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Investigating The Population Dynamics of an Avian Apex Predator Across an Urban Gradient

Donna Marain
dmolf001@fiu.edu

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FLORIDA INTERNATIONAL UNIVERSITY

Miami, Florida

INVESTIGATING THE POPULATION DYNAMICS OF AN AVIAN APEX PREDATOR ACROSS AN URBAN GRADIENT

A dissertation submitted in partial fulfillment of

the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

BIOLOGY

by

Donna Marain

2020

To: Dean Michael R. Heithaus
College of Arts, Sciences and Education

This dissertation, written by Donna Marain, and entitled Investigating the Population Dynamics of an Avian Apex Predator Across an Urban Gradient, having been approved in respect to style and intellectual content, is referred to you for judgment.

We have read this dissertation and recommend that it be approved.

Daniel Gann

Dale E. Gawlik

Michael Heithaus

Gary Rand

Philip Stoddard

Joel Trexler, Major Professor

Date of Defense: November 5, 2020

The dissertation of Donna Marain is approved.

Dean Michael R. Heithaus
College of Arts, Sciences and Education

Andrés G. Gil
Vice President for Research and Economic Development
and Dean of the University Graduate School

Florida International University, 2020

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ABSTRACT OF THE DISSERTATION

INVESTIGATING THE POPULATION DYNAMICS OF AN AVIAN APEX PREDATOR ACROSS AN URBAN GRADIENT

by

Donna Marain

Florida International University, 2020

Miami, Florida

Professor Joel Trexler, Major Professor

Predators are often the focus of conservation efforts. They can be useful sentinel species, umbrella species, and flagship species. Predators can also be the first guild lost when ecosystems are under stress, especially from anthropogenic land-use change. Raptors can be an exception to this trend, filling the role of apex predators across the urban gradient. South Florida contains the Everglades ecosystem and one of the fastest growing human populations in the country. In the current study, I investigated the population dynamics of South Florida’s most abundant hawk: the Red-shouldered Hawk (*Buteo lineatus*, RSHA) across the urban gradient.

South Florida is home to its own subspecies of RSHA (*Buteo lineatus extimus*), which has heretofore received little formal study. I first observed breeding attempts to quantify the productivity of the southern subspecies. South Florida RSHAs were found to be equally productive in urban and exurban areas and produced 1.8 ± 0.6 fledglings per successful nest, about average for this species. I developed habitat maps around each nest using remote sensing, but land cover was not related to the likelihood of nest success.

I then placed cameras in nests to observe the prey items fed to chicks. Adults fed primarily reptiles (58%) and amphibians (18%). I also partnered with three wildlife rehabilitation hospitals to screen RSHAs that perished in their care for anticoagulant rodenticides (ARs). The Environmental Protection Agency restricted the sale of ARs to the public in 2008 in part to reduce secondary poisoning to wildlife like raptors. Despite these restrictions and the low rate of mammal consumption among local birds, 49% of RSHAs screened had been exposed to ARs.

Finally, I investigated the genetic diversity of RSHAs and found evidence for a genetic bottleneck, reduced genetic diversity, and inbreeding in the focal population. My study found RSHAs in South Florida to be very flexible in their diet and nest sites but also found reduced genetic diversity and high rates of exposure to toxins. Additional research is needed to determine whether the population is increasing, stable, or declining in the rapidly urbanizing region.

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CHAPTER 1

INTRODUCTION

Predators are often chosen as the focus of conservation efforts (Clucas et al. 2008, Sergio et al. 2008). At times, these species are chosen for their public appeal to garner support and/or funding for conservation efforts (Clucas et al. 2008, Sergio et al. 2008). Iconic taxa are known as flagship species. Other times, predators are the focus of conservation efforts for their ecological role in the ecosystems where they live (Sergio et al. 2008). Predators can be keystone species, shaping their environment more than would be expected on the basis of their abundance (Sergio et al. 2008). Predators can be umbrella species; protecting the large areas covered by their territories extends protections to species with smaller home ranges (Sergio et al. 2008). Predators can be sentinel species because many aspects of their natural history (large home ranges, territoriality, long-lifespan, etc.) make them especially vulnerable to ecosystem disturbances (Sergio et al. 2008). These ecosystem functions can be very species- and ecosystem-specific, therefore research is needed to verify the links between the desired conservation outcome and the species of conservation interest (Sergio et al. 2008).

One ecosystem disturbance that is often detrimental to predators is anthropogenic land-use change, especially urbanization (Fischer et al. 2012). The largest apex predators are often absent in human-dominated landscapes, allowing small predators to fill the ecological role of top predators in urban areas (Fischer et al. 2012). One notable exception to the replacement rule includes avian predators (raptors), many of which successfully hunt and breed in cities worldwide (White et al. 2017). Now that more than half the world’s population and over 80% of Americans live in cities, urban raptors can serve as backyard ambassadors, increasing residents’ awareness and concern for the environment more broadly (Davis 2018). Urban raptors can also provide desirable ecosystem services such as rodent control (Hindmarch and Elliott 2014) or scavenging carcasses (Huijbers et al. 2015). Of course, not all raptors are able to successfully inhabit urban places (Chace and Walsh 2006) and even those that do may not use the most highly urbanized city centers (White et al. 2017).

In the United States, Florida is in the top five most populous states with the third fastest population growth rate (Reece et al. 2013). Florida is home to many unique species and subspecies of animals because it served as a glacial refuge during the last glacial maximum and today boasts a subtropical climate unique in the country (Eo et al. 2010, Barrowclough et al. 2019). South Florida, specifically Miami-Dade, Broward, and Palm Beach counties, is where much of Florida's human population growth has occurred since the 1960s (Nijman and Clery 2015). At the same time, Miami-Dade County is the only county in the contiguous United States with two National Parks within its borders (Nijman and Clery 2015). To protect the unique biodiversity of the region, all three counties contain political boundaries which divide developable land to the east from protected natural lands to the west (Nijman and Clery 2015). The stark juxtaposition of protected natural lands and a very highly urbanized population center provides an excellent study setting for examining whether raptors are able to adjust to high levels of urbanization.

I chose to examine various aspects of the life history of Florida's most abundant hawk: the Red-shouldered Hawk (*Buteo lineatus*) in my dissertation research. The Red-shouldered Hawks within the study area belong to a Florida endemic subspecies, *B. l. extimus* that has received very little study previously. In South Florida, Red-shouldered Hawks often serve as the avian apex predator because large raptors are less abundant than the RSHA (eBird 2020). Therefore, my dissertation serves two important purposes: providing the first formal natural history information for the subspecies as well as examining the adaptability of an avian apex predator to a rapidly urbanizing landscape.

Dozens of raptor species have been found to inhabit urban areas, but not all have established breeding populations (Hager 2009). Even among species that do breed in urban areas, few have higher reproductive output than their exurban conspecifics (Kettel et al. 2018). Reproduction, mortality, immigration, and emigration are the fundamental processes that determine population growth rates (Steenhof and Newton 2007). In a long-lived, highly mobile, cryptic guild like raptors, tracking immigration, emigration, and mortality can be time-consuming and challenging (Wiens and Reynolds 2005). Quantifying reproductive rates can provide the quickest insight into an important contributing factor to population persistence. In Chapter II, I followed Red-shouldered Hawk breeding attempts at both urban and exurban nest sites across the tri-county area for three years to determine rates of nest success and productivity. I also developed habitat maps for a 500-meter area surrounding each nest using WorldView2 satellite imagery to investigate whether likelihood of reproductive success correlated with the habitat surrounding a nest.

