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The Effect of Area on Resource Competition among Migrant Birds at a Stopover Site

Sara Marie Beall

THE EFFECT OF AREA ON RESOURCE COMPETITION AMONG MIGRANT BIRDS AT
A STOPOVER SITE

by

SARA MARIE BEALL

(Under the Direction of C. Ray Chandler)

ABSTRACT

Few studies have focused on the habitat and resource requirements of migratory landbirds
along migration routes. Habitat fragmentation may exacerbate the costs of migration by
reducing food availability and/or increasing competition at crowded stopover sites. I
predicted that smaller forest fragments would have higher densities of birds, and that birds
would compete for food more intensely in smaller fragments. I examined seven forest
fragments of varying size (0.68 ha – 5.69 ha) at Savannah National Wildlife Refuge in three
migration periods between Spring 2007 and Spring 2008. I set up netted exclosure pairs to
examine the relationship among fragment size, bird density and resource abundance. I
found that in Fall 2007 and Spring 2008, the density of migrant birds was higher in smaller
fragments. In all three field seasons, the density of resident birds was higher in smaller
fragments than in larger fragments.   Birds did depress arthropod abundance in Spring
2007 and 2008, but there was no relationship with hammock size. Birds did not have a
measurable effect on fruit resources in the fall. The higher density of both migrants and
residents in smaller hammocks indicates that birds are responding to area during stopover.
The difference between arthropod abundance in exclosure pairs indicates that birds use
this food resource, and provides evidence for food competition.

NDEX WORDS: Stopover Site, Exclosures, Neotropical, Migrant, Migration, Competitio

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Migration is part of the annual cycle of many species of birds (Alerstam and Lindstrom 1990). In some cases migratory birds may be able to make long, continuous flights across geographic barriers such as the Gulf of Mexico (Moore et al. 1990). But if there is available habitat to make a stopover, birds use stopover sites along migration routes to rest and replace energy reserves. During stopover migrants must exploit unfamiliar habitats, which increases predation risks, and yet maintain a high rate of fat deposition to avoid a late arrival to breeding or wintering grounds (Moore et al. 1990). If migrants survive migration, but replenish fat stores at a slower rate due to inadequate stopover habitat, a delay in passage could result in reduced reproductive success or mortality after arriving on the breeding grounds (Petit 2000).

Habitat requirements during stopover are especially important because humans are affecting this process by fragmenting or eliminating critical stopover sites (Stratford and Robinson 2005). Habitat loss or fragmentation is especially perilous to Neotropical migrants due to the high physiological costs of long-distance migration. Stopover ecology parameters, especially habitat quality, resource competition, and avian density- habitat size relationships, are important links in measuring the effects of habitat loss and fragmentation on Neotropical migrant populations.

Despite its ecological and conservation significance, relatively little is known about site selection and the habitat or resource requirements of migratory landbirds. Far more research has focused on ecology at breeding and wintering sites (Moore et al. 1990, 1993).

Thus, there are few studies to draw broad conclusions about stopover ecology. For example, migrants as a group have different foraging behaviors and habitat requirements (Moore et al. 1990), and may even show different preferences between spring and fall migration (Hutto 1985, Keller and Yahner 2007). But, some generalizations are possible. For example, when available, many species use the same habitat types during migration as in the breeding season (Petit 2000). However, recent rates of habitat loss may force species to adapt to increasingly isolated or poor quality stopover sites.

Previous studies support additional patterns in stopover-site selection. Migrants may choose a site based on size (Keller and Yahner 2007). Of sites of a given size, habitat quality is important. Finally, habitat quality and the migrant preferences may change according to the season or state of the bird (Hutto 1985).

Habitat area is presumably an important variable in stopover site selection. As area increases, so does species richness and abundance (see MacArthur and Wilson 1967, Blake and Karr 1987). Some bird species are area-sensitive in the breeding season and restricted to larger tracts of land (Galli et al. 1976, Ambuel and Temple 1983, Howe 1984, Keller and Yahner 2007). A study on riparian corridors along the Altamaha River, in the same region as my study site, found a significant positive relationship between corridor width and probability of occurrence in breeding season of Northern Parulas *(Setophaga americana)*, White-eyed Vireos *(Vireo griseus)*, and Red-eyed Vireos *(Vireo olivaceus)* (Hodges and Krementz 1996). If we assume that migrants choose stopover-site habitats that are similar to breeding season habitats, (Petit 2000), then we can draw conclusions about stopover site selection based on breeding season studies. However, this remains largely speculative.

Beyond the size of a stopover site, habitat quality should be an important parameter of stopover site quality. Migrants use habitat non-randomly within stopover sites, indicating that migrants respond to habitat quality (Moore et al. 1990). Some patterns have emerged that show migrants use habitat structure as an indicator of habitat quality. Studies (Blake and Hoppes 1986, Martin and Karr 1986) have shown that migrants prefer patchy vegetation or tree-fall gaps, perhaps because of a higher density of insects and fruit-bearing vegetation. Abiotic resources such as the amount of light in the understory may be a cue for birds to sample a habitat (Martin and Karr 1986), which in high-quality sites may lead to the accumulation of individuals. Abundance and species richness of mixed landbird flocks during fall migration was highest in habitats with corresponding high degrees of habitat heterogeneity, such as forest-edge habitat (Rodewald and Brittingham 2002, 2004). A comparison of coastal woodlands in Louisiana was consistent with a positive correlation between habitat diversity and migrant use. Disturbed habitat, with a reduced and less diverse understory, was not used as frequently by early migrants and specialist foragers (Barrow et al. 2000).

Habitat quality and migrant preferences may change according to the physiological or behavioral state of the bird (Hutto 1985). For example, Wilson's Warblers *(Cardellina pusilla)* preferred willow-dominated habitat, with a higher abundance of arthropods, in the spring, but in fall switched preference to forest-edge habitat, perhaps because of a difference in migratory strategy between seasons (Yong et al. 1998). In another instance, woodland migrants in fall most frequently used mature edge-dominated and scrub-sapling stage forests, most likely because of a corresponding high availability of fruiting vegetation

(Rodewald and Brittingham 2004). Fruit availability was a determinant for fall migrants using successional habitats (Suthers et al. 2000) and, along with arthropod abundance, was found to be more significant than habitat structure when explaining migrant density (Buler et al. 2007). Thus, habitat quality can be high or low depending on the season, available resources, and foraging requirements of the migrants.

The condition of the bird affects habitat selection and use. Wood Thrush *(Hylocichla mustelina)*, Veery (*Catharus fuscescens*), Swainson's Thrush (*C. ustulatus*) and Gray-cheeked Thrush (*C. minimus*) foraging behavior was affected by energetic condition upon arrival (Yong and Moore 2005). In a lab experiment of induced migratory disposition (physiological and behavioral changes to prepare the bird for migration), Moore and Simm (1985) found that Yellow-rumped Warblers (*Setophaga coronata*) foraged more efficiently pre-migration and during the migration period. Habitat use and the pace of migration between spring and fall migration may be further determined by sex and age constraints (Moore et al. 1990). For example, Wilson's Warblers use stopover habitat differentially by sex in the spring and age in the fall (Yong et al. 1998).

Predicting how a bird of a given state selects among stopover sites of various size and quality is complicated by ongoing human impacts. In particular, patterns of stopover site use cannot be predicted without considering the effects of habitat loss and fragmentation on habitat use. Fragmentation is a conversion of large area of continuous habitat, into smaller vegetation patches, of potentially differing habitats (Faaborg et al 1995). Fragmentation can occur naturally, through flooding or fire, but more often fragmentation is a result of human activity. Biologists across several disciplines have

expressed concern over increasing rates of habitat loss and the impact of fragmentation on the viability of wildlife populations (Debinski and Holt 2000).

Fragmentation affects migrant species at each stage of their life cycle, but results may not be consistent among seasons and species (Keller and Yahner 2007). Fragmentation of breeding habitat increases nest predation and brood parasitism, and reduces reproductive success (Temple and Cary 1988, Robinson et al. 1995, Robinson 1989). Conversion of forest to agriculture habitat also affects migrants at wintering sites. In a seven-country study of habitat use at Neotropical wintering sites, ground-feeders such the Ovenbird *(Seiurus aurocapillus)*, Northern Waterthrush *(Parkesia noveboracensis)*, Wood Thrush *(Hylocichla mustelina)*, Gray-cheeked Thrush *(Catharus minimus)* and Kentucky Warbler *(Geothlypis formosus)* were rarely or never found in agricultural habitat (Robbins et al. 1989).

The effects of fragmentation on birds during the migratory period are less well known. The influences can be difficult to assess fully in species such as Neotropical migrants, which move between temperate breeding grounds and tropical wintering grounds. The MacArthur-Wilson theory of island biogeography may be used to model broad effects of habitat fragmentation. However, the MacArthur-Wilson theory is complicated in migrants who vary in behavior and physical state, are selecting unfamiliar habitats, and are often under the constraints of weather or geographic barriers (Faaborg et al. 1995).

Fragmentation clearly affects the two main parameters that migrants use to choose stopover-site habitat: size and habitat quality. Fragmentation increases the proportion of

edge habitat, which may negatively affect some area-sensitive migrant species that primarily use forest-interior habitat (Faaborg et al 1995, Temple and Cary 1988). Species that are able to exploit edge or early successional habitat may exclude area-sensitive species from using smaller fragments (Ambuel and Temple 1983). Fragmentation may induce crowding in smaller fragments and alter the proportion of area-sensitive species. In one study, the abundance of generalist species stayed the same, while the abundance of area-sensitive Neotropical migrants declined as fragments got smaller (Schmiegelow et al. 1997).

Fragmentation may convert forest to natural early succession, agricultural, or edge habitat, but urban development leads to a near-total habitat loss. Urbanization of habitat influences migrant species richness. Species such as the Worm-eating Warbler *(Helmitheros vermivorus)*, Scarlet Tanager *(Piranga olivacea)*, Ovenbird *(Seiurus aurocapillus)* and Black-and-white Warbler *(Mniotilta varia)* may be particularly sensitive in these areas (Stratford and Robinson 2005). An examination of avian habitat use at a landscape level must consider the overall proportion of urban and wild habitats.

As habitats along migration routes are increasingly fragmented, birds may be forced to use stopover sites of lesser quality, either in size or available resources. The smaller sizes of stopover sites might affect not only abundance or diversity, but also avian density. Some studies have found both positive and negative area-density relationships of migratory birds during migration periods. Migrant species diversity and total abundance in spring migration increased with shelterbelt size in South Dakota, independent of vegetation heterogeneity and shelterbelt isolation (Martin1980). However, Martin found an

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increase in overall migrant density with a decrease in area. Somershoe and Chandler (2004) found that migrant density was higher in smaller oak hammocks in the spring, and the pattern was unexplained by differences in vegetation. If smaller fragments have higher density, then competition for food resources may be greater in small fragments than in larger fragments.

Some species are negatively affected by an increase in fragment size. The presence of Gray Catbird *(Dumetella carolinensis)* , European Starling *(Sturnus vulgaris)*, Song Sparrow *(Melospiza melodia),* Common Grackle *(Quiscalus quiscula)*, and Red-winged Blackbird *(Agelaius phoeniceus)* was negatively correlated with patch size during spring migration in Pennsylvania (Keller and Yahner 2007). Quantifying stopover patterns of avian density and community interactions, such as competition, is crucial to predicting habitat use and halting the decline of migrant populations.

