MOVEMENT ECOLOGY OF A MIGRATORY SONGBIRD (TREE SWALLOW, *TACHYCINETA BICOLOR*): STAGED MIGRATION AND WINTER ROOST DYNAMICS

AN ABSTRACT
SUBMITTED ON THE NINTH DAY OF MARCH 2015
TO THE DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
OF THE SCHOOL OF SCIENCE AND ENGINEERING
OF TULANE UNIVERSITY
FOR THE DEGREE
OF
DOCTOR OF PHILOSOPHY

BY

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ABSTRACT

In this dissertation I examine the non-breeding-season movement ecology of a migratory songbird, the Tree Swallow (*Tachycineta bicolor*). Specifically, I focus on both seasonal migration (group-level movements) and the formation of communal roosts (individual-level movements). Using a combination of remote and direct tracking methods, I show first that southeastern Louisiana is an important and unique stopover site for this species during autumn migration. Tree Swallows tracked with geolocators from three separate breeding areas spent on average 30 days at this site before migrating to their main overwintering areas, a much longer period of time than traditional songbird migratory stopovers. Next, using historical Doppler weather radar data, I compare the annual dynamics of occupancy patterns, roost-site consistency, and autumn migration phenology between Louisiana- and Florida-arriving swallows, another important non-breeding area for this species. Arrival to Louisiana occurs over a much shorter time window than in Florida, and relative abundance decreases throughout the middle winter months in Louisiana before an increase again during spring migration. In Florida, swallows arrive much more gradually, and relative abundance remains high throughout the winter, more akin to a traditional winter site. For both locations the variation in autumn arrival phenology can be partly explained by the amount of precipitation along

the respective flyways: in general, higher rainfall along the Mississippi and Atlantic flyways is associated with later arrival to both Louisiana and Florida, respectively.

Having shown that the roosts are generally in the same location each night, I next focus on the causes and consequences of individual movements. Using radio-telemetry, I show that swallows have high, but not perfect, roost site fidelity from night to night, but do occasionally switch between roosts. Roosts thus form a network connected by the movements of individuals between them. I develop an individual-based model to show that this pattern of roost dynamics can be explained by individuals showing a high level of roost-site fidelity combined with a some amount of conspecific attraction to their nearest neighbors. Other real-world roost dynamics emerge from the model when these two parameters (roost fidelity and conspecific attraction) are independently adjusted. By extending the model to include the transmission of infectious diseases, I show theoretically that these roost dynamics can affect the spread of a disease throughout the population when the disease is spread via density-dependent transmission mode, but if the disease is spread via frequency-dependent transmission mode, infection rate is not affected by roost dynamics and spreads evenly across the parameter space. This can have consequences for species that form communal roosts or other types of social networks, especially in a world with increasing emerging infectious diseases.

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Burney provided much needed advice on catching swallows at their roosts and finding roosts on radar; and I thank him for his help attaching radio transmitters in the field.

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INTRODUCTION

"A great number of birds also go into hiding; they do not all migrate, as is generally supposed.... Swallows, for instance, have been often found in holes, quite denuded of their feathers…."
-Aristotle, 350 BCE, The History of Animals, Book VIII

"Swallows certainly sleep all the winter. A number of them conglobulate together, by flying round and round, and then all in a heap throw themselves under water, and lye in the bed of a river."
-Samuel Johnson, as quoted in Life of Johnson, by Boswell, 1791

"Oct 30 1821, New Orleans - The day Warm, Swallows Plenty and quite as gay in their flight as in June — to find here those Birds in aboundance 3 Months after they have left the Midle States, and to Know that they Winter Within 40 Miles in Multitudes is one of the Gratifications the Most Exquisite I ever Wish! to feel in Ornithological Subjects and that Puts compleat Dash over all the Nonsense Wrote about their Torpidity during Cold Weather; No Man could ever have enjoyed the Study of Nature in her all Femine Bosomy Wild and err so Wide"
-J. J. Audubon, Journal of New Orleans, 1820-1821

In the 4th Century B.C.E. and probably earlier, in order to explain the disappearance of swallows and other birds during the cold months of winter, people believed that they hid themselves and hibernated, emerging when the weather turned warm again. Swallows and kites would dive beneath the water and spend the cold months under the mud; storks and doves would hide themselves in trees.

The idea more or less persisted for more than two thousand years, but not everyone believed it; and when in 1820 John James Audubon moved to southeastern Louisiana to work on his book and paintings, one of his 'Gratifications' was to dispel the myth once and for all: "Being extremely desirous of settling the long-agitated question respecting the migration or supposed torpidity of Swallows, I embraced every opportunity of examining their habits, carefully noted their arrival and disappearance, and recorded every fact connected with their history" (Audubon 1929). The many mentions of Tree Swallows (*Tachycineta bicolor*), or his "little favourites . . . . the green-baked white-belied [sic] swallow", in his New Orleans journal attest to this goal:

> [February 21, 1821]: "Saw Many Green Baked White Belied Swallows to day . . . All of them very Lively and not exibiting much of the Muddy Appearance that immersion in the Swamps about this City would undoutedly give them, [if they] had they remained buried in it since Last December . . ."
>
> [October 27, 1821]:"Green Back Swallows Gamboling over the City and the River the Whole day… [I] have great Hopes of ascertaining their Winter quarters Not far from [here]".
>
> [January 28, 1822]: "Thermometer at 40°. Having seen the Hirundo viridis continually, and the H. purpurea or Purple Martin beginning to appear, I discontinued my observations."

And with these observations, he dispelled one of the major ornithological myths that had persisted since before the time of Aristotle.

We now know that migration is quite common in the bird world, and is also prevalent in mammals, fish, and insects (Dingle 2014). The behavior ranges from the long-distance trans-hemispheric journeys of bar-tailed godwits (*Limosa lapponica*) (Gill et al. 2005) to smaller-scale altitudinal migrations of many New World tropical birds (e.g. Boyle 2008). Recent technological and methodological advances have greatly facilitated the study of migration (Robinson et al. 2009, Bridge et al. 2011), from direct tracking of individual birds with satellite telemetry (Martell et al. 2001), radio telemetry (Cochran 1987) and geolocators (Stutchbury et al. 2009) to indirect tracking or remote sensing with isotope analysis (Marra et al. 1998), Doppler radar (Diehl et al. 2003), and citizen science data (Hurlbert and Liang 2012). These advances have led to major breakthroughs and fascinating discoveries not just about seasonal migration, but other types of organismal movements including seed dispersal (Wright et al. 2008), foraging (Louzao et al. 2014), and nomadism (Mueller et al. 2011). The burgeoning field of movement ecology (Nathan et al. 2008) reflects an attempt to incorporate these studies into a general framework to aid in the study of, and promote the formation of hypotheses about, organismal movement.

In this dissertation, I explore two movement behaviors of Tree Swallows: seasonal migration and the formation of communal roosts. The first two chapters examine migration and group movements of roosts (population-level movements), while the last two chapters explore some of the causes and consequences of communal roosting (individual-level movements). I incorporate various methods to study, quantify, and understand these movements, including tracking of individuals (geolocators and radio telemetry), tracking at the species level (Doppler weather radar and citizen-science [eBird] data), and individual-based (or agent-based) modeling.

The Tree Swallow has been very well studied during the breeding season for many decades, and this “model organism” (Jones 2003) has provided insight into mating systems and reproductive behavior (Stutchbury and Robertson 1987, Dunn et al. 1994), spatial relationships and individual movements (Robertson and Rendell 1990, Shutler and Clark 2003), and variation in life-history traits (Dunn and Winkler 1999, Hussell 2003). However, its non-breeding season ecology, including movements outside the breeding area, is much less studied, and this dissertation is an attempt to both scratch the surface of this large topic and to appreciate what Audubon noticed of them two centuries ago: “What knowledge these Litle [sic] Creatures possess and how true they are in their Movements” (Audubon 1929).

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Chapter One

Integrating information from geolocators, weather radar, and citizen science to uncover a key stopover area for an aerial insectivore[1]

ABSTRACT

Determining the distribution of stopover and overwintering areas for migratory animals is essential for understanding population dynamics and building predictive models. Tree Swallows (*Tachycineta bicolor*) are small songbirds that breed across North America. Data from Doppler weather radar and eBird indicate that Tree Swallow numbers increase throughout October and November in southeastern Louisiana, but then decrease during December. We thus hypothesized that southeastern Louisiana is a stopover area used by Tree Swallows during fall migration before moving to further overwintering areas. We tested this hypothesis by attaching light-logging geolocators to Tree Swallows at five breeding sites spanning the species' breeding range from British Columbia to Nova Scotia, and then tracking their fall migration routes, stopover sites, and wintering locations. Of 38 individuals that returned the following breeding season, 11 birds from

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three breeding sites (Saskatchewan, Wisconsin, Ontario) used southeastern Louisiana as a stopover site. Arrival date and duration of stay closely matched observations from both eBird and radar data. From Louisiana, most swallows continued their migration to one of three wintering sites: peninsular Florida, the Bahamas, and the Yucatán Peninsula, whereas two birds remained until spring within 200 km of the stopover area. Our results suggest that southeastern Louisiana is an extended stopover site for Tree Swallows that originate from a wide geographic range on the breeding grounds, and demonstrate how geolocators, combined with other sources of movement information, reveal habitat use throughout the annual cycle.

INTRODUCTION

Understanding factors that influence population dynamics of migratory organisms requires knowledge of habitat use and movements throughout the annual cycle (Sherry and Holmes 1995, Norris and Marra 2007, Faaborg et al. 2010). Most studies describing migratory connectivity have focused on connecting breeding areas with primary over-wintering sites (e.g. Hobson and Wassenaar 1997, Chamberlain et al. 1997, Kelly et al. 2005, Boulet et al. 2006, Norris et al. 2006). However, many migrant birds move between one or more stopover sites during their autumn and spring migrations (Moore 2000), and determining locations of stopover sites is a critical step for both conservation (Mehlman et al. 2005) and building population models to predict how migratory animals will respond to environmental change (Warnock et al. 2004, Sheehy et al. 2011).

For most small-bodied birds, we only have information on use of stopover sites at a limited number of long-term banding sites (e.g., DeSante et al. 2003, Fransson et al.

2005, Priestley et al. 2010). Identifying stopover sites can be challenging because of the difficulty of directly tracking individuals during migration. Furthermore, determining whether stopover sites are used by multiple breeding or non-breeding populations requires information on movements across a species' range. Recent advances in light-logging geolocators now make it possible to follow daily movements of individuals throughout the annual cycle (e.g., Stutchbury et al. 2009, Bairlein et al. 2012, Fraser et al. 2012), providing opportunities for identifying stopover sites and estimating how many breeding or non-breeding populations use these sites during migration.

Tree Swallows are small (ca. 20 g) migratory birds that breed throughout much of North America (Winkler et al. 2011). Shortly after breeding, individuals aggregate in large nocturnal roosts that form near breeding grounds (Burney 2002, Norris et al. unpublished data). After one to two months, individuals migrate south to their wintering grounds, located along the Atlantic and Gulf coasts of southeastern North America, Mexico, Central America, and the Caribbean (Winkler et al. 2011), where they also form roosts, some of which contain well over a million birds (Burney 2002). However, direct linkages among specific breeding, stopover, and wintering areas, as well as details of migration phenology, are unknown in Tree Swallows and most other songbird species.

In this paper, we first use citizen science (eBird) records and weather radar to show that Tree Swallows arrive in the lower Mississippi Valley in southeastern Louisiana en masse in October and November, use abundant sugarcane fields as roosting habitat, and then appear to significantly decrease in number post-sugarcane-harvest, migrating out of the area towards their main over-wintering sites. Based on these observations, we examined the hypothesis that southeastern Louisiana is used primarily as a stopover site by Tree Swallows before individuals continue towards over-wintering sites. An alternative explanation is that swallows do not actually leave southeastern Louisiana, but that the sugarcane harvest forces swallows to disperse to smaller roosts that are not readily visible on radar. To examine these hypotheses, we attached light-level geolocators to birds at five breeding sites across North America to track their fall migration routes, stopover sites, and wintering locations.

METHODS

Locating Tree Swallow Roosts using NEXRAD Doppler Weather Radar. Our study area in southeastern Louisiana for both radar and eBird data is a circle with a radius of 175 km centered near Slidell, Louisiana, USA, at the KLIX Doppler weather radar station (30°20'N, 89°49'W). This circle covers all of southeastern Louisiana and much of southern Mississippi (figure 1.1A). We chose 175 km radius as the cutoff because beyond that roosts are less easily detectable on radar. The United States has 159 WSR-88D radar stations throughout the country, continuously scanning the aerosphere for precipitation patterns. Often birds, bats, and insects are also detected in radar data (Kunz et al. 2008, Chilson et al 2012a). The WSR-88D program was introduced in the early 1990s, and these data are archived and freely available online from the National Climatic Data Center (http://www.ncdc.noaa.gov). In the non-breeding season, many swallow species ascend at dawn from their nocturnal roosts in large numbers into the aerosphere. Large swallow and martin roosts appear on morning Doppler weather radar as 'ring-echoes', an annulus (or semi-annulus) of pixels that expands with each successive sweep of the radar beam (figure 1.1A-C; Russell and Gauthreaux 1998, Winkler 2007). Roost-rings expand until either birds descend below the altitude detected by radar, or density of birds becomes too low for detection by the radar beam.

We downloaded WSR-88D Doppler weather data from the National Climatic Data Center for station KLIX in Slidell, Louisiana, from October 2011-April 2012. We scanned radar data visually each morning during the hour following local sunrise, and noted suspected Tree Swallow roosts within the study area. Locations, habitat, and species composition for most of these roosts were verified by visiting the roosts. Though we did not visit each roost in person, roosts that were not visited displayed the roost-ring structure on radar that is diagnostic of Tree Swallows (i.e., speed of departure and shape of roost-ring), and were located in typical roosting habitat (*Phragmites* reed beds) known to attract numerous Tree Swallows based on eBird data. For each radar scan in which a roost-ring appeared, we drew a circle around the roost annulus (or semi-circle) using a web-based application (developed by D.R.S.). The application automatically calculates the radius and latitude and longitude of the center of each roost-ring. Although estimating numbers of birds within Doppler weather radar scans remains problematic (Russell and Gauthreaux 1998, but see Chilson et al. 2012b), we use the maximum detectable radius of the expanding roost rings as an index that is positively related to roost size. However, we do not yet understand the precise relationship between roost size and maximum radius, which may be nonlinear. For each roost, we calculated the maximum detectable radius, and for each day that roosts appeared, we summed the maximum detectable radii of all roosts.

Estimating bird distribution eBird records. eBird is a citizen-science based program run jointly by the National Audubon Society and the Cornell Lab of Ornithology that collects bird observations. eBird is a repository of tens of millions of bird sightings submitted by birders around the world (Wood et al. 2011), and millions of new observations are submitted every month. Thus, this resource reflects spatial and temporal patterns of the distribution and abundance of birds. We downloaded eBird data from the Avian Knowledge Network (http://www.avianknowledge.net) from 2006-2011 for the same study area from which we analyzed radar data. We calculated the proportion of eBird reports submitted each day that included Tree Swallows, a value we refer to as frequency. Following Hurlbert and Liang (2012), we used frequency of Tree Swallow reports rather than abundance of Tree Swallows to reduce bias that may be introduced by the sighting of extremely large roosts. For example, an observer visiting a large roost site in the morning or evening may submit an observation of a million swallows whereas an observer in the same area of more dispersed foraging birds during the day may report much smaller numbers. A linear regression of frequency of Tree Swallow reports versus total number of reports ($R^2 < 0.01$, $F = 1.1$, df = 1 and 211, $P = 0.30$) verified that the total number of reports submitted to eBird does not influence the frequency of Tree Swallow observations within those reports.

Geolocators. In summer 2011, we deployed geolocators (Lotek Wireless model MK12-S, with 10-mm light stalk) on adult Tree Swallows ($n = 177$) at five breeding sites across North America: Wolfville, Nova Scotia (45°6'N, 64°21'W; $n = 30$); Long Point, Ontario (42°39'N, 80°26'W; $n = 33$); Saukville, Wisconsin (43°23'N, 88°01'W; $n = 35$);

Saskatoon, Saskatchewan (52°13’N, 106°04’W; *n* = 40); and Prince George, British Columbia (53°50' N, 122°57' W; *n* = 39). We attached geolocators with a modified leg-loop backpack harness (Stutchbury et al. 2009), which had a combined mass of ≤ 1.0 g (< 5% of body mass). Prior to deployment, we calibrated each geolocator in two distinct phases. Static (off-bird) calibration was used to identify changes in light sensitivity between the two time periods before deployment and after retrieval the following year. For these calibration periods, we placed geolocators on the roof of a building near the deployment site at Long Point, Ontario, and away from artificial light for seven days in early June 2011 and again in July 2012. Using a light threshold value of 5 on the arbitrary scale of 0 to 64 used in BASTrack software (British Antarctic Survey 2010), we determined that there were similar average sun elevation angles for the two time periods (-5.38˚ pre-deployment, -5.34˚ following retrieval). After geolocators were deployed on birds, we performed dynamic on-bird calibration for each bird for the period after nesting and before migration when birds were still at or near their known breeding location but no longer using nest boxes (mean duration ± SD = 17 ± 6 days). The start of migration is defined here as a pronounced movement of ≥100 km from the breeding site that resulted in another location in the same direction the next day. Sun angle values determined this way more accurately reflected conditions during deployment by accounting for potential shading effects caused by a bird’s behavior (Fudickar et al. 2011, Lisovski et al. 2012). We considered calibration on the breeding grounds (shortly after breeding) to be sufficient for the entire annual cycle because swallows generally roost in *Typha* marshes in both the breeding (Dunn & Whittingham 2005; but see Hayes & Cohen for western populations) and non-breeding season (this study). We used each geolocator-specific sun angle determined during dynamic calibration to plot estimated locations using Bird Tracker (British Antarctic Survey 2010). On-bird sun angles ranged from -4.05˚ to -5.34˚, and resulted in a mismatch with true breeding locations by an average 50.6 ± 22 km in latitude (range: 11–98 km) and 55.2 ± 29 km in longitude (range: 24–99 km). Geolocator positions during this period were accurate to within an average distance of 81.7 ± 24 km.

Following visual inspection of twilight transitions in TransEdit (British Antarctic Survey 2010) to remove obvious outliers caused by unusual shading events or behavior, we used live calibration sun angles calculated for each geolocator to estimate birds' latitude and longitude using midnight locations. Because estimating latitude is problematic during the equinox periods when day length is equal at all latitudes, we excluded 15 days on either side of the equinoxes (as in Fraser et al. 2012). To determine location probabilities (e.g. Bächler et al. 2010) during the main stopover and over-wintering locations, we used the KDE and Isopleth commands in the Geospatial Modeling Environment (Beyer 2012) to produce 50% and 95% kernel density estimates.

RESULTS

Radar and eBird . The summed daily radii of all Tree Swallow roosts located on Doppler radar from October 2011 to April 2012 increased throughout October, peaked in mid-November, began to decrease in December, and remained low throughout the rest of the study period. October through December 2011 is the period in which eight roosts were located in sugarcane fields along the lower Mississippi Valley (table 1.1; figures 1.2 and 1.3). By the end of December, sugarcane had been completely removed. Figure 1.2 shows a vertical bar at 23 December, after which no sugarcane roosts appeared on radar, and both roost radii and eBird frequencies decreased.

To correlate the arrival and departure of geolocator-bearing birds with changes in the aggregate number of swallow roosts detected on radar, we fitted logistic curves to changes in the numbers of swallow roosts as seen on Doppler radar from October through December. The curves were fitted using the ‘glm’ function in the stats-package of the R programming language by specifying a binomial distribution and a logit link (R Development Core Team 2011). From these curves, calculated separately for increase and decrease in roost numbers, we calculated the 90th percentiles of curves as arrival and departure windows, respectively. We calculated inflection points of arrival and departure curves to estimate mean arrival and departure dates from radar data, and compared these to mean dates from geolocator birds. Mean arrival and departure dates from radar were 17 October and 29 November, respectively. Arrival and departure windows were between 6 - 28 October and 31 October – 29 December, respectively.

The proportion of total eBird reports that include Tree Swallows (Tree Swallow frequency) also increased sharply during October 2011, peaked in early November 2011, and began to steadily decrease throughout the rest of the winter and into spring (mean number of reports submitted per week = 206, SD = 72; figure 1.2). Averaged weekly frequency of Tree Swallow reports for five years (2006-2010; mean number of reports submitted per week = 348, SD = 91) also shows a similar pattern of a peak in late October and early November and a gradual decline throughout the rest of winter (figure 1.2, dashed red line), suggesting that 2011-12 was not an atypical year for eBird reports.

Radar and eBird data were positively correlated (Pearson's $r = 0.43$, $t = 5.0$, df = 114, $P < 0.001$).

Geolocators. We retrieved 38 geolocators (21%) in 2012 from the 5 deployment sites (table 2.1): 2/39 from British Columbia; 11/40 from Saskatchewan; 6/35 from Wisconsin; 13/33 from Ontario; and 6/30 from Nova Scotia.

Of the 38 Tree Swallows that returned with geolocators, 11 (29%) spent some time in southeastern Louisiana during early winter before moving to their main over-wintering site (figure 1.4). These birds originated from three breeding sites: 8/11 (73%) from Saskatchewan, 2/6 (33%) from Wisconsin, and 1/13 (8%) from Ontario. Excluding one bird whose arrival date was masked by the equinox, mean arrival date (± SD) to Louisiana was 20 October (± 5 d), and mean departure date was November 22 (± 18 d; figure 1.3). Eight of the 11 birds that used southeastern Louisiana arrived within the 6-28 October arrival window as calculated from the radar data, and mean arrival date from birds with geolocators three days earlier than mean arrival date estimated from radar.

Nine of 11 birds departed Louisiana during the sugarcane roost departure window, and the mean departure date of birds with geolocators was seven days earlier than departure date estimated from radar. These nine birds left Louisiana destined for three distinct over-wintering regions in the Yucatán Peninsula, Mexico ($n = 7$), peninsular Florida ($n = 1$), and the Bahamas ($n = 1$; figure 1.5). For four birds whose mean estimated winter position was over water, we chose the nearest location on land (mean difference ± SD = 79 ± 47 km). For one bird whose mean winter location was located more than 200 km over the Gulf of Mexico, we chose the nearest point on land to the south. We made this decision even though the Texas coast was closer because unusual sensor shading between the autumn and spring equinoxes is known to artificially increase latitude estimates in the Northern Hemisphere (Lisovski et al. 2012). Mean distance travelled to wintering locations after stopping over in Louisiana was 1225 ± 168 km.

Two birds (geolocator numbers 840 and 841; figure 1.5) remained within 230 km of the stopover area for the rest of the winter. We did not include these birds in the calculation of mean departure date from the geolocator data. One bird moved slightly NE from the study area, and departure date of the other bird was difficult to estimate. This was due to consistency in longitude estimates combined with latitude-masking caused by the equinox (see Methods for further details). The other 27/38 swallows did not travel to southeastern Louisiana as a stopover site, and instead used other stopover sites closer to their breeding origin before migrating to their over-wintering areas (Norris et al. unpublished data).