One of the primary factors that contributes to reproductive success in raptors is prey availability (Kettel et al. 2018). At the start of the breeding season, adult females must achieve an above average body condition in order to produce eggs and/or eggs that are likely to hatch (Weibe and Bortolotti 1995, Newton 2010). The importance of prey availability continues after hatching. Many raptor species exhibit increased aggression between siblings, including siblicide, when food resources are scarce (Morandini and

Ferrer 2015). The diet breadth and preferred prey of raptors is consistently found to be a determining factor for which species inhabit and breed in urban areas because many prey species are absent from urban locations (Boal 2018, Kettel et al. 2018). In Chapter III, I placed cameras in a subset of nests across the urban gradient to record prey deliveries adult hawks made to chicks. Cameras were set to record continuously for 14 hours, beginning an hour before sunrise and ending an hour after sunset each day. Prey items were identified to class (Aves, Mammalia, Reptilia, etc.) and the amount of time spent feeding each item was recorded to the nearest second as a proxy for biomass.

In long-lived species, adult mortality is often found to have a larger impact on population persistence than reproductive output (Monzón and Friedenberg 2018). Urban environments contain many anthropogenic sources of mortality that are absent from exurban areas (Hager 2009). A growing body of research has documented the high rates of exposure to anticoagulant rodenticides (ARs) in urban raptors (Murray 2017). The United State Environmental Protection Agency restricted the sale of ARs to the public in 2008, partly to reduce the risk of secondary poisoning in raptors (Murray 2017). Research is needed to determine whether the AR risk to raptors persists despite these regulations. In Chapter IV, I partnered with three wildlife rehabilitation hospitals in my tri-county study area to collect any Red-shouldered Hawks that died during their course of care. I then removed the livers from these birds and sent them to the Iowa State University Veterinary Diagnostic Laboratory to be screened for nine ARs. Red-shouldered Hawks have only been included in one prior study of AR exposure in raptors (Weir et al. 2018), perhaps because the commensal rodents targeted by ARs are not a typical prey item of this species, and no prior study has examined AR exposure in any raptor in Florida.

Because demographic studies of raptors can be time-consuming and challenging, genetics can be a useful alternative pathway to investigate population persistence (Booms et al. 2011). Only a single sampling event is necessary per individual and a limited number of samples from a population may provide sufficient information to answer conservation questions (Hale et al. 2012). Genetic sampling can be non-invasive and does not require the researcher to encounter the animal (Martínez-Cruz and Camarena 2018). In Chapter V, I examined the genetic diversity at nine microsatellite loci in Red-shouldered Hawks sampled in my tri-county study area. The California subspecies of Red-shouldered Hawk is known to have suffered a genetic bottleneck within the last 200 years, which coincides with human population growth in that state (Hull et al. 2008). I tested Florida birds for a genetic bottleneck and compared their measures of genetic diversity to those of the California and eastern United States Red-shouldered Hawk subspecies. Finally, I investigated whether the population of Red-shouldered Hawks was panmictic across my study area by testing for isolation-by-distance and differentiation between birds collected in urban areas versus exurban areas.

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CHAPTER II

BREEDING ECOLOGY OF THE SOUTH FLORIDA RED-SHOULDERED HAWK (*BUTEO LINEATUS EXTIMUS*)

ABSTRACT – Many raptor species with large ranges are made up of subspecies that vary in their morphology, behavior, and local ecological niche. These subspecies are often the focus of conservation efforts and therefore require their own study. The subspecies of Red-shouldered Hawk (*Buteo lineatus extimus*) that occurs in South Florida has yet to receive any formal study into its breeding ecology. Eighty-two breeding attempts of this subspecies were observed over three years, 62 of which included incubation, and 47 of which resulted in fledglings. The productivity at successful nests was 1.86 ± 0.6 nestlings. In addition, habitat maps for a 500-meter radius around each nest were developed using WorldView2 satellite imagery. Six land cover classes were mapped: dense wetland, sparse wetland, grass, trees, water, and impervious surface. Hawks nested in a wide variety of habitats and no relationship was found between land cover variables and the likelihood of nest success. Though palm trees were the most frequently chosen nesting place, nests in palms failed as often as they succeeded. Compared to Red-shouldered Hawks in other parts of the country, the present study found an average productivity rate and a much more diverse set of nest sites, both the structures on which the hawks nested and the habitats surrounding those structures.

Key words: remote sensing, nesting, productivity, habitat, urban

The distributions of many raptor species can span entire continents, if not the globe. Consequently, these raptor species can be made up of several subspecies that exhibit different plumages (Talbot et al. 2017), morphologies (Baladrón et al. 2015), and behaviors (Vrezec et al. 2018) resulting in each subspecies occupying its own unique ecological niche in its environment. Many subspecies were described decades or centuries ago using plumage and morphological characteristics. In recent years, controversy has surrounded the use of avian subspecies designations in conservation because genetic investigations often fail to find genetic differentiation between described avian subspecies (Zink 2004, Phillmore and Owens 2006). Despite the controversy, US law still uses subspecies designations to indicate which populations fall under conservation management (Haig et al. 20016).

Florida boasts several avian subspecies thanks to its unique geologic history compared to the rest of the continental United States as well as its present-day subtropical climate (Eo et al. 2010, Barrowclough et al. 2019). Because the peninsula served as a refuge during the last glacial maximum, genetic investigations into modern-day Florida subspecies tend to find sufficient genetic differentiation from mainland populations to support their subspecies designations (Eo et al. 2010, Barrowclough et al. 2019). Florida is also especially vulnerable to two of the top threats to birds this century: habitat loss caused by anthropogenic land-use changes and climate change (Reece et al. 2013, Rosenberg et al. 2019).

The Red-shouldered Hawk of southern Florida (*Buteo lineatus extimus*) is one such subspecies that has morphologic (Jacobs and Jacobs 2002), behavioral (Ogden 1974), and genetic (Barrowclough et al. 2019) distinctions from its mainland conspecifics. The Red-shouldered Hawk species was once thought to contain five subspecies: *B. l. elegans* in the western United States, *B. l. texanus* in eastern Texas, *B. l. alleni* in the southeastern United States, *B. l. lineatus* in the Northeast and Midwest, and *B. l. extimus* in South Florida (Hull et al. 2008). However, recent genetic work has found significant genetic variation (Φ_{ST}=0.08, $P < 0.001$) among birds in only three regions of this species' range: California, Florida, and the eastern United States (Barrowclough et al. 2019). Despite its status as the most abundant hawk in the state, where it often fills the ecological niche of top avian predator because of the low abundance of large raptors, no study has yet characterized the breeding biology of Red-shouldered Hawks in South Florida (Toland 2003, eBird 2020).

Red-shouldered Hawks have been found to avoid or thrive in urban areas in different parts of their range. Red-shouldered Hawks were found to avoid urban areas most strongly of seven raptor species studied in New Jersey (Bosakowski and Smith 1997), but thrive in urbanized areas of Ohio (Dykstra et al. 2009) and California (Rottenborn 2000). Two factors play a critical role in predicting which raptors will inhabit and reproduce in urban areas: their natural habitat and their diet (Boal 2018). Red-shouldered Hawks in South Florida often rely on open wetlands, a very different habitat from the forested landscapes where they have been previously studied (Morrison et al. 2007). Forest dwelling raptors are more likely to inhabit urban places than marshland birds (Boal 2018). And while raptors with a generalist diet are found in urban areas more often (Boal 2018), only bird specialists consistently experience higher reproduction when breeding in urban habitats (Kettel et al. 2018).