Resource competition may fluctuate with landbird density and fragment size. Species with similar resource requirements compete for resources, with the possibility that one species may inhibit the success of or eliminate the presence of the other (Connell 1961). Prey behavioral changes, time of day, mode of predator searching, or microhabitat depression may cause resource depression and in turn influence competition (Charnov et al. 1976).

Resource competition is common in birds. Field studies show that avian distributions and densities may be due to exploitative competition for food. Local populations of seed-eating sparrow species in Arizona are limited by food availability (Dunning and Brown 1982). When resources are limited, behaviorally dominant species

may actively or passively displace competitors. Red-headed Woodpeckers *(Melanerpes erythrocephalus)* forced out Red-bellied Woodpeckers *(M. carolinus)* in a floodplain where acorns were a limiting resource (Williams and Batzli 1979). Aggressive encounters between Philadelphia Vireos and Red-eyed Vireos were more frequent when there was an overlap in the species' activity ranges (Robinson 1981). Predation studies at the same site have shown that birds depress arthropod abundance (Holmes at al 1979), suggesting that resource competition may occur (Holmes et al 1979, Robinson 1981).

Some studies have found evidence of resource competition in migrants at stopover sites. During spring migration, variation in fragment size and migrant density may affect resource abundance, resulting in varying levels of competition (Moore and Yong 1991). Resource competition varies within a site based on migration timing, foraging strategies, and resource distribution. Early migrants may deplete clumped resources such as fruit in isolated stopover sites. This could prevent adequate fuel deposition for later migrants, especially in late fall when arthropods may be limited (Ottich and Dierschke 2003).

In the presence of decreased or depleted resources due to competition, migrants may be subject to slower rates of fat deposition. A study in Louisiana showed birds that stop at sites with a high migrant density replenish energy reserves more slowly than at sites with a lower migrant density (Moore and Yong 1991). Neotropical migrants must replenish fat stores at stopover sites to refuel and continue the journey; a failure at this level could affect probability of reproductive success or survival. Resource competition may reduce food abundance and increase stopover time, delaying migrant arrival at breeding or wintering grounds (Moore and Yong 1991).

To examine the relationship between resource competition and bird abundance and density, studies have used exclosures to exclude birds from selected trees or branches. Bird exclosure experiments have shown that birds can depress food resources on breeding grounds (Holmes et al 1979) and at stopover sites (Moore and Yong 1991, Ottich and Dierschke 2003). An exclosure experiment comparing avian predation in shade- and sun-grown coffee fields (Greenberg et al. 2000) found that birds depressed the numbers of caterpillars in both agrosystems. A study on Checker-throated Antwrens *(Myrmotherula fulviventris)* in Panama showed they deplete aerial leaf litter prey items outside of exclosures by almost 50% (Gradwohl and Greenberg 1982).

To maintain stopover sites and manage migrant species, land managers need to understand the patterns of stopover site selection, the relationship between area and bird densities, and the conditions in which competition for resources may occur. The objective of this study was to examine the effects of forest fragment size on food-based competition among migratory birds at a stopover site (Savannah National Wildlife Refuge). I used avian counts and predator exclosures to quantify the degree of resource exploitation during spring and fall migration. I addressed two specific predictions. First, I predicted that migrant density would be higher in smaller fragments (Somershoe and Chandler 2004). Second, I predicted that resource availability would decrease with an increase in migrant density and abundance. Lower resource availability would then lead to more intense resource competition in smaller fragments (Figure 1).
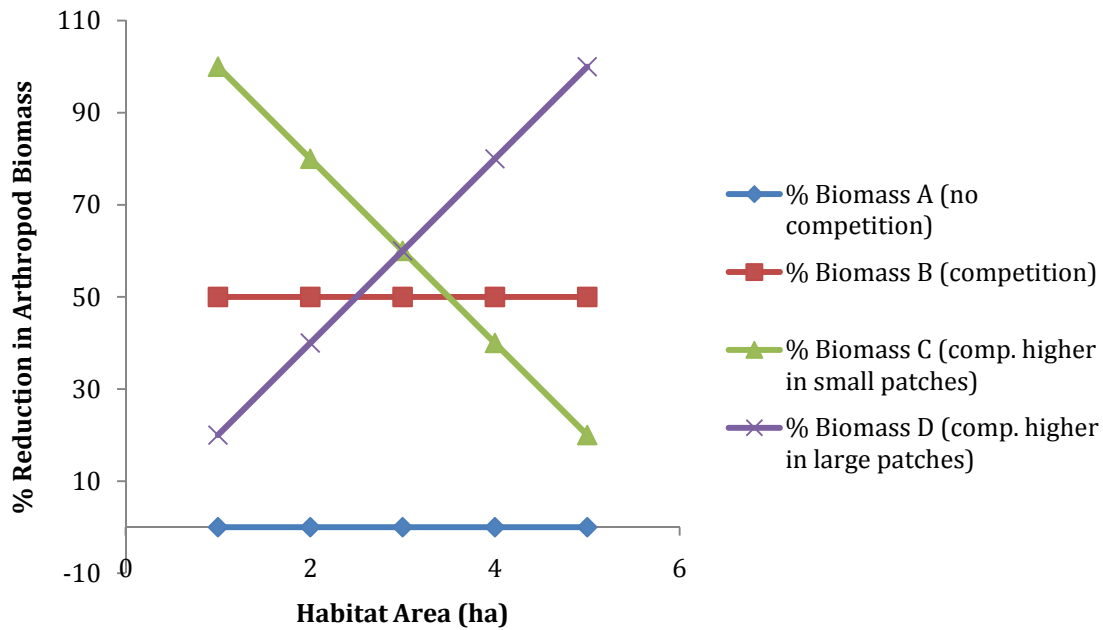
Figure 1. The predicted effects of habitat size on the percent reduction in arthropod biomass (exclosure vs. control). If size is a significant factor, then Line C will be the resulting pattern.

CHAPTER 2

MATERIALS AND METHODS

Study Site: This study took place at the Savannah National Wildlife Refuge (SNWR)

in Jasper County, South Carolina. SNWR (32° 15′ N, 81° 11′ W) is on the lower coastal

plain, 29 km from the Atlantic Ocean. The refuge is composed of isolated oak hammocks

surrounded by extensive freshwater marshes (Figure 1). These marshes are managed by

refuge staff within impoundments enclosed by pedestrian and vehicle-accessible dikes,

which provide access to oak hammocks of varying size. Somershoe and Chandler (2004)

have shown that Neotropical migrants use oak hammocks as stopover sites during spring

and fall migration.

Oak hammocks within SNWR, which grow on areas of slightly higher elevation, are

comprised primarily of oaks (mostly *Quercus virginianus*), sweetgum (*Liquidambar

styraciflua*), sugarberry (*Celtis* spp.), and chinaberry (*Melia azedarach*). Understory and

edge species are chinese tallow (*Sapium sebiferum*). cherry laurel (*Prunus caroliniana*), saw

palmetto (*Serenoa repens*), greenbrier (*Smilax spp*), mulberry (*Morus spp*), wax myrtle

(*Myrica cerifiera*)*,* yaupon (*Ilex vomitoria*) and beautyberry (*Callicarpa americana*). For

details of vegetation see Somershoe (2000).

I chose seven hammocks to represent a range of hammock sizes (Figure 2). These

hammocks were isolated from each other by freshwater marsh and wetland habitat, and

were at least 75 m from the next closest hammock.

Research Protocol: My study took place at the SNWR during spring (2007, 2008) and

fall migration (2007). Spring sampling took place from April 1 to May 25, 2007, and April 4

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to May 15, 2008. Fall sampling occurred from September 17 to November 18, 2007. I quantified avian density and species composition in each hammock, as well as the availability of avian food resources (arthropods or fruit) across the migration season. I used bird exclosures paired with accessible control sites to measure arthropod availability in the spring (as found on *Prunus caroliniana,* the most common shrub in all hammocks*)* and fruit availability (*Ilex vomitoria,* the most common fruiting shrub in all hammocks*)* in the fall.

     Bird censusing. Migrant and resident landbird density and species composition was estimated by walking line transects in each hammock (Bibby 2000). I conducted transect counts within 4 hours after sunrise or 2 hours before sunset. Each hammock was sampled approximately twice per week. It was not always possible to sample all the hammocks on the same day. I visited hammocks in a random order each day to reduce potential temporal bias. All calling birds during transects were recorded with a Saul Mineroff Electronics SME-ATR55 shotgun microphone and an Olympus VN-3100PC digital recorder.

     Line transects were conducted by slowly walking at a pace of approximately 15m/min through the long axis of each hammock, and recording all birds seen and heard, within 50 m from the transect. Repeat calls or sightings from the same bird (for example, if the bird was foraging along the length of the transect) were not counted. I began the transect approximately 10 m outside the edge of each hammock, and extended the transect 10 m beyond the opposite edge to insure that I was surveying the entire hammock. Birds flying over the hammock without stopping, or calling from outside the hammock, were not counted. I distinguished birds detected as residents or migrants based on the Partners in

Flight Classification (Hunter et al. 1993). Bird count data from transect counts was used to

calculate the relative density of birds per 0.5 ha of hammock.

Fixed points, at least 200 m apart, were flagged in each hammock. Due to spacing

constraints, most hammocks had only one point, but the two largest hammocks were large

enough to have two fixed points in each. All points were at least 25m from the edge of the

hammock. Point counts consisted of a five-minute habituation period, immediately

followed by a five-minute recording period. All birds seen and heard were noted, as well as

their approximate distance (less than 25m, 25-50m, 50-75m, or 75m+) from the observer.

Birds that I determined to be calling from a point beyond the confines of the hammock

were not counted. Point counts were conducted for comparative data with transect counts,

and point count data are in Appendix A. Transect counts provided more detailed

descriptions of individuals and species surveyed, and are used for the statistical analysis in

the Results.

Arthropod availability: Exclosures of Bird-X® bird-deterrent netting were installed

around cherry laurel (*Prunus caroliniana)* branches in a paired design. I chose cherry laurel

because it was abundant in all hammocks, and because birds forage among its branches (R.

Chandler, personal communication). A branch was selected as a bird exclusion site and

covered with netting. It was paired with a similar control branch, on a different tree, that

was free of netting and accessible to birds. Branches were chosen based on a visual

assessment of size, height from ground, and number of leaves. Pairs were sampled by

branch-clipping to quantify any differences in arthropod availability due to the hammock

size. Between 20 to 23 pairs were set-up in two of the smaller (less than 1.5 ha) and two of

the larger (more than 3.0 ha) hammocks. For logistical purposes, it was not possible to install an adequate number of exclosure pairs in all seven hammocks.

The netting had a 2 cm mesh size, to prevent access by birds and other vertebrates, but allow access by arthropods. Netting was draped over randomly selected branches or plants to form an exclosure approximately 1x1x1m. Treatment pairs were evenly spread throughout the hammocks. No plant was sampled more than once in a field season to avoid induced chemical defenses that might affect arthropod foraging. Treatment and control pairs were no more than 10 m apart (Holmes et al. 1979) and were chosen based on visually similar leaf density and understory height. Treatment pairs were placed at a height of approximately 20 - 300 cm to account for differences in avian understory use. Exclosures were left undisturbed for 2 - 6 weeks prior to branch-clipping.

