varying influence on the outcome of each species nests, with Bewick's Wren ($\beta = 2.027$) having the least impact, followed by the Black-tufted Titmouse ($\beta = 2.72$), with the largest influence seen in the Ash-throated/Brown-crested Flycatcher ($\beta = 3.57$). Taking what we know about the generalistic nesting behavior of the Bewick's Wren, it is not surprising that they showed the lowest influence by the cavity type. The Black-tufted Titmouse and the flycatchers both had high nesting success when they built their nest in an abandoned woodpecker cavity, and despite the Bewick's Wren having the lowest of the three groups, it still had high rates of success. Overall, the discrepancy between the number of successful nests in abandoned woodpecker cavities and naturally occurring ones is stark (see Table 6). These results support previous literature that cavity nesting birds tend to have high success rates, this in contrast to cup nesting or ground nesting birds that tend to have much lower success rates especially compared to their cup nesting or ground nesting counterparts (Li and Martin 1991, Martin 1995, Mouton and Martin 2018). This has been hypothesized to be because of the hidden nature of eggs and chicks within a cavity compared to the exposed contents of other nest types.

Based on the results of both the raw nesting success or failure and the results of model averaging the fitted models, the cavities left behind by woodpeckers are extremely valuable to local SCN birds. Nest failure in natural cavities was lower than previously suggested in the literature for cavity nesting birds, with failure rates ranging from ~ 50-75%. This is contrasted by the high success rates within abandoned woodpecker nests, ranging from 84 to 94%. This may be due, in part, to the extreme temperature of the region. Just like the woodpecker, these SCN birds may be preferentially choosing live trees in an attempt to protect their eggs and chicks from the high heat of the day.

The cavities left behind by woodpeckers had characteristics that were more favorable for cavity nesting birds compared to naturally occurring cavities. Woodpecker cavities were significantly different from naturally occurring cavities; nests were higher within the tree, the tree was less decayed, and the DBH was larger. Additionally, the woodpecker cavities were more likely to be occupied than naturally occurring ones which may potentially be a limiting resource in some areas. For example, both early-seral and grassland biomes had lower base levels of pre-existing cavities than the woodland and shrubland biomes (see Table 7). Considering that SCN birds are reliant on pre-existing cavities to create their nests, the factors that drive the creation and design of the woodpecker's cavity may then dictate the success of these local cavity nesting birds.

4.6. Management Implications

My study provides useful information on nesting selection of both a key ecosystem engineer and secondary cavity nesting birds in south Texas. My results indicate that the common secondary cavity nesting birds of south Texas may rely on the cavities left behind by the woodpecker, and that the woodpecker actively sought out areas of specifically high insect availability. To protect and manage for these cavity nesting birds managers should avoid removing trees with large DBHs that have multiple cavities as these cavities may be crucial to many species. Specifically, the secondary cavity nesting bird's abundances were significantly different between biome types that had various levels of forestation. This may indicate that the persistence of trees with DBHs large enough for functional cavities are crucial nesting spots for cavity nesting birds in biomes with few numbers of available trees, such as grasslands or early seral. However, while the influence of the woodpecker was slightly lessened in the heavily forested biomes (scrubland and woodland), secondary cavity nesting birds still had higher rates of success in abandoned woodpecker cavities than in natural cavities, again indicating the importance of protecting and managing for woodpeckers in areas with secondary cavity nesting bird populations.

Further research into the habitat requirements of the Golden-fronted Woodpecker will give more information as to where they are establishing their home ranges, and thus give more information as to how the secondary cavity nesting bird assemblage may be influenced. Decayed trees in southern Texas may not be as valuable to primary and secondary cavity nesters, as has previously been shown in studies in more northern areas. Rather, I have shown that live trees of DBH large enough to support active cavities are preferred by the woodpecker, and thus, the secondary cavity nesting birds. Protecting cavity nesting birds in areas similar to my study location will include protecting areas with the above-mentioned nesting tree requirements, with emphasis in biomes with already few woody trees.