We followed Red-shouldered Hawk breeding attempts in three South Florida counties over three breeding seasons to quantify their productivity because this basic natural history information has not been quantified for this subspecies before. We also used remote sensing to characterize the habitat surrounding both successful and unsuccessful nests for two reasons: in order to allow comparisons between territories in this region and other states and to attempt to relate land-cover characteristics to breeding outcomes in this population.

Methods

The study took place in Miami-Dade, Broward, and Palm Beach counties in Florida (Fig. 1) beginning in the first week of January and ending during the first week of May in 2017, 2018, and 2019. North-south boundary lines split each county nearly in half, with state- and federally protected Everglades wetlands to the west and human-dominated landscapes to the east (Nijman and Clery 2003). Population growth in these three counties has quintupled to over five million people since the 1960s, with development expanding westward to house the growing populace (Nijman and Clery 2003).

In studies of breeding raptors, nest surveys are commonly conducted before leaf-out in the spring when stick nests are detectable in the trees (Miller et al. 2015, Millsap 2018). However, most south Florida trees (except for cypress trees) do not experience abscission. We found Red-shouldered Hawk nests by playing conspecific calls in areas known to have Red-shouldered Hawk activity through eBird and direct reports to the corresponding author. If adult hawks responded by calling or flying towards the researcher, their behavior was then monitored until they resumed normal behavior that revealed the site of their nest, i.e., nest building. Sites where hawks responded to conspecific calls were then visited at least once every two weeks until the outcome of the breeding attempt was clear. Breeding attempts were defined to include breeding activity observed (e.g. copulation) but no nest found, nest building but no incubation, incubation but no hatching, nest fell to the ground with no replacement clutch attempted, a replacement clutch was laid which either succeeded or failed, chicks hatched but none fledged, or chicks fledged. Similar to Dykstra et al. (2009), chicks were assumed to have fledged if they appeared to be at least three weeks old. Statistics were only conducted on the 62 breeding attempts with observed incubation. The type of structure on which the nest was built and the number of chicks fledged, if any, were also noted.

Because the study area encompassed three counties, each with their own land-cover classification schemes, we developed standardized maps to compare all nesting sites. We used WorldView2 (WV2) satellite imagery to characterize the habitat within a 500-meter radius of each nest. Five-hundred meters was chosen to conform with previous investigations of the habitat surrounding the nests of this species (Rottenborn 2000, Dykstra et al. forthcoming 2020), but also appeared appropriate on the basis of the behavioral observations of the hawks in the current study.

The WV2 satellite images were geometrically and atmospherically corrected to percent reflectance values in eight bands of the electromagnetic spectrum. The spatial resolution of the data was 4 m^2 (2 m x 2 m). We mapped six broad land-cover categories (1) dense wetland (i.e., dense cattail, wetland shrubbery, or floating vegetation) where the hawks are unlikely to hunt but these areas likely still provide habitat for prey, (2) sparse wetland, where the hawks hunt, (3) grass, also likely used for hunting, (4) trees, which provide nesting places, (5) impervious surface (including buildings, roads, gravel levees, and sand), and (6) deep water. Concurrent data collected from nest cameras showed Red-shouldered Hawks in the study area ate a wide variety of both terrestrial and aquatic prey such as walking catfish (*Clarias batrachus*), juvenile American alligators (*Alligator mississippiensis*), Common Galinules (*Gallinula galeata*), green iguanas (*Iguana iguana*), and various snakes, rabbits, rodents, and more (DM, 2020, unpubl. data), which informed our determinations of prey habitat.

Satellite images, when available, were chosen from January or February of 2017, 2018, or 2019 because the time frame corresponded to when adult hawks were choosing their nest sites. Training points were digitized for each of the six land-cover classes on the WV2 satellite image within each 500-meter circle in ArcMap 10.5 (ESRI, Redlands, CA). A minimum of 121 and a maximum of 537 training points were placed in each 500-meter circle for a total of 10,034 training points across the 53 nest sites (Fig. 2). Fifty-three nest sites were mapped because at some sites, hawks switched nest trees between years. Land cover surrounding the nests varied widely. We then read the 500-meter circles and the training points into Program R (R Development Core Team 2012) using the RGDAL package (Bivand et al. 2017), extracted the spectral data from the relevant satellite image using the RASTER package (Hijmans 2014), merged the spectral information of the satellite image to the training points in each land-cover class. The merged data were used to train random-forest classifiers (Liaw and Wiener 2002) to then predict the land-cover class of all pixels within each 500-meter circle using the RASTER package.

Minimum-mapping units were used to aggregate small clusters of pixels into the surrounding land-cover type. Minimum mapping units for each land-cover type were as follows: 40 pixels for dense wetland, 40 pixels for sparse wetland, 20 pixels for grass, 20 pixels for water, 10 pixels for trees, and 10 pixels for impervious surfaces. Impervious surface and trees received the smallest minimum-mapping units because they often occurred in narrow strips that could still be of biological significance to the hawks, whereas wetlands rarely occurred in such small configurations.

For the accuracy assessment, we evaluated maps to be at least 90% accurate with an accuracy confidence of 95%. We used the formula $N = \frac{B\Pi_i(1-\Pi_i)}{b_i^2}$ from multinomial sampling theory, where Π is the proportion of the class closest to 50% cover, B is the critical value associated with the upper tail of the Chi-squared distribution, b is the allowable error of the estimate, and N is the number of points to randomly sample, evenly distributed across all land-cover classes. Each randomly placed point was assigned a land-cover class by examining the spectral signature of the satellite image. The land-cover class assigned to the accuracy assessment points was then cross-tabulated with the predicted land-cover class in the corresponding map to generate a confusion matrix. The mapping was iterative, samples were added at each iteration until all land-cover classes were at least 90% accurate.

Binomial logistic regressions were used to relate reproductive outcomes (chicks fledged or not) to the amount of each land-cover type in each 500-meter circle surrounding the 62 nest trees where incubation was observed, the kind of structure in which the birds nested (palm or not palm), and the nest site location (urban, edge, or exurban). Breeding success was modeled for isometric log ratio transformed land cover proportions. Land-cover proportions were all included in a general model, run separately in univariate models, and two aggregations were also tested in univariate models: combining the sparse and dense wetland categories into a single wetland category and combining sparse wetland with grass because these were thought to be the best land-cover types for hunting. Only the one binary reproductive dependent variable was examined because reproductive outcomes were too variable and nest observations too few to support more nuanced investigations. Kruskal-Wallis tests were used to test for differences between groups. Means are reported with standard deviations.

Results

Over the three years of the study, we observed 82 breeding attempts at 41 nest sites (Fig. 3). We observed incubation during 62 breeding attempts and observed fledgling-age chicks during 47 breeding attempts. Once incubation was observed, 76% of nests were successful. Only four of the 47 breeding attempts with chicks were found after chicks had hatched. Among the 20 sites where we did not observe egg-laying, we did not find nests at 11 of these and nine had nest-building, but no observed incubation. These 20 nests were not included in any of the statistical analyses. Among the 15 unsuccessful nests with observed incubation, failures were split between nests falling out of the tree during incubation with no replacement clutch observed (*n*=5), extended incubation (>two months) with no chicks observed (*n*=5), an abrupt abandonment of the breeding attempt during incubation (*n*=3), and disappearance of the chicks before fledging age (*n*=2). Replacement clutches were definitively observed on two occasions when incubation was observed on one nest that produced no chicks and then incubation was initiated in another nest. One replacement clutch succeeded, fledging two chicks, and one failed.