Branch-clipping was used to collect cherry laurel branches at intervals throughout the spring migration season (Moir et al. 2005). Plastic trash bags (49.2 liters) were placed around the selected branch before clipping, to mimimize arthropod knockdown outside of the bag. The branches did not contain any fruits at the time of clipping. Branches were then clipped and sprayed with a non-residual solution of 0.02% pyrethrin to chemically knockdown arthropods. Branches (including stem and leaves) were left to air-dry, then weighed to the nearest 1.0g and examined for presence of arthropods. Arthropods were oven-dried for 2 weeks, then weighed to (mg). I quantified the arthropod relative abundance by calculating the dried arthropod biomass (g) per 100 g of branch mass, including leaves. Because branches for exclosure pairs were chosen based on visual similarity, a biomass comparison accounted for any differences in branch length or number

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of leaves. I then calculated the percent difference in arthropod abundance between netted treatment (T) and accessible control (C) pairs ([T-C]/T x 100). I used this measurement to estimate intensity of competition among hammocks of varying size across the migration season.

Fruit availability: I used the same procedure to set-up exclosures around yaupon (*Ilex vomitoria)* to determine fruit availability to birds during the fall migration season. Only female (*I. vomitoria* is dioecious) fruiting branches were used, and a control branch of similar size and berry density was chosen within 10 m of each treatment. Exclosures were no larger than 2x2x2m. Three treatment pairs were selected in each of the seven hammocks. Periodically throughout the migration season I counted both ripe berries (more than 50% red) and unripe berries (more than 50% green) on treatment and control branches. I assumed that berries would fall from the treatment and control branches at an equal rate, so fallen fruit was not counted. The difference in percent of ripe berries between treatment and control branches was used to quantify the berry availability across the fall migration season. The premise of using the percentage of ripe berries was that although berries will ripen at an equal rate both inside and outside of the exclosures, a lower total percentage of ripe berries in bare control branches would be an indication that birds are competing for fruit.

Analysis: The statistical analysis was done using JMP software (SAS Statistical Software, version 8.0.2). I compared exclosure and bird census data among hammocks of varying size in linear regressions to look for differences in resource competition.

The transects were of varying length, based on the hammock size. The transect

counts included all birds seen or heard within 50 m of the transect. To compare data among hammocks, I needed to use a density measure that would account for the differences in size. I used the number of birds/0.5 ha because the smallest hammock surveyed was approximately 0.5 ha in size. I used the mean number of birds per day for each hammock as an approximation of the total birds in that hammock. I calculated the total area measured in transect counts by measuring 50 meters to either side of the transect, along the total length of the transect. I then used Google Earth to measure the total area surveyed for birds (count area). I used linear regression to determine the relationship between avian density and hammock size.
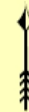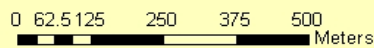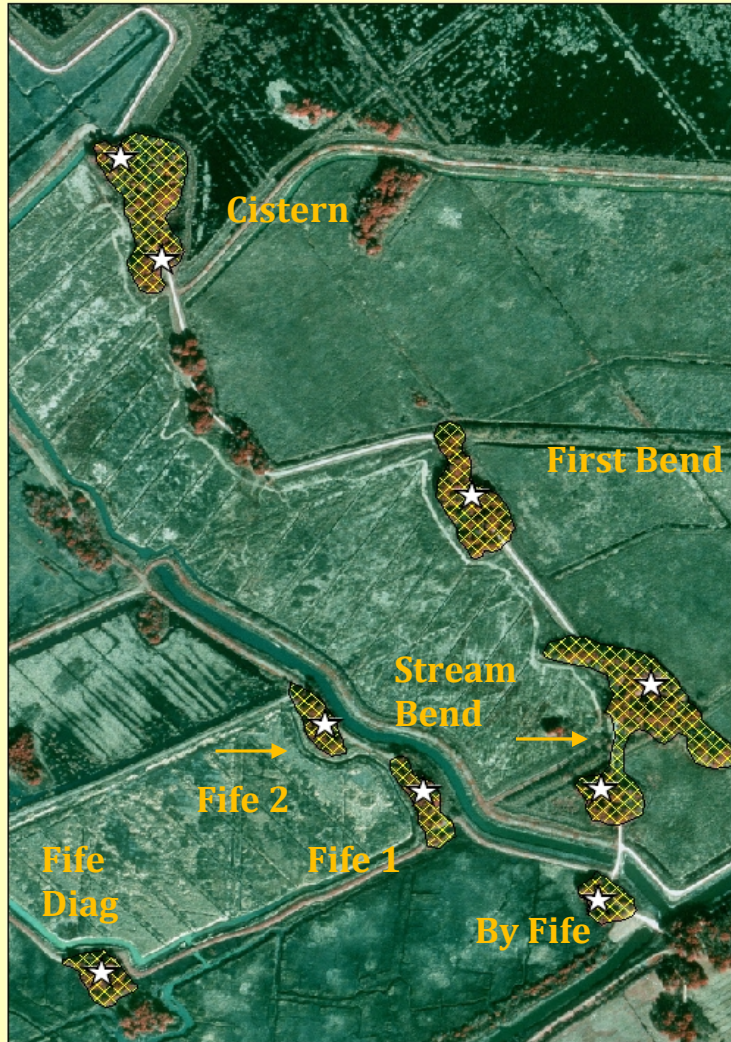
Figure 2: Location and size of study sites at Savannah National Wildlife Refuge. The hammocks range in size from smallest, Fife Diag (0.68 ha), By Fife (0.72 ha), Fife 2 (0.75 ha), Fife 1 (1.27 ha), First Bend (1.68 ha), Cistern (2.64 ha) and Stream Bend (5.69 ha).

CHAPTER 3

RESULTS

Spring Migration: I conducted transect surveys to establish that migrants use

Savannah National Wildlife Refuge as a stopover site. I surveyed (point counts and

transects) at Savannah National Wildlife Refuge on 25 days in 2007. In 2008 I conducted

transect surveys on 11 days, and point counts on an additional 11 separate days (Appendix

A). The mean number of individuals per transect in 2007 was highest at 17 ± 9.0 SE on

April 30, and in 2008 was 6.29 ± 0.9 SE on April 26 (Figure 3). This corresponds with the

peak migration dates of April 29 to May 3 (2007) and April 6 to April 11 (2008). The mean

total number of species per transect per day was highest at 13 ± 1.4 SE on May 2, 2007

(Figure 4), and was 22 on April 7 2008.

2007: In 2007 the density of residents was lower in larger hammocks than in

smaller hammocks. (Figure 5, top; Table 2) but the density of migrants was higher in larger

hammocks than in smaller hammocks (Figure 5, top). There was a significant negative

regression between the number of resident species (the mean number per 0.5 ha) and

hammock size (Figure 6, top), but a not significant positive regression between the number

of migrant species and hammock size (Figure 6, top).

A total of 20- 23 exclosure pairs were sampled in each hammock (Table 1). There

was a difference in arthropod abundance between exclosure and control sites (Figure 7).

Differences in arthropod abundance between exclosures and paired control sites did not

vary with hammock size, (Figure 7, top).

2008: In 2008, there was a negative relationship between hammock size and the density of birds observed for both residents (Figure 5, bottom; Table 2) and migrants (Figure 5, bottom). There was a negative relationship between the number of resident species and hammock size (Figure 6, bottom), but no relationship between migrant species and hammock size (Figure 6, bottom).

A total of 20 – 23 exclosure pairs were sampled in each hammock (Table 1). Differences in arthropod abundance (percent difference between treatment and control arthropod density) among hammock sizes were not statistically significant (Figure 7, bottom).

Table 1. A summary of arthropod exclosure sampling, Savannah National Wildlife Refuge, April 1- May 25 (2007) and April 4- May 15 (2008).