4.7. Conclusions

Since woodpeckers within my study seemed to choose their nesting locations based on insect availability, and given that all of the SCN birds present within the study were insectivorous, there may be additional gains from nesting within an active woodpecker territory. SCN birds may be enticed to nest in an area due to the increased numbers of cavities created by the active woodpecker pair. Once established, they not only get the benefit of nesting within a cavity that is more structurally sound and designed for incubation of eggs and young, they may also benefit from the increased amounts of insects in the area, which may have been chosen by the woodpecker initially. I also suggest that the stark difference in cavity success and failures seen between natural and abandoned woodpecker cavities and the strong trend of live trees predicting nest success of the cavity nesters is indicative of the extra effort woodpeckers expend to protect their eggs and chicks from the south Texas summer heat. The tendency of the Golden-fronted woodpecker to excavate live trees over highly decayed trees may be indicative of a larger global trend; woodpeckers in more northern areas may not require the thermoregulation of live trees with higher water content due to lower breeding season temperature but woodpeckers in arid/semi-arid areas may rely on this more energy costly method. My results open up new avenues for study on the temperature effects and the cavity design of woodpeckers at different latitudes.

The Golden-fronted woodpecker acts as an ecosystem engineer, as both its nesting locations and cavity design may influence SCN birds who also rely on the stability of their cavity to protect their nests. Additionally, the avian community as a whole may be indicative of these increased insect loads around woodpecker territories, as both avian species richness and abundance was positively correlated with the presence of woodpecker home-ranges. The fact that several insect orders within my study and the avian community as a whole showed a positive correlation with both the home-range of the woodpecker, their presence within a site, and with their shared nest characteristics with SCN birds suggests that the Golden-fronted Woodpecker is an active ecosystem engineer within this southern Texas system, and potentially a more important component of the avian assemblage than previously determined.

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APPENDIX A

AVIAN SPECIES RELATIVE ABUNDANCE

Index of avian species' relative abundances found on sites occupied by a Golden-fronted Woodpecker (Occupied) and those without (Unoccupied). Species detected though auditory and visual point count identification. Data collected in spring and summer of 2019 across the San Antonio Viejo Ranch, East Foundation, TX.

Species		Relative Abundances	
Common Name	Scientific Name	Occupied	Unoccupied
Ash-throated Flycatcher	*Myiarchus cinerascens*	68	29
Audubon's Oriole	*Icterus graduacauda*	4	1
Barn Swallow	*Hirundo rustica*	4	1
Brown-crested Flycatcher	*Myiarchus tyrannulus*	35	8
Black-crested Titmouse	*Baeolophus atricristatus*	84	18
Bell's Vireo	*Vireo bellii*	1	0
Bewick's Wren	*Thryomanes bewickii*	101	55
Blue-gray Gnatcatcher	*Polioptila caerulea*	4	4
Brown-headed Cowbird	*Molothrus ater*	15	14
Blue Grosbeak	*Passerina caerulea*	2	1
Black Vulture	*Coragyps atratus*	2	0
Bronzed Cowbird	*Molothrus aeneus*	3	1
Black-tailed Gnatcatcher	*Polioptila melanura*	3	1
Black-throated Sparrow	*Amphispiza bilineata*	65	56
Bullock's Oriole	*Icterus bullockii*	5	0
Cactus Wren	*Campylorhynchus brunneicapillus*	12	1
Carolina Wren	*Thryothorus ludovicianus*	3	0
Cassin's Sparrow	*Peucaea cassinii*	100	72
Curve-billed Thrasher	*Toxostoma curvirostre*	2	0
Clay-colored Sparrow	*Spizella pallida*	8	2
Common Ground-Dove	*Columbina passerina*	13	13
Chihuahuan Raven	*Corvus cryptoleucus*	15	17
Chipping sparrow	*Spizella passerina*	1	0
Couch's Kingbird	*Tyrannus couchii*	10	1
Common Nighthawk	*Chordeiles minor*	6	7
Common Pauraque	*Nyctidromus albicollis*	7	1
Crested Caracara	*Caracara cheriway*	6	4

Appendix A: Avian Species Relative Abundance continued.