Productivity at nests with documented incubation was 1.42 ± 0.94 (*n*=58) and for successful nests 1.86 ± 0.6 (*n*=43) (the four nests found post-hatching were not included in either calculation). Two chicks was the most common number fledged from successful nests (*n*=28), followed by single chicks (*n*=14), and three chicks (*n*=5). Nests were built most often in palm trees (*n*=17), followed by pine trees (10 native, 5 non-native), mahogany/oak trees (*n*=13), cypress trees (*n*=8), human structures (n=5, one metal walkway over water, one roof of a small concrete shed with solar panels, two electricity poles, and one wedged between metal scaffolding and an exterior wall), one large dead snag used three years in a row, and one nest built in between thin trees. Of the 41 nest sites, 14 had observed breeding activity (ranging from two adults sitting together during the pre-laying period to successfully fledging chicks) all three years of the study, 12 in two years, and 16 in one year. There was no difference in the proportion of any land-cover class surrounding nests used for one, two, or three years (*P*>0.05). Of the 14 nest sites with breeding activity in all three years, only two successfully produced chicks every year.

The first observation of incubation occurred most frequently in the second week of February, though in 2018, incubation was observed at two nests in the first week of January (both failed, though one laid a successful replacement clutch in mid-February). Chicks began to leave the nest for nearby branches most frequently in late April and early May, but the time span between the earliest observation of branching and the latest could be as much as eight weeks, from late March to late May. Subadult (1-year old) birds were observed breeding on three occasions, all at urban nests: one subadult male successfully fledged one chick with an adult female at a shopping mall, one subadult female successfully fledged two chicks with an adult male at a botanical garden, and one subadult female was observed copulating with an adult male but no nest was found at this site at an urban wetland preserve. One adult male nesting at a remote highway rest-stop managed to successfully fledge a chick despite an old, healed, severe humerus fracture.

Forty-eight of the observed breeding attempts were in exurban areas, 23 in urban areas, and 11 were located at the border of urban and exurban land. The results of the accuracy assessment were as follows: sparse wetland 94% accurate, trees 91%, impervious surface 99%, dense wetland 93%, grass 91%, and water 99% accurate. Percent coverage of each land-cover category ranged from 0-68% for dense wetland (μ=13% ± 19%), 0-79% for sparse wetland (μ=28% ± 25%), 0-62% for grass (μ=11% ± 13%), 0-38% for water (μ=9% ± 9%), 0-71% for trees (μ=26% ± 21%), and 1-62% for impervious surface (μ=14% ± 15%). Impervious surface was the only land-cover category that was mapped in every circle because of the nature of nest searches; vehicles were the only mode of transportation available for nest searches.

No relationship was found between the land-cover class data in any configuration (multivariate or univariate) and the likelihood of fledging chicks (P >0.05, Fig. 4). No difference was found between nest site location (urban, exurban, and edge) and the likelihood of fledging chicks (P >0.05). A Kruskal-Wallise test determined that productivity was not significantly different at successful urban nests (2 ± 0.63), successful exurban nests (1.75 ± 0.64 young), and successful nests at the edge of these two categories (1.75 ± 0.46, P>0.05). Chicks were eight times less likely to successfully fledge out of nests in palm trees compared to non-palm nest structures (P=0.001). Despite palm trees being the most frequently chosen nest site, nests in palms failed (n=9) as often as they succeeded (n=8). Other kinds of nest trees of similar height were available at 14 of the 17 breeding attempts with palm nests. Of the nine failures in palm tree nests, four fell, three had extended incubation, one appeared abandoned during the incubation stage, and one appeared abandoned after hatching but before fledging. Only 3 of 15 pine nests failed, only 1 of 13 nests in a mahogany or oak tree failed, only 1 of 8 nests in a cypress tree failed, and only 1 of 5 nests on human structures failed.

Discussion

The productivity of the Red-shouldered Hawks observed in this study is towards the middle of the range reported for this species (1-2.8 chicks per successful nest, Townsend 2006, Dykstra et al. forthcoming 2020). However, previous anecdotal reports from Everglades National Park suggest that three-sibling nests might have once been more common in a portion of my study area (Ogden 1974). Among breeding attempts where incubation was observed, 76% of nests successfully fledged young, which is among the higher rates reported in previous studies (55-74% Townsend 2006). Previous study of the RSHA in other states has found predation, either of adults or nestlings, to be a frequent cause of nest failure (Townsend 2006, Miller et al. 2015). Predation on RSHAs was never directly observed during this study; instead, here nests frequently failed during incubation, either because the nest fell to the ground, often with broken eggs inside, or resulted from extended periods of incubation without observations of chicks. Laying dates were also much earlier than for conspecifics elsewhere in the country (i.e., over one month earlier than Ohio birds, Dykstra et al. forthcoming 2020), which is to be expected because of known correlations between avian laying dates and latitudinal climate variation (Carrillo and González-Dávila 2010). Similar laying dates were reported for a conspecific population in central Florida (Morrison et al. 2007).

More research is needed to determine why Red-shouldered Hawks in South Florida so often built their nests in palm trees despite high rates of failure. Red-shouldered Hawks are also reported to nest in palm trees in California, but in contrast to this study, more fledglings were produced from nests in palms in California compared to nests in native cottonwood trees (Rottenborn 2000). Across their entire range, red-shouldered hawks were only reported to have nested on human structures six times prior to my study (Dykstra et al. forthcoming 2020). All nesting that occurred on human structures in my study were located in Stormwater Treatment Areas 2 and 3/4, both large constructed wetlands surrounded by earthen levees designed to remove phosphorus from polluted water from Lake Okeechobee before it reaches Everglades National Park to the south (Beck et al. 2013). Because these wetland cells are designed to be inundated, with only the levees above water for driving and electricity poles, trees are exceedingly rare. When present in these two STAs, trees were nearly always solitary and occupied by a Red-shouldered Hawk nest. This landscape contrasted sharply with nests at college campuses, business parks, and shopping malls in South Florida that had high amounts of impervious surface and/or tree cover within a 500-meter radius. Other nests were found within 500 meters of the ocean or with as little as 5% of the surrounding habitat considered good hunting habitat (grass and sparse wetland). The habitat variability surrounding successful nest sites in my study contrasts with prior studies where increasing forest cover correlates with reproductive success (Dykstra et al. forthcoming 2020) and higher occupancy rates (Henneman and Anderson 2009).

No relationships were found between the composition of any of the land-cover variables or nest site location (urban, exurban, edge) and the likelihood of nest success. Studies of Red-shouldered Hawks in urban areas in California and Ohio have also found no effect of urbanization on the reproductive success of Red-shouldered Hawks (Rottenborn 2000, Dykstra et al. forthcoming 2020). Many studies of raptor breeding biology use much longer study periods to investigate these relationships because raptor breeding is inherently variable from year to year (Stout et al. 2006, Dykstra et al. 2009). Even among the 14 nest sites with observed breeding activity in each year of the study, only two succeeded in fledging chicks each year. Clearly, additional factors, not just surrounding land cover, contribute to nest success or failure in this population. Future telemetry work is recommended to determine breeding season home range sizes for the Florida subspecies.

Hawks successfully fledged a similar number of young in urban, exurban, and edge nests, even when more than half of the habitat surrounding their nest was impervious surface. Our results are encouraging because the human population of South Florida has quintupled over the last fifty years and is still growing, with the urbanization to match (Nijman and Clery 2003). The adaptability of the local subspecies of Red-shouldered Hawks documented herein is perhaps an encouraging sign for the continued persistence of this unique subspecies in this area where it often fills the ecologically vital role of avian apex predator.