	Fife Diag (0.68 ha)	Fife 1 (1.27 ha)	Cistern (2.64 ha)	Stream Bend (5.69 ha)
2007				
Exclosure Pairs	n= 20	n= 23	n= 22	n= 20
Days sampled	4	4	4	3
Mean percent difference (T-C/T)	95.28	96.27	33.66	85.82
Highest percent difference And Date	98.9, May 11	97.5, May 27	95.1, May 22	92.5, May 25
2008				
Exclosure Pairs	n= 20	n= 21	n= 20	n= 23
Days sampled	5	5	5	5
Mean percent difference (T-C/T)	36.37	63.54	37.9	87.38
Highest percent difference and date	95.6, May 17	100, April 198	59.7, May 17	88.2, April 13
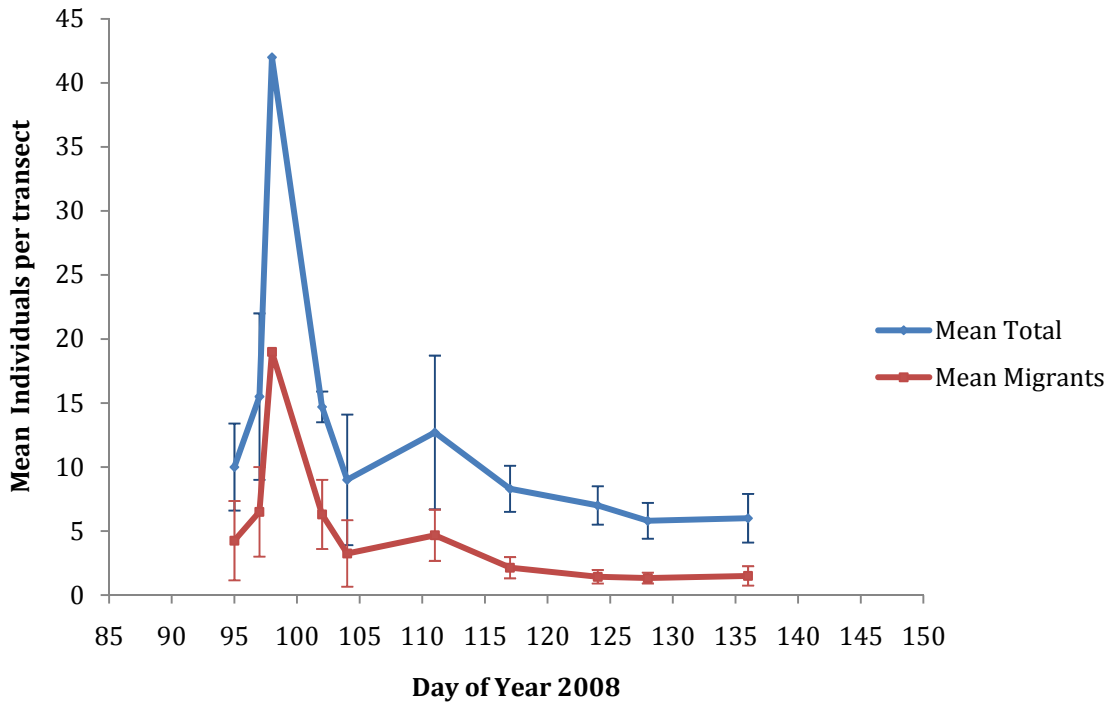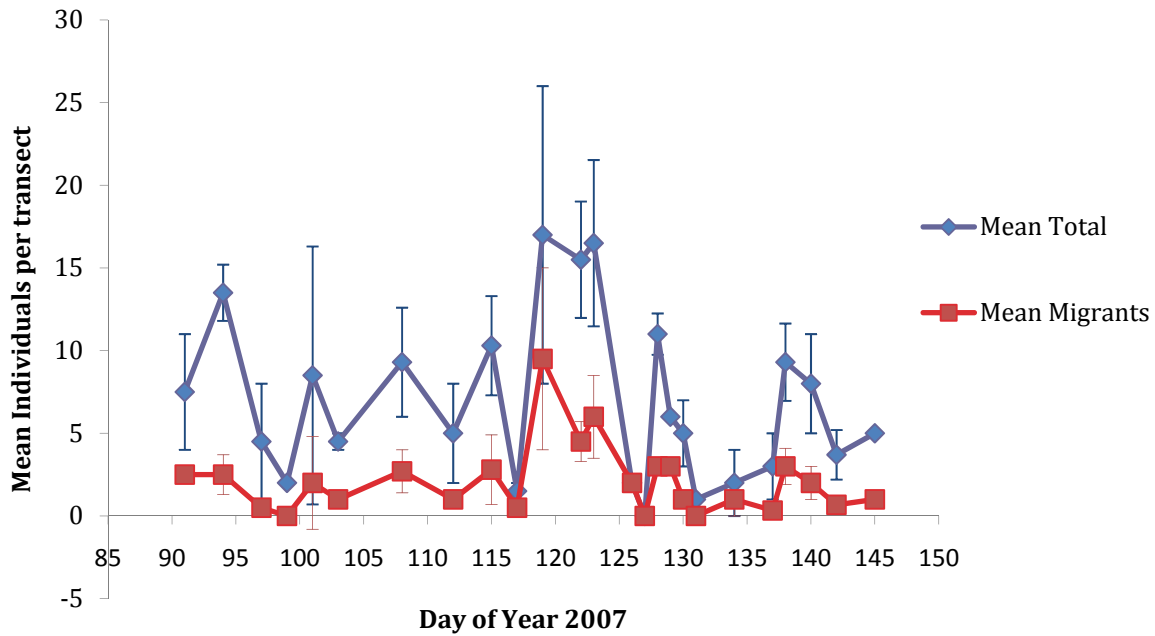
Figure 3. Mean individuals observed (both residents and migrants, per transect per day), during transect counts 2007 (top) and 2008. Day 115= April 25 (2007); Day 115= April 24 (2008).
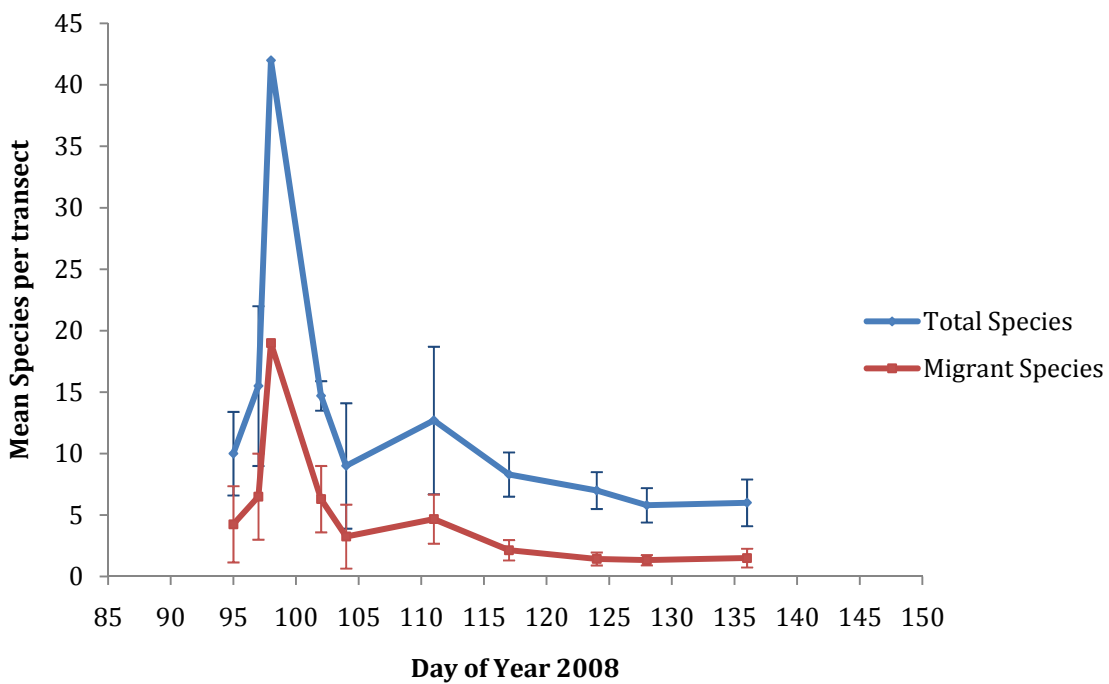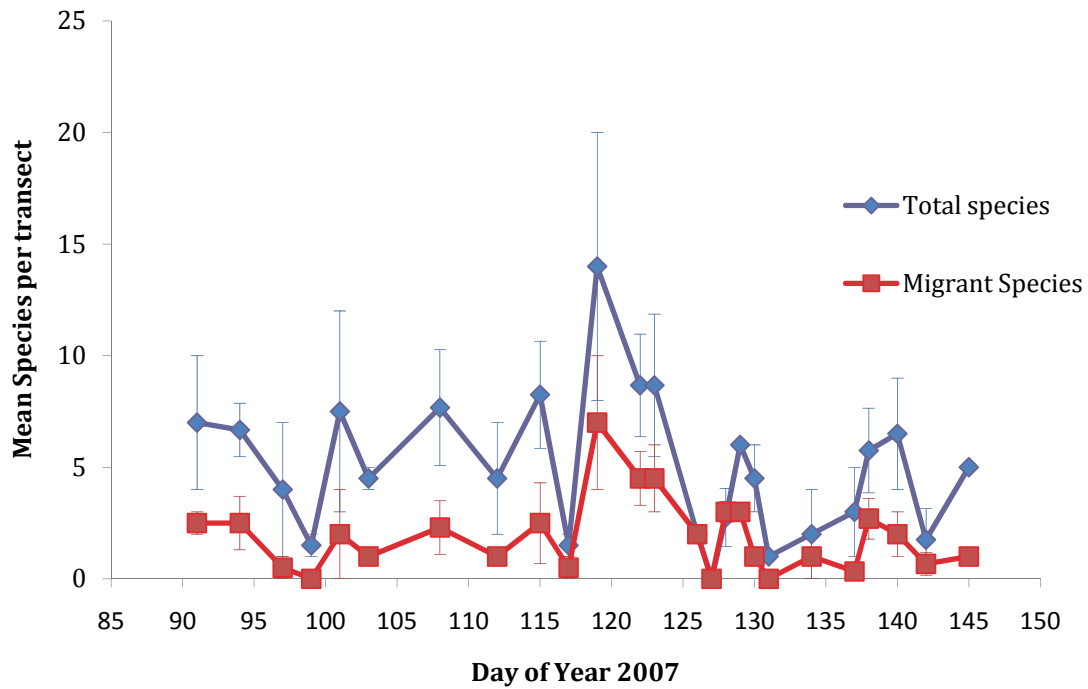