DISCUSSION

We demonstrate how data from geolocators can be used to examine hypotheses about habitat use in a period of the annual cycle that is extremely challenging to study. From citizen science and radar observations, we generated the hypothesis that southeastern Louisiana is used as stopover site by Tree Swallows during fall migration. Our geolocator data largely supported this hypothesis because most of the Tree Swallows with geolocators that went through Louisiana arrived by the beginning of November, and most had left by the middle of November and into early December (figure 1.3). Our results also suggest that southeastern Louisiana is used as a stopover area by several breeding populations of Tree Swallows across North America, and an over-wintering site by some individuals, before the birds continue on to a variety of primary overwintering areas.

This area of the northern Gulf coast, which is the southern end of the Mississippi Flyway, is used by many species of migratory birds as an autumn stopover, most notably Neotropical migrants that are preparing for a trans-Gulf flight to Central America (Able 1972, Moore 2000). The large number of Tree Swallows that use southeastern Louisiana each autumn suggests that this area is an important stopover site during fall migration of this species, but the significance of this region for annual-cycle processes is not yet fully understood. As more tracking data are becoming available for migratory birds, it is clear that migration strategies can be complex, composed of previously unknown major stopover sites (this study) and even multiple wintering areas (e.g. Stach et al. 2012).

Stopover sites can be used for many reasons, including molt or refueling for the migration itself (Warnock 2010). Most adult Tree Swallows captured in the study area in late October and November have already completed molt (Laughlin et al. unpubl. data), supporting previous claims that Tree Swallows complete pre-basic molt prior to, and in some cases during, their journey southwards (Stutchbury and Rohwer 1990). Therefore, this area is not used as a molting area before heading towards the final wintering areas. It is possible that southeastern Louisiana is a stopover area to accumulate fat reserves for crossing the Gulf of Mexico, as do many other Neotropical migrant species. However, these stopover bouts typically last less than one week (Woodrey and Moore 1997). Tree Swallows with geolocators stayed on average 32 d in southeastern Louisiana. Swallows that crossed the Gulf to the Yucatan appeared to have done so in less than one day, whereas birds that migrated on towards Florida appeared to have done so over land, not water. It does not seem likely, therefore, that swallows would require a month to gain fat reserves prior these flights.

Another, not mutually exclusive possibility, is that sugarcane fields provide a high-quality roosting habitat in an area that has lost more than 5,000 km^2 of wetlands over the last century (Couvillion et al. 2011). It is perhaps not coincidental that the departure of Tree Swallows with geolocators is concurrent with gradual harvest of sugarcane fields that cover over 1600 km^2 statewide and mature around the time when southbound Tree Swallows arrive. When swallows arrive each fall, the sugarcane crop is at its full height (ca. 4 m), and covers an almost continuous area along the banks of the lower Mississippi River. Sugarcane harvest usually begins in early November, in many places at once, and lasts for nearly two months, creating a checkerboard-pattern of available roosting habitat that gradually disappears until the crop is completely removed. Numbers of Tree Swallows in sugarcane roosts appear to decrease as harvest continues, and though it is difficult to quantify, roosts of well over a million birds decrease to the tens of thousands near the end of harvest (Laughlin et al., unpubl. data). From a stopover perspective, it appears that the sugarcane fields are used as stopover habitat for Tree Swallows during October through December, and wetland areas are used as over-wintering habitat for birds that remain. In spring, radar and eBird data suggest another influx of swallows on their northward migration (figure 1.2). Only wetland roosts are used during this time period, as the sugarcane has not yet grown to sufficient height for roosting by swallows.

Does the sugarcane harvest drive most swallows out of southeastern Louisiana, or could it also be a gradual decrease in winter temperatures that suppresses the local food supply of flying insects? Most likely it is a complex combination of factors. Anecdotal evidence for this question comes from the New Orleans Journal of John James Audubon, who in October of 1822 wrote extensively of the “white-bellied” swallows that were abundant during October, but seen throughout the winter months only in warmer winters (Audubon 1929). This suggests that this pattern of a large number of Tree Swallows funneling through the southern end of the Mississippi Flyway each autumn may not be a recent phenomenon. It is important to note, however, that some Tree Swallows do remain in the area and use southeastern Louisiana as their main over-wintering site after the sugarcane harvest, as two of the birds with geolocators did (figure 1.3). It is difficult to quantify how many Tree Swallows remain in the area, but Tree Swallows roosts form in wetland areas post-harvest (and are large enough to show up on the stationary NEXRAD radar stations), and Tree Swallows remain an important part of the area’s avifauna throughout the entire winter.

Our study combines three independent sources of data to discover a key autumn stopover area for several distinct populations of Tree Swallows. To our knowledge, this is the first study to combine citizen science data (eBird) with Doppler radar data to discover a potential spatiotemporal pattern in the abundance of birds. We then used an individual tracking device that tested and provided strong evidence for our hypothesis about the southeastern Louisiana staging area. Combining multiple sources of data enables us to test hypotheses about habitat use patterns throughout the annual cycle. Our results suggest that southeastern Louisiana is likely a key stopover site for migratory Tree Swallows from central North America. Removal or degradation of this site would, therefore, likely influence multiple breeding and non-breeding populations (Sheehy et al.

2011), which could have knock-on effects for the entire migratory network of this species (Taylor and Norris 2010).

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Table 1.1 Location and duration of all Tree Swallow roosts as seen on Doppler weather radar station KLIX, Slidel, LA, from October 2011 - April 2012.

Roost name and number	Location (lat/lon)	Habitat	Start Date	End date	Duration (d)
1. Edgard	30.03, -90.53	Sugarcane	11-Oct	20-Dec	70
2. Vacherie	29.97, -90.80	Sugarcane	12-Oct	9-Dec	58
3. Luling	29.94, -90.39	Sugarcane	12-Oct	20-Dec	69
4. Lockport	29.62, -90.49	Sugarcane	14-Oct	9-Dec	56
4. Thibodeaux	29.73, -90.80	Sugarcane	17-Oct	11-Nov	25
5. Plattenville	30.02, -91.02	Sugarcane	17-Oct	30-Nov	44
6. Iberville	30.17, -91.16	Sugarcane	17-Oct	18-Nov	32
7. Baton Rouge	30.48, -91.27	Sugarcane	17-Oct	5-Nov	19
8. Pearl River S.	30.22, -89.59	Wetland	5-Nov, 29-Feb[a]	20-Nov, 16-Mar[a]	15, 17[a]
9. N. Pontchartrain	30.39, -90.17	Wetland	28-Dec	21-Feb	56
10. MS Delta	29.36, -89.30	Wetland	9-Jan	20-Apr	101

[a] Roost appeared in November, dissolved, and formed again in February 2012

Table 1.2. Timing and onward migration distances of Tree Swallows using southeastern Louisiana as a late-fall stopover site

Band number	BAS Geolocator number	Sex	Breeding site	Southeast Louisiana Arrival date	Southeast Louisiana Departure date	Southeast Louisiana Stopover duration (d)	Wintering region	Distance from LA to main wintering site (km)
2321-10994	794	M	SK	4-Oct[a]	18-Nov	45[a]	Yucatan	1202
2321-10851	832	F	SK	16-Oct	12-Nov	27	Yucatan	974
1851-75491	474	F	WI	21-Oct	18-Nov	28	E. Mexico	1359[b]
2351-32559	790	M	SK	21-Oct	18-Nov	28	Yucatan	1342
1671-55771	840	M	SK	21-Oct	15-Apr[a]	177[a]	Southern US	125
2321-11763	846	M	SK	21-Oct	11-Nov	21	E. Mexico	1386
2321-11377	851	F	SK	21-Oct	11-Nov	21	E. Mexico	1360
2311-93640	763	F	ON	25-Oct	25-Dec	61	E. Mexico	1255
2321-10896	799	M	SK	26-Oct	6-Nov	11	Bahamas	1226
2351-32201	841	M	SK	31-Oct	1-Jan	62	Southern US	204
1831-01663	472	M	WI	2-Nov	22-Nov	20	Florida	930

[a] date influenced by effect of latitude estimates close to autumnal equinox.

[b] winter location shifted north by sensor shading. See text for further explanation.

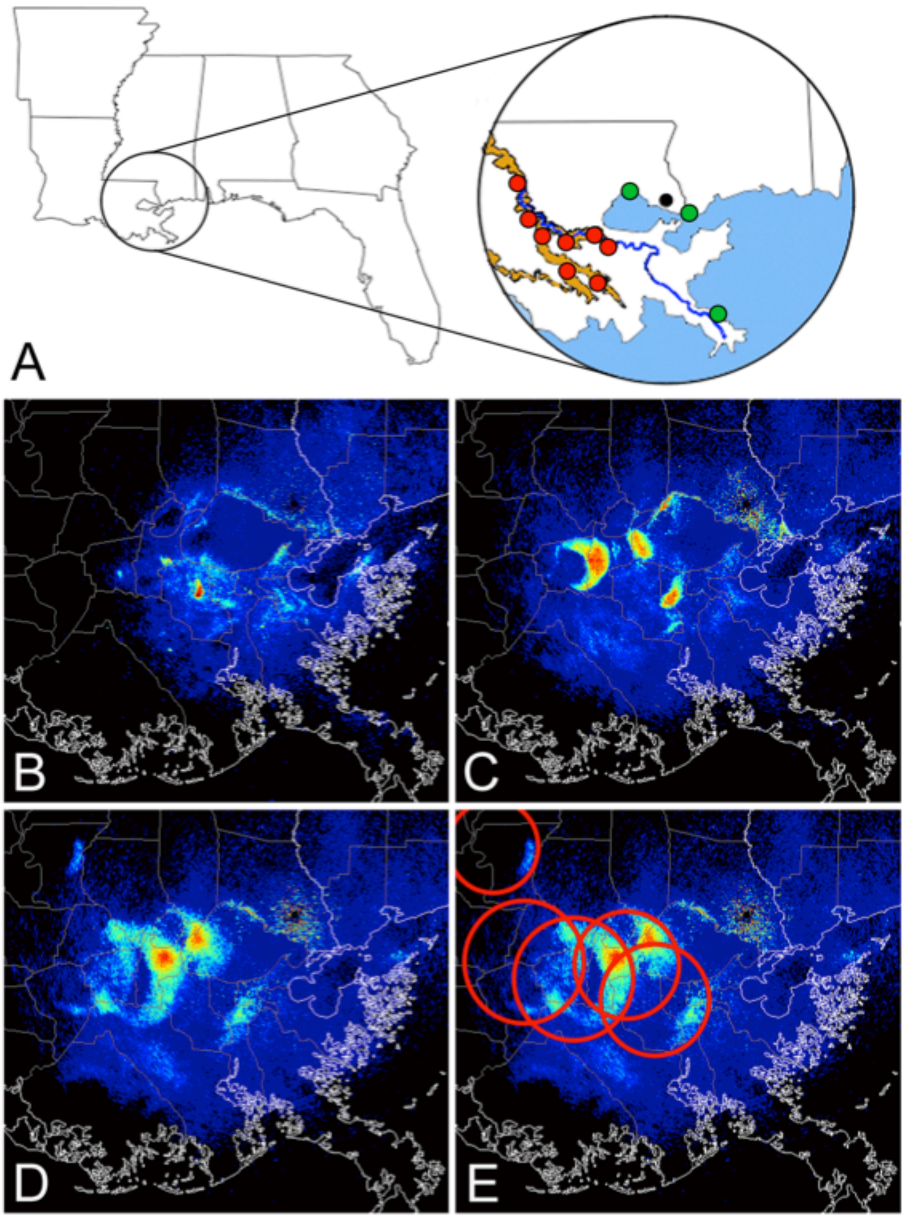

Figure 1.1. Panel A: Map showing study area in Louisiana. Black circle is study area for radar and eBird data: a circle of radius 175 km centered at KLIX radar station near Slidell, LA (black dot at center of circle). Red dots are sugarcane roosts, green dots are wetland roosts, blue line is Mississippi River, and brown area is approximate extent of sugarcane production in study area. Panels B-E: Example of successive Doppler radar images from station KLIX on 1 November 2010 in the hour following local sunrise.

Panels B-D show the emergence and subsequent expansion of five Tree Swallow roosts (successive panels are approximately 20 min apart). Panel E is the same scan as the third, but shows the manually added circles over roosts from which we calculated roost radii. Roosts are (from west to east): Baton Rouge, Plattenville, Vacherie, Edgard, and Luling.

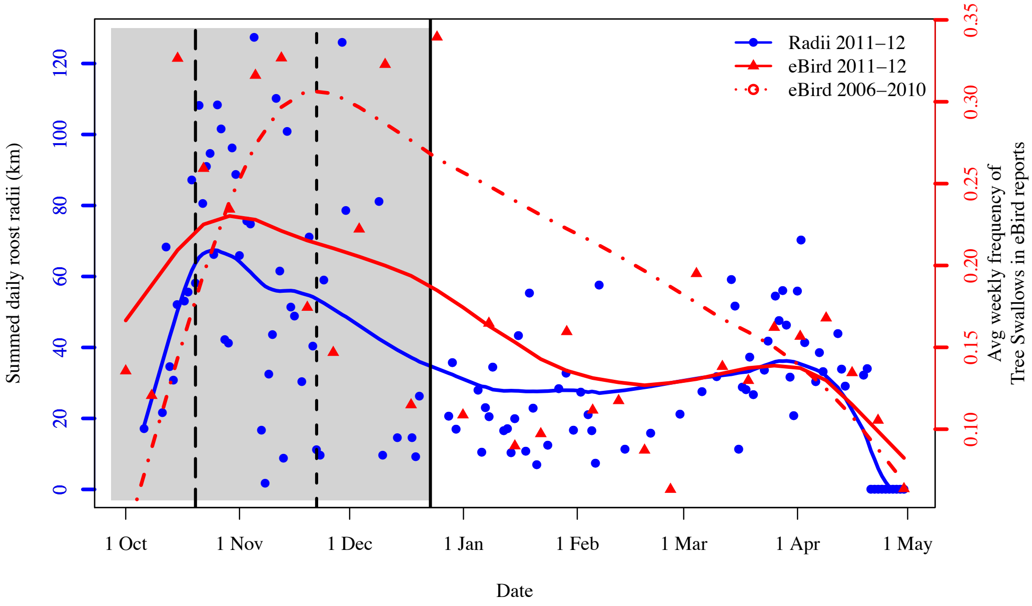

Figure 1.2. Daily summed roost-ring maximum radii (left y-axis, blue circles) and averaged weekly frequency of eBird reports that contain Tree Swallows (right y-axis, red triangles), and their associated smoothing curves, for October 2011 through April 2012. Dashed red curve represents averaged daily eBird frequency of Tree Swallows reports for October through April 2006-2010, on the same right y-axis scale. Shaded area represents duration of sugarcane roosts; roosts in the non-shaded area are in wetlands. Long-dashed vertical line represents mean arrival date for swallows with geolocators (20 October), and short-dashed vertical line is mean departure date for swallows with geolocators (22 November).

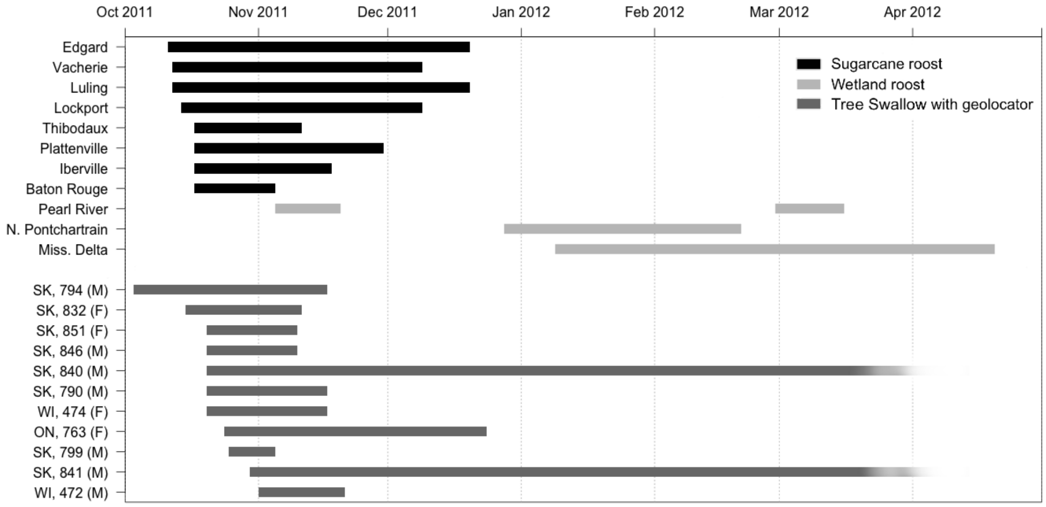

Figure 1.3. Timeline showing the location and duration of Tree Swallows roosts that appeared on NEXRAD radar station KLIX in Slidell, LA from October 2011-April 2012 (black bars are sugarcane roosts, light gray bars are wetland roosts), and the breeding-ground origin (SK = Saskatoon, Saskatchewan, WI = Saukville, Wisconsin, ON = Long Point, Ontario), geolocator number, sex, and approximate arrival, duration, and departure date of Tree Swallows fitted with geolocators that stopped over in southeastern Louisiana in 2011. The spring departure dates of two birds were masked by the equinox, and are here faded to reflect this uncertainty.

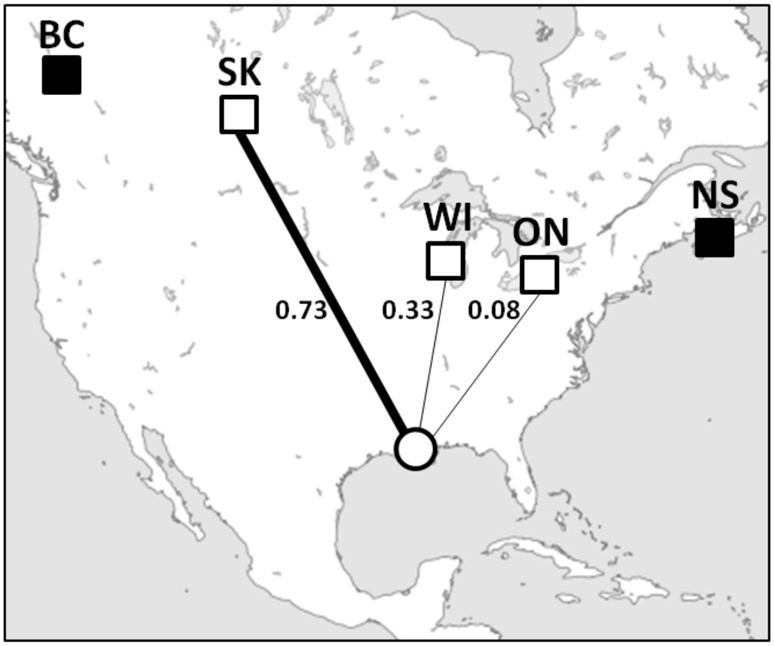

Figure 1.4. Map showing the breeding sites (SK: Saskatoon, Saskatchewan, WI: Saukville, Wisconsin, ON: Long Point, Ontario; hollow squares) of Tree Swallows fitted with geolocators that staged in southeastern Louisiana (hollow circle). For two of the breeding sites (BC: Prince George, British Columbia, NS: Wolfville, Nova Scotia; black squares) none of the individuals travel through Louisiana during fall migration. Numbers represent the proportion of individuals from each breeding site that staged in southeastern Louisiana, and the thickness of the connecting lines is proportional to the percentage of all geolocator-fitted birds that staged in southeastern Louisiana.

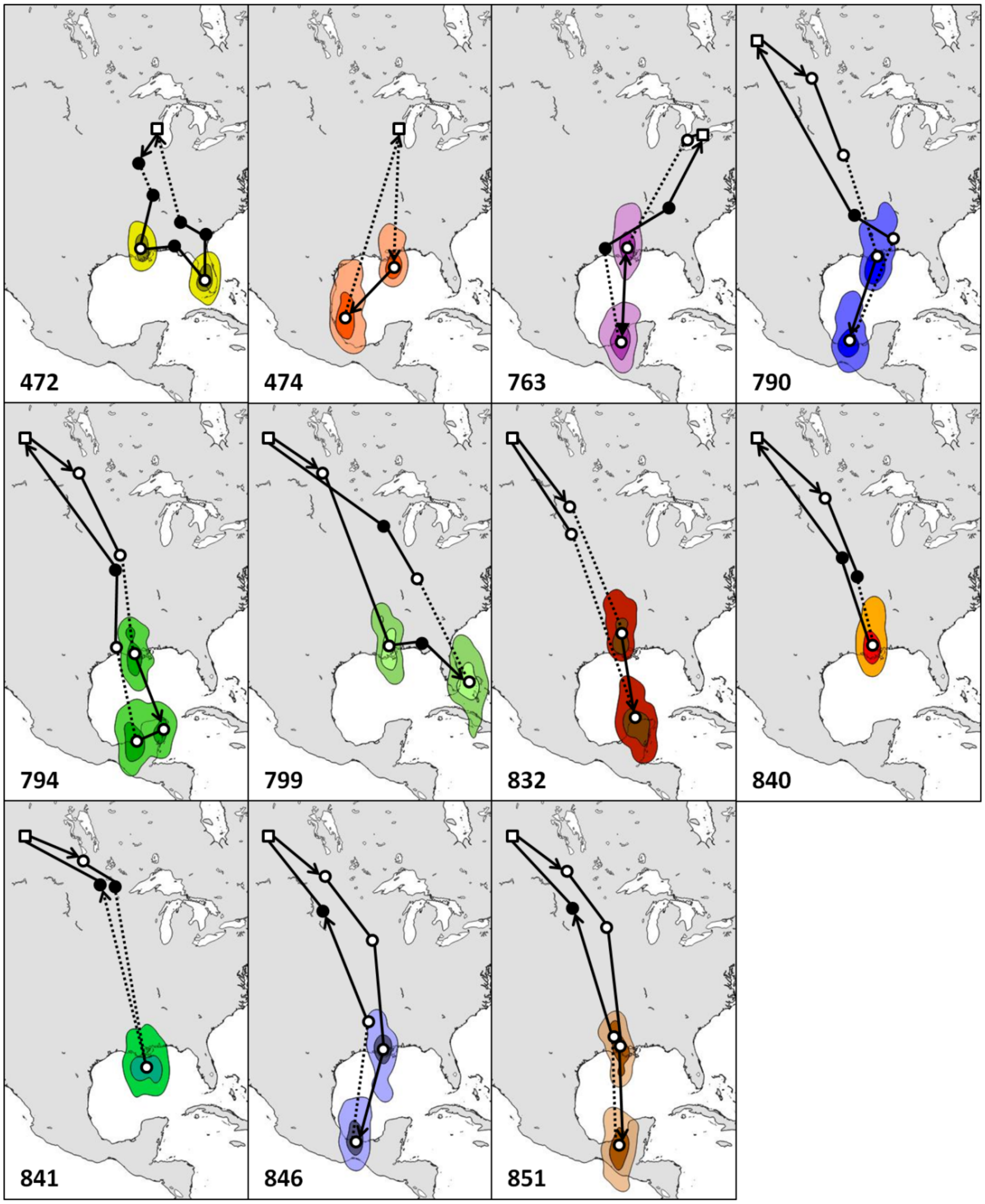

Figure. 1.5. Maps showing migration routes and kernel density polygons of stopover and over-wintering locations for all 11 Tree Swallows that used southeastern Louisiana as a stopover area during Fall migration in 2011. Each panel represents a single individual with 95% kernel density polygons located within 50% kernel density polygons in each

stopover and wintering period. Migration routes are presented as solid lines, with dotted lines representing gaps in location estimates due to equinox periods. Hollow dots represent mean locations where birds remained for longer than 7 days, solid dots represent single locations to illustrate the route taken, hollow squares represent breeding sites (as in figure 1.4), and numbers refer to geolocator number (as in table 1.2).