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Figure Captions

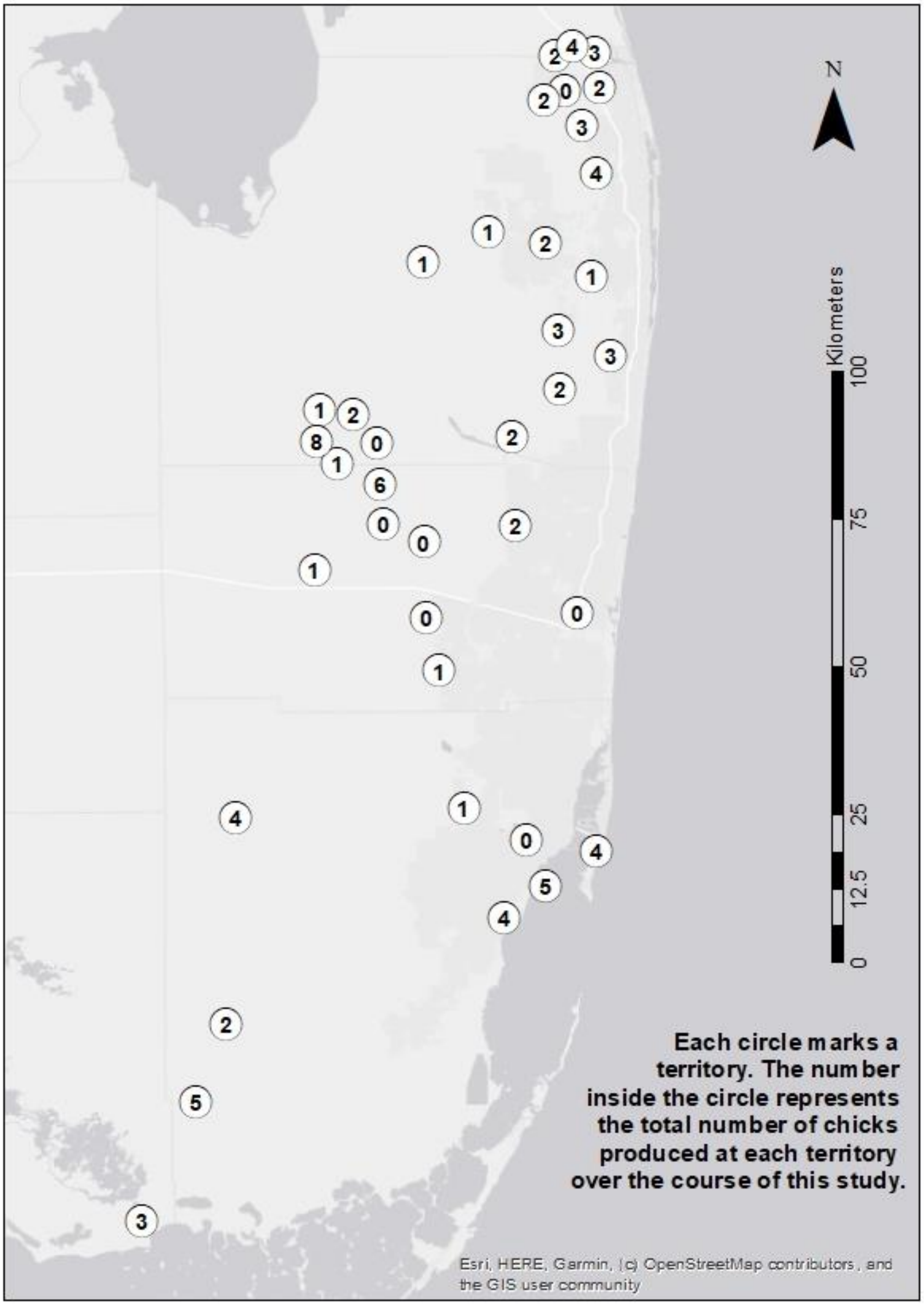
Figure 1. Map of study area with nest sites.

Figure 2. Example habitat map. This nest site had the second highest proportion of impervious surface. It is located at a very popular shopping mall.

Figure 3. Visual representation of breeding Red-shouldered Hawk breeding observations in Miami-Dade, Broward, and Palm Beach counties in spring 2017, spring 2018, and spring 2019.

Figure 4. The proportion of each land-cover type within 500 meters of unsuccessful and successful nests.