Figure 4. Mean number of species (residents and migrants, per transect per day), during transect counts Spring 2007 and Spring 2008. Day 115= April 25 (2007); Day 115= April 24 (2008).
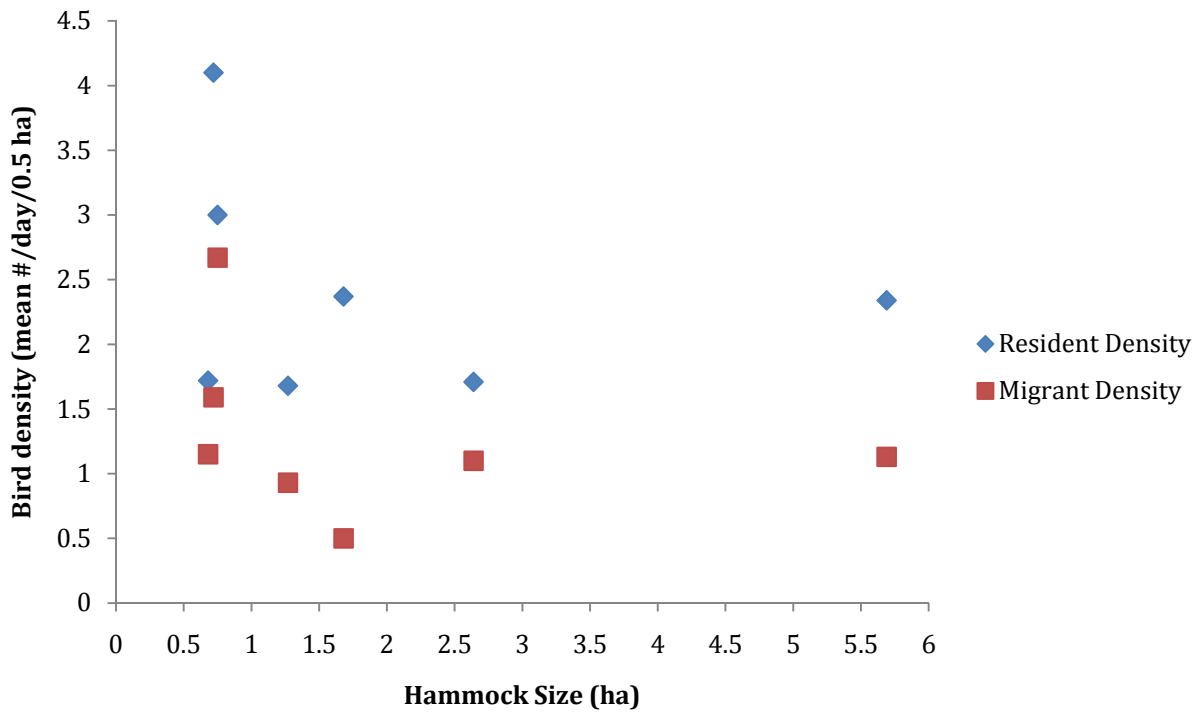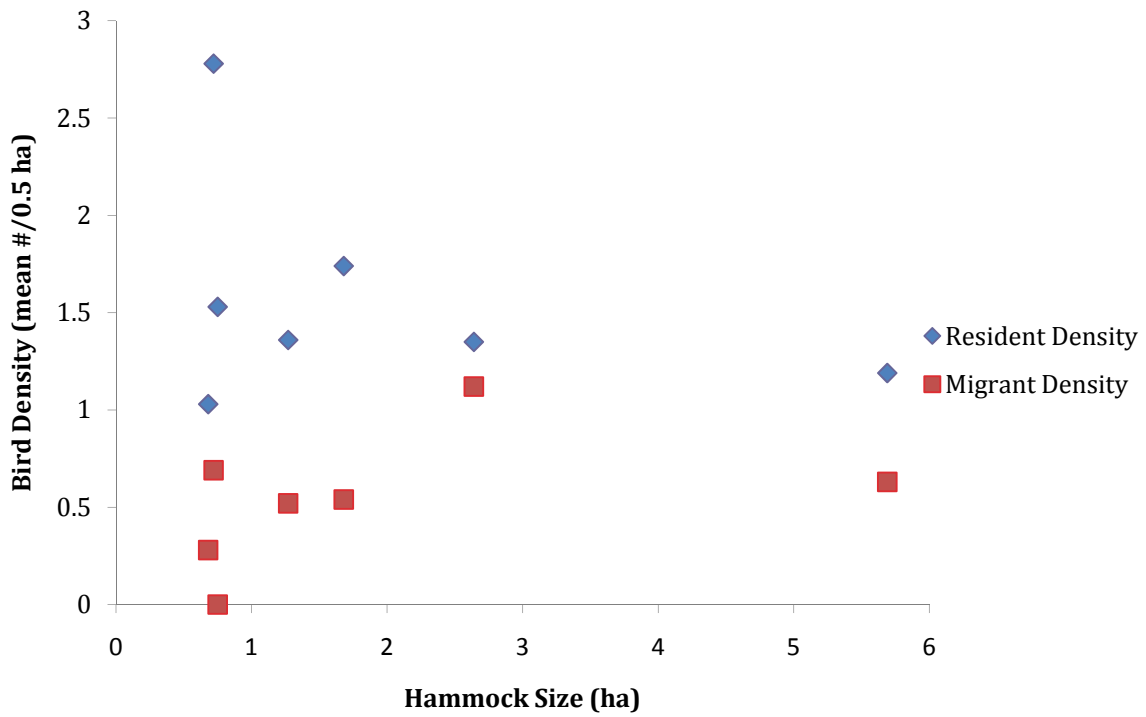
Figure 5. Density of individuals (mean number observed per day per 0.5 ha) found among hammocks of varying sizes in Spring 2007 (top) and 2008.
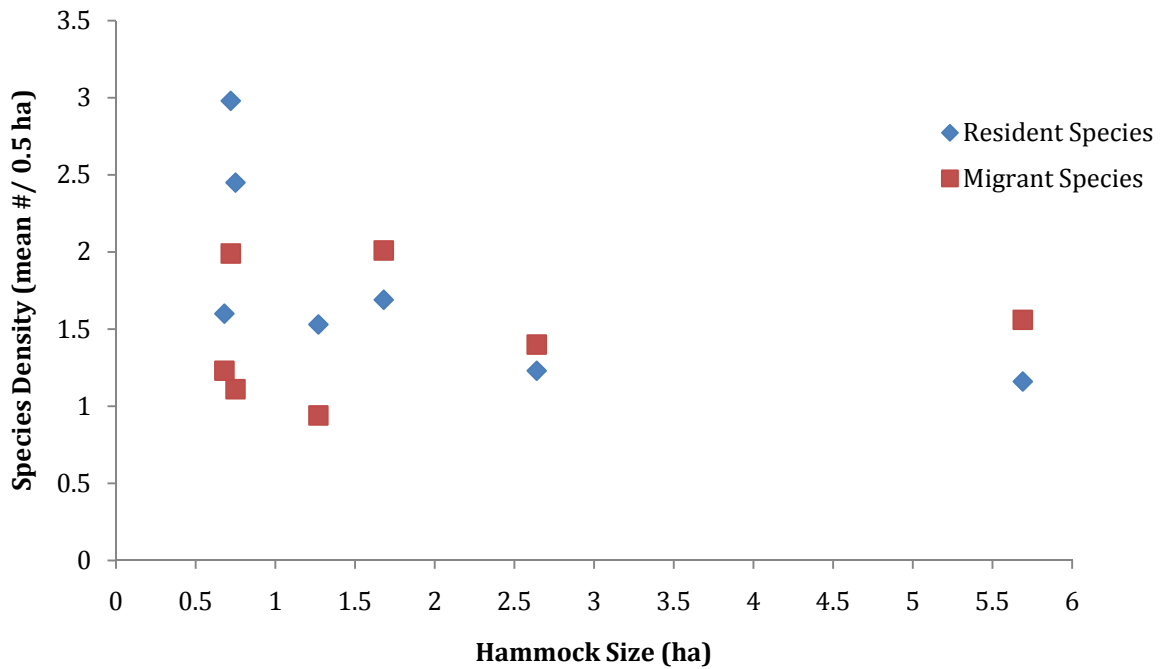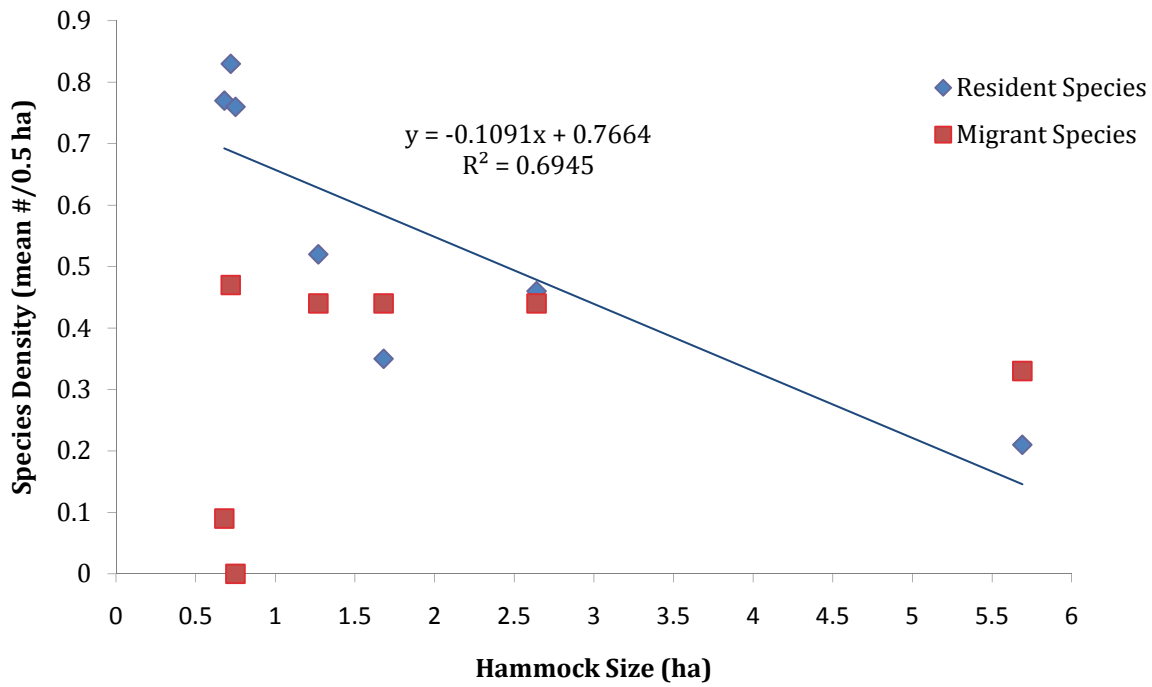
Figure 6. Mean Species Density during transect counts in Spring 2007 (top) and 2008. Mean resident species density was significantly higher in smaller hammocks in 2007 (F=11.36, p<0.05, R^2=0.694)
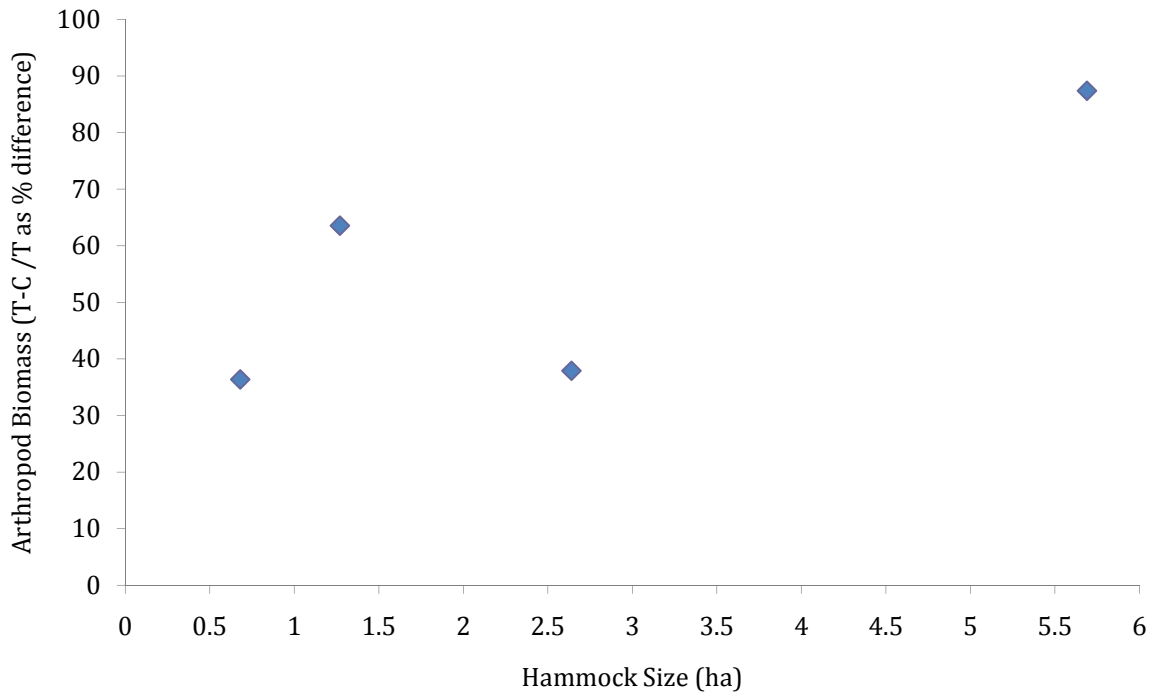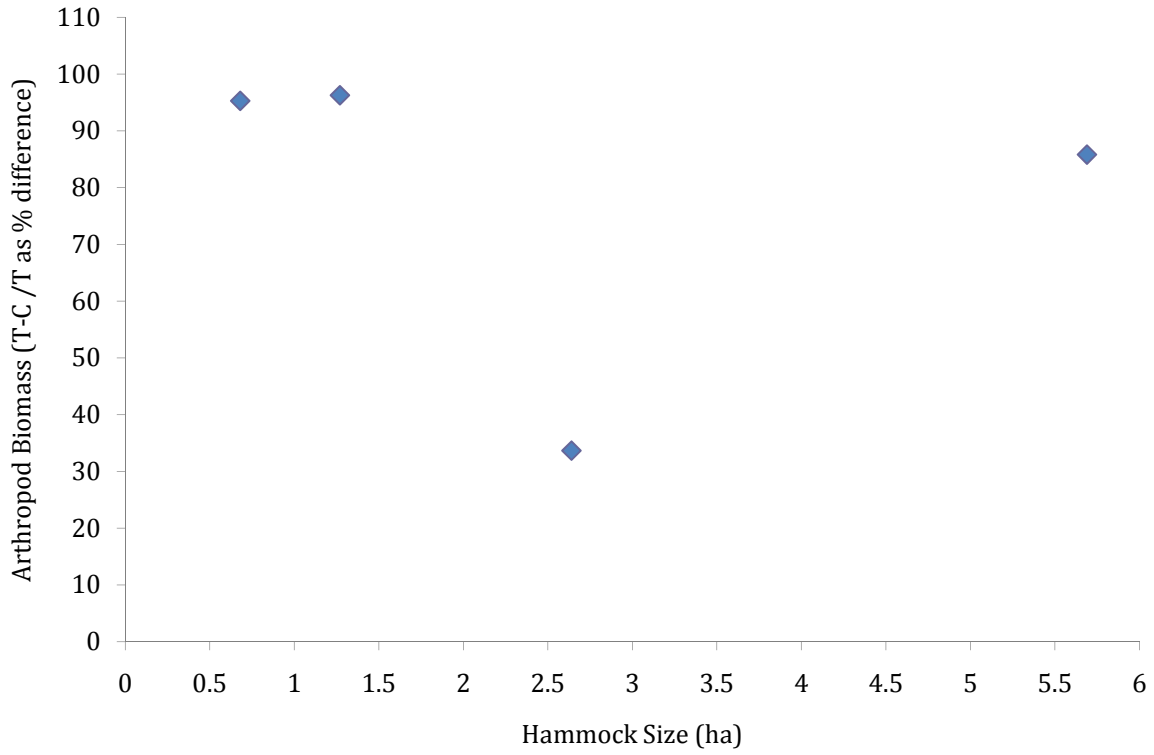
Figure 7. Arthropod Density (as T-C/T % difference) among hammock sizes in Spring 2007 (top) and 2008.