CHAPTER TWO

Autumn migration phenology, occupancy patterns, and roost-site consistency of Tree Swallows in Louisiana and Florida

ABSTRACT

Understanding annual movement dynamics of migratory animals is critical to understanding full life cycle biology and predicting their responses to global change. Remote sensing can capture a broad picture of population-level movement dynamics. In this study, we used historical data from weather surveillance radar (NEXRAD) to compare the autumn migration phenology, winter occupancy patterns, and roost-site consistency of Tree Swallows from 1996 – 2012 at two key sites in their winter range (southeastern Louisiana and central Florida). Variation in mean arrival date in both Louisiana and Florida can partly be explained by precipitation along their respective migration flyways, but arrival in Louisiana occurred over a much shorter time window than in Florida. In all study years in Louisiana, swallows used sugarcane fields as roost sites during their long autumn stopover and prior to the December harvest, after which most of the swallows departed the area until spring migration. Roost locations were much more consistent from year to year than would be expected by random chance and were generally high in Louisiana even in the contiguous habitat of sugarcane fields. In Florida,

occupancy patterns were consistent with a traditional winter site, but roost-site locations were less consistent and many roost sites appeared to be used only sporadically.

INTRODUCTION

Movement ecology is an emerging field of research seeking to understand the causes and consequences of all types of organismal movement (Nathan et al. 2008). Animal movements in particular range in scale from long-distance migration to breeding dispersal and smaller-scale foraging trips. It is perhaps best to approach the study of animal movement as an optimization (Hansson and Åkesson 2014) in which the different scales of movements have evolved to confer fitness benefits to the movers.

Recent advances in technology have facilitated the study of animal movements (Bridge et al. 2011). Direct tracking of individuals was once restricted to large organisms that could carry satellite transmitters (e.g. Berthold et al. 1995), but the advent of light-sensing “geolocators” has heralded a new era of research into the year-round journeys of songbirds that weigh as little as 15 g (Stutchbury et al. 2009, McKinnon et al. 2013). Other methods to track animal movements include remote sensing via weather radar (Diehl et al. 2003) and citizen-science projects that incorporate large-scale observational records (Sullivan et al. 2014). In this study, we used data from Doppler weather radar stations located along the northern Gulf of Mexico to compare the movement dynamics of Tree Swallows (*Tachycineta bicolor*) at two sites on its wintering grounds.

Tree Swallows are small migratory songbirds that breed across much of North America and Canada. They are well studied on the breeding grounds where they readily breed in nest boxes constructed at several long-term breeding sites (Jones 2003). During the non-breeding season, Tree Swallows (hereafter TRES) aggregate in enormous communal roosts each night, sometimes containing a million or more individual birds, and the morning roost departures are so dense they appear on Doppler weather radar as expanding rings of pixels (Winkler 2006, Laughlin et al. 2013).

Long-term Breeding Bird Survey results have indicated population declines of many migrant birds in general and aerial insectivores in particular, including TRES, especially in northeastern North America (Nebel et al. 2010). Nest box occupancy trends of TRES have corroborated this spatial pattern of decline (Shutler et al. 2012). The reasons for these declines are as yet unknown, though increased agricultural intensification (Paquette et al. 2013) and insecticide use on the breeding grounds (Gibbons et al. 2015) may play a role. A better understanding of annual movement dynamics of this species is important in order to know where to focus research efforts on the causes of these declines.

In a previous study, we showed that southeastern Louisiana is an important non-breeding site for Tree Swallows from across its breeding range (Laughlin et al. 2013), and we know from geolocator data that individuals that breed in northeastern North America migrate along the Atlantic coast to winter in Florida (D. R. Norris et al. unpublished data). We thus focus our current study on these two important stopover and wintering areas. Here, we use current and historic radar data from Doppler weather radar stations in southeastern Louisiana and central Florida to examine three components of TRES movement ecology: 1) We calculate annual variation in autumn migration phenology and relate this to climate variables along the respective flyways; 2) We quantify the occupancy patterns throughout the non-breeding season to better understand the role of each site during the annual cycle; and 3) We calculate annual roost-site consistency at these two important stopover and wintering areas. This study is, to our knowledge, the first to use historical Doppler radar data as a remote sensing tool to compare the movement ecology and dynamics of two populations of birds during the non-breeding season.

METHODS

a. Study area and period. Our study took place in southeastern Louisiana and central Florida during the non-breeding season. Specifically, our study occurred between the dates of 15 September and 15 May, from 1996 to 2013 in three 175-km-radius circles centered on three WSR-88D radar stations: KLIX in Slidell, LA (30˚20′12.35″ N, 89˚49′31.93″ W), KTBW in Tampa, FL (27˚42′19.371″ N, 82˚24′06.30″ W), and KLMB in Melbourne, FL (28˚06′47.21″ N, 80˚39′14.60″ W) (figure 2.1).

b. Importing radar data and TRES roost annotation. We downloaded Level-II radar data from the National Climatic Data Center (see Acknowledgements) from the three NEXRAD stations, and focused on the one hour before and one hour after local sunrise during which TRES roosts appear and dissipate on radar. Depending on the mode in which the radar station is running (e.g. clear-air or precipitation modes), the antenna rotates every 6 or 10 minutes, outputting a 360° image of the radar data. We imported these images into a webtool (designed by D.R.S.) that allows users to scan relevant radar data to locate diagnostic patterns of swallow roosts and annotate them as they expand in successive radar sweeps. This involves drawing a circle that encompasses the roost-rings, increasing the radius of the circle as the roost-ring expands with each successive sweep of the radar beam. TRES roosts appear on radar approximately 15 – 20 minutes before sunrise and expand over the next hour until the ring dissipates (Laughlin et al 2014) due to either the birds descending lower than the radar beam or because their density decreases to an extent where the radar no longer picks them up. For each day of the study period, we visually scanned the radar images from each station starting at 45 minutes before sunrise until 45 minutes after sunrise and annotated each TRES roost that appeared. Each roost annotated was stamped with a date, location, and length (in km) of the maximum roost-ring radius before it dissipated on the screen.

To verify the species composition of the roosts that we annotated, we visited and ground-truthed a subset of the sites in person. From ground-truthing, we determined three criteria that identify a roost as a TRES roost, rather than another species. The criteria were: 1) The appearance on radar occurred between 15 – 20 minutes before local sunrise; 2) The roost shape on radar had to be in a circular or semi-circular pattern; and 3) the habitat from which the roost emerged had to be either a wetland reed bed (*Typha* or *Phragmites*) or a sugarcane field. Only roost-rings that matched all these criteria were included in the study.

Because of the overlap in radar coverage of the two stations in Florida, some TRES roosts appeared on both radar stations. To avoid double counting the radii of these overlapped roosts, we used the maximum radii reported for that roost on a given day between the two stations and discarded the other. Radar data was sparse or intermittent for three years during the study period (2001-02 in Louisiana and 1997-98 and 1998-99 in Florida) due to station anomalies, upgrades, or outages. These years were removed from the analysis.

c. Radar-estimated occupancy verified with eBird. For each annotated TRES roost we measured the maximum roost-ring radius before the roost dissipated on radar and used this as a proxy for roost size. Estimating the number of birds aloft in a given radar sweep is problematic for a number of reasons (see Buler and Diehl 2009, Chilson et al. 2012). Though we do not yet understand the exact relationship between the maximum radius of a roost-ring on radar and the number of birds in that roost (which could be non-linear), the relationship is positive (Laughlin et al 2013). To measure the occupancy of TRES in the study areas, we summed the maximum radius of each roost visible on radar for each day, a metric we refer to as summed daily radii (hereafter SDR). This metric provides a measure of both occupancy (presence or absence) and also relative abundance.

To verify that SDR is a good representation of Tree Swallow occupancy and relative abundance patterns in the study area, we compared our radar-estimated measures with those calculated from eBird data. eBird is a popular (and growing) citizen science program run through the Cornell Lab of Ornithology in which birders submit checklists of birds seen or heard in a particular area and time, providing an unprecedented overview of the spatiotemporal distribution and abundance of birds in North America (Sullivan et al. 2014). We calculated the frequency of TRES from all eBird complete checklists from 2008-2012 that were within our study area (before 2008, eBird data are too sparse to provide an accurate picture of occupancy patterns in our study areas). For each year and location, we plotted the 5-day-average SDR from the radar data with the 5-day-average frequency of TRES occurrence in eBird lists (hereafter eBird frequency). We then fit generalized additive models (GAMs) through SDR and eBird frequency data and calculated the Pearson's correlation coefficient between the fitted GAMs from SDR and eBird. Further, to test for a positive relationship between the average number of daily reports submitted to eBird and the Pearson's correlation coefficient between radar and eBird GAM predictions, we regressed the annual correlation coefficients with the annual average number of eBird reports for each year. We hypothesized that the GAMs from SDR would be correlated with those from eBird data and that as the mean number of daily eBird checklists increases, so too would the correlation between the GAM fits of SDR and eBird data.

d. Winter occupancy patterns. In a previous study, we showed that TRES occupancy decreased throughout November and December in Louisiana during the 2010 - 2011 study period (Laughlin et al. 2013). Here, we extend the study temporally to data going back to the mid-1990's, and also spatially by including Florida. We hypothesized that Louisiana dynamics would be similar to that of Laughlin et al. (2013), that is, as an extended stopover site indicated by a peak in SDR in autumn then a drop during the remaining winter months, whereas data from Florida would show more traditional winter-site dynamics (indicated by a plateau pattern of SDR). To compare winter TRES occupancy patterns between Louisiana and Florida, for each year during the study period we plotted the 5-day-average SDR and fit a GAM through the data. We visually inspected the plots to determine occupancy patterns of TRES throughout the study period. Additionally, we plotted the 16-year-average SDR for both sites and the 5-year-average TRES eBird frequency to compare visually how TRES occupy each location on average and to test whether SDR and eBird frequency show the same patterns of occupancy.

e. Roost-site consistency. A previous study showed that TRES roosts are generally located in the same area for long periods of time within a season, and therefore radar-estimated roost locations create clusters of points when plotted onto a map (Laughlin et al. 2014). Here, we tested whether or not such roost-site consistency is also found across seasons in Louisiana and Florida. To calculate roost-site consistency across the study period, we first plotted the radar-estimated roost locations for each year and study site and developed a set of coordinates for each TRES roost location used during the study. For those roosts not ground-truthed, the roost-rings needed to meet a set of three diagnostic tests to be included in the data set: 1) timing of dawn roost departure was between 15 – 20 minutes before local sunrise, 2) the roost-ring had a circular or semi-circular appearance, and 3) the location was in appropriate roosting habitat (*Typha*, *Phragmites*, or sugarcane field). Every roost that we discovered by radar that met these conditions and was ground-truthed was a TRES roost. For each year, we performed cluster analysis on the points using the *pam* function in the package ‘cluster’ (Maechler et al. 2015) in R and included an initial set of centroids (coordinates of roosts used) for that year. The resulting clusters were assigned a roost ID with an associated location (the geographic centroid of the cluster) and a name (usually the nearest city, road, or other defining feature).

We calculated a roost consistency value (RC) for each roost, defined simply as the proportion of years during the study period that the roost site was used. To verify that RC was not a by-product of distance from the radar station (i.e., the possibility that the roost was in use but not detected in some years because of it's distance to the nearest NEXRAD station), we regressed RC by distance to the station.

f. Migration phenology. To examine annual variation in timing of TRES autumn migration during the study period, we calculated the arrival window and mean arrival date (MAD) in Louisiana and Florida. Arrival window was defined as the number of days between the first roost appearing on radar and the first peak of the GAM fit through the SDR for a given year, and mean arrival date (MAD) was defined as the temporal midpoint of the arrival window (figure 2.2). For the Louisiana site, we also calculated mean autumn departure date (MDD), defined as the temporal midpoint between the first peak of the GAM fit and the next local minimum (figure 2.2A).

We tested whether climate variables at the winter study site or along the respective migratory flyway can explain any of the variation in MAD at both locations and MDD in Louisiana. We downloaded climate data (mean monthly maximum temperature and total monthly precipitation) from the North American Regional Reanalysis (available from the National Center for Atmospheric Research, see Acknowledgements) at three pre-defined points along both the Mississippi migration flyway and the Atlantic migration flyway, as well as at the two study areas. We chose three sites in both the Mississippi and Atlantic flyway (figure 2.1) that were predicted to be high in TRES occupancy during September and October based on visual inspection of the Tree Swallow STEM model created by Fink et al. (2010). STEMs (Spatiotemporal Exploratory Models) produce maps that predict weekly occurrences and relative abundances of species across the Western Hemisphere based on an algorithm that incorporates presence data (eBird reports) and relevant habitat variables (Fink et al. 2010). For both Louisiana MAD and Florida MAD, we performed 4 multiple regressions of mean monthly maximum temperatures and total monthly precipitation at the three corresponding flyway sites and the wintering site during the time span in which MAD or MDD occurred, and compared models using AIC (Akaike 1974). We used the *lm* and *extractAIC* functions in the stats package for R (R Core Team 2014) for the regression and AIC calculations, respectively.

RESULTS

a. SDR and verification with eBird. We documented and annotated 9,872 unique TRES roost departures (n=2736 in Louisiana and n=7136 in Florida) during the study period. Our use of the daily summed radii of roost-rings measured from Doppler radar data (SDR) to approximate the temporal occupancy and relative abundance of TRES in our study area agrees well with occupancy measures calculated using eBird data (figure 2.2). When plotted together, SDR and frequency of TRES on eBird reports are highly correlated (table 2.1), and these correlations increase as the mean number of daily eBird reports increases (figure 2.3).

b. Patterns of TRES occupancy. On average, large TRES roosts begin to form in early October, predominantly in sugarcane fields along the lower Mississippi river and its tributaries. Summed daily radii as measured on Doppler radar (SDR), our proxy for

TRES occupancy, generally increased quickly throughout October, peaked in late October or early November, and decreased during November and December. TRES relative abundance remained low (but was non-zero) until spring migration when the roosts began to increase in size, followed again by a decrease to zero as the swallows finally departed this location to migrate to their northern breeding sites, usually by late April. This pattern of an autumn peak, a decrease throughout the winter, and a (smaller) peak again in spring was repeated each year of the study. Data from eBird reports corroborate this pattern (figure 2.2A, table 2.1). Pearson's correlation coefficient between radar-estimated TRES occupancy and eBird-estimated occupancy is high and significant for the 5 years that we compared (2008-2012).

In Florida, large TRES roosts form in mid to late October and SDR increases more gradually than in Louisiana. SDR fluctuates during the winter months of December through February in some years, but there is generally no decrease in SDR suggesting a large TRES departure mid-winter as in Louisiana (figure 2.2B). Florida appears to function as a more typical over-wintering site with almost constant occupancy throughout the winter. As in Louisiana, eBird corroborates this pattern, showing a later increase in TRES frequency than in Louisiana and more of a plateau-pattern than the repeated up-and-down pattern found in Louisiana. Pearson's correlation coefficient is likewise high and significant for Florida SDR and eBird occupancy estimates (table 2.1).

c. Roost-site consistency. We documented a total of 17 locations within 175 km radius of KLIX station in Louisiana that TRES use as roost sites (table 2.2). Of these 17 sites, ten were located in sugarcane fields and seven were in *Typha* or *Phragmites* reed beds along lake edges, bayous, or rivers. Mean roost-site consistency in Louisiana was 0.6, that is, on average a roost site was detected in 60% of the years during the study period (figure 2.4A). 35% of roost sites in Louisiana were used in more than 80% of the years, and three of 17 sites were used every year.

In Florida, we documented 44 sites used at least once as a TRES roost location during the study period (table 2.2). Mean roost-site consistency was lower in Florida, with an average of 0.44. 14% of roost sites in Florida were used in 80% of the study years, but only one site in Florida was used in all study years (figure 2.4B). Despite these apparent differences in RC between Louisiana and Florida, a Student's t-test revealed no significant difference between the two sites (t = -1.78, P = 0.088).

The distance between a roost site and the nearest radar station was not correlated in Louisiana (P = 0.614) or in Florida (P = 0.351). Roost sites further from the radar stations were just a likely to appear on radar as roost sites close to the stations, indicating that proximity to a radar station did not influence RC values of roosts.

d. Autumn migration phenology. Mean arrival date (MAD) in Louisiana as measured from GAMs fit to SDR data ranged from 12 October (in 2002 and 2004) to 27 October (in 1998) and had a mean of 18 October and standard deviation of 4.3 days. Arrival window ranged from 20 days (in 2005) to 40 days (in 2007) (figure 2.5A), with a mean of 27.9 and standard deviation of 6.4 days. Mean autumn departure date in Louisiana (MDD) ranged from 7 November (in 2002) to 11 December (in 2009) and had a mean of 22 November and standard deviation of 10.7 days.

In Florida, MAD ranged from 29 October (in 2006) to 3 December (in 2009) with a mean of 14 November and standard deviation of 9.6 days. Arrival window ranged from 45 days (in 2010) to 95 days (in 2003) (figure 2.5B), with a mean of 62.9 days and standard deviation of 15.4 days. MADs in Louisiana and Florida in concurrent years are not correlated with each other; that is, later arrival in Louisiana in a particular year is not paralleled by later arrival in Florida, indicating that the two flyways are independent of each other.

We performed linear regressions of mean maximum monthly temperatures and total monthly precipitation at each of the three respective flyway sites and at the study sites to explain variation in MAD and compared models using AIC. In Louisiana, we used October climate variables because MAD fell within October. The two top models, precipitation at MF1 and at MF2, had very similar AIC values and were both more than 2 AIC units lower than the next-best model indicating a significant difference (Sakamoto et al. 1986). Both models showed a positive relationship between precipitation along the flyway and arrival to Louisiana (figure 2.6A). That is, higher total October precipitation was associated with later arrival to Louisiana. In Florida, MAD fell mostly within November, and we thus used November climate variables. The model with the lowest AIC value was precipitation at AF1, the closest flyway site from Florida, again with a positive relationship between total precipitation and MAD (figure 2.6B). All other models to explain MAD in Florida had AIC units more than 3 units away from the top model and had very similar AIC values.

The final model used to explain mean autumn departure date from Louisiana (MDD) included only the variable November precipitation: as total precipitation increased, MDD decreased (table 2.3).

DISCUSSION

Winter occupancy patterns. Results from our occupancy pattern analysis reaffirm the unique role that southeastern Louisiana plays as an extended autumn stopover site for TRES. We showed previously that TRES tracked with geolocators in 2011-12 from three distinct breeding areas stopped over in this region for a month, on average, before continuing to their main overwintering area (Laughlin et al. 2013). The current study shows that similar dynamics occur every year, with relative abundance of TRES swelling during October and dissipating throughout November and December. In this sense, southeastern Louisiana acts as an initial winter site during the non-breeding season of TRES in a movement behavior that is much more complex than traditional to-and-fro models of migration would suggest. Tracking studies of other species are likewise revealing complex non-breeding season movement patterns, including long stopovers and multiple wintering areas (e.g., Fraser et al. 2012, Stach et al. 2012).

Central Florida, by contrast, appears to be a traditional winter site for TRES, where relative abundance is much more stable throughout the winter months. However, data on individual movements in this area are lacking. Annual fluctuations in occupancy as measured with SDR, together with the fact that some roosts dissipate in mid-winter while others form later in the season elsewhere (Laughlin et al. *unpublished data*) suggest that the movement dynamics in Florida may be more akin to itinerancy, in which TRES may be tracking resources by moving en masse throughout the season. Such dynamics have been reported in Barn Swallows on their winter grounds in sub-Saharan Africa (van den Brink et al. 2003). It would be informative to correlate the spatial dynamics of roost locations with local rainfall patterns, for example, to test whether TRES form new roosts mid-winter because they are tracking food supplies.

Roost-site consistency. Though a Student's t-test shows a non-significant difference between the RC values of Florida versus Louisiana roost sites, it is informative to look at the frequency distribution of the data (figure 2.4). Out of 44 possible roost sites in Florida, only one site was used in every year of the study, compared to 3 of 17 sites in Louisiana used every year. What differences between Louisiana and Florida might influence the different roosting behaviors of these swallow populations? One possibility is the role that each site plays in the annual-cycle biology of TRES. Louisiana acts as a stopover site for the majority of swallows that pass through during autumn migration, whereas Florida appears to be a more traditional winter site. Roosting behaviors might be different for stopover versus overwintering sites as has been suggested for Barn Swallows in Europe and Africa (Loske 1986). This may be an unlikely possibility for the present study, as Louisiana acts as both a stopover and overwintering site.

Another possibility might be the continuous versus discrete roosting habitat that differentiates Louisiana from Florida. Sugarcane fields cover thousands of relatively continuous hectares in southeastern Louisiana. Many of the sugarcane roosting sites that are used each night throughout one season (prior to the harvest) are used in subsequent years as well. The roosting habitat in Florida is made up of discrete reed beds and *Typha* marshes in clay settling ponds of phosphate mines. These areas may undergo periodic drying and therefore may not be available every year as appropriate roosting habitat. One of the recent major roost sites (Duette) in Florida appeared during the last few years as a clay settling pond of a phosphate mine filled up with Typha reeds. Satellite imagery reveals that this site was not appropriate roosting habitat 15 years prior to this study, whereas now it is one of the major TRES roost sites in central Florida.

Autumn migration phenology. Arrival to these winter sites (MAD) was best explained by precipitation along the flyway in both LA and FL, which suggests the trend that TRES may be more responsive to precipitation during migration than to temperature. For most migrant birds, the factors that drive migration away from the breeding grounds each autumn are not well understood. It is thought that long-distance migrants may be more influenced by photoperiod when deciding when to initiate migration, and less influenced by local environmental cues.