Figure 1



Esri, HERE, Garmin, (c) OpenStreetMap contributors, and the GIS user community

Figure 2

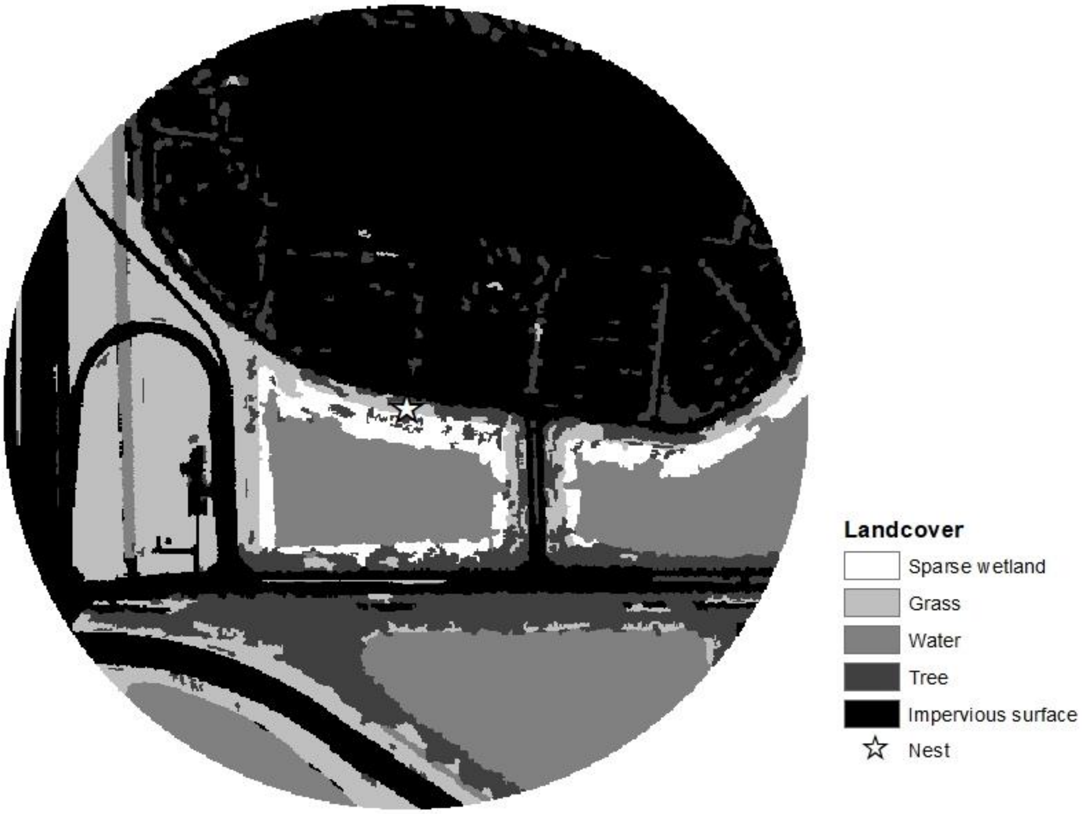

Landcover
Sparse wetland
Grass
Water
Tree
Impervious surface
Nest

Figure 3

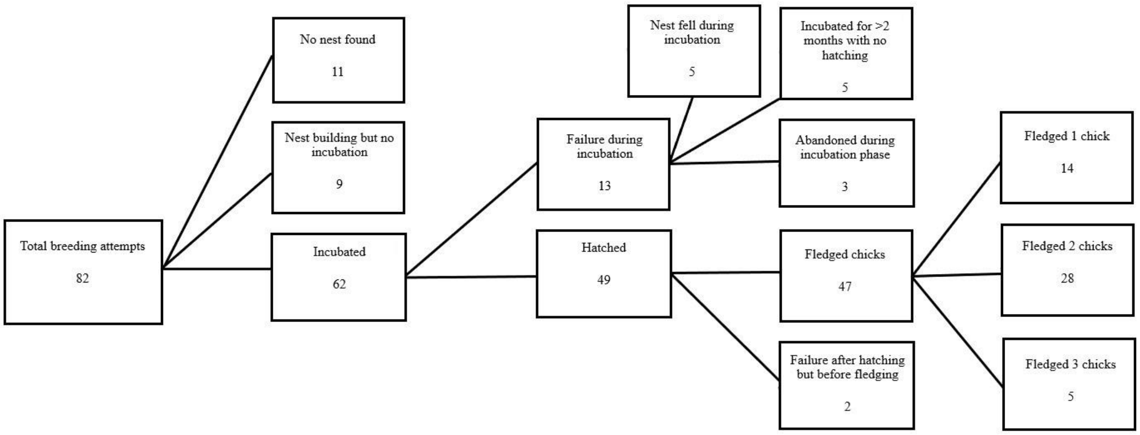
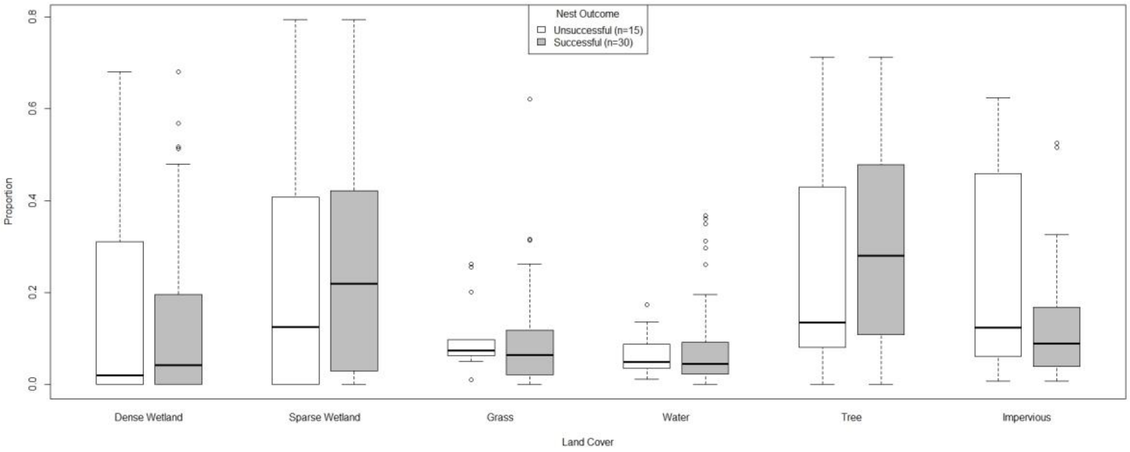

Total breeding attempts
82
No nest found
11
Nest building but no incubation
9
Incubated
62
Failure during incubation
13
Hatched
49
Nest fell during incubation
5
Incubated for >2 months with no hatching
5
Abandoned during incubation phase
3
Fledged chicks
47
Failure after hatching but before fledging
2
Fledged 1 chick
14
Fledged 2 chicks
28
Fledged 3 chicks
5

Figure 4


Nest Outcome
☐ Unsuccessful (n=15)
▨ Successful (n=30)
Proportion
0.0
0.2
0.4
0.6
0.8
Dense Wetland
Sparse Wetland
Grass
Water
Tree
Impervious
Land Cover

CHAPTER III

BREEDING SEASON DIET OF THE RED-SHOULDERED HAWK (*BUTEO LINEATUS EXTIMUS*) IN SOUTH FLORIDA

Abstract

Red-shouldered Hawks (*Buteo lineatus*) are the most abundant hawk species in Florida, often serving as the top avian predator in a variety of habitats. A distinct subspecies (*Buteo lineatus extimus*) is found in South Florida, one of the most rapidly urbanizing areas of the country, but the diet of the subspecies has not yet been documented. The present study characterized the diet Red-shouldered Hawks provided to their nestlings in South Florida using nest cameras at two nests in spring 2018 and four nests in spring 2019. Seventy-two percent of 1,024 recorded prey deliveries were identifiable to class. Reptiles and amphibians were the most frequently consumed prey classes, but mammals and birds likely provided more biomass per item as determined by their partitioning times (defined as starting when an adult began tearing the prey item and ending when the last of the prey item was consumed). Prey delivery rates ranged from 0.35 items per hour to 1.39 items per hour, a lower range than rates previously quantified for Red-shouldered Hawks in other states (0.66-1.89 items per hour). Each pair successfully fledged all nestlings, though they provided a wide variety of prey amounts and types. More research is needed to determine whether prey amount and/or type affects reproductive success of Red-shouldered Hawks nesting in the urban and exurban habitats of South Florida.

Key words: diet, Florida, urban, partitioning time, nest camera

Red-shouldered Hawks (*Buteo lineatus*) are adaptable generalists in both their habitat and dietary needs across their range (Dykstra et al. 2018). The red-shouldered hawk is the most abundant hawk species in Florida and in South Florida, and they often fill the ecological niche of top avian predator in a variety of habitats because large raptors are not abundant (Toland 2003, eBird 2020). A distinct subspecies (*Buteo lineatus extimus*) is found only in South Florida and anecdotal reports suggest a number of differences between this subspecies and its conspecifics elsewhere, such as its reproductive output, size, and habitat preferences (Jacobs and Jacobs 2002, Morrison et al. 2007). The metropolises of South Florida are newer and more populous than many in the United States (Nijman and Clery 2003), which may present a conservation challenge to these hawks if they are unable to adapt to the extensive urbanization.

Two factors play a critical role in predicting which raptors will inhabit and reproduce in urban areas: their natural habitat and their diet (Boal 2018). Red-shouldered Hawks (*Buteo lineatus*) have been found to avoid or thrive in urban areas in different parts of their range (Bosakowski and Smith 1997, Dykstra et al. 2009). One study found suburban Red-shouldered Hawks in Ohio ate roughly the same prey species observed at exurban nests elsewhere (Dykstra et al. 2003), which is expected considering the similarity of the suburban and exurban habitats studied, both at least partially forested with tall trees close to water (Dykstra et al. 2000). However, the Red-shouldered Hawks in South Florida rely on open wetlands, a very different habitat from the forested landscapes where they have been previously studied (Morrison et al. 2007). Forest dwelling raptors are more likely to inhabit urban places than marshland birds (Boal 2018). And while raptors with a generalist diet are found in urban areas more often than raptors with specialist diets (Boal 2018), only bird specialists consistently experience higher reproduction when breeding in urban habitats compared to exurban habitats (Kettel et al. 2018).

Both diet and habitat preferences need to be considered when investigating the potential consequences of urbanization for a raptor population. Therefore, the present study characterized the diet of Red-shouldered Hawks in various habitats across South Florida. The study presents the first data on the diet of this subspecies and is the southernmost study of Red-shouldered Hawk diets.

Methods

This study took place in Miami-Dade, Broward, and Palm Beach counties in Florida in April and May of 2018 and in March through May of 2019 (Fig. 1). North-south boundary lines split each county nearly in half with state- and federally protected Everglades wetlands to the west and developed areas to the east (Nijman and Clery 2003). Population growth in these three counties has quintupled to over five million people since the 1960s, with development expanding westward to house the growing populace (Nijman and Clery 2003).