Table 2. Statistical Analysis of the Effects of Area on Resident and Migrant Abundance and Species Diversity, Spring 2007 and 2008 (d.f. = 1,6; *= $p<0.05$).

Area	F	P	R^2
Transects 2007			
Mean Resident Individuals (Density)	0.719	0.435	0.126
Mean Migrant Individuals (Density)	1.01	0.362	0.168
Mean Resident Species	11.36	0.019*	0.694
Mean Migrant Species	0.303	0.606	0.057
Exclosures 2007			
Arthropod Density (g arthropod/ 100g branch) as the % difference between netted treatment and bare control	0.064	0.824	0.031
Transects 2008			
Mean Resident Individuals (Density)	0.263	0.630	0.050
Mean Migrant Individuals (Density)	0.441	0.536	0.081
Mean Resident Species	3.28	0.130	0.396
Mean Migrant Species	0.089	0.777	0.0176
Exclosures 2008			
Arthropod Density (g arthropod/ 100g branch) as the % difference between netted treatment and bare control	2.81	0.236	0.583

Fall Migration: I conducted transect surveys on 22 days in 2007, from September 17 to November 18 (Figure 10). The highest mean number of migrants was 5.5 ± on October 29 (Figure 8). The mean species observed in all hammocks varied throughout the season (Figure 9; Appendix B).

There was a negative regression between mean density and hammock size for both residents and migrants (Figure 10). There was a significant negative relationship between resident and migrant species density and hammock size (Figure 11). Statistical analysis summarized in Table 3.

Three exclosure pairs in each hammock (n=7) were examined for amount of ripe fruit. Although bird densities were higher in smaller hammocks, smaller hammocks had a larger amount of available (ripe) fruit, but the difference among hammocks was not significant (Figure 12). There was no difference in available fruit when birds were excluded from selected branches (Figure 12).
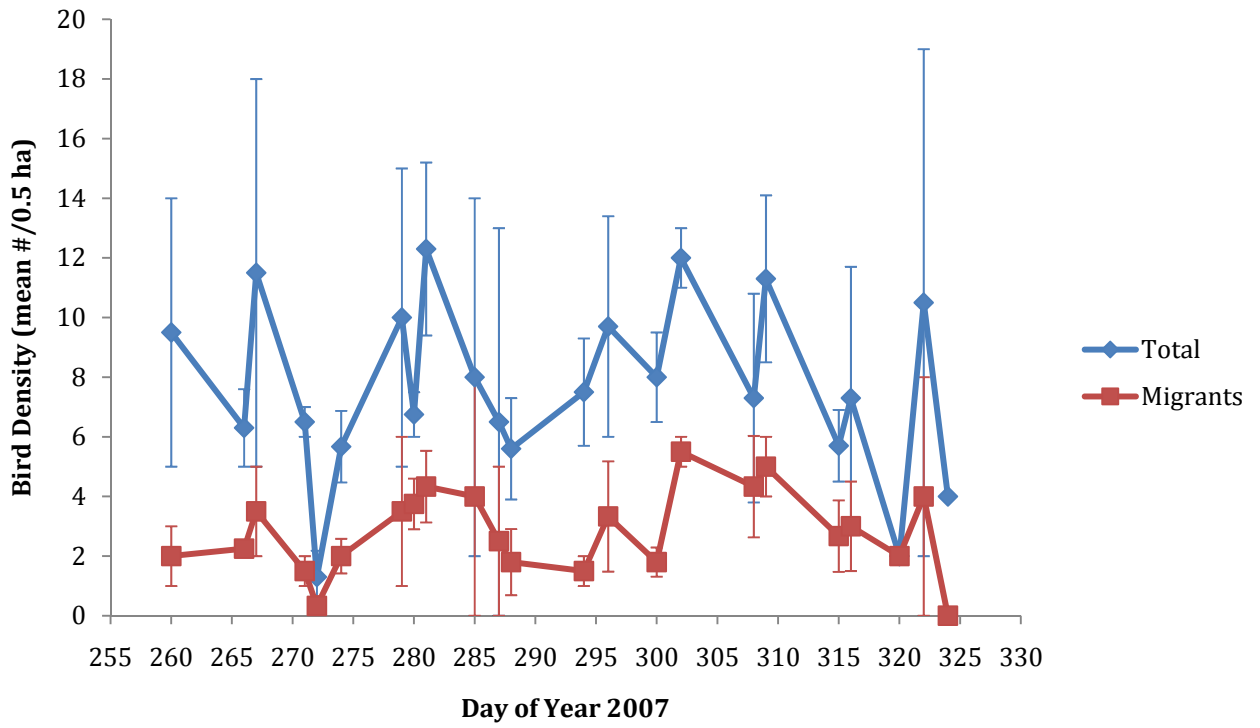
Figure 8. Mean individuals observed per transect per day. Day 290 = October 17.
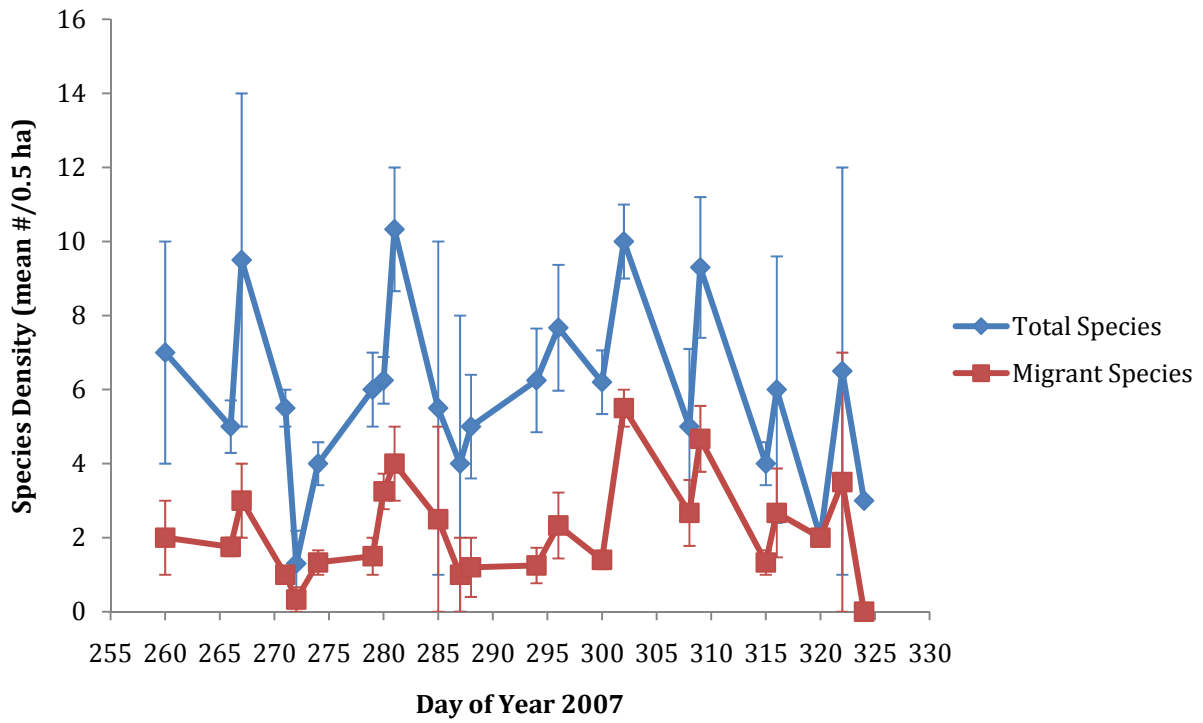
Figure 9. Mean species observed per transect per day. Day 290 = October 17.
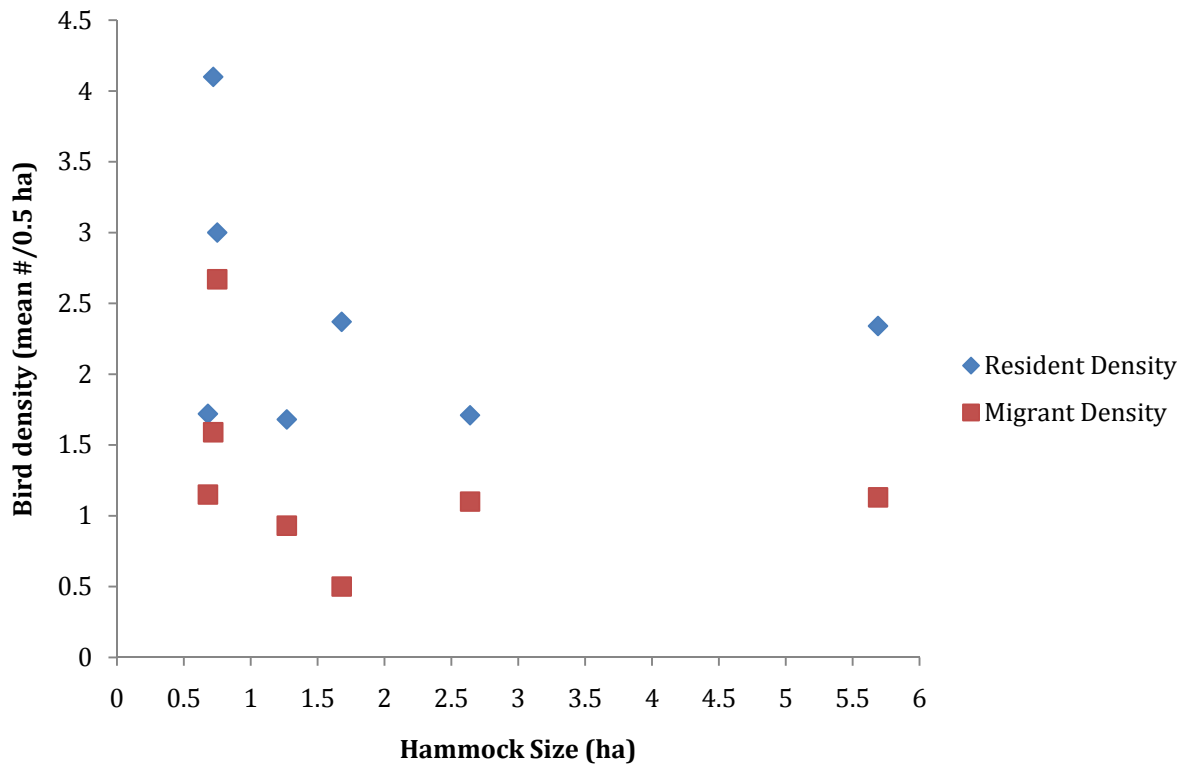
Figure 10. Mean density (mean per day/0.5ha) of birds among hammock sizes in Fall 2007.
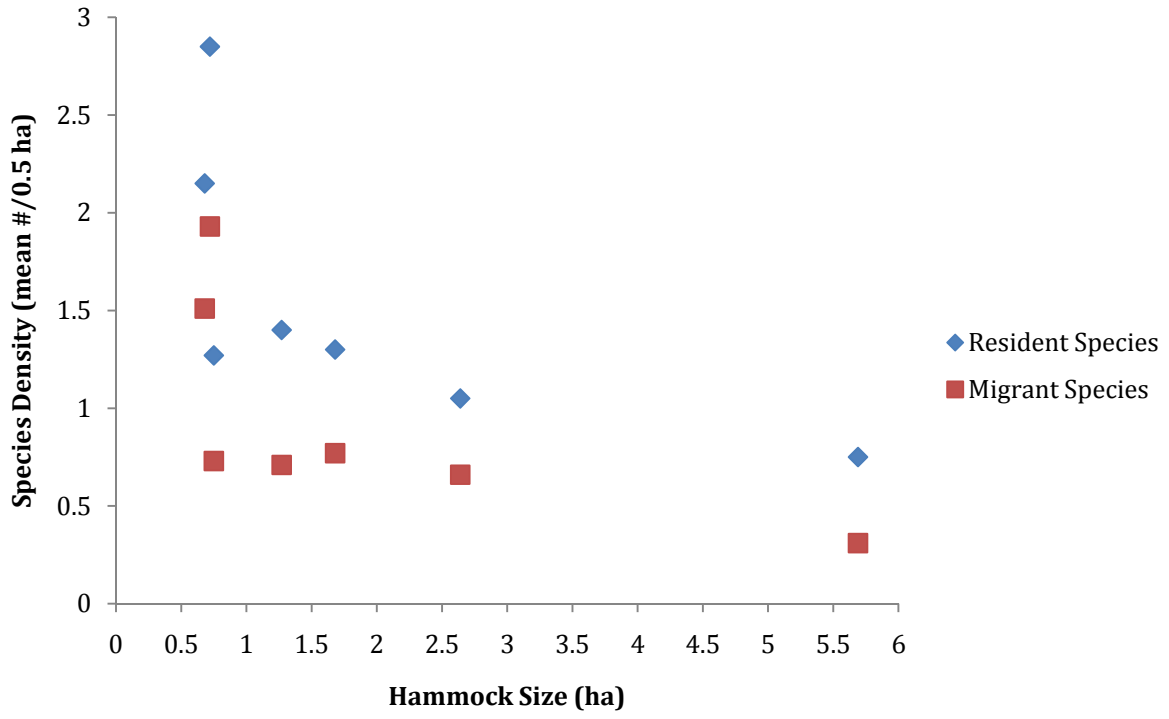
Figure 11. Mean species density among hammock sizes in Fall 2007.
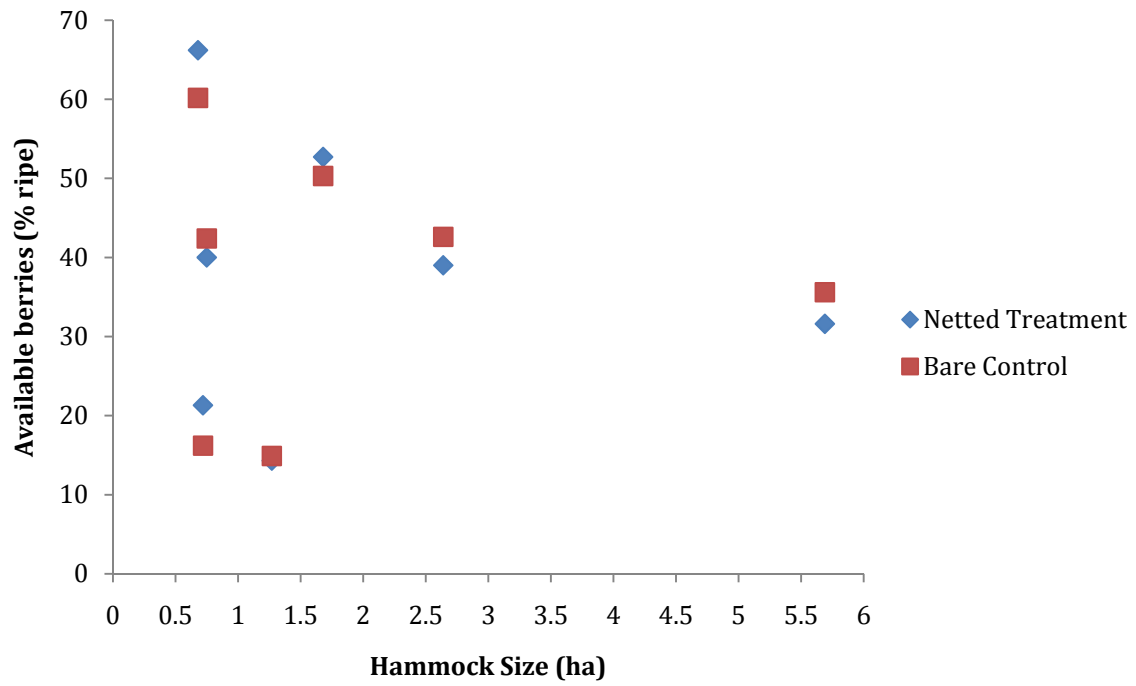
Figure 12. The percentage of ripe yaupon fruit among hammock sizes in Fall 2007.