Studies of spring migration have shown that some migrants have advanced their spring migration due to warmer springs (Lehikoinen et al. 2004, Gordo 2007), or have shown that some migrants have not advanced their spring migration (Jenni and Kéry 2003) and their populations have declined as a result (Møller et al. 2008). Temporal mismatch between the timing of peak food abundance and the timing of breeding season arrival is a major area of study. Autumn migration dynamics are much less studied than spring migration when birds are returning to their breeding grounds to initiate breeding. However, autumn migration is an important component to the annual life-cycle biology of migrant birds, not least of which is because it is the first journey that every migratory bird undertakes. The timing of autumn migration may be influenced by events on the breeding grounds. Further, mismatches on the wintering grounds due to altered migration dynamics have not yet been explored to our knowledge.

Our arrival and departure metrics were based on the aggregated sizes of communal roosts as they appeared on radar. Because of this, we were able to avoid the often-confounding metrics based on sightings or captures of individual birds, which can unduly influence first arrival and mean arrival metrics. Our metric of first roost date, the date on which the first communal roost appears on radar, may be robust to such measures because communal roosts that appear on radar cannot be considered outliers or spurious first arrivals. Roosts that appear in sugarcane fields in Louisiana need to reach a certain size before they appear on radar at distances of those in our study. Initial data suggest that a roost of only 2,000 birds, for example, does not appear on Doppler radar when the roost is situated 100 km away from the radar station, as the Edgard, Louisiana roost is. This roost is usually the roost that first appears on radar (Laughlin et al. *unpublished data*), but does not appear until it has reached the size of several thousand birds at least. Thus first roost date is not influenced by the often left-tailed distribution of early-arriving birds.

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Table 2.1. Pearson's correlation coefficient between GAM fit to radar SDR and GAM fit to frequency of TRES on eBird reports and mean number of daily reports to eBird (in parentheses).

Year	Louisiana, cor / (mean number daily reports)	Florida, cor / (mean number daily reports)
2008-09	0.48 (5.5)	0.85 (24.7)
2009-10	0.4 (8.0)	0.89 (49.7)
2010-11	0.76 (22.2)	0.82 (54.4)
2011-12	0.87 (24.3)	0.95 (80.9)
2012-13	0.86 (32.7)	0.9 (115.5)

Table 2.2. Roost IDs, locations, roost consistency value (RC), distance to the nearest radar station, and habitat of the 17 Louisiana and 44 Florida roosts used during the study period.

Louisiana

Roost ID	Latitude	Longitude	RC	Dist to radar station (km)	Habitat
Edgard	30.032	-90.495	1.00	72.77	sugarcane
Vacherie	29.978	-90.746	0.94	97.17	sugarcane
Luling	29.907	-90.356	1.00	69.95	sugarcane
Baton Rouge	30.483	-91.272	0.81	139.81	sugarcane
Iberville	30.127	-91.151	0.50	129.55	sugarcane
Plattenville	30.030	-91.000	0.44	118.02	sugarcane
Supreme	29.866	-90.976	0.44	122.58	sugarcane
Thibodeaux	29.675	-90.774	0.69	117.42	sugarcane
Raceland	29.631	-90.470	0.31	100.15	sugarcane
Mandeville	30.402	-90.183	0.88	35.23	wetland
Pearl River	30.227	-89.582	0.56	26.50	wetland
Maurepas	30.245	-90.360	0.25	52.49	wetland
Bayou La Loutre	29.797	-89.552	0.56	65.56	wetland
St Catherines Island	30.195	-89.761	0.13	16.90	wetland
Mississippi Delta	29.350	-89.279	1.00	121.78	wetland
Morgan City	29.748	-91.284	0.63	155.29	wetland

Table 2.2 (cont.)

Florida

Roost ID	Latitude	Longitude	RC	Dist to radar station (km)	Habitat
Lake Woodruff	29.082	-81.430	0.33	132.73	wetland
Lake Monroe	28.898	-81.296	0.11	106.62	wetland
Turnbull	28.885	-80.889	0.11	91.07	wetland
Lake Jessop	28.747	-81.193	0.22	88.32	wetland
St Johns NWR	28.563	-80.926	0.67	59.83	wetland
Lake Louisa	28.412	-81.696	0.28	106.61	wetland
E Lake Tohopekaliga	28.333	-81.289	0.28	66.50	wetland
Lake Poinsette	28.340	-80.830	0.50	32.01	wetland
Lake Tohopekaliga	28.228	-81.393	0.44	72.60	wetland
Lake Washington	28.169	-80.778	0.11	14.76	wetland
Lake Alfred	28.116	-81.711	0.44	82.69	wetland
Lake Hatchineha	28.070	-81.363	0.94	70.70	wetland

Table 2.2 (cont.)

Florida

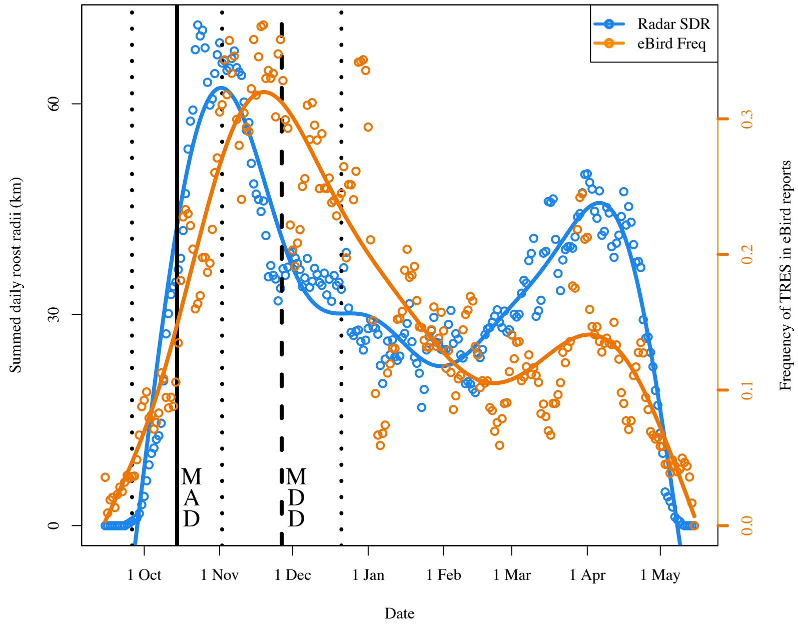
Roost ID	Latitude	Longitude	RC	Dist to radar station (km)	Habitat
Broadmoor Marshes	27.965	-80.764	0.22	19.45	wetland
S Broadmoor Marshes	27.867	-80.734	0.28	28.06	wetland
St Sebastian	27.801	-80.593	0.11	34.50	wetland
Yeehaw Junction	27.663	-80.963	0.22	58.44	wetland
Blue Cypress	27.663	-80.690	1.00	50.09	wetland
Lakewood Park	27.525	-80.379	0.22	68.78	wetland
Adams Ranch	27.519	-80.549	0.11	66.37	wetland
Fort Drum S	27.499	-80.682	0.11	65.22	wetland
Orange Ave	27.440	-80.593	0.11	81.73	wetland
Lake Istokpoga	27.381	-81.289	0.39	101.99	wetland
Lykes	27.190	-81.126	0.61	111.26	wetland
Okeechobee NW	27.190	-80.897	0.28	103.17	wetland
Okeechobee NE	27.124	-80.682	0.56	109.38	wetland
Okeechobee E	27.006	-80.445	0.33	124.74	wetland
Okeechobee W	26.954	-81.208	0.44	141.67	wetland
Brooksville	28.583	-82.488	0.19	99.25	wetland
Tampa	28.235	-82.577	0.56	62.39	wetland
Lake Parker	28.064	-81.962	0.31	63.03	wetland
Hopewell	27.841	-82.088	0.38	37.96	wetland
Bradley	27.762	-81.896	0.81	47.43	wetland
Cockroach Bay	27.689	-82.510	0.13	8.43	wetland
Four Corners	27.650	-82.066	0.56	32.43	wetland
Hardee Lakes	27.650	-81.933	0.31	45.50	wetland
Duette	27.512	-82.133	0.19	35.45	wetland
Sarasota	27.374	-82.421	0.56	36.93	wetland
Laurel	27.157	-82.392	0.88	58.22	wetland
Deep Lake	27.164	-81.755	0.50	89.57	wetland
Rotonda	26.927	-82.295	0.44	87.02	wetland
Bermont Rd	26.993	-81.652	0.69	107.36	wetland
Cecil Webb	26.816	-81.955	0.25	108.02	wetland
LaBelle	26.711	-81.311	0.67	154.50	wetland
Corkscrew Swamp	26.395	-81.674	0.11	162.57	wetland

Table 2.3. Model selection results showing the AIC and ΔAIC values for the regression modelsof climate variables explaining variation in MAD in Louisana and Florida.

Model	AIC	ΔAIC
Louisiana MAD ~		
MF2_precip	46.45	0
MF1_precip	46.69	0.24
LA_precip	48.73	2.28
MF2_temp	49.15	2.7
LA_temp	49.42	2.97
MF1_temp	49.56	3.11
MF3_temp	49.63	3.18
MF3_temp	49.66	3.21
Florida MAD ~		
AF3_precip	66.28	0
AF2_precip	69.66	3.38
AF3_temp	70.09	3.81
FL_precip	70.68	4.4
AF1_precip	70.68	4.4
FL_temp	70.77	4.49
AF2_temp	70.88	4.6
AF1_temp	70.9	4.62

Figure 2.1. Map showing study areas (blue circles of approximately ~175-km radius centered at radar stations) and locations along the Mississippi (MF1, MF2, MF3) and Atlantic flyways (AF1, AF2, AF3) from which we downloaded climate data.

A. Louisiana



B. Florida

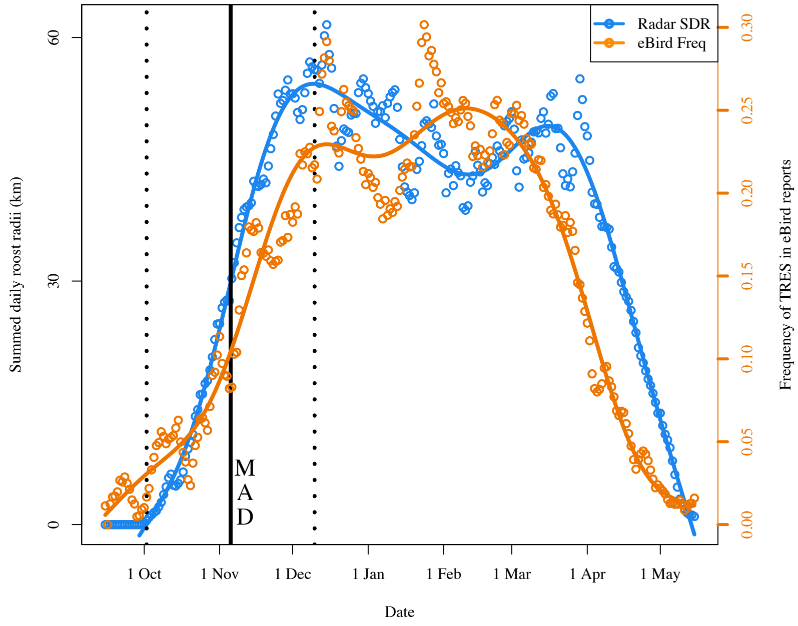


Figure 2.2. Plot showing 16-year averages of summed daily roost radii (SDR) (blue dots) and frequency of TRES on eBird reports (orange dots) and their associated GAM fit lines (colored lines) in A. Louisiana and B. Florida. Black short dashed vertical lines are, from

the left, first roost date, peak arrival date, and second local minimum, from which MAD (solid black vertical line) and MDD (long-dashed vertical line in Louisiana only) were calculated.

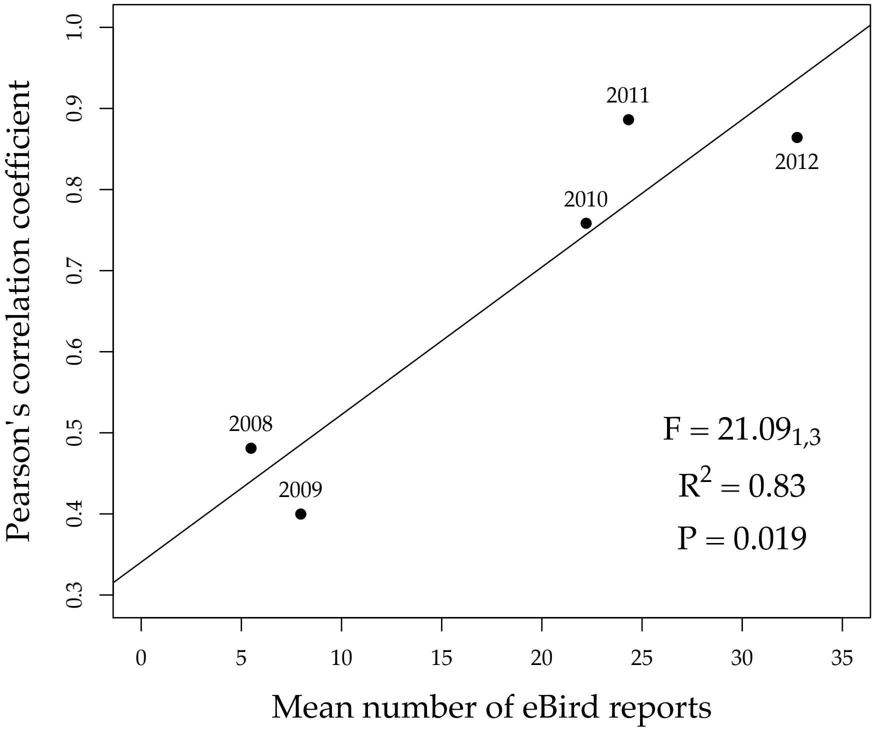
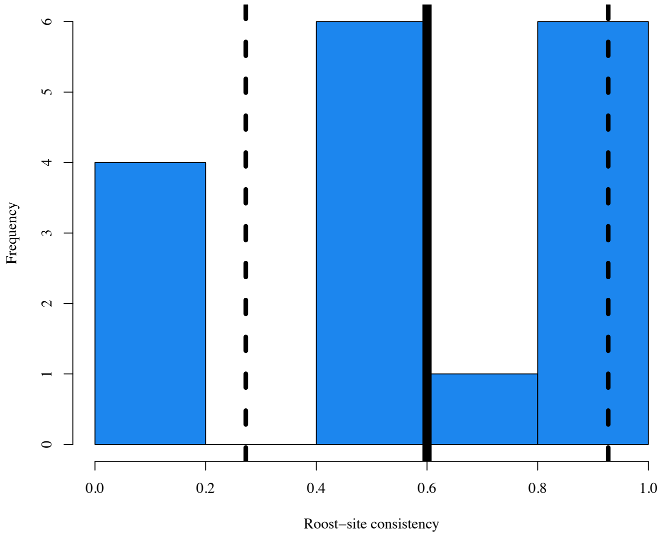


Figure 2.3. Relationship between the mean number of daily eBird reports and the Pearson's correlation coefficient of summed daily roost radii (SDR) and frequency of TRES on eBird reports.

A. Louisiana



B. Florida

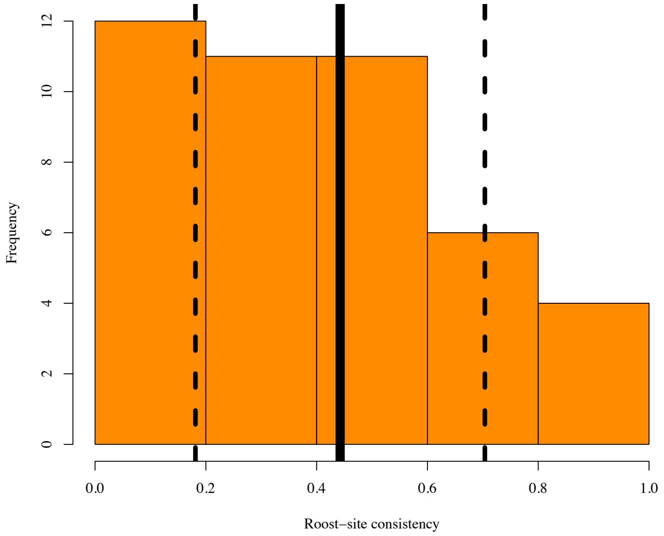
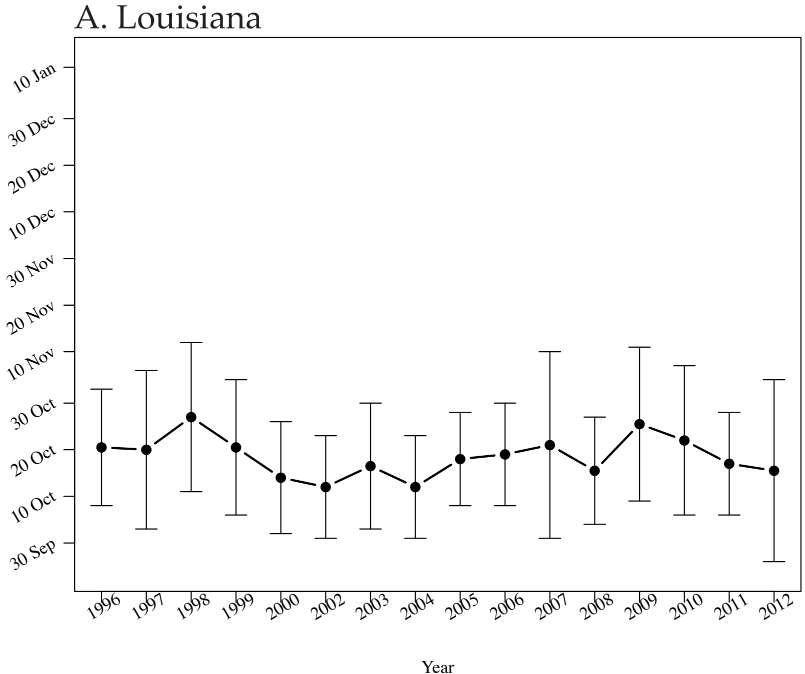
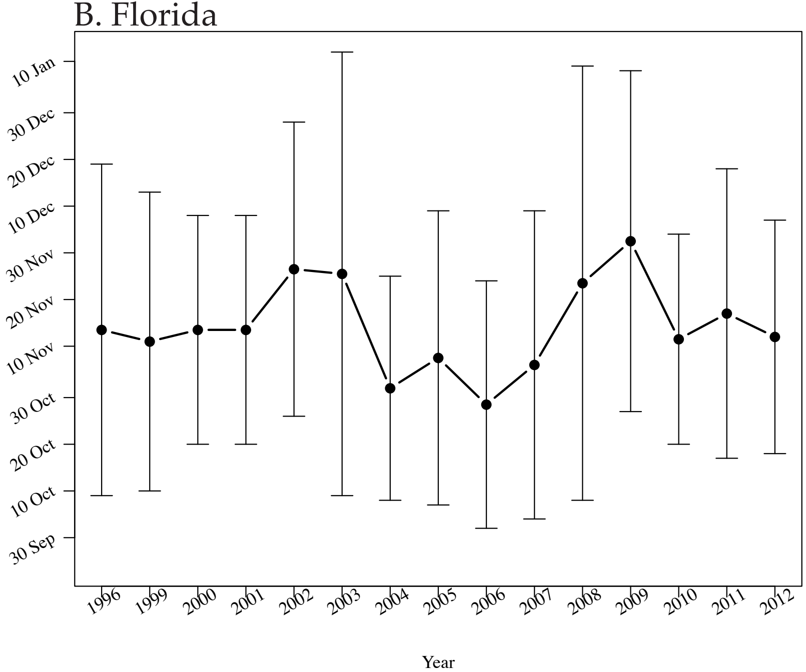


Figure 2.4. Frequency of roost-site consistency of A. Louisiana and B. Florida. Black vertical line shows mean and dashed lines are standard deviations.



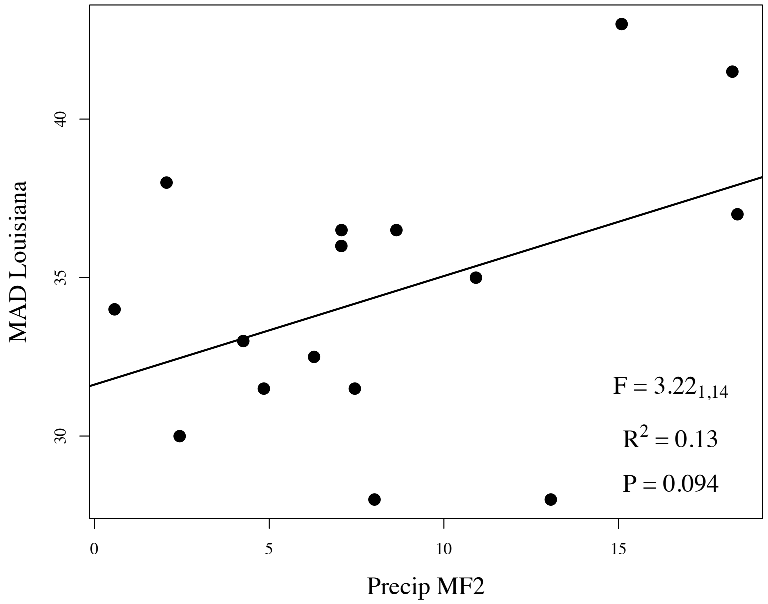
A. Louisiana



B. Florida

Figure 2.5. Mean arrival date (MAD) and arrival window (bars) for A. Louisiana and B. Florida.

A. Louisiana MAD and total precip (cm) at MF2



B. Florida MAD and total precip (cm) at AF3

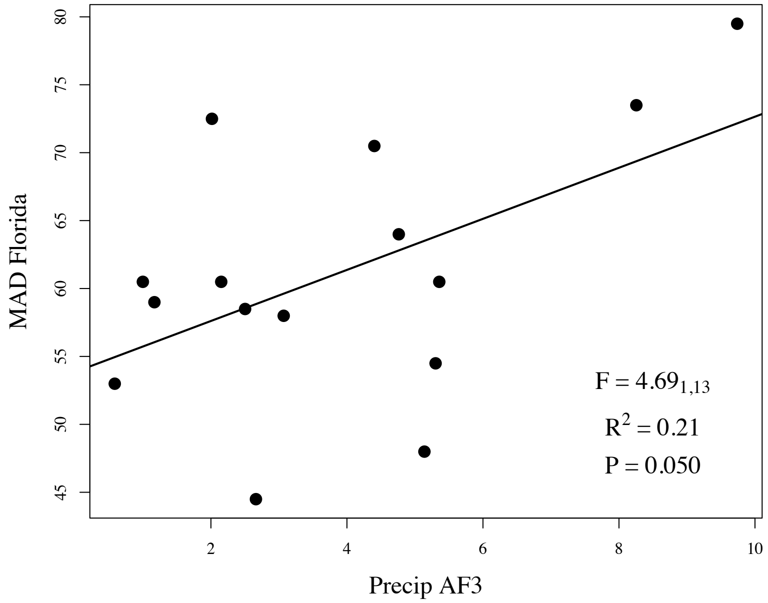


Figure 2.6. Plots showing relationship between total precipitation at points along flyway and MAD for A. Louisiana and B. Florida.