In many studies of breeding raptors, nest surveys can be conducted before leaf-out in the spring when stick nests are visible in the trees (Miller et al. 2015, Millsap 2018). However, most south Florida ecosystems (except for cypress swamps) are vegetated year-round. Red-shouldered Hawk nests were found by playing conspecific calls in areas known to have Red-shouldered Hawk activity through eBird and direct reports to the author. If adults responded by calling or flying towards the researcher, their behavior was monitored until the hawks returned to their nest-site location. At times, this required several trips.

Nests were found on federal land in Everglades National Park and Arthur R. Marshall Loxahatchee National Wildlife Refuge, on state land in the stormwater treatment areas, on county land such as parks and highway rest stops, and on private land among suburban homes, university campuses, and business parks. Nest cameras could only be installed where nest trees and habitat were suitable and accessible, and where permission was granted by the landowner or land manager. When camera installation was possible, either qualified tree climbers or a biologist in a mechanical lift approached the nest. A waterproof 24-hour color/infrared security camera (product no. PC177IRHR-8, Supercircuits, Austin, Texas, USA.) was mounted roughly 0.6 m above the nest while the camera view was checked with a handheld video monitor (model HLT 71, Haier, Camden, South Carolina, USA.). Each camera was covered with camouflage-patterned tape to reduce its conspicuousness to the birds. The cameras were connected by a 60-foot cable to a mini digital video recorder (model AKR-200, Seorim Technology Co., Ltd., Seoul, South Korea) located in a waterproof tub at the base of the tree. Also inside the tub was a deep-cycle marine battery that powered the system. A programmable timer (CN101 DC 12V 16A Digital LCD Power Programmable Timer Time Switch Relay, FAVOLCANO, Fort Lee, New Jersey, USA.) was included to limit recording to 14 hours per day beginning an hour before sunrise and ending an hour after sunset. Batteries and SD cards were replaced every three days. In the first year of the study, two nest cameras were installed before egg-laying, but at both nests the pair built a new nest in a nearby tree. Therefore, all subsequent camera installations were conducted after eggs had hatched at approximately two to four weeks of age (Table 1). Nestlings were lowered to assistants on the ground during camera installation, which took 15 to 90 minutes depending on the site. All nestlings present at the start of recording fledged successfully at all recorded nests. Recording began immediately and ended once nestlings began to branch and cameras were removed at least one month after the cessation of recording to ensure the nest was no longer in use.

All recordings were scored by the author to ensure consistency in prey identifications. Prey were identified to class because video quality was insufficient for species identification in most cases, though identifications below the class level were noted when possible. Partitioning time in seconds was also recorded, defined following Sonerud et al. (2014), as beginning when an adult began tearing prey to feed to nestlings and ending when the last of the prey item was consumed. If the adult paused while feeding for longer than 30 seconds, the amount of time spent not feeding was subtracted from the partitioning time. Partitioning time was not recorded if nestlings fed themselves. If two prey items were fed at once, partitioning time was not recorded for either item. Instances of sibling aggression, including pecks at a sibling's head or body and pulls on a sibling's feathers or skin, were also recorded if they occurred during prey deliveries because many raptor species exhibit aggression between siblings, including siblicide, when prey delivery rates are insufficient to maintain all chicks (Morandini and Ferrer 2015). Video between prey deliveries was not reviewed for aggressive behaviors. Prey delivery rates were calculated using only complete recording days, defined as days for which all 14 hours of recording were available with no gaps. Levin's index ($B=1/\Sigma p_i^2$, where p is the proportion of each identifiable prey class in the diet) was calculated as a measure of diet breadth at each nest (Levin 1968). Kruskal-Wallis rank sum tests were used to determine partitioning times differed significantly for different prey types and among nests, followed by Dunn's tests with a Bonferroni correction for multiple comparisons to identify significantly different groups.

Results

Prey delivery to nestlings was tracked at six Red-shouldered Hawk nests over the course of my study, for periods ranging from 16 to 29 days (Table 1). Two nests were recorded in 2018 and four nests were recorded in 2019. Three of the six nests were located in federally protected parks, one (STA 1) in state protected wetlands, one (150th Avenue) in a suburban yard that bordered county-protected wetlands, and one in a large private botanical garden in a suburban area (Fairchild Tropical Botanical Garden). One nest (STA1) had a single nestling, one nest (Mahogany Hammock) had three nestlings, and the remaining four had two nestlings each. All nestlings present at the beginning of recording were raised to fledging. In total, 1,568 hours of video captured 1,024 prey deliveries across all nests; 71.5% of prey deliveries were identifiable to class and 72% had a partitioning time. Eighty-four complete recording days were recorded, which totaled 1,176 hours of video (Table 1). Unidentifiable items were often consumed quickly, providing limited opportunity for identification (Fig. 2). Identifiable prey items came from seven classes: 58% Reptilia, 18% Amphibia, 10% Mammalia, 9% Aves, 3% Actinopterygii, 2% Malacostraca, and a negligible percentage of Insecta. Not all classes were consumed at each nest (Table 2). Examples of prey species from each class are listed in Table 2. Reptiles and amphibians were consumed at all nests and mammals were consumed at five of six nests.

Partitioning times of mammals and birds were significantly larger than those for reptiles and amphibians (Kruskal-Wallis test, $X^2 = 223.09$, df = 6, $P < 0.001$, Fig 2). Reptiles accounted for 46%, birds 20%, mammals 19%, amphibians 11%, and the remaining prey classes together made up less than 5% of partitioning times. Prey delivery rates varied from 0.35 items per hour to 1.38 items per hour (Table 1). Four nests (Fairchild, Loxahatchee, Mahogany Hammock, and 150th Ave) delivered prey most often between 0800 and 1200, whereas Pa-hay-okee and STA1 lacked a peak delivery time (Fig. 3). Partitioning times varied only slightly between nests, although the nest at 150th Avenue was notable for its low average partitioning time and the nest at STA1 was notable for its high average partitioning time (Fig. 4). Of 223 recorded prey deliveries at the 150th Avenue nest, 177 had a partitioning time and 140 of those partitioning times were 15 seconds or fewer, which agreed with the high proportion of unidentifiable prey items at this nest (Table 2). The parent birds at STA1 were the only ones that did not deliver reptiles most often, but instead delivered birds most often (Table 2).

Instances of sibling aggression ranged from zero to 24 at each of the five nests with siblings (Table 1). The only nest in the study with three siblings (Mahogany Hammock) had the highest incidence of prey deliveries accompanied by sibling aggression (20 out of 88 total observed prey deliveries).

Discussion

Red-shouldered Hawks eat more mammals in their northern range and more amphibians and reptiles in their southern range (Strobel and Boal 2010). My study demonstrated that Red-shouldered Hawks in South Florida generally conform to the continent-wide pattern. However, in Arkansas, Georgia, and Missouri, amphibians are the most common prey item (up to 46%) and reptiles are secondary (up to 26%). The Florida birds studied herein consumed reptiles most frequently (58%) and amphibians secondarily (18%), which is most similar to Red-shouldered Hawks in Texas (31% reptiles, 8% amphibians). Reptiles and amphibians were the only prey classes consumed by nestlings in all six nests in this study and constituted 76% of identifiable prey items. Though mammals made up only 10% of identifiable prey items in this study, concurrent research found 49% of Red-shouldered Hawk carcasses from three South Florida wildlife hospitals had anticoagulant rodenticides present in their livers upon their death, a hazard likely limited to the urban and agricultural areas of South Florida (Chapter IV).