Species		Relative Abundance	
Common Name	Scientific Name	Occupied	Unoccupied
Eastern Screech-Owl	*Megascops asio*	14	1
Eurasian Collared-Dove	*Streptopelia decaocto*	1	2
Field Sparrow	*Spizella pusilla*	2	2
Golden-fronted Woodpecker	*Melanerpes aurifrons*	96	42
Great Horned Owl	*Bubo virginianus*	7	0
Great Kiskadee	*Pitangus sulphuratus*	2	0
Green Jay	*Cyanocorax yncas*	9	2
Greater Roadrunner	*Geococcyx californianus*	35	24
Great-tailed Grackle	*Quiscalus mexicanus*	1	0
Hooded Oriole	*Icterus cucullatus*	1	0
House Wren	*Troglodytes aedon*	1	1
Lark Sparrow	*Chondestes grammacus*	23	15
Long-billed Thrasher	*Toxostoma longirostre*	19	2
Ladder-backed Woodpecker	*Dryobates scalaris*	2	0
Least Flycatcher	*Empidonax minimus*	1	0
Lesser Nighthawk	*Chordeiles acutipennis*	13	0
Loggerhead Shrike	*Lanius ludovicianus*	1	6
Mourning Dove	*Zenaida macroura*	91	67
Northern Bobwhite	*Colinus virginianus*	165	116
Northern Cardinal	*Cardinalis cardinalis*	144	117
Northern Harrier	*Circus cyaneus*	1	0
Northern Mockingbird	*Mimus polyglottos*	105	88
Olive Sparrow	*Arremonops rufivirgatus*	44	30
Olive-sided Flycatcher	*Contopus cooperi*	1	0
Painted Bunting	*Passerina ciris*	122	99
Pyrrhuloxia	*Cardinalis sinuatus*	88	80
Savannah Sparrow	*Passerculus sandwichensis*	1	0
Scaled Quail	*Callipepla squamata*	5	7
Scissor-tailed Flycatcher	*Tyrannus forficatus*	32	39
Swainson's Hawk	*Buteo swainsoni*	1	1
Turkey Vulture	*Cathartes aura*	4	6
Vermilion Flycatcher	*Pyrocephalus obscurus*	10	2
Verdin	*Auriparus flaviceps*	15	9
Western Kingbird	*Tyrannus verticalis*	1	1
White-eyed Vireo	*Vireo griseus*	26	23
White-tipped Dove	*Leptotila verreauxi*	4	1
White-winged Dove	*Zenaida asiatica*	6	2
Yellow-billed cuckoo	*Coccyzus americanus*	26	21

APPENDIX B

CANDIDATE MODEL LIST

Logistic Regression candidate models and null model predicting the success or failure of cavity nesting birds. Data was collected on cavity nesting birds, post fledging, across the SAV Ranch, East Foundation during 2019. Decay state of the nesting tree = Decay, amount of cavity that is covered by vegetation = Nest Cover, whether the nest was located in an abandoned woodpecker cavity or a naturally occurring one = Nest Type, the height of the cavity in the nesting tree = Height, the diameter of the nesting tree at breast height = DBH, the diameter of the cavity entrance hole = Hole, the depth of the cavity = Depth. Candidate models were used for mode averaging.

Bewick's Wren (n = 79)	logLik	AICc	ΔAICc	Weight
M1: Decay + Nest Cover + Nest Type	-11.672	32.520	0.000	0.185
M2: Decay + Nest Type	-13.420	33.526	1.005	0.112
M3: Decay + Nest Cover + Nest Type + Height	-11.465	34.748	2.227	0.061
M4: Decay + Nest Cover + Nest Type + DBH	-11.498	34.815	2.295	0.059
M5: Decay + Nest Cover+ Nest Type + Hole	-11.573	34.964	2.443	0.054
M6: Decay + Nest Cover + Nest Type + Depth	-11.650	35.117	2.597	0.050
M7: Decay + Nest Type + DBH	-13.008	35.193	2.673	0.049
M8: Decay + Nest Type + Depth	-13.381	35.938	3.418	0.033
M9: Decay + Nest Type + Height	-13.412	36.001	3.481	0.032
M10: Decay + Nest Type + Hole	-13.416	36.009	3.489	0.032
M11: Decay + Nest Cover	-15.113	36.912	4.391	0.021
M12: Decay + Nest Cover + Nest Type + DBH + Height	-11.189	37.002	4.482	0.020
Null Model	*-47.650*	*97.35*	*31.3106*	*3E-08*

Appendix B: Candidate Model continued.