CHAPTER THREE

Behavioral drivers of communal roosting in a songbird: a combined theoretical and empirical approach[2]

ABSTRACT

Communal roosting is a taxonomically widespread phenomenon, with considerable variation in patterns of roost dynamics. Some organisms roost together in different locations each night (or day) while others roost in traditional locations each night, sometimes switching between roosts in the roost network. The behaviors that drive roost-site selection and the resulting patterns are not well understood. We created an individual-based model that simulates the daily aggregation of organisms into communal roosts. In the model, individuals move according to a movement rule integrating two independently-adjustable, behavioral drivers: roost fidelity, which leads individuals back towards their previous nights' roost; and conspecific attraction, which leads individuals to congregate towards nearest conspecific neighbors. The model predicts that variable levels of aggregation will emerge under different combinations of these drivers, ranging from

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no aggregation to complete aggregation of individuals into their previous roosts. We tested to see which combination of drivers best predicts patterns of roost use in our study system of Tree Swallows (*Tachycineta bicolor*) in southeastern Louisiana in fall. Using Doppler weather radar data, we show that Tree Swallow roost sites remain consistent from night to night, and the birds return to one of several traditional roosts. Using radio telemetry, we show that individuals switch between these traditional roosts at minimum 22% of the time. Our results suggest that the formation of large communal roosts in Tree Swallows is driven by a combination of moderate conspecific attraction and strong, but not perfect, roost fidelity.

INTRODUCTION

Animal aggregations have fascinated people for centuries: ungulates migrating across the Serengeti, a school of fish eluding a predator, or a flock of birds turning simultaneously. In each, vast numbers of individuals seem to act as one organism. Historically, these behaviors were only thought possible by 'collective thinking', by the same thoughts and intentions moving through the group as a whole (Selous 1931). These collective behaviors are now being explored using individual-based modeling (Grimm and Railsback 2003; Sumpter 2010), and many of these models have shown that population-level aggregations can be explained by simple individual-level movement rules (Camazine et al. 2001; Couzin and Krause 2003).

Communal roosting, here defined as an aggregation of unrelated conspecifics that spend the diurnal or nocturnal resting period together, is a taxonomically widespread behavior found in mammals (bats and primates; Kunz 1982; Anderson 1998), birds

(Eiserer 1984), fish (Clough and Ladle 1997), insects (Vulinec 1990; Grether and Switzer 2000), and even some flatworms (Reynierse et al. 1969). Communal roosting occurs at many scales, from tens to millions of individuals. In birds and bats especially, roosts can be very large, with millions of individuals aggregating at one place each day (night), and repeating the process each day (night) throughout a season or, in some cases, all year. It is important to distinguish between a communal roost and a breeding colony, because the evolutionary consequences of joining either can be quite different (Barta and Giraldeau 2001). In the case of colonial breeding, an individual has no choice but to return to the same colony each night in order to feed nestlings. In communal roosting, an individual may have access to several roosts, or it may choose to roost solitarily, and it is not necessarily committed to returning to the same place each night. It is the communal roost in this context, and not a colony, that we discuss for the remainder of this study.

Much of the research on communal roosting has focused on the evolution and fitness benefits of this behavior (Beauchamp 1999). Several theories have been put forward to explain this widespread behavior, such as predator dilution (Lack 1968), the information-center hypothesis (Ward and Zahavi 1973), and the patch-sitting hypothesis (Caccamise and Morrison 1986), and each theory has some empirical support. However, the individual behaviors that drive the daily return to one of potentially several roost sites have not been fully examined. Because evolution acts most strongly at the individual level, understanding the individual dynamics of roosting behavior is prerequisite for understanding the causes and consequences of communal roosting. How does an individual choose where, and with whom, to roost on a given day? What behaviors are involved in this decision-making process? Possible behavioral drivers include: roost site fidelity, where individuals remember and return to the same roost site each night; aggregation due to conspecific attraction, where individuals aggregate with nearest neighbors into groups; habitat selection, where multiple individuals select the same type of habitat because it protects from adverse weather or helps in thermoregulation; proximity to important food sources; and chemicals (pheromones) deposited at roost sites that attract conspecifics to that site.

Many species that aggregate in roosts often use the same roosting site(s) from night to night and year to year (Eiserer 1980; Lewis 1995; Grether and Donaldson 2007); some traditional avian roost sites can be in use for more than a century (Marples 1934; Hutchinson 1989). Of those organisms that make use of traditional roost sites, some studies report that individuals are faithful to only one of several possible traditional roosts (McCracken and Bradbury 1981; Leyrer et al. 2006), while other studies have shown that the individual composition at traditional roost sites is fluid between successive roosting periods (Kurta et al. 1996; Grether and Switzer 2000; Conklin and Colwell 2007). Even within the same species, different patterns can emerge. For example, Morrison and Caccamise (1985) report that some radio-tagged European Starlings (*Sturnus vulgaris*) were always faithful to a particular roost in one portion of their study area, whereas others often switched between a different set of major and minor roosts in a different portion of their study area. It is clear from the literature on roosting behavior that roost selection is a highly variable behavior, but no studies to our knowledge have tried to tease apart the different behavioral drivers on the existing patterns of aggregation.

The behavioral mechanisms driving roost site selection may be understood in light of self-organization theory (Camazine et al. 2001), in which complex collective behaviors are examined using individual rules (Sumpter 2010). Our general thesis is that roosting patterns in many species can be explained as an emergent property of a system in which individuals move according to multiple concurrent behavioral drivers that are identical between individuals, without the need for differentiation of individuals between 'leaders' and 'followers' (e.g. Sueur et al. 2010).

Here we present an individual-based model that simulates the daily aggregation of individuals into roosts using a movement rule that incorporates two behavioral drivers: roost site fidelity (*RF*) leading individuals to return to their previous roost, and conspecific attraction (*CA*) leading individuals to congregate with their current nearest neighbors (i.e., not necessarily the ones they roosted with previously). Our model assumes that the entire habitat is suitable for roosting and thus does not include habitat selection. These two drivers (*RF* and *CA*) are independently adjustable and can work in concert or alone on individuals in our model. We show that these two drivers can produce multiple roosting patterns when combined at different strengths even though all individuals move according to the same rule.

We specifically explored the roosting behavior of Tree Swallows in the sugarcane fields of the lower Mississippi River Valley. We show, using radar data, that roost locations are highly consistent from night to night. One hypothesis that would explain this is that individual birds are returning each night to the same place, i.e. exhibiting near-prefect site fidelity. We tested this hypothesis by conducting a radio telemetry study, and determined that night-to-night individual return was approximately 78% at most. Our individual based model shows that the pattern observed in Tree Swallows (high roost location consistency with high, but not perfect, individual roost fidelity) can be explained if the individuals are driven by high roost fidelity combined with moderate conspecific attraction.

METHODS

1. Model description

We use the ODD (Overview, Design concepts, Details) protocol for describing individual-based models developed by Grimm et al. (2006, 2010) as a guide for model description. The code is implemented in the R programming language (R Core Team 2013).

Purpose of model

We developed an individual-based model that simulates the movement of individuals in the final stage of the day when they are returning to roosts. For Tree Swallows, this is approximately the final two hours before sunset. The purpose of this model is threefold: to 1) simulate roosting dynamics of autonomous individuals that follow the same movement rule, 2) study the patterns of roosting dynamics that emerge by varying the levels of the two behavioral drivers, and 3) apply the model results to empirical data from our study system of Tree Swallow roosting behavior in southeastern Louisiana. Our main question was: can a simple movement rule based on two behaviors, applied to each individual, accurately replicate the roosting dynamics of our study system?

Entities, state variables, and scales

The basic model consists of 5000 autonomous individuals moving across a homogeneous 30 x 30 grid space for a total of 45 time steps. Individuals are characterized by their current location on the grid, and by their previous night's roost (i.e., their 'original' roost), which is randomly chosen for each individual from one of four pre-specified locations. The grid space is bounded on each side. The grid cells are homogenous in that they all represent equally suitable roosting habitat; a cell's characteristics are its location within the grid and the number of individuals it contains. Four of the grid cells represent the 'original' roost sites, roosts that individuals have been previously assigned as their previous nights' roost. These are located evenly spaced across the square grid so that proximity between roosts and edges may only minimally affect the movements of the individuals. Roost 1 is located at (10,10), roost 2 at (10,20), roost 3 at (20,10), and roost 4 at (20,20; figure 3.1). Each model simulation (e.g. each combination of the two behavioral drivers) runs on a 1-day time step, after which time the results and model properties are calculated. Within this one day, individuals move one at a time according to the movement rule (described below) for a total of 45 time steps.

The model is not spatially explicit but represents an abstracted version of our study system. The grid size is such that an individual would be able to cross it within the specified number of time steps, and therefore the resulting roost patterns are not a consequence of limited time. We chose the parameter values and initial conditions (grid size, number of individuals, number of time steps, and evenly spaced roosts) as the most conservative arrangement that could demonstrate interesting dynamics.

Process overview and scheduling

The movement of an individual from one time step to the next is determined by weighted random sampling of the 'neighborhood cells', i.e. the 9 grid cells surrounding and including the current location of each individual (Fig. 1b). Individuals move one at a time, and the new position of the individual is updated before the next individual moves.

The probability of any individual moving from cell *j* into cell *i* is equal to the weight of cell *i* divided by the sum of the weights of all neighborhood cells:

$$P_{ij} = \frac{W_i}{\sum_{k=1}^{9} W_k} \qquad \text{(Eqn. 1)}$$

Weights are assigned to neighborhood cells using the formula

$$W_i = 1 + (\gamma_{RF})(d_i) + (\gamma_{CA})(p_i) \qquad \text{(Eqn. 2)}$$

where *i* is one of the nine neighborhood cells, γ_{RF} is the strength of roost fidelity, and γ_{CA} is the strength of conspecific attraction. d_i is the "improvement" in units of distance that would be achieved by moving into cell *i*, i.e., the difference between the individuals' current distance to its original roost and the distance between cell *i* and the individual's original roost. Distance improvements that are less than zero are truncated to zero (that is, no additional weight is given to grid cells further away from the original roost than where the individual is currently located). p_i is the number of birds in cell *i* multiplied by a constant. d_i and p_i values are expressed in units such that one unit change in either has the same effect on W_i. Individuals move to neighboring cell *i* with a probability proportional to the weight W_i assigned to the cell. We vary both γ_{RF} and γ_{CA} independently between 0 and 1 such that when $\gamma_{RF} = 1$, all individuals have a very strong probability to move towards their original roost, and when $\gamma_{CA} = 1$, all individuals have a very strong tendency to congregate with nearest neighbors. In the absence of any behavioral drivers (i.e., when $\gamma_{RF} = 0$ and $\gamma_{RF} = 0$), the weight of each neighborhood cell, W_i, equals 1 (i.e., the lowest value possible), and individuals thus perform a random walk. If γ_{RF} is fixed at 0 and γ_{CA} is increased, W_i increases solely in proportion to the number of conspecifics in cell *i*. Likewise, if γ_{CA} is fixed at 0 and γ_{RF} is increased, W_i increases only for those cells closer to the individuals' original roost than the individuals' current location.

At the end of each simulation, we defined the resulting roosts and their locations using the following algorithm. The grid cell containing the largest number individuals is the location of the first roost, and the size of this roost is the number of individuals within the 9-cell neighborhood centered at this cell. These cells are then excluded from the grid and the process is repeated for the cell containing the second largest number of individuals, and so on, until all cells with more than 25 individuals are accounted for.

Design concepts

Basic principles. The model addresses a basic behavioral question, that is, how should an individual decide in which direction to move when settling down for the resting period? A simple movement rule that incorporates two behavioral drivers (*roost fidelity* and *conspecific attraction*) is varied to explore this question. These behavioral drivers have empirical support from not only roosting systems of several taxa, but other life-history traits as well, such as breeding systems (*breeding site fidelity*) and migration (*travel with conspecifics*).

Emergent Model Properties. We measure three important model properties that emerge from the behaviors of the individuals:

1) Individual return rate (*IRR*) is defined as the proportion of all individuals 'at roost' that returned to their original roost. 'At roost' individuals are those whose final position is within the 9-cell neighborhood of one of the roosts that formed according to the above algorithm. Individuals not at roost are not included in the calculation of *IRR*.

2) Roost-location consistency (*RC*) is a measure of whether roosts form in the same locations or in random locations each night and is quantified as the number of the four 'original' roosts that re-formed divided by the total number of roosts that formed. In cases where all four roosts re-formed but no other roosts formed, *RC* is equal to 1. In cases where new roosts formed but not in any of the original sites, *RC* is equal to 0.

3) Aggregation index (*AI*) is defined as the variance to mean ratio of the number of birds in each grid cell, re-scaled between 0 (no aggregation of individuals) and 1 (complete aggregation of all individuals into the original roosts).

Initialization

The model is initialized by defining where 'original' roosts are located on the grid space, assigning one original roost to each of 5000 individuals, and placing each individual at a random location on the grid space. The model proceeds through the 45 time steps, moving each individual independently according to the movement rule. We ran eight model simulations for each combination of *RF* and *CA*, and averaged the model properties resulting from each combination.

2. Field study of Tree Swallow roosts of southeastern Louisiana

Study species

Tree Swallows are small (~ 20 g) insectivorous migratory birds that breed across northern North America from Nova Scotia down to North Carolina in the east, westward into Alaska and down the west coast into southern California (Winkler et al. 2011). During the non-breeding season, Tree Swallows congregate in communal nocturnal roosts, spending the night on the leaves of wetland grasses such as *Typha* or *Phragmites*. Often roosts contain well over 1 million individuals (Winkler 2006) and are usually large enough to be detected by Doppler weather radar (see below). In southeastern Louisiana, Tree Swallows arrive each year in September and October and form communal roosts in sugarcane fields, at least until the sugarcane is harvested (Laughlin et al. 2013). One large communal roost (with > 1 million individuals) usually descends into two or three adjacent 40 km^2 fields of sugarcane just after local sunset. The birds disperse from the roost, sometimes several tens of km away, just before local sunrise. Anecdotally and confirmed by radar data, swallows use the same fields in which to roost each night, and even each year, despite the availability of large tracts of mature sugarcane lining the riverbanks in southeastern Louisiana.

Study area

Our fieldwork took place in southeastern Louisiana in an area with a radius of approximately 150 km centered on the weather radar station KLIX near Slidell, LA (30° 20’ N, 89° 49’ W), from October - December 2010. Beyond 150 km from the radar station, bird roosts are difficult to detect and accurately locate (Kelly et al. 2012). The landscape within this area is composed of bottomland and upland forests, fresh and brackish marshes and swamps, lakes, agricultural areas (mostly sugarcane), and urban centers.

The use of NEXRAD to locate roosts

We located roosts and monitored their status during the study period using Doppler weather radar data. The WSR-88D weather surveillance radar (or NEXRAD) was established in the United States in the mid-1990’s. There are currently 159 NEXRAD stations across the U.S., continuously monitoring the atmosphere for precipitation patterns. In addition to precipitation, however, large-scale movements of animals can also be detected by this technology (Gauthreaux et al. 2008). NEXRAD radar has been used to study the mass movements of birds (Russell et al. 1998; Diehl et al. 2003), insects (Larkin 1991; Westbrook and Wolf 1998), and bats (Horn and Kunz 2008; Frick et al. 2013), at scales much larger than those possible from the ground. In southeast Louisiana, Tree Swallows arrive each fall from their northern breeding grounds in September, and the large roosts begin to appear on radar in early to mid-October (Laughlin et al. 2013).

We downloaded NEXRAD imagery from station KLIX starting 0.5 hours before sunrise to 1 hour after sunrise every day from 1 October to 31 December 2010. We visually scanned these images to locate all Tree Swallow roosts within our study area. Many features of Tree Swallow roosts are diagnostic when they appear on radar imagery. Tree Swallows emerge from the roost between 15 and 20 minutes before local sunrise, and gain altitude a few hundred meters into the aerosphere before dispersing from the roost site. This appears on radar as a ‘roost ring-echo’, an annulus of pixels that expands outward with each successive sweep of the radar beam (Russell et al. 1998). The habitat in which a roost appears is also diagnostic; Tree Swallows roost in tall wetland grasses such as *Typha* or *Phragmites*, or in mature sugarcane fields that resemble *Phragmites* reedbeds. When such a roost appeared on the radar imagery, we labeled the roost by drawing a circle around it using a roost-labeling webtool (designed by DRS), enclosing the pixels of the roost. The location of each roost for each day was defined as the center of the circle in the first scan in which the roost was detected. All roosts that appeared on radar during our study period were labeled and ground-truthed to verify species composition.

Radar data analysis

To test whether the radar-estimated roost locations formed in random or consistent locations each night, we performed a cluster analysis on the radar-estimated roost locations. We used the *pamk* function in the R package ‘fpc’ (Hennig 2013) to first calculate the maximum number of medoids in the data. A medoid is similar to the median of a cluster of points, and is the point in the data that minimizes the distance between it and all other cluster members. The data were partitioned around the medoids using the average silhouette width to estimate the optimum number of clusters in the data (Kaufman and Rousseeuw 1990). Average silhouette widths above 0.70 indicate that a strong structure exists in the data, and the number of clusters is robust. If roosts formed in the same places each night, the radar-estimated roost locations will group into defined clusters, whereas random roost locations will not cluster into groups. We tested whether variation around the medoids was correlated with distance from the radar station by fitting a linear model between cluster variation and distance to KLIX radar station. Due to both the curvature of the Earth and the slightly raised tilt of the radar beam (at minimum 0.5 degrees above horizontal), roosts farther away from the radar station do not appear as consistently as the roosts closer to the station (Kelly et al. 2012). Birds emerging from the roosts on the perimeter of the radar detection limit need to attain greater heights to be detected by the radar beam, and are thus potentially dispersed farther from the actual roost location before the roost-ring appears on radar.

The use of radio telemetry to measure individual movements between roosts

We explored the movements of individual birds by attaching miniature radio transmitters (PicoPip Ag376, Lotek Wireless, Newmarket, Ontario) to 29 birds. Swallows were captured with mistnets at one centralized roost near Vacherie, LA (29° 28’ N, 90° 48’ W) on the evening of 6 November, 2010. The transmitters weighed 0.6 g, approximately 3% of the total body weight of Tree Swallows. Radios were attached to a piece of fabric which was glued to the bases of bare feathers on the back of the bird between the wings (Dunn and Whittingham 2005) using Loctite ® cyanoacrylate. We attached the transmitters at dawn at the Vacherie roost, all on the same morning, and the birds were released on site.

Over the next six weeks, we surveyed four roosts (located by Doppler radar) with radio receivers several times per week in order to document and quantify each bird’s pattern of roost usage. The surveys took place within 50 m of the roost site after the birds had descended into the sugarcane to roost.

Ground-truthing of roost locations

The approximate roost locations were first established by scanning the radar imagery each morning. These were supplemented by reports from local bird watchers and farmers, who also provided us with roost locations used by Tree Swallows in previous years. We then visited each location to verify that the roosts detected with radar were Tree Swallow roosts, and to mark the exact location of the roost. Roosts form very quickly in the evening, and it was not possible to verify the exact location of more than one or two roosts per night. Roost locations not detected visually were verified using radio telemetry (i.e., triangulation of the strength of the signals from birds carrying radios verified the locations of the roosts).

RESULTS

1. Model Results

The model predicts several different patterns of roosting dynamics depending on the relative strengths of the two behavioral drivers, ranging from no aggregation at all, where individuals end up in random places each night and show no signs of grouping, to complete aggregation, where all individuals end up back in their originally assigned roosts, and many scenarios in between.

Figure 3.2 displays the roost sizes and locations from six representative emergent patterns. In scenarios with no conspecific attraction or roost fidelity ($\gamma_{RF} = 0$ and $\gamma_{CA} = 0$), individuals move randomly, no roosts form and all model properties are at their minimum value $IRR = RC = AI = 0$ (Fig. 2A). When $\gamma_{RF} = 0$, as γ_{CA} increases, new roosts form in different (random) locations, and the roosts are more numerous but smaller in size. Figure 3.2B shows the results where $\gamma_{RF} = 0$ and $\gamma_{CA} = 1$, in which 32 new roosts formed with a mean of 154 individuals (± 61) in each roost. Return rate is close to zero in these instances because roost location is random and the original roosts re-form only coincidentally. Individuals also associate with, and roost alongside, different individuals each night. In this scenario, $IRR = 0.011$ (± 0.007), $RC = 0.046$ (± 0.02), and $AI = 0.062$ (± 0.009). Fig. 2C shows the results when both parameters are set to relatively low values ($\gamma_{RF} = 0.07$, $\gamma_{CA} = 0.03$). Here, roost fidelity is strong enough to ensure that the original four roosts re-form, but the conspecific attraction also drives the individuals to congregate with their nearest neighbors, leading to a significant amount of roost-switching (28% of individuals are now located in a different roost than the one where they were originally assigned). Since both γ_{RF} and γ_{CA} are relatively low, only 78% of all individuals are at a roost, while the rest of the individuals are still scattered throughout the middle portion of the grid-space (Fig. 2C). In this scenario, *IRR* = 0.558 (± 0.028), *RC* = 0.95 (± 0.093), and *AI* = 0.145 (± 0.008).

In scenarios where γ_{CA} and γ_{RF} are both moderately high, the original roosts tend to re-form, in addition to several smaller roosts. In figure 3.2D, for example, the original roosts contain a mean of 913 (± 79) individuals, whereas the new roosts average 254 (± 69) individuals. Here, *IRR* = 0.375 (± 0.024), *RC* = 0.420 (± 0.047) and *AI* = 0.274 (± 0.041). With mid-level γ_{CA} and high γ_{RF} (e.g. Fig. 2E), all four original roosts re-form, no new roosts form (*RC* = 1.0), most of the individuals are at roost (99%), and individuals return to their original roosts at a rate of 75%. Despite a significant rate of roost-switching (25%), the roosts are in the same locations and are of the same size as the original roosts (1242 ± 49 individuals). In this scenario, *IRR* = 0.751 (±0.011), *RC* = 1.0 (± 0.0) and *AI* = 0.571 (± 0.112). Figure 3.2F displays the results in which $\gamma_{RF} = 1.0$ and $\gamma_{CA} = 0$. All original roosts re-form, and all individuals return to their original roosts. All model properties reach their maximum: *IRR* = 1.0 (± 0.0), *RC* = 1.0 (± 0.0), and *AI* = 0.998 (± 0.001).