Table 3: Statistical Analysis of the Effects of Area on Resident and Migrant Abundance and Species Diversity, Fall 2007 (d.f.= 1,6; *=p<0.05).

Area	F	P	R2
Transects			
Mean Resident Individuals (Density)	1.13	0.337	0.184
Mean Migrant Individuals (Density)	3.31	0.129	0.398
Mean Resident Species	4.01	0.102	0.445
Mean Migrant Species	3.88	0.106	0.437
Exclosures			
Treatment Branches (Netting)	0.114	0.749	0.022
Control Branches	0.00	0.999	7.5×10^{-7}

CHAPTER 4

DISCUSSION

Hammocks at Savannah National Wildlife Refuge attract migrants in spring and fall (Figure 4,6). The migrant and resident birds depress food resources in the form of arthropods (Figure 9), but do not affect fruit abundance (Figure 16). Although the bird density varies with hammock size, I did not find a significant relationship between competition and hammock size (Figure 9).

I found that migrant density was higher in smaller hammocks in two of three field seasons, and resident density was higher in smaller hammocks in all three seasons. Previous studies have established that smaller fragments can have a higher density of migrants (Martin 1980, Martin 1981, Somershoe and Chandler 2004). Competition for resources may occur in a small forest fragment with a high density of birds (Moore and Yong 1991). Although I found that competition is taking place, this effect did not vary in any consistent way among hammock sizes. Birds had a negligible effect on the percentage of available ripe yaupon berries, and the average percentage of available yaupon berries was not influenced by hammock size. Birds depleted food resources in a measureable way, a condition of competition (Moore and Yong 1991). However, this was not signigicant.

Avian Density- Exclosure Data Relationships: Quality food resources are extremely important to migrants at stopover sites, to provide fuel to complete the journey. Migrants may choose stopover sites based on the abundance of food resources. Insectivorous migrant densities were positively correlated with arthropod abundance at stopover sites

along the Mississippi coast (Buler et al. 2007), and in central Pennsylvania (Rodewald and Brittingham 2004). Exclosure treatments have shown that birds depress arthropod abundance (Moore and Yong 1991, Gradwohl and Greenberg 1982, Sanz 2001, Holmes et al. 1979).

Higher avian densities in small hammocks should lead to a measureable difference in arthropod abundance. I found that birds did depress the arthropod abundance in each of the four hammocks tested. The degree that arthropod abundance was diminished ranged from approximately 30% to 95%, although the arthropod abundance pattern in 2008 was opposite the pattern in 2007 (Figure 7). The percentage difference in arthropod density (between netted treatment and bare control branches) in the largest hammocks was consistent between 2007 and 2008. I expected to find that the percentage difference in arthropod density (between netted treatment and bare control branches) would be higher in smaller hammocks, indicating more intense food competition. In 2007 the percent difference in arthropod density was over 90% in each of the two smallest hammocks, while in 2008 it was between 30-60%. However, Spring 2007 was the only field season where the density of migrants was not higher in smaller hammocks(Figure 5, top), so migrant density does not explain the variation in competition among hammocks. Further, resident density that year was not proportionately higher to account for increased foraging pressure.

Abiotic factors such as temperature and rainfall, and biotic interactions related to the timing and intensity of migration, may explain the year-to-year variation. The effects of abiotic changes would be more pronounced in edge habitat (Faaborg et al. 1995), which describes the two smallest hammocks where arthropods were sampled. In 2007 the influx

of migrants was more diffuse and prolonged throughout the season, and even at the day

when I observed the highest mean number of individuals, it was still half the number

detected in the peak of 2008 (Figure 3).

The timing of fruiting for yaupon berries varies from year to year. In Fall 2006,

yaupon trees did not begin to put out green berries until late October/ early November,

and the proportion of fruiting female trees was approximately 75% less than in Fall 2007

(S. Beall, personal obervation). Migrant density and resource competition may follow a

different pattern in years where the fruit supply is diminished. Fruit abundance and quality

are habitat cues which attract migrants, and are correlated with an increase in resource

exploitation (Suthers et al. 2000), and frugivorous migrant density is correlated with fruit

abundance (Buler et al. 2007).

Avian Density- Hammock Area Relationships: Species-area relationships state that

bigger fragments will have more individuals and more species (Faaborg et al. 1995, Galli et

al. 1976, MacArthur and Wilson 1967). I found that although larger fragments had a higher

total number of birds, the density of birds per area was actually higher in smaller

fragments. The higher density may be attributed to edge effects. A broad definition of edge

habitat is any intersection of more than one landscape element (Yahner 1988). The effect

of edge habitat on migrant populations may manifest as some area-sensitive species

avoiding edge habitats (Parker et al. 2005). However, other studies (Ambuel and Temple

1983, Blake 1983, Blake and Karr 1987) have established that ecological generalists,

species which have flexible area and foraging requirements, are more common in smaller

forest fragments. These generalist, non-area-sensitive species may be attracted to edge

habitat. Some species, such as the Song Sparrow and Gray Catbird, may even preferentially choose smaller fragments during migration (Keller and Yahner 2007). Many of the resident species I detected are habitat generalists with no area requirements. A higher density of residents may be a cue to generalist migrants that the habitat is suitable as a stopover.

The width of edge habitat in relation to the total dimension of the fragment can be determined by examining the functionality of the habitat to wildlife (Yahner 1988). By these edge parameters, I expected that any hammock in which I did not find species which breed in the forest- interio (eg: Yellow-billed Cuckoo or Black-and-White Warbler), to be classified as nearly all edge. As such, I consider the smallest hammocks, Fife 2 (0.75ha) and Fife Diag. (0.68 ha), to be entirely edge-habitat.