Ash-throated/Brown-crested Flycatcher (n = 102)	logLik	AICc	ΔAICc	Weight
M1: Decay + DBH + Origin + Hole	-38.417	87.458	0.000	0.127
M2: Decay + Orign + Hole	-39.564	87.541	0.083	0.121
M3: Decay + Nest Cover + Origin + Hole	-39.233	89.090	1.632	0.056
M4: Decay + Nest Cover + Origin + DBH + Hole	-38.134	89.152	1.694	0.054
M5: Decay + Origin + Depth + Hole	-39.308	89.242	1.784	0.052
M6: Decay + Origin + DBH + Height + Hole	-38.252	89.387	1.929	0.048
M7: Decay + Origin + DBH + Depth + Hole	-38.261	89.406	1.948	0.048
M8: Decay + Origin + DBH	-40.561	89.535	2.077	0.045
M9: Decay + Origin + Height + Hole	-39.455	89.535	2.077	0.045
M10: Decay + Origin	-41.766	89.777	2.319	0.040
M11: Decay + Nest Cover + Origin + Depth + Hole	-38.959	90.802	3.343	0.024
M12: Decay + Nest Cover + Origin + Height + Hole	-39.023	90.930	3.472	0.022
M13: Decay + Nest Cover + Origin + DBH + Height + Hole	-37.872	90.936	3.477	0.022
M14: Decay + Nest Cover + Origin + DBH + Depth + Hole	-37.957	91.106	3.647	0.020
M15: Decay + Origin + DBH + Height	-40.277	91.178	3.720	0.020
M16: Decay + Origin + Depth + Height + Hole	-39.162	91.209	3.751	0.019
M17: Decay + Origin + DBH + Depth + Height + Hole	-38.060	91.312	3.854	0.018
M18: Decay + Nest Cover + Origin + DBH +	-40.344	91.313	3.854	0.018
M19: Decay + Nest Cover + Origin	-41.503	91.419	3.961	0.017
M20: Decay + Origin + Height	-41.549	91.511	4.052	0.017
M21: Origin + Hole	-42.719	91.682	4.224	0.015
M22: Decay + Origin + DBH + Depth	-40.557	91.738	4.280	0.015
M23: Decay + Origin + Depth	-41.751	91.914	4.456	0.014
Null Model	*-67.350*	*136.74*	*49.2824*	*2.5E-12*

Golden-fronted Woodpecker (n = 55)	logLik	AICc	ΔAICc	Weight
M1: Decay + Nest Cover	-12.655	31.781	0.000	0.267
M2: Decay + Nest Cover + DBH	-12.319	33.439	1.657	0.117
M3: Decay + Nest Cover + Hole	-12.607	34.014	2.233	0.087
M4: Decay + Nest Cover + Height	-12.636	34.072	2.290	0.085
M5: Decay + Nest Cover + Depth	-12.640	34.080	2.299	0.085
M6: Decay + Nest Cover + DBH + Depth	-12.207	35.639	3.857	0.039
M7: Decay + Nest Cover + DBH + Hole	-12.249	35.723	3.941	0.037
M8: Decay + Nest Cover + DBH + Height	-12.319	35.862	4.081	0.035
M9: Decay + Nest Cover + Height + Hole	-12.567	36.358	4.577	0.027
Null Model	*-32.227*	*66.530*	*34.749*	*7.6E-09*

Appendix B: Candidate Model continued.

Black-crested Titmouse (n = 39)	logLik	AICc	ΔAICc	Weight
M1: Decay + Nest Cover + Origin	-11.672	32.520	0.000	0.185
M2: Decay + Origin	-13.420	33.526	1.005	0.112
M3: Decay + Nest Cover + Origin + Height	-11.465	34.748	2.227	0.061
M4: Decay + Nest Cover + Origin + DBH	-11.498	34.815	2.295	0.059
M5: Decay + Nest Cover + Origin + Hole	-11.573	34.964	2.443	0.054
M6: Decay + Nest Cover + Origin + Depth	-11.650	35.117	2.597	0.050
M7: Decay + Origin + DBH	-13.008	35.193	2.673	0.049
M8: Decay + Origin + Depth	-13.381	35.938	3.418	0.033
M9: Decay + Origin + Deight	-13.412	36.001	3.481	0.032
M10: Decay + Origin + Hole	-13.416	36.009	3.489	0.032
M11: Decay + Nest Cover	-15.113	36.912	4.391	0.021
M12: Decay + Nest Cover + Origin + DBH + Height	-11.189	37.002	4.482	0.020
Null Model	*-26.917*	*55.940*	*23.422*	*1.52E-06*