Figure 3.3 shows how the resultant model properties (return rate, *IRR*; roost consistency, *RC*; and aggregation index, *AI*) change as the strength of roost fidelity (γ_{RF}) and conspecific attraction (γ_{CA}) increase. *IRR* and *RC* are highly correlated; as the original roosts re-form at a higher rate than new roosts are forming (i.e., as *RC* approaches 1), individuals also are returning to their original roosts at a higher rate (i.e., *IRR* also approaches 1). One exception to this is the scenario in figure 3.2E, where *RC* = 1.0, but *IRR* is 0.75. At these levels of fidelity and attraction, all the original roosts form in the same place, but not all individuals return to their original roosts, as they are drawn into different roosts by conspecific attraction.

2. Field-study results

Radar analysis: Roost location and consistency

Our radar analysis shows that Tree Swallows formed 10 roosts within our study area and that the locations of the roosts are consistent from night to night. The radar-estimated Tree Swallow roost locations clustered into 10 distinct groups (average silhouette width = 0.72). Figure 3.4 displays the locations of the clusters as defined by partitioning of the medoids and the size of the circles is proportional to the variance of the cluster members to cluster medoid. About 70% of the variance in estimated location within each cluster was explained by a positive linear relationship with distance from the radar station KLIX (Figure 3.5), as expected if variance of radar-estimated roost locations is mostly due to radar 'error' than to the roosts actually changing location from night to night.

Our ground-truthing of roost locations is in agreement with these findings. The roosts were located in the same set of sugarcane fields every night that we visited them (n = 81 roost-nights). Most often, the birds used the same field as the previous night, but sometimes shifted a few fields away, but were always within the same 2 – 3 km^2 area. This consistency is despite a considerable amount of unused homogeneous habitat of sugarcane lining the banks of the Mississippi River in southeastern Louisiana.

Radio telemetry: Individual movements between roosts

We detected signals from 23 of the 29 radio-tagged birds at least twice each over the telemetry surveillance period ($\overline{x}$ = 7.2 detections per bird, sd = 4.9). We missed receiving signals from many birds not because they were not at a roost on a given night, but because we could not visit every roost every night. Fifteen of these birds were detected in ≥ 3 unique roosts over the next 6 weeks ($\overline{x}$ = 2.7 different roosts per bird, sd = 0.9), including one bird that was detected in 5 different roosts. Two birds were detected in only the Vacherie roost where we attached the radios. However, signals from these two birds were not detected each time the Vacherie roost was surveyed, indicating that they did not use the Vacherie roost each night – but since they were not detected at a different roost, we did not count these absences as roost-switches.

In all, we collected 173 detections of the radio-tagged birds during the study. Of these detections, 103 (60%) were made at the same roost as the bird was previously detected, and 71 (40%) were made at a different roost than the bird was previously detected. If we count only those detections that were on consecutive nights (n=63), we documented 14 roost-switches and 49 roost-returns, for an individual return rate of about 78%. This is a conservative estimate; by only counting those switches that occurred on consecutive nights, we ignore 39 switches (23% of all re-sightings) that did not occur on consecutive nights, and probably more switches occurred than we documented as well.

If a bird did switch roosts, it chose to roost significantly closer (on average 15.71 km nearer) to their original roost than would be expected if they were choosing alternate roosts randomly (paired t-test, t = -3.54, df = 13, p = 0.004).

DISCUSSION

Synthesis of model and field results

Our field results combined with the model suggest that the pattern of Tree Swallow roosting dynamics can largely be explained by individuals exhibiting a combination of moderately high roost-site fidelity coupled with moderate conspecific attraction. The radar data indicate that roost-location consistency is high; roosts form in the same places each night, which requires a fairly high level of individual roost-fidelity. The radio-telemetry data show that individuals switch between these stable roosts at a rate of at least 22% each night, indicating that fidelity to the roost site is not perfect, and that birds are sometimes attracted towards conspecifics into other roosts. Individual swallows appear to have a fairly high propensity to return to the same roost that they used the previous night. This is evidenced both in the return rates that we calculated as a whole (> 60% return rate to previous roost) and in the fact that if a bird did switch roosts from one night to the next, it usually switched to an available roost closer to, rather than further from, where it roosted the previous night. Each bird appears generally drawn towards its previous roosting location, but can be diverted to a different roost site via conspecific attraction. These findings are most consistent with the pattern shown in figure 3.2E, in which the roost locations are highly stable from one night to the next, but individuals switch between the roosts at a rate of about 25%.

In our study species, it is not clear whether individuals switching between stable roost locations occurs throughout the non-breeding range, or even throughout the non-breeding season. Roost lability (that is, the degree to which individuals switch between traditional roost sites) in swallows may be a function of distances between roosts. The sugarcane roosts in our study area have an average distance of ~ 20 km between them. However, Van den Brink (2003) reports the re-capture of a Barn Swallow (*Hirundo rustica*) on the wintering grounds in Africa at two different communal roosts 114 km apart, suggesting that roost lability may not be uncommon in hirundinine communal roosts, but further study is required.

Model parameters and assumptions

To simplify our model, we made several assumptions about the roosting system that may affect the results of the model. For example, we did not create a spatially explicit grid in which habitat selection and/or the location of food resources plays a role. The addition of such parameters would allow us to examine hypotheses regarding the roles of spatial heterogeneity, habitat loss and/or food patchiness on aggregative dynamics. The roosting literature is rich in examples in which these parameters play an important role in roosting dynamics. Morrison and Caccamise (1985) showed that adult starlings joined roosts located close to rich supplemental food supplies, while Lambertucci and Ruggiero (2013) showed that Andean condors (*Vultur gryphos*) select roost sites that protect them from adverse climate and anthropogenic disturbances. Moreover, if individuals choose roosting sites based on certain habitat characteristics that are rare in the environment, then aggregations may form unintentionally (Beauchamp 1999). However, habitat selection is scale-dependent and we did not include it in the model since, in our study-system, the roosting area is a relatively homogeneous habitat of sugarcane fields. At larger scales, the swallows are certainly choosing to roost in sugarcane rather than in other available wetland vegetation. But at the smaller scale that we are modeling, we cannot discern why swallows consistently choose one sugarcane field over another.

Field Study

We attached radios to individuals at only one roost, all on the same day, and this precludes addressing some interesting questions about roost fidelity in our system. For example, had we attached radios to birds at several roosts, we could have measured variability in roost fidelity among roosts, as has been shown in other studies (e.g., Morrison and Caccamise 1985). Further, we were not able to survey every communal roost every night - which may have led to inflated estimates of roost fidelity. We were only able to detect individuals on consecutive nights 63 times, of which 14 were at different roosts than the previous night. However, we missed signals from many birds each night, probably because we could not survey each roost in the study area every night.

Application of model to other systems

Despite the simplicity of our two-parameter model, it is able to replicate the dynamics of our study system and some others, and represents a starting point in the understanding of how different behaviors can drive roost dynamics across taxa. At one extreme, high conspecific attraction but no roost-site fidelity drive the patterns shown in Fig 2B, where roost locations change frequently and individuals show no propensity to return to their previous roost. These patterns resemble those seen in California Quail (*Callipepla californica*) (Yadon 1956) and Long-tailed Bats (*Chalinolobus tuberculatus*) (O'Donnell and Sedgeley 1999). At the other extreme, high roost-site fidelity with no conspecific attraction drive the patterns shown in Fig. 2F, where roost locations are fixed (termed traditional roosts) and individuals always return to the same roost. Such patterns have been observed in the greater spear-nosed bat (*Phyllostomus hastatus*) (McCracken and Bradbury 1981) and the Red Knot (*Calidris canutus canutus*) (Leyrer 2006).

Intermediate patterns shown in Fig. 2C-2F where there is some degree of individuals switching between traditional roosts are driven by different levels of roost fidelity and conspecific attraction. This pattern, termed roost lability, has been shown to occur at varying levels in communal roost systems of several bird species (e.g., European Starlings (Morrison and Caccamise 1985), Common Grackles (*Quiscalus quiscula*), American Robins (*Turdus migratorius*) (Morrison and Caccamise 1990) and American Crows (*Corvus brachyrhyncos*) (Caccamise et al. 1997)) as well as several bat species, (e.g., noctule bats (*Nyctalus noctula*) (Krontwitter 1988), Daubenton's bats (*Myotis daubentonii*) (Rieger 1996) and Indiana bats (*M. sodalis*) (Kurta et al. 1996)). Clough and Ladle (1997) discovered that in stream-swelling dace (*Leuciscus leuciscus*), individually marked fish switched between two patches of nighttime habitat used by larger groups of dace, describing for one of the first times 'roost'-use in fish. Roost lability is also prevalent in some insect roost systems, such as in rubyspot damselflies (*Hetaerina Americana*; Grether and Switzer 2000) and in harvestman (Opiliones, *Prionostemma* sp.; Grether and Donaldson 2007)

Though we modeled day-to-day roost fidelity here, we expect that similar mechanisms may apply on longer time scales. Many communally roosting species, including Tree Swallows, return to the same roost sites annually, not only daily. Roost fidelity may thus be an important driver for the formation and maintenance of communal roosts on both small (daily) and large (annual) time scales.

General insights from the model

Our model suggests that very large communal roosts do not form under situations of conspecific attraction alone (Fig. 2B, Fig. 3C). In the model, only when individuals return to traditional roost sites are the roosts of considerable size (Fig. 2E and 2F) and aggregation index is consistently high (Fig. 3C). Conklin and Colwell (2008) suggested a similar idea in reference to associations between individuals within shorebird roosts. The idea that migratory organisms that form massive communal roosts on the wintering grounds, such as Tree Swallows and other aerial insectivores, as well as many bat species, can only do so by returning to the same roost locations year-after-year has important implications for the conservation of winter habitat. Habitat loss that prevents the formation of roosts at traditional roost sites could cause mortality for many of the individuals dependent on these sites. Continual and widespread habitat loss could thus lead to population declines, as has been observed on the breeding grounds for Tree Swallows (Nebel et al. 2011; Shutler et al. 2012) and other roosting aerial insectivores such as Purple Martins (*Progne subis*) (Sauer et al. 2011; Tarof and Brown 2013).

In our model, all individuals move according to the same movement rule; in this case, there are no pre-specified ‘leaders’ or ‘followers’. However, as the strengths of roost fidelity and conspecific attraction increase, interesting dynamics emerge that are reminiscent of leader/follower dynamics. Depending on the number of surrounding conspecifics, each individual at each time step has an opportunity to be either a leader (heading straight back to previous roost) or a follower (attracted to a large aggregation). In those cases where individuals end up in a different roost than they were in before, they followed the other individuals who were heading back to their previous nights' roost. Biro et al. (2006) have shown empirically and theoretically that leaders can emerge in pigeon homing flights when individuals are conflicted about the directional preference of the flight route. In such cases, no pigeons began the flight as leaders, but during the course of the flight some individuals began to follow a leader while others split from the group.

Modeling the interactions of different individual-level behaviors has increased our understanding of the movements and emergent patterns of fish schools, insect swarms, and bird flocks (Parrish & Hamner 1997; Sumpter 2010). Our study adds to the growing body of literature on individual-based modeling and self-organization in complex systems, and provides a framework for understanding the many patterns of roost dynamics found in natural systems. We show that many unique, and real, population-level patterns of roost formation and maintenance can emerge by modeling simple individual-level behaviors.

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Table 3.1. Definitions of model parameters and emergent properties

Parameter	Symbol	Range	Definition
Strength of conspecific attraction (CA)	γ_{CA}	0 - 1	Value multiplied by proportion of conspecifics in cell (p_i) and added to cell weight
Strength of roost fidelity (RF)	γ_{RF}	0 - 1	Value multiplied by distance improvement from current position to cell position (d_i) and added to cell weight
Property	Symbol	Range	Definition
Individual return rate	IRR	0 - 1	Proportion of roosting birds that returned to their assigned roost
Roost-location consistency	RC	0 - 1	Number of original roosts that re-formed divided by total number of roosts
Aggregation index	AI	0 - 1	Variance to mean ratio of the number of individuals in each grid cell, re-scaled between 0 and 1.

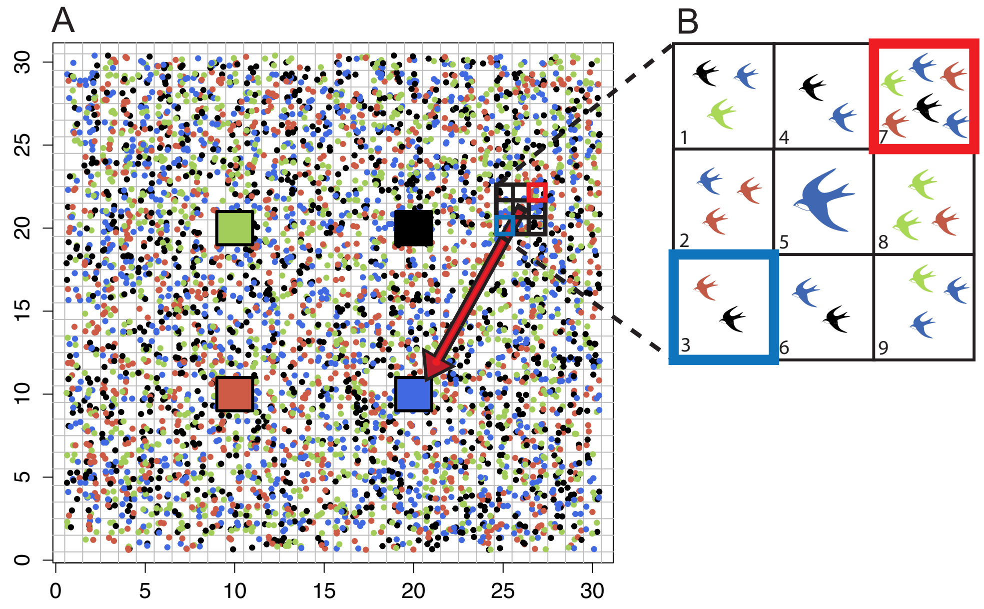


Figure 3.1. Model grid space and close-up of neighborhood cells surrounding and containing an example individual. A. The 30 x 30 grid showing the initial randomly scattered individuals across the grid before the initiation of movement. Dots are individuals, color coded according to which roost they were assigned (colored boxes). Individuals are shown slightly offset from the cell they belong in to avoid overlapping. B. Example close-up of the neighborhood cells surrounding and containing one individual (in cell 5) whose original roost was at (20,10), the blue roost. Under scenarios of high *CA*, cell 7 (red outline) would have the highest weight because it contains the largest number of individuals. Under scenarios of high *RF*, cell 3 (blue outline) would have the highest weight because it is the cell closest to the individuals' original roost (blue square).

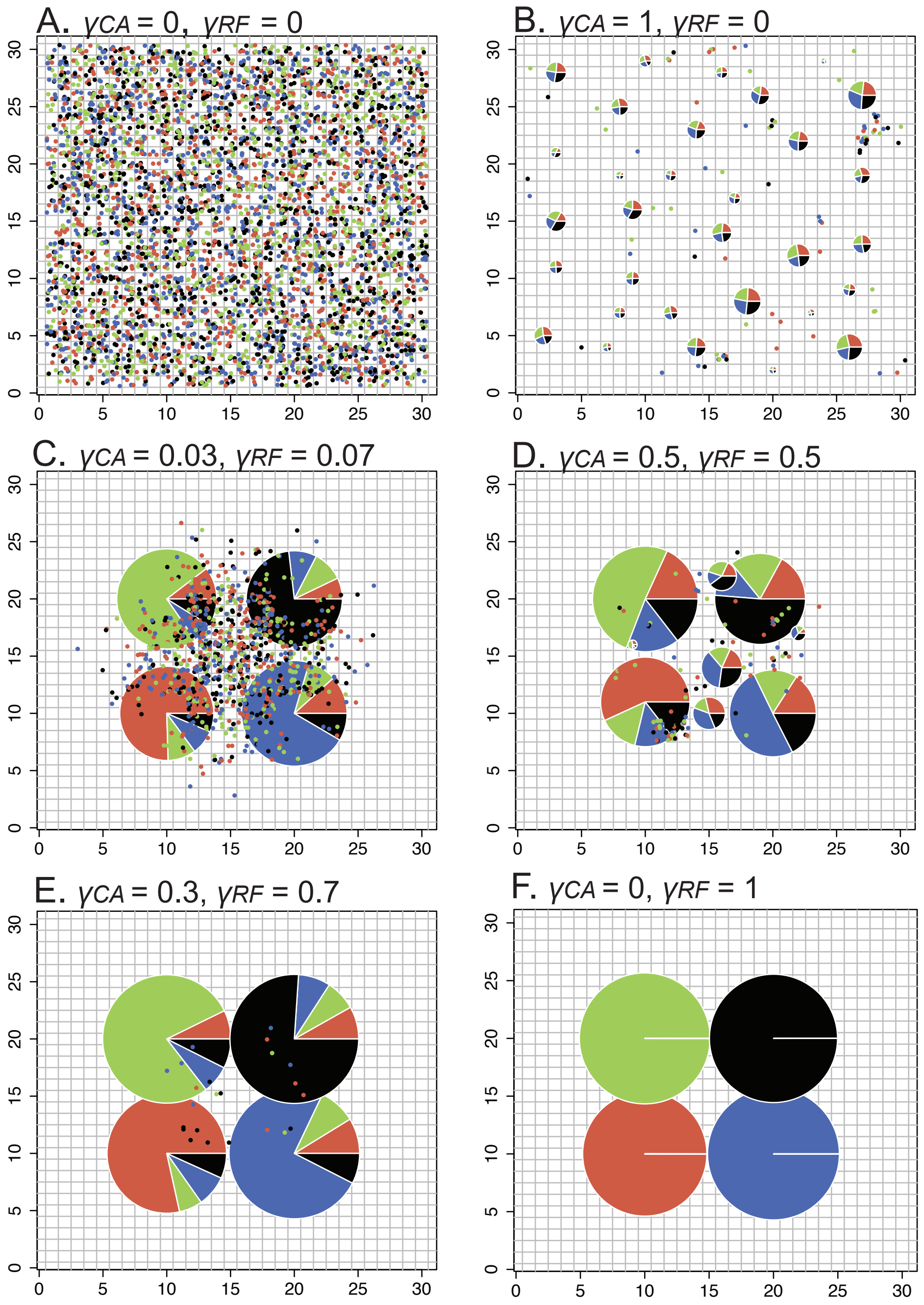
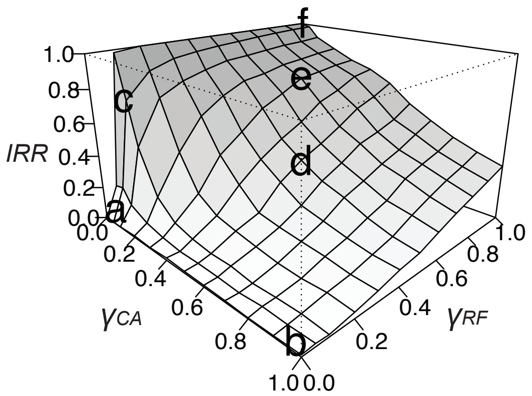


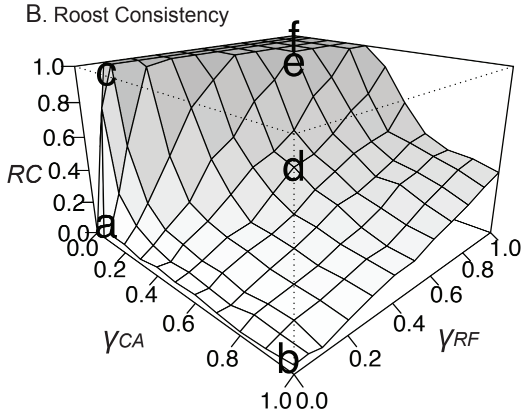
Figure 3.2. Six unique patterns generated by the model from different combinations of γ_{CA} and γ_{RF}. Floating pie charts represent the location, size, and individual composition of the roost (i.e., proportion of individuals from each original roost, color-coded by which roost they originated from). A. No aggregation at all. B. Small roosts form in random

locations across the grid, but none of the original roost re-form. C. All original roosts re-form but not all birds return to a roost. D. All original roosts re-form, plus a few smaller ‘satellite’ roosts. E. All original roosts re-form and most birds (> 95%) are at roost. This scenario most closely approximates the results from the present empirical work on Tree Swallow roosts. F. All original roosts re-form, and all individuals return to their original roost.

A. Individual Return Rate



B. Roost Consistency



C. Aggregation Index

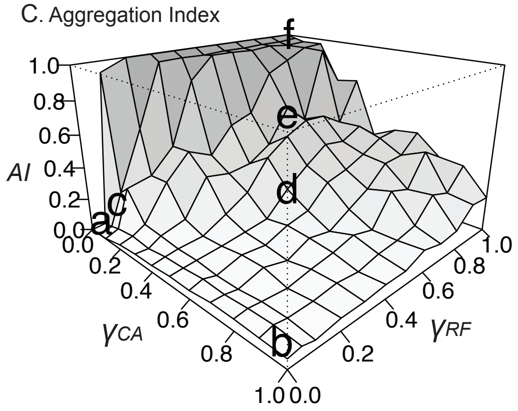


Figure 3.3. 3D plots of the three model properties plotted as a function of increasing parameter values. A. Individual return rate (*IRR*), B. roost consistency (*RC*), and C. aggregation index (*AI*). The symbols 2a – 2f refer to the different scenarios in Figure 2, showing the locations of these six scenarios on the parameter space.

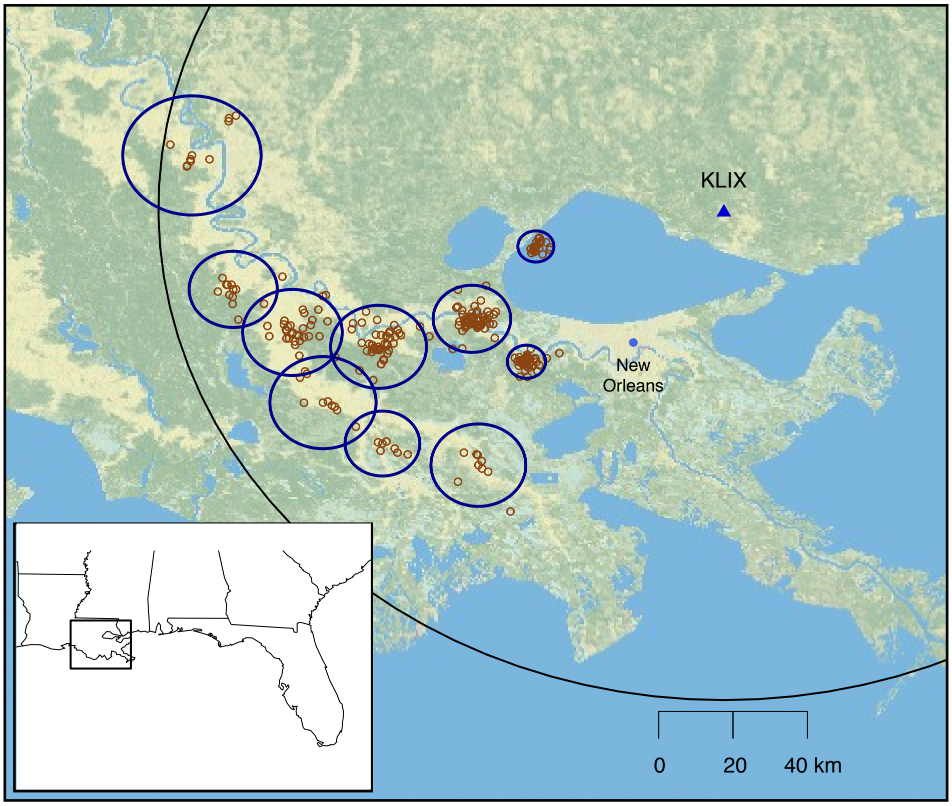


Figure 3.4. Map of southeastern Louisiana showing the circular study area (black circle), location of KLIX radar station, and radar-estimated locations of all Tree Swallow roosts from October – December 2010 (brown circles). The blue circles display the results of the clustering algorithm, and the radius of each circle is proportional to the variance of each estimated location within each cluster to the medoid of that cluster (showing how location variance increases with distance from radar station). See text for further details.