In Spring 2007, the migrant density was higher in larger hammocks, while the resident density was smaller in larger hammocks. In larger hammocks that are not entirely edge habitat, a higher density of resident individuals may compete via interference competition with the migrants (Ambuel and Temple 1983). Lower resident density may serve as cue of habitat quality to area-sensitive migrants such as the Black-throated Green Warbler, which I detected only in one of the two largest hammocks.

Because spring immediately precedes the breeding season, there may be behavioral differences in stopover site selection between spring and fall migration. In Spring, species that are forest-interior breeders may begin to select stopover habitat that more closely mimics a suitable breeding habitat (Keller and Yahner 2007).

However, in fall the pressure to breed is over, and migrants may have fewer area-habitat requirements along migration routes. In a study of forest-patch use in

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Pennsylvania, several species which I also identified at SNWR (Red-bellied Woodpecker, Blue-headed Vireo, Eastern Wood-Pewee, Red-eyed Vireo, Black-throated Blue Warbler, and Black-throated Green Warbler) were more likely to be found in larger fragments in spring migration. However, these species were not more likely to be found in larger hammocks in fall migration (Keller and Yahner 2007). Of the afore-mentioned species, I found only the Blue-headed Vireo and Red-bellied Woodpecker in both spring and fall. The Red-bellied Woodpecker was equally abundant in all hammocks. However, the Blue-headed Vireo was only found in larger hammocks in the Spring, but in the fall I detected the species in a hammock as small as 0.68ha (Fife Diag).

Less strict habitat-area requirements explain the difference at SNWR in bird densities between Spring and Fall 2007. In the fall, the negative relationship with area was stronger for both resident and migrant density than in the spring.

Martin (1981) suggested that a higher density of birds in smaller shelterbelts in South Dakota was due to species which feed outside of the shelterbelts. The hammocks at Savannah National Wildlife are surrounded by marsh, where forest-dwelling species are not likely to feed. A previous study found that migrant density was higher in smaller hammocks at Savannah National Wildlife Refuge, and that these differenced were irrespective of differences in vegetation structure and composition (Somershoe and Chandler 2004).

The higher density of both migrants and residents in smaller hammocks indicates that birds are responding to area during stopover at Savannah National Wildlife Refuge. Higher densities in smaller hammocks support the idea that edge habitats are attractive to

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generalist bird species. The evidence suggests that competition for food may be more intense in smaller hammocks, although year-to-year variation demands further study. Future research on area requirements of migrating birds, and the relationship between avian density and resource availability, will help in the conservation of stopover site habitat and migrant bird populations.

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APPENDIX A

Species list for 2007 and 2008 spring migration periods. Numbers indicated the total number of times each species was observed in that hammock each year.

	Fife 2 (0.75 ha) 2007/08	Fife Diag (0.68 ha) 2007/08	First Bend (1.68 ha) 2007/08	Fife 1 (1.27 ha) 2007/08	By Fife (0.72 ha) 2007/08	Stream Bend (5.69 ha) 2007/08	Cistern (3.44 ha) 2007/08
Migrants							
Northern Bobwhite *(Colinus virginianus)*	0/0	0/0	1/0	0/0	0/0	0/0	0/0
Yellow-billed Cuckoo *(Coccyzus americanus)*	0/0	0/0	0/0	1/1	0/0	0/0	1/0
Acadian Flycatcher *(Empidonax virescens)*	0/0	0/0	0/0	0/0	1/0	0/1	0/0
Great-Crested Flycatcher *(Myiarchus crinitus)*	0/0	0/0	0/1	0/1	0/5	3/1	4/1
Brown Creeper *(Certhia Americana)*	0/0	0/0	0/0	0/0	0/0	0/0	1/0
Yellow-Throated Vireo *(Vireo flavifrons)*	0/0	0/0	0/0	0/0	0/0	1/0	1/0
Blue-headed Vireo *(Vireo solitarius)*	0/0	0/0	0/0	0/0	0/0	0/1	1/0
Red-Eyed Vireo *(Vireo olivaceous)*	0/0	0/0	0/2	0/2	1/0	1/0	1/2

House Wren *(Troglodytes aedon)*	0/0	0/0	0/1	0/1	0/0	0/0	0/0
Marsh Wren *(Cistothorus palustris)*	0/0	0/0	1/0	2/0	0/1	2/0	1/1
Ruby-Crowned Kinglet *(Regulus calendula)*	0/0	0/0	0/1	0/1	0/0	1/1	1/0
Hermit Thrush *(Catharus guttatus)*	0/0	0/0	0/0	0/0	0/0	0/0	2/0
Gray Catbird *(Dumetella carolinensis)*	0/0	0/0	0/1	1/1	0/2	1/4	0/0
Northern Parula *(Parula Americana)*	0/0	0/0	2/1	0/1	0/1	3/2	7/0
Yellow Warbler *(Dendroica petechia)*	0/0	0/1	0/0	0/0	0/0	0/0	0/0
Black-throated Blue Warbler *(Dendrioca caerulescens)*	0/0	0/0	1/1	0/1	0/0	0/1	0/1
	Fife 2 (0.49 ha) 2007/08	Fife Diag (0.53 ha) 2007/08	First Bend (1.15 ha) 2007/08	Fife 1 (1.24 ha) 2007/08	By Fife (1.57 ha) 2007/08	Stream Bend (3.08 ha) 2007/08	Cistern (3.44 ha) 2007/08
Yellow-Rumped Warbler *(Dendroica coronata)*	0/1	0/12	1/9	¼	1/5	1/8	0/6
Black-Throated Green Warbler *(Dendroica virens)*	0/0	0/0	0/0	0/0	0/0	0/1	0/0

Species							
Pine Warbler *Dendroica pinus)*	0/0	0/0	0/0	1/0	0/1	3/0	0/0
Palm Warbler *(Dendroica palmarum)*	0/0	0/0	0/0	0/0	0/2	0/0	0/0
Hooded Warbler *(Wilsonia citrina)*	0/0	0/0	0/0	0/0	0/0	0/2	0/0
Black-and-White Warbler *(Mniotilta varia)*	0/0	0/0	1/1	0/1	0/0	0/1	0/0
American Redstart *(Setophaga ruticella)*	0/0	0/0	0/1	0/1	0/0	0/1	0/0
Red-Breasted Grosbeak *(Pheucticus ludovicianus)*	0/0	0/0	0/0	0/0	0/0	0/0	0/1
Blue Grosbeak *(Guiraca caerulea)*	0/0	0/0	0/0	0/0	0/0	3/0	1/0
Prothonotary Warbler *(Protonotaria citrea)*	0/0	0/0	0/0	0/0	0/0	0/0	2/0
Northern Waterthrush *(Seiurus noveboracensis)*	0/0	0/1	0/0	0/0	0/0	0/2	0/0
Common Yellowthroat *(Geothlypis trichas)*	0/5	2/0	2/7	1/7	¾	6/6	12/2
Summer Tanager *(Piranga rubra)*	0/0	0/0	0/0	0/0	0/0	0/1	0/0

House Finch *(Carpodacus mexicanus)*	0/0	0/0	1/0	0/0	0/0	1/0	0/0
Indigo Bunting *(Passerina cyanea)*	0/1	0/0	0/0	1/0	0/0	0/0	1/0
Painted Bunting *(Passerina ciris)*	0/0	0/0	0/0	1/0	0/0	0/3	0/0

	Fife 2 (0.49 ha) 2007/08	Fife Diag (0.53 ha) 2007/08	First Bend (1.15 ha) 2007/08	Fife 1 (1.24 ha) 2007/08	By Fife (1.57 ha) 2007/08	Stream Bend (3.08 ha) 2007/08	Cistern (3.44 ha) 2007/08
Swamp Sparrow *(Melospiza Georgiana)*	0/0	0/1	2/0	0/0	0/1	1/1	1/0
White-Throated Sparrow *(Zonotrichia albicollis)*	0/0	0/0	½	0/2	0/2	2/1	0/2
Bobolink *(Dolichonyx orzyvorous)*	0/1	0/0	0/0	0/0	0/0	0/0	0/0
Brown-Headed Cowbird *(Molothrus ater)*	0/2	0/0	0/1	0/1	0/1	0/1	0/1
Orchard Oriole *(Icterus spurious)*	0/0	0/0	0/0	1/0	1/1	0/2	0/0
Northern Oriole *(Icterus galbula)*	0/0	0/0	0/0	0/0	2/0	2/0	2/1

Residents

Mourning Dove *(Zenaida macroura)*	1/3	2/2	8/5	5/5	4/12	7/10	6/3
Red-Bellied Woodpecker *(Melanerpes carolinus)*	4/5	3/1	7/7	2/7	6/12	10/9	10/5
Downy Woodpecker *(Picoides pubescens)*	0/0	0/0	2/1	0/1	0/1	0/0	0/0
Hairy Woodpecker *(Picoides pubescens)*	0/0	0/1	0/0	0/1	1/0	0/0	1/0
Pileated Woodpecker *(Dryocopus pileatus)*	0/0	0/0	0/1	0/0	0/0	0/0	2/0
Blue Jay *(Cyanocitta cristata)*	2/1	2/1	2/6	2/6	1/3	7/12	6/2
Fish Crow *(Corvus assifragus)*	0/0	0/0	0/0	0/0	0/0	0/0	1/1
Tufted Titmouse *(Baeolophus bicolor)*	0/1	0/2	2/2	½	1/5	0/9	3/1
Carolina Chickadee *(Poecile carolinensis)*	0/0	0/0	0/0	0/0	2/0	5/3	1/1

	Fife 2 (0.49 ha) 2007/08	Fife Diag (0.53 ha) 2007/08	First Bend (1.15 ha) 2007/08	Fife 1 (1.24 ha) 2007/08	By Fife (1.57 ha) 2007/08	Stream Bend (3.08 ha) 2007/08	Cistern (3.44 ha) 2007/08
Brown Creeper *(Certhia Americana)*	0/0	1/0	1/0	0/0	1/0	0/0	4/0
Carolina Wren *(Thyrothorus ludovicianus)*	0/2	1/5	6/8	6/8	9/8	12/10	5/4
Northern Mockingbird *(Mimus polyglottos)*	0/0	0/0	0/0	0/0	0/0	1/1	1/0
Brown Thrasher *(Toxostoma rufum)*	1/3	2/0	6/5	1/5	6/7	9/6	1/0
Northern Cardinal *(Cardinalis cardinalis)*	7/9	2/1	7/1	7/1	3/7	7/14	10/5
Eastern Towhee *(Pipilo erythropthalmus)*	1/0	0/0	2/1	0/1	0/8	3/3	0/1
Red-Winged Blackbird *(Agelaius phoeniceus)*	0/1	0/1	0/3	0/3	1/3	0/1	0/1
Brown-Headed Cowbird *(Molothrus ater)*	0/0	0/0	0/0	0/0	0/0	0/0	0/0
Common Grackle *(Quiscalus quiscula)*	0/0	1/0	0/0	0/0	0/4	0/2	0/0

Boat-Tailed Grackle *(Quiscalus major)*	0/0	0/1	0/0	0/0	0/0	0/0	0/0