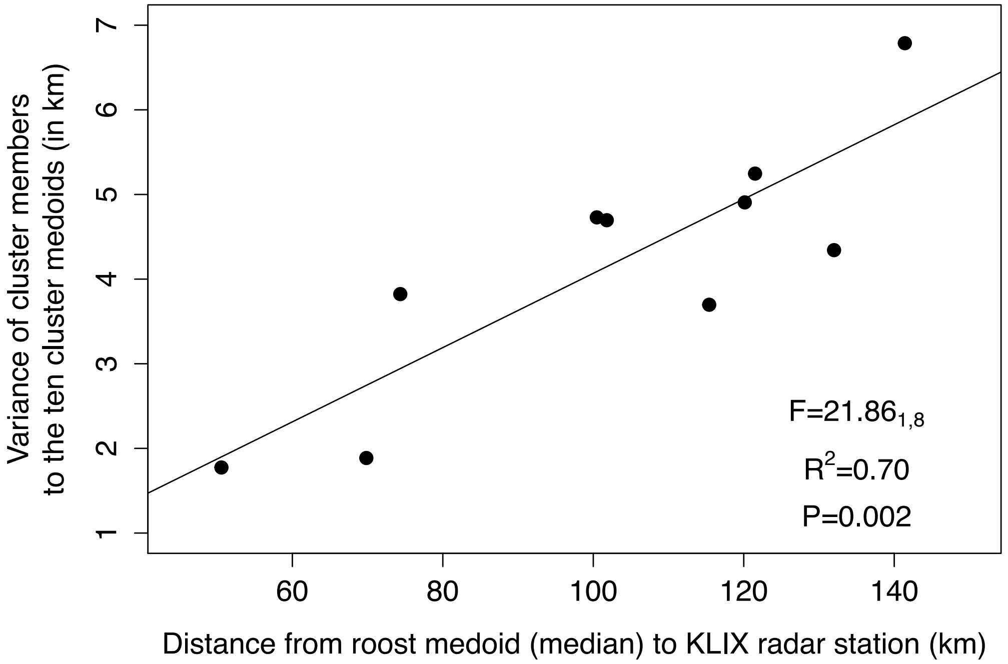


Figure 3.5. Relationship between the distance from cluster medoids (i.e., roost location medians, see text for details) to KLIX radar station and the variance of cluster medoids to cluster members. Variance in roost location detected by radar increases with distance from radar station.

CHAPTER FOUR

Conspecific attraction and the spread of infectious diseases at communal roosts

ABSTRACT

Communal roosting is a widespread behavior but potentially results in increased pathogen transmission. In a previously published model, we showed how the interaction of individual behaviors (roost fidelity and conspecific attraction) results in different roost dynamics including group sizes and intermixing between roosts. Here, we extend the model to explore how different behaviors and disease transmission modes affect the spread of an infectious disease. Our results show that infection remains isolated to a single roost when there is no roost switching but can spread quickly even under low levels of intermixing. However, when conspecific attraction (intermixing) is high and exceeds roost fidelity, the spread rate of diseases that have a density-dependent transmission mode is dramatically slowed. Spread rate of diseases with frequency-dependent transmission are not influenced by the strength of conspecific attraction or roost fidelity provided there is some level of intermixing. We discuss how results of this model can be applied widely to the dynamics of disease outbreaks at communal roosts and other animal aggregations, and show that knowledge of both the aggregative

dynamics of the species and the transmission mode of the disease are important to predict how the disease will spread at sites of aggregation.

INTRODUCTION

Emerging infectious diseases are a threat to both wildlife populations and to human public health, and their effects are exacerbated by human-induced global change (Epstein et al. 2003). Of the emerging diseases affecting humans, 75% of them are zoonotic, that is, able to be transmitted between humans and wildlife (Taylor et al. 2001). It is therefore vital to understand infection dynamics of such diseases to predict how wildlife and human populations may be affected (Daszak et al. 2000) and to determine the efficacy of control strategies (Hallum and McCracken 2011).

Dynamics of different diseases are influenced by many, often interacting, factors. One factor is transmission processes, for example air- versus vector-borne diseases, or those spread via direct versus sexual contact. These processes lead to different modes of transmission, depending on the disease in question. Historically, models of disease dynamics assumed a linear relationship between population density and probability of infection (Kermack and McKendrick 1927, Anderson and May 1979), a mode of transmission referred to as ‘density-dependent’ transmission. More recently, other transmission modes have been introduced in order to account for the often-complex relationships between the rate of disease spread and numbers of infected versus susceptible individuals (McCallum et al. 2001). In sexually transmitted diseases for example, the probability of infection depends less on the number of infected individuals in the population and more on the social contacts between individuals. Different transmission modes can be thought of as belonging to a continuum, with density-dependent transmission at one end, and ‘frequency-dependent’ transmission, where the probability of infection is based on the prevalence of disease in the population (i.e., the proportion of infected individuals), at the other end (Antonovics et al. 1995).

Another factor that affects disease dynamics are the social behaviors of species, e.g. communal versus solitary breeding/roosting , which affect contact rates of individuals (Altizer et al. 2006). White-nose Syndrome (WNS), for example, is a fungal disease spread amongst bats that aggregate during hibernation and has caused large-scale population declines in eastern North American bat species (Frick et al. 2010). Roosts of American Robins (*Turdus migratorius*) have been implicated as amplification foci for West Nile virus in portions of the US (Diuk-Wasser et al. 2010). Likewise, phocine distemper virus is pathogenic in pinnipeds, especially Harbor Seals (*Phoca vitulina*), and is spread between individuals at their ‘haulouts’, or sites of aggregation on land (Swinton et al. 1998).

Communal roosting in animals, here defined as aggregations of conspecifics during the inactive period of the diurnal cycle (Grether et al. 2014), is a taxonomically widespread social behavior. It has been described in mammals such as bats (Kunz 1982), primates (Hamilton 1982), and pinnipeds (Thompson 1989); fish such as stream-swelling dace (Clough & Ladle 2005); many species of birds (Eiserer 1984, Beauchamp 1999); and also invertebrates such as damselflies (Grether & Switzer 2000), butterflies (Mallet 1986), arachnids (Cockerill 1988), and planarians (Reynierse et al. 1969). The benefits of communal roosting include decreased risk of predation via predator dilution or avoidance (Hamilton 1971), increased awareness of food resources via information sharing (Ward &

Zahavi 1973), and thermoregulatory benefits of huddling close together (Eiserer 1984). The costs associated with this behavior include increased competition for food or mates (Beauchamp 1999), and increased rates of pathogen or parasite transmission between individuals in close contact with each other (Krause & Ruxton 2002).

The dynamics of communal roosting varies both among and within species. Group size of communal roosts can vary by several orders of magnitude, even within species. Some roosts may contain a few to a dozen individuals, others several hundred to thousands of individuals, while large communal roosts of some bats and birds can contain more than a million individuals. Roosting behavior also varies temporally. Many birds form communal roosts only during the non-breeding (or winter) season (Eiserer 1984), and some bats hibernate together in caves during the winter (O'Shea and Bogan 2003). Some female bats form maternal roosts in early summer (Kunz 1982) but not at other times of the year.

Additionally, the consistency of the location of roosts and individuals intermixing between them varies among species. Some species, such as California quail (*Callipepla californica*) and long-tailed bats (*Chalinolobus tuberculatus*) form roosts in new locations each night (Yadon 1956, O'Donnell and Sedgeley 1999), whereas other organisms that roost communally often use 'traditional' sites from night to night and year to year (Eiserer 1984). Among those species that make use of traditional roost sites, different individual dynamics can occur. In radio-telemetry studies of Red Knots (*Calidris canutus canutus*) and the greater spear-nosed bat (*Phyllostomus hastatus*), individuals always returned to the same roost each night, despite the presence of other roosts of the same species in close proximity (McCracken and Bradbury 1981, Leyrer et al. 2006). In most other studies, however, individual birds, bats, and invertebrates switched between roost sites, creating roost systems that are interconnected by the movements of individuals between them (Morrison and Caccamise 1985, Kronwitter 1988, Grether and Switzer 2000, Laughlin et al. 2014).

In a previous paper we showed, using an agent-based model, that different individual behaviors interact to produce different patterns of roost location consistency and roost switching (Laughlin et al. 2014). In the basic model, individuals aggregate into roosts by following a movement rule that incorporates two independently adjustable behaviors: *roost fidelity* (causing an individual to return to its original roost) and *conspecific attraction* (causing an individual to aggregate with its nearest neighbors). Varying these two parameters leads to different roost dynamics, including systems with different roost sizes and levels of intermixing between roosts. Here, we extend this model to include infectious disease to examine, generally, how the speed of disease spread within a population is affected both by roost dynamics and by the transmission mode of the disease. The question in this study is twofold: 1) how do different aggregative behaviors interact to drive the spread of a disease throughout a population and 2) what effect does the transmission mode of the disease have on the speed of transmission under different roosting behaviors and dynamics?

METHODS

I. Description of basic model

Our original agent-based model simulates the formation of communal roosts in one day by individuals all following the same movement rule (Laughlin et al. 2014). The model is initiated with 5,000 individuals randomly scattered across a 30 x 30 cell lattice. Each individual has been randomly assigned to a 'previous roost', one of four evenly spaced locations on the grid where the individual roosted during the previous night. The movement rule consists of two individually adjustable parameters: roost fidelity (γRF, where an individual tends to return to its previous roost) and conspecific attraction (γCA, where an individual tends to aggregate with its nearest neighbors). Each parameter was varied between 0 – 1 (in 0.1 increments), resulting in a total of 121 unique combinations of γRF and γCA. At the end of the model run, the model properties calculated include individual return rate (IRR – the proportion of individuals that returned to their previously assigned roost) and roost consistency (RC – the proportion of new roosts that are one of the original four). For full details, see Laughlin et al. (2014).

II. Modifications to the basic model

a. Extension to multiple days. We extended the model beyond the one-day scenario by repeating the 45 timesteps that represent the daily roost return time for 50 days. At the start of the first day all individuals are assigned to one of four initial roosts as in Laughlin et al (2014). Each day all 5000 individuals are randomly scattered across the 30 x 30 lattice. Subsequent roost formation is simulated by a movement rule with inputs, γRF and γCA that is the same for all individuals as described in Laughlin et al (2014). At the end of 45 timesteps, aggregations of more than 25 individuals (within a 9-cell neighborhood) are designated as roosts and all individuals in the aggregation are assigned to that roost. If the individual does not end up in a roost at the end of a day, then the last roost in which it occurred or to which it was assigned originally remains the roost assigned to that individual. At the end of each model run, the 50-day averages of four emergent model properties are calculated: *individual return rate* (IRR), *roost consistency* (RC), *number of roosts* (NR) and *roost size* (RS) (table 4.1). We also examined the emergent properties over time for each parameter combination to verify that no trends or sudden changes exist, and that the mean value of the 50-day run reflects the dynamics accordingly.

b. Disease dynamics. Individuals can be in one of two possible states: Susceptible (S) or Infected (I). At model initiation on day one, all individuals began as S except for one randomly selected individual designated as I. Once infected, individuals remain infected and do not recover and are not removed, following the standard S-I model of disease dynamics. Infection of susceptibles only occurs at roosts; susceptible individuals that are outside a roost at the end of each day cannot become infected. Within a roost, the mean number of infected individuals that a susceptible encounters each night (such that it would become infected), λ, depends on the transmission mode:

1) Under density-dependent transmission, λ is a function of the *number* of infected individuals *I*, at roost *r*:

$$\lambda = \beta I_r \qquad \text{(Eqn. } \mathit{1}\text{)}$$

where β is the transmission coefficient in units of per individual per unit time, and I_r is the number of infecteds in roost *r*; and

2) Under frequency-dependent transmission, λ is a function of the *proportion* of infecteds at roost *r*:

$$\lambda = \frac{\beta' I_r}{S_r + I_r} \qquad \text{(Eqn. } \mathit{2}\text{)}$$

where β' is the transmission coefficient in units of time^{-1}, (that is, the rate at which a susceptible makes contact with other hosts; Begon et al. 2002) and $S_r + I_r$ is the total number of individuals in roost *r*. For comparison purposes, β (in density dependent transmission, eq. 1) and β' (in frequency-dependent transmission, eq. 2) were scaled such that the probability of infection at a roost with N_r = 1000 individuals with the same number of I was the same for density- and frequency-dependent transmission (i.e., β = β' / N_r). At the end of each day, within each roost, the probability of a susceptible becoming infected is the probability that the susceptible encountered more than zero infecteds. We assume the number of infecteds encountered is drawn from a Poisson distribution with mean λ as defined above, so that:

$$P(S \rightarrow I) = 1 - e^{-\lambda} \qquad \text{(Eqn. } \mathit{3}\text{)}$$

The model simulates 50 days, during which we measure the prevalence of the disease (proportion of all infected individuals; PI_t) at the end of each day, *t*, for each of the 121 combinations of parameters *γRF* and *γCA* and for each transmission mode. To examine infection rate as a function of model parameters, we compared the prevalence after 10, 20, 30, and 50 days under both frequency- (FD) and density-dependent (DD) transmission. We ran a multiple linear regression to determine the effect of independent variables *γRF* and *γCA* and their interaction on prevalence on day 20 (PI_{20}) and day 50 (PI_{50}) for each transmission mode. Additionally, we calculated the linear correlations of PI_{20} and PI_{50} with the mean values of all emergent model properties using Pearson's product-moment correlation to test which properties are most strongly correlated with the variation of infection under each transmission mode. To verify that differences between transmission modes were not the result of infectivity scaling, we tested additional values of β such that N_r = 260 and N_r = 1215. We ran these alternate disease dynamics on the same simulation of movements so that stochastic movement behaviors did not influence the comparison between β values.

RESULTS

Roost dynamics and emergent model properties of the 50-day model

When $\gamma CA = 0$ and $\gamma RF = 0$, no roosts form (that is, no grid cell contains more than 25 individuals at the end of each day). As γRF increases but γCA remains fixed at zero, all four original roosts form each day with no additional roosts, even when γRF is low, and all individuals return to their previous roosts. As the strength of γCA increases and $\gamma RF > 0$, individuals initially return to previously established roosts but also switch between these original roosts at increasing rates. When $\gamma CA > \gamma RF$, small new roosts begin to form in addition to the original roosts, and when γCA is much greater than γRF, the original roosts may not form at all and roost formation occurs randomly across the grid each day.

As in the original one-day model (Laughlin et al. 2014), mean individual return rate (IRR) and mean roost consistency (RC) increase with increasing γRF, and decrease with increasing γCA. Mean roost size (RS) likewise increases with increasing γRF and decreases with increasing γCA. Mean number of roosts (NR), however, is negatively correlated with these properties: fewer daily roosts are associated with larger roost sizes and with more individuals returning to their previous roosts (larger RS and IRR).

Disease transmission dynamics

a. Disease dynamics as function of parameter combinations. When $\gamma CA = 0$ and $\gamma RF = 0$, total infection under both density- and frequency-dependent transmission (PI_{50_FD} and

PI_{50_DD}) are approximately 0 (figure 4.1). Because infection only occurs at roosts, the disease remains isolated in the one initially-infected individual under these conditions because no roosts form. As *γRF* increases but *γCA* remains fixed at zero, PI_{50_FD} and PI_{50_DD} never exceed approximately 0.25 because no roost switching occurs and the disease remains isolated at the roost into which it was introduced (figures 4.1 and 4.2) which was 1 of 4 initial roosts. All individuals at the roost containing the infected individual eventually become infected, but no individuals at other roosts are exposed. When individuals are subject to conspecific attraction (that is, when *γCA* starts increasing), they begin to switch between roosts, allowing infection to spread to other roosts; infection can thus reach the entire population under certain parameter combinations (figures 4.1 and 4.2).

The ability of the disease to spread when *γRF* and *γCA* are both > 0 is different for frequency- and density-dependent transmission. Under frequency-dependent transmission, the strength of *γRF* and *γCA* do not affect the ability of the disease to spread throughout the population (figures 4.1 and 4.2). The variation of PI_{20_FD} within the parameter space (figure 4.1B) is caused by stochasticity in the model and is independent of *γRF* and *γCA* (See table 4.2 for regression results). However, under density-dependent transmission, the parameter combinations do influence infection dynamics. When *γRF* is high and *γCA* is low, the disease saturates the population much faster than when *γRF* is low and *γCA* is high (figure 4.2B). As *γCA* increases, the ability of the disease to spread is dampened (figure 4.1). The parameter combinations explain 53% of the variance in infection after 20 days (PI_{20_DD}) and 58% of the variation after 50 days (PI_{50_DD}) (table 4.2).

b. Disease dynamics related to model properties. The model properties, RS and NR are strongly negatively correlated with each other such that there are situations with many small roosts and situations with a small number of large roosts. Examining the relationship of infection rate with the emergent model properties (table 4.2) shows that, under frequency-dependent transmission, none of the model properties are strongly correlated with variation in disease prevalence after 20 days, while after 50 days the disease has saturated the population under all parameter combinations and there is thus no variation to explain. The rate of infection is nearly identical in situations where there are many small roosts and where there are few large roosts (figure 4.3A). Under density-dependent transmission, however, roost size (RS) is strongly correlated with variation in PI_{20_DD}, and all model properties are significantly correlated with variation in PI_{50_DD} (table 4.2). Under density-dependent transmission, infection increases with increasing individual return rate (IRR), roost size (RS), and roost consistency (RC), but decreases with increasing number of roosts (NR). In situations where there are many small roosts, infection is dampened compared to situations where there are few large roosts (figure 4.3B). Figure 4.4 displays the model property values in the parameter space.

c. Effects of rescaling β. Infection rate increased when $N_r = 260$ and decreased when $N_r = 1215$, but results were not qualitatively different; that is, under increasing γCA and decreasing γRF, the disease spread is suppressed under density-dependent, but not frequency-dependent, transmission (figure 4.5).

DISCUSSION

This study highlights the dynamic role that conspecific attraction can have on disease dynamics in species that form social aggregations. If there is no conspecific attraction to individuals in other roosts, infection will not spread no matter the mode of transmission, either because roosts do not form (if animals do not exhibit roost fidelity) or roost membership is stable and no individuals switch between roosts. In the latter case, the disease spreads within any roost in which it was introduced but no further. These results are analogous to some real-world disease dynamics of social animals. Manlove et al. (2014) studied bighorn lamb (*Ovis canadensis*) mortality in years with and without pneumonia infection, and found that in years with infection, lamb mortality was associated with subpopulation membership because limited or no movements between subgroups restricted the spread of the disease. Similarly, Langwig et al. (2015) found that White-nose Syndrome (WNS) is transmitted between bats mostly at bat hibernacula between which individuals do not move, rather than at communal roosts between which individuals do move (e.g. Willis and Brigham 2004). As such, transmission of this highly pathogenic fungal disease may be restricted to particular hibernacula.

Weak conspecific attraction allows diseases to spread rapidly throughout the population because individuals begin to switch between roosts, leading to higher contact rates between individuals in different roosts. At mid to high levels of roost fidelity and low but non-zero levels of conspecific attraction, infection throughout the population is rapid because in general, higher roost fidelity leads to larger roosts (and therefore more susceptible individuals are exposed). Under density-dependent transmission, the probability of infection per susceptible is identical in large or small roosts that have the same number of infected individuals. In large roosts, there will be more individuals exposed daily than in small roosts, and disease spread is faster under these conditions. These results are consistent with studies that examined the relationship between disease prevalence and group size. In general, group size is positively correlated with infection intensity and prevalence (Côté and Poulin 1995, Patterson and Ruckstuhl 2013).

However, under density-dependent transmission, strong conspecific attraction reverses this, i.e. slows or prevents the spread of disease. This seems counter-intuitive but can be explained by noticing that strong attraction to each other but not to specific sites results in the formation of many small aggregations such that only a small number of susceptible individuals will be exposed to the small number of initially infected individuals, resulting in slower spread. Similarly, Griffin and Nunn (2011) simulated the spread of an infectious pathogen in social networks that differed in levels of community modularity (i.e., the extent to which the population is divided into subgroups) and found that increasing modularity led to decreased pathogen success (Griffin and Nunn 2011). Our findings likewise show that infection is slowed when the population is split into small groups (roosts), but also indicate importantly that increases in the movement rates of individuals between small roosts do not increase infection rates (i.e., infection is slowed at small roosts despite unstable group membership).

Major differences in disease dynamics emerge between the two transmission modes we modeled. The strength of attraction to conspecifics (provided it is not zero) does not affect the always-rapid spread of a disease that has frequency-dependent transmission. Smaller roosts have much greater probability of infection per susceptible (i.e., λ) than larger roosts under frequency-dependent transmission, assuming the same number of infected individuals at small versus large roosts. This may be expected to lead to increased rates of infection at small versus large roosts but larger roosts with N infected individuals have a greater number of susceptibles than smaller roosts with N infected individuals, so the number of new infected individuals per day is higher in larger roosts despite the lower λ. Higher λ but smaller number of susceptibles in small roosts versus the lower λ but larger number of susceptibles in large roosts leads to relatively even spread of infection for all parameter combinations under frequency-dependent transmission. Because frequency-dependent transmission is clearly more robust to variation in roost size, these results suggest that this transmission mode may be more informative when modeling disease dynamics in systems where roost size and/or roost switching rates are unknown or vary.

There are many examples of diseases that are apparently spread through roost systems or aggregative behavior. The varying roosting behaviors of birds can influence the spread of disease throughout a population. For example, American Robins (*Turdus migratorius*) form large communal roosts after the breeding season and on the wintering grounds, and these aggregations have been implicated as amplification foci for West Nile virus (Diuk-Wasser et al. 2010, but see Krebs et al. 2014). As such, human infection of WNV may be increased in areas where communal robin roosts occur. Though WNV is mostly a vector-borne disease, bird-to-bird transmission has been documented in communal roosts of crows (Dawson et al. 2007). Sociality in animals often changes seasonally and seasonal increases in gregariousness can lead to increased infection rates (reviewed by Altizer et al. 2006). House finches (*Haemorhous mexicanus*), for example, aggregate in the winter, especially at feeders, leading to increased transmission of mycoplasmal conjunctivitis (Hosseini et al. 2004). Phocine distemper virus is spread amongst Harbor seals at their haulouts where seals aggregate seasonally on sea ice or beaches (Swinton et al. 1998). We see this even in humans: the classic example is that increased contact rates among schoolchildren in the fall and winter often lead to seasonal outbreaks of measles and mumps, whereas outbreaks during summer months with decreased social contacts occur less often (London and Yorke 1973).

Likewise, though bats vary in their social and roosting behaviors, the North American bats most affected by White-nose syndrome (WNS) are all species that hibernate in aggregations during the winter (Cryan et al. 2010), where transmission of the disease is most prevalent (Langwig et al. 2015). It is currently not known whether WNS is spread via a frequency- or density-dependent mode (Foley et al. 2011) or some other mode, and the transmission mode may in fact be different for different species (Langwig et al. 2012). Predicting disease dynamics in this system would be aided by a better understanding of where and when bat-to-bat transmission occurs, together with the movement dynamics of bats between roosts and hibernacula prior to hibernation.

Potential extensions of the model

Our model provides a framework in which disease dynamics can be understood in organisms that aggregate daily or seasonally. We do not model a specific disease in a specific organism, but rather show generally how aggregative behaviors can interact to affect transmission of a hypothetical disease throughout a population that forms communal roosts. Many modifications of the model input and output are possible to help shed light on specific disease systems.

Habitat selection. In our model, the matrix is a 30x30 grid in which any cell is potential roosting habitat. It would be straightforward to make the model spatially explicit by adding a habitat matrix onto the grid, which would allow us to model the effects of habitat fragmentation on roosting dynamics and disease spread within such systems. A real-world example of such a process is in pinniped aggregations. Seals and walruses aggregate during certain portions of the annual cycle, and it is generally assumed that diseases such as phocine distemper virus are transmitted between individuals at such haulouts rather than in the water (Swinton et al. 1998). Melting sea ice due to global warming has caused haulout habitat loss, forcing pinnipeds into much larger aggregations than seen historically (Lavigne and Schmitz 1990). These larger-than-average aggregations would exacerbate disease spread throughout the population, especially in instances where transmission is all or partly density-dependent.

Variation in individual-level behaviors. One feature of our model is that all individuals follow the same movement rule for a given parameter combination. This is not always the case in real systems, where individuals may vary in their movement behaviors. Leader-follower dynamics (e.g. Biro et al. 2006), for example, will influence the movements of individuals, and in our model would lead to different roost configurations and individual return rates. Likewise, in our model an individual's infectious state does not affect its behavior; that is, once an individual becomes infected, it does not move less, use fewer roosts, or aggregate less often then susceptible individuals. However, empirical evidence suggests that infectious diseases can alter both individual- and group-level roosting behavior. American Crows infected with WNV, for example, undergo significantly reduced movements between communal roosts (Ward et al. 2006). Langwig et al. (2012)

found that little brown myotis bats (*Myotis lucifugus*) alter their roosting behavior in response to WNS infection. They found that bats clustered in hibernacula at much higher rates prior to infection, but after WNS detection, the number of bats roosting singly was 17 times greater than before detection. In these examples, infection can either increase roost fidelity (as in crows) or decrease conspecific attraction (as in myotis bats); it is thus clear that different diseases alter behaviors of individuals in different ways, introducing feedbacks into the disease dynamics.

Social network analysis. Another way of exploring the results of this type of model would be to output a social network (Krause et al. 2007) from the movement results and then calculate network metrics, such as centrality (Borgatti 2005) or exclusivity (Sih et al. 2009) in order to determine which metrics are most closely associated with infection rate. More usually, in social network analysis, these network metrics are inputs to the model and are systematically varied to examine their influence on social dynamics. Griffin and Nunn (2012), for example, examined the influence of community modularity on infection rate throughout a network and found that increased modularity (i.e., the degree to which the population split into subgroups) slowed the rate of infection, analogous to our results in which density-dependent infection rate was weakened in systems with many small roosts.

Transmission mode. Probably the most important component in disease modeling is the transmission function (McCallum et al. 2001) as disease dynamics are greatly influenced by the choice of function used in the modeling process (Dwyer et al. 2000, Fenton et al. 2002). The assumption of a linear relationship between population density and probability of infection (Kermack and McKendrick 1927, Anderson and May 1979) is not valid for all disease dynamics, for example sexually transmitted diseases (STDs) and vector borne pathogen dynamics. Frequency-dependent transmission is generally used in models of STD dynamics, where the number of sexual encounters per individual does not necessarily increase as a function of population density (Anderson and May 1991, Thrall et al. 1993). Likewise in vector-borne pathogen dynamics, the probability of a host becoming infected may not increase with host density, but is more related to vector dynamics and behavior (Antonovics et al. 1995). However, the complexities of real-world transmission dynamics often require variations on these basic functions. Ryder et al. (2007) built a model in which they combined frequency- and density-dependent transmission, varying the levels of each transmission function in order to simulate systems in which both types of transmission occur. Our model reinforces the distinction between frequency- and density-dependent transmissions, and can incorporate other transmission modes if the system in question requires, including non-linear functions (e.g. Barlow 2000, Fenton et al. 2002).

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Table 4.1. Definitions of model parameters and emergent properties

Parameter	Symbol	Range	Definition
Conspecific attraction	γCA	0 – 1	Value multiplied by proportion of conspecifics in each neighborhood cell
Roost fidelity	γRF	0 – 1	Value multiplied by distance improvement from current position to each neighborhood cell
Transmission coefficient	β or β'	0.5 / 0.0005	Frequency- and Density-dependent (respectively) coefficient used to calculate probability of infection (see Equations 1 & 2).

Property	Symbol	Range	Definition
Individual return rate	IRR	0 - 1	50-day mean proportion of roosting birds that returned to their previous day roost
Roost consistency	RC	0 - 1	50-day mean of proportion of original roosts that re-formed, divided by total number of roosts
Roost size	RS	0 - ~1,250	50-day mean of number of individuals within each roost
Number of roosts	NR	0 - ~35	50-day mean number of unique roosts at end of model run
Proportion infected	PI_t	0 - 1	Proportion of infected individuals after day t

Table 4.2. Results of multiple regression of PI_{20_FD}, PI_{20_DD}, and PI_{50_DD} with model parameters and Pearsons's correlation coefficient of PI_{20_FD}, PI_{20_DD}, and PI_{50_DD}

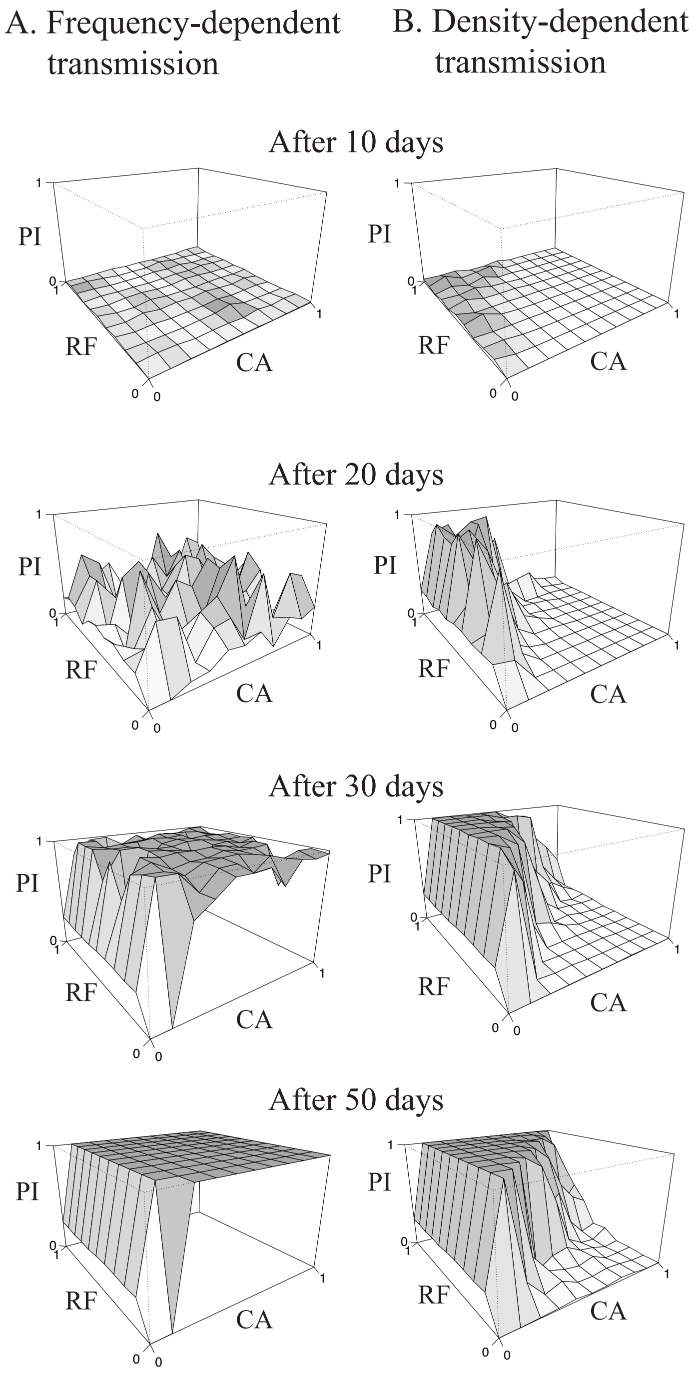
As function of model parameters and their interaction

Model	$F\text{-value}_{DF}$	R^2	P-value	γRF	γCA	Interaction
PI_{20_FD}	$1.685_{3,117}$	0.017	0.174	0.33	0.19	0.697
PI_{20_DD}	$45.84_{3,117}$	0.53	< 0.0001	< 0.0001	0.117	< 0.0002
PI_{50_DD}	$55.42_{3,117}$	0.58	< 0.0001	0.0004	< 0.0001	0.00213

Correlations with model properties

Model	IRR	RC	NR	RS
PI_{20_FD}	-0.1	0.02	0.03	-0.06
PI_{20_DD}	0.74*	0.63*	-0.6*	0.8*
PI_{50_DD}	0.5*	0.7*	-0.76*	0.63*

* denotes P-value < 0.0001. No asterisk denotes non-significant P-value for correlation tests.


A. Frequency-dependent transmission

B. Density-dependent transmission

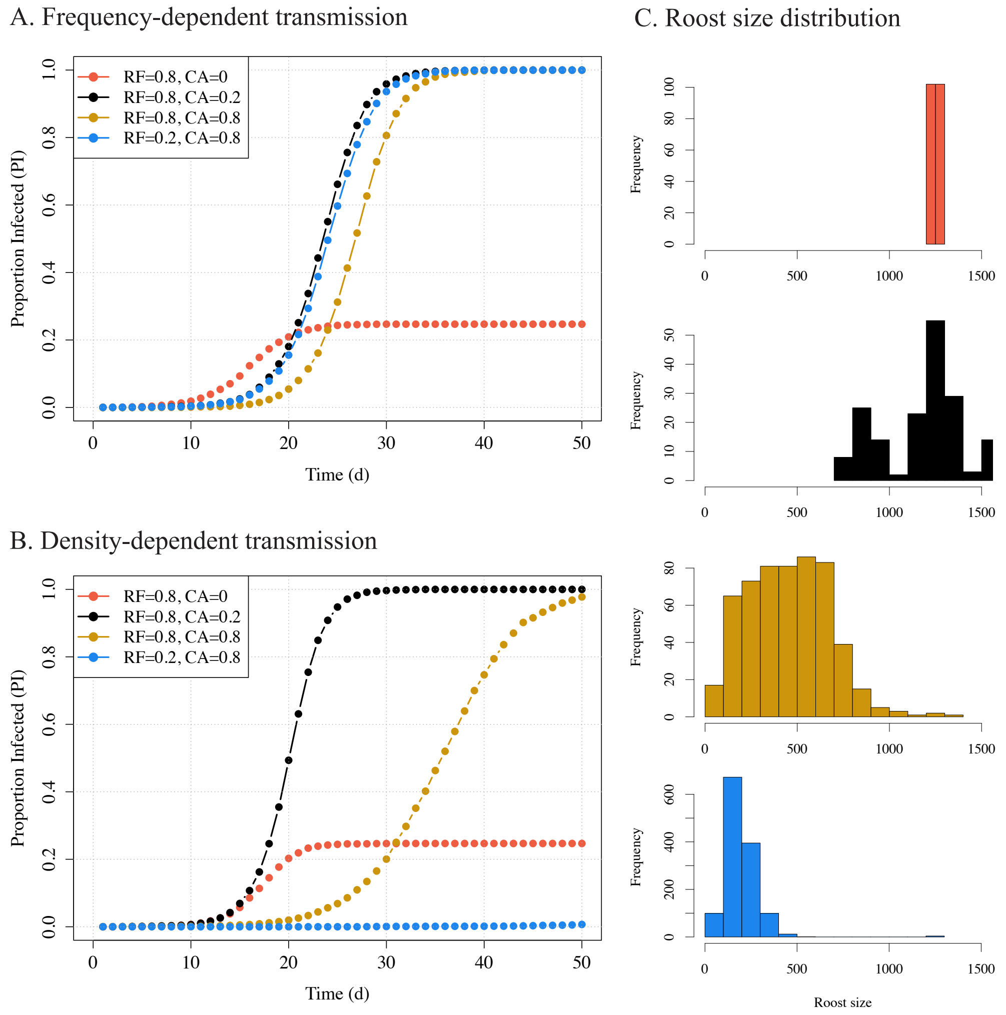
After 10 days

After 20 days

After 30 days

After 50 days

Figure 4.1. *γRF* and *γCA* parameter space showing the proportion of the population infected (PI) after 10 days, 20 days, 30 days, and 50 days under A. frequency- (left column) and B. density-dependent (right column) transmission.



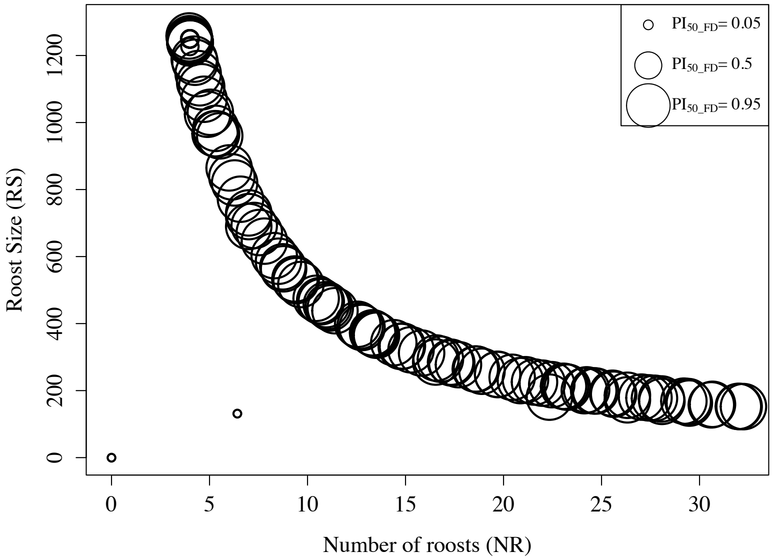
A. Frequency-dependent transmission

B. Density-dependent transmission

C. Roost size distribution

Figure 4.2. Proportion infected (PI) as a function of time (50 days) for four representative parameter combinations. A. Under frequency-dependent transmission, for most combinations where CA > 0, infection spreads evenly. B. Under density-dependent transmission, infection is fastest when *γRF* is high and *γCA* is low (black), medium when *γRF* and *γCA* are approximately equal (brown), and slowest when *γRF* is low and *γCA* is high (blue). C. Roost size distributions for the four representative parameter combinations color-coded accordingly.

A. Frequency-dependent transmission



B. Density-dependent transmission

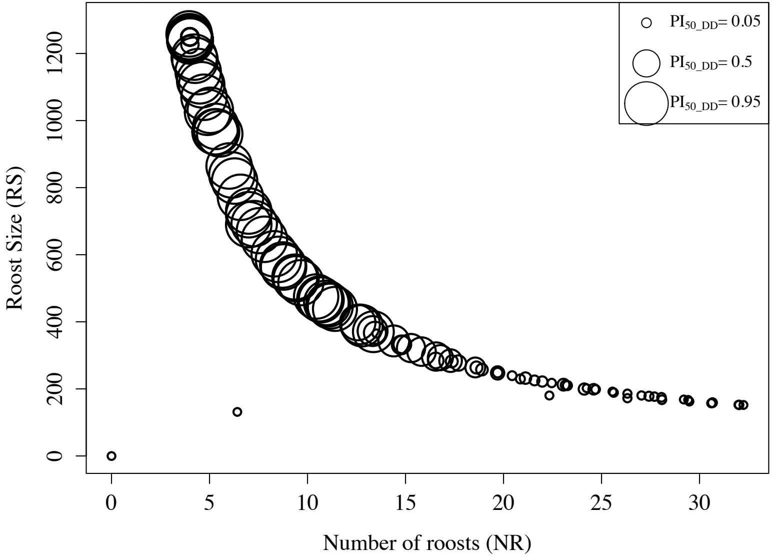
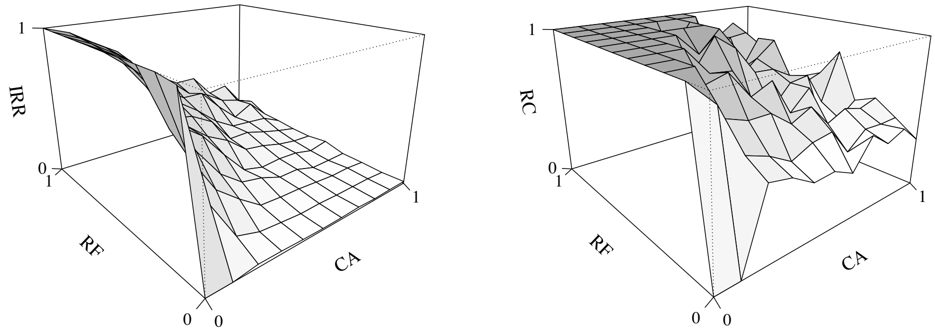
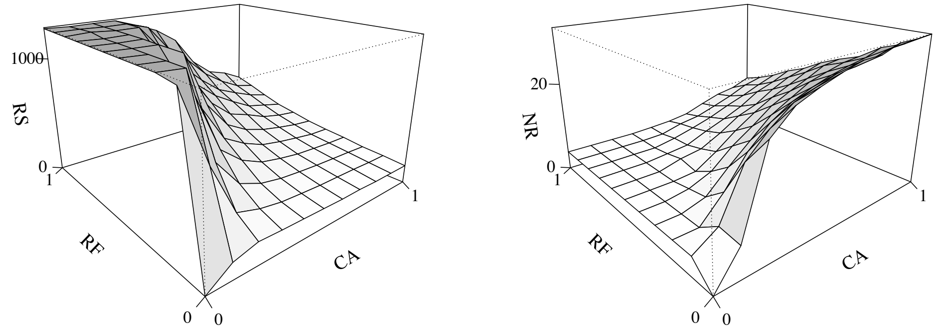


Figure 4.3. Relationship between roost size (RS) and number of roosts (NR) for all model runs. The size of the circle corresponds to the proportion of infected population after 50 days (PI_{50}) under A. frequency-dependent transmission, and B. density-dependent transmission.


A. Individual return rate (IRR)

B. Roost consistency (RC)


C. Roost size (RS)

D. Number of roosts (NR)

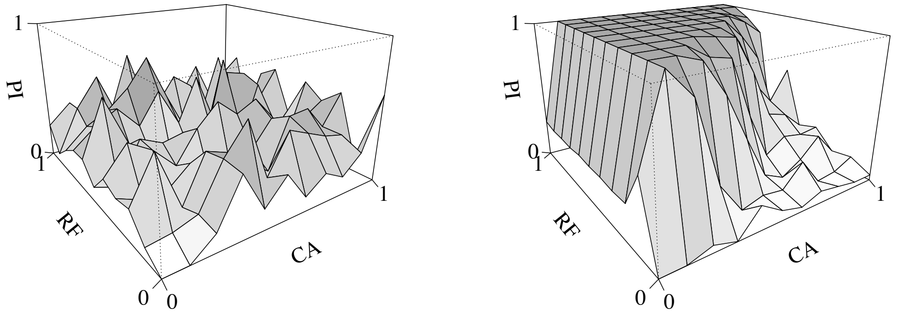
Figure 4.4. Emergent model properties as a function of *γRF* and *γCA* : A. Individual return rate (IRR), B. mean roost consistency (RC), C. mean roost size (RS), and D. mean number of roosts (NR).

Frequency-dependent transmission

Density-dependent transmission

A. PI_{20_FD} when $N_r = 260$

B. PI_{20_DD} when $N_r = 260$



C. PI_{20_FD} when $N_r = 1215$

D. PI_{20_DD} when $N_r = 1215$

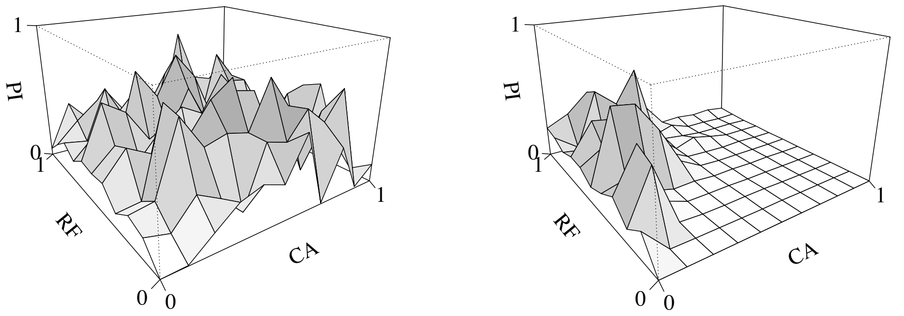


Figure 4.5. PI_{20} when β is scaled to A. $N_r = 260$ and C. $N_r = 1215$ under frequency-dependent transmission, and B. $N_r = 260$ and D. $N_r = 1215$ under density-dependent transmission

BIOGRAPHY

Andrew Laughlin was born in Pittsburgh, PA in 1975, graduated High School in 1993, and attended Calvin College where he graduated with a BA in English/Classics in 1997. After deciding to pursue a career in ecology, he enrolled in post-baccalaureate courses from AB-Tech and UNC Asheville before entering East Tennessee State University where he earned a MS in Biological Sciences in 2010. After completing his Ph.D. in ecology, he is looking forward to catching up on the many novels he has had to put on hold, playing and writing more music for guitar, and playing a lot more with his kids before they grow up. He, along with his wife Laura and three children (Ramona, Astrid, and Reuben) will be re-locating in the summer of 2015 to Asheville, NC, birthplace of their two daughters.