Though mammals and birds represented only 19% of identifiable prey items in this study, they represented 39% of partitioning time for all identifiable prey items. Mammals and birds required longer partitioning times than reptiles and amphibians (Fig. 2), which suggests they provided more biomass per item. Because prey items were not identified to species in the current study, biomass could not be estimated. However, for adult females of six raptor species in Norway and Sweden, partitioning time varies only as a function of prey body mass, not prey type, which strongly suggests that partitioning time can be an index for prey biomass (Sonerud et al. 2014).

Despite the differences in habitat, prey delivery rates, and prey types, all hatchlings in the current study fledged. The highest prey delivery rate (1.38 items/hr) was documented at the 150th Avenue nest, where parent hawks brought back dozens of small items consumed too quickly to identify. The 150th Avenue nest was also the only one to have identifiable insects among its prey items, suggesting perhaps some or many of the quickly consumed, unidentifiable items were also insects. Prey delivery rates for Red-shouldered Hawks across the United States range from 0.66 items per hour to 1.89 items per hour (Townsend 2006). Individual nests in the present study fell well below this previously published range and still successfully fledged all nestlings. Red-shouldered Hawks in South Florida produce fewer nestlings on average and grow to a smaller adult size than their conspecifics elsewhere in the country, which may partially explain their success in my study with low prey delivery rates (Jacobs and Jacobs 2002). Only two of the five nests with siblings displayed notable amounts of sibling aggression, at Fairchild during 20 out of 265 total prey deliveries and Mahogany Hammock during 24 out of 88 total prey deliveries. Mahogany Hammock, the only nest with three siblings, was recorded later in the nestlings' development, and had comparable prey delivery rates to nests that contained only two nestlings. These factors could explain the sibling aggression at Mahogany Hammock.

The Fairchild nest was the only nest recorded in the urban portion of the study area and had the lowest diet breadth of all six nests (Table 2). At the Fairchild nest, reptiles were the main prey item (175 of 265 total prey items) and green iguanas (*Iguana iguana*) made up 44% of the reptiles. Iguanas are one of the most visible non-native animal species at the Garden, with a very dense breeding population. At another urban nest site, where permission to record was denied, multiple blue land crab (*Cardisoma guanhumi*) carapaces were observed under the Red-shouldered Hawk nest, but it is unknown what proportion of the diet they constituted. Blue land crabs were one of the most visible animal species at this site, with a dense breeding population. Some studies of other urban raptors have found a similar specializing of the prey base at urban nests, e.g., pigeons for urban Cooper’s Hawks (*Accipter cooperii*) in Arizona (Estes and Mannan 2003) and; non-native rodents for Barn Owls (*Tyto alba*) in Argentina (Teta et al. 2012).

The current study is the first to describe the breeding-season diet of Red-shouldered Hawks in South Florida. Adults at some nests in the study delivered less food to the nest than has been previously published for conspecifics across the country. Each of the six nests studied here showed unique patterns of prey composition and prey delivery rates, yet all pairs were successful in raising their entire brood. An investigation is needed to determine whether prey amount and/or prey identity affect population persistence for this species in the urban and exurban portions of its range in South Florida. However, the study demonstrates that Red-shouldered Hawks in South Florida are highly flexible in prey use, leading to successful fledging of nestlings. Such adaptability may benefit them in coping with changing patterns of human land use.

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Table 1. Summary data by nest. Dates recorded are followed in parentheses by the number of days in that period. Age represents the approximate age of nestlings at the start of recording. Total prey deliveries represent all prey deliveries recorded throughout recording. Sibling aggression represents the number of prey deliveries during which siblings displayed aggressive behaviors across all prey deliveries during the study. All subsequent data are calculated for complete recording days only (CRDs, days with no interruptions during the entire 14-hour period).

Data	Study Sites					
Nest	150th Ave	Fairchild	Loxahatchee	Mahogany Hammock	Pa-hay-okee	STA 1
Location	Suburban yard bordering county-protected wetlands	Private botanical garden surrounded by suburban homes	National Wildlife Refuge	Everglades National Park	Everglades National Park	State-protected wetlands
Dates recorded	11-28 April 2019 (18)	30 April - 28 May 2019 (29)	12 April-3 May 2018 (22)	11-26 March 2019 (16)	13 April-15 May 2018 (33)	28 March-19 April 2019 (23)
Age	4 wks	2 wks	3wks	4 wks	2 wks	3 wks
Sibling aggression	0	24	4	20	1	N/A
Total prey deliveries (PDs)	223	265	260	88	90	98
# of CRDS	10	25	20	4	7	18
PDs during CRDS	193	242	250	48	47	88
Average PDs per CRD	19.3	9.68	12.5	12	6.7	4.89
Average PDs per hour	1.38	0.69	0.89	0.86	0.48	0.35
Average PDs per hour per nestling	0.69	0.35	0.45	0.29	0.24	0.35

Table 2. Count of prey classes consumed at each nest and their Levin's index of diet breadth. Observed prey types identified to the lowest taxonomic category are as follows: **Actinopterygii**, Walking catfish (*Clarias batrachus*); **Amphibia**, unidentified frogs; **Aves**, Common Gallinule (*Gallinula galeata*), Common Yellowthroat (*Geothlypis trichas*), Eastern Screech Owl (*Megascops asio*), House Sparrow (*Passer domesticus*), unidentified passerines and herons; **Insecta**, unidentified grasshoppers; **Malacostraca**, unidentified crayfish; **Mammalia**, juvenile eastern gray squirrel (*Sciurus carolinensis*), unidentified rodents and rabbits; **Reptilia**, American alligator (*Alligator mississippiensis*), Cuban knight anole (*Anolis equestris*), green anole (*Anolis carolinensis*), green iguana (*Iguana iguana*), unidentified lizards, snakes, and turtles.

Prey Type	Study Sites					
	150th Ave	**Fairchild**	**Loxahatchee**	**Mahogany Hammock**	**Pa-hay-okee**	**STA 1**
Actinopterygii	2	-	2	4	15	-
Amphibia	30	8	71	12	7	3
Aves	-	6	18	-	2	40
Insecta	3	-	-	-	-	-
Malacostraca	-	-	-	7	4	-
Mammalia	13	17	20	4	2	20
Reptilia	54	175	78	47	43	28
Unidentifiable	121	59	71	17	17	7
Levin's index	2.60	1.36	3.01	2.25	2.48	2.96

FIGURE LEGENDS

Figure 1. Map of the study area.

Figure 2: Partitioning times of each prey class. The central line represents the median, the box encloses the first and third quartile of these data, and the top and bottom hashmarks extend to 1.5 times the interquartile range or the furthest data point, whichever is smaller. Data points beyond 1.5 times the interquartile range are not shown. Letters above each plot indicate significant differences between prey classes as determined by Kruskal-Wallis rank sum tests followed by Dunn's tests with a Bonferroni correction for multiple comparisons.

Figure 3. Density plot of prey deliveries during each hour of complete recording days by nest. 95% confidence intervals were calculated by bootstrapping 1000 replicates of the original dataset, then calculating the confidence interval for the density of prey deliveries during each hour at each nest in the bootstrapped data. Sample sizes are the number of prey deliveries on complete recording days (Table 1).

Figure 4: Boxplot of partitioning times at each nest. The central line represents the median, the box encloses the first and third quartile of these data, and the top and bottom hashmarks extend to 1.5 times the interquartile range or the furthest data point, whichever is smaller. Data points beyond 1.5 times the interquartile range are not shown. Letters above each plot indicate significant differences between nests as determined by Kruskal-Wallis rank sum tests followed by Dunn's tests with a Bonferroni correction for multiple comparisons.

FIGURES

Figure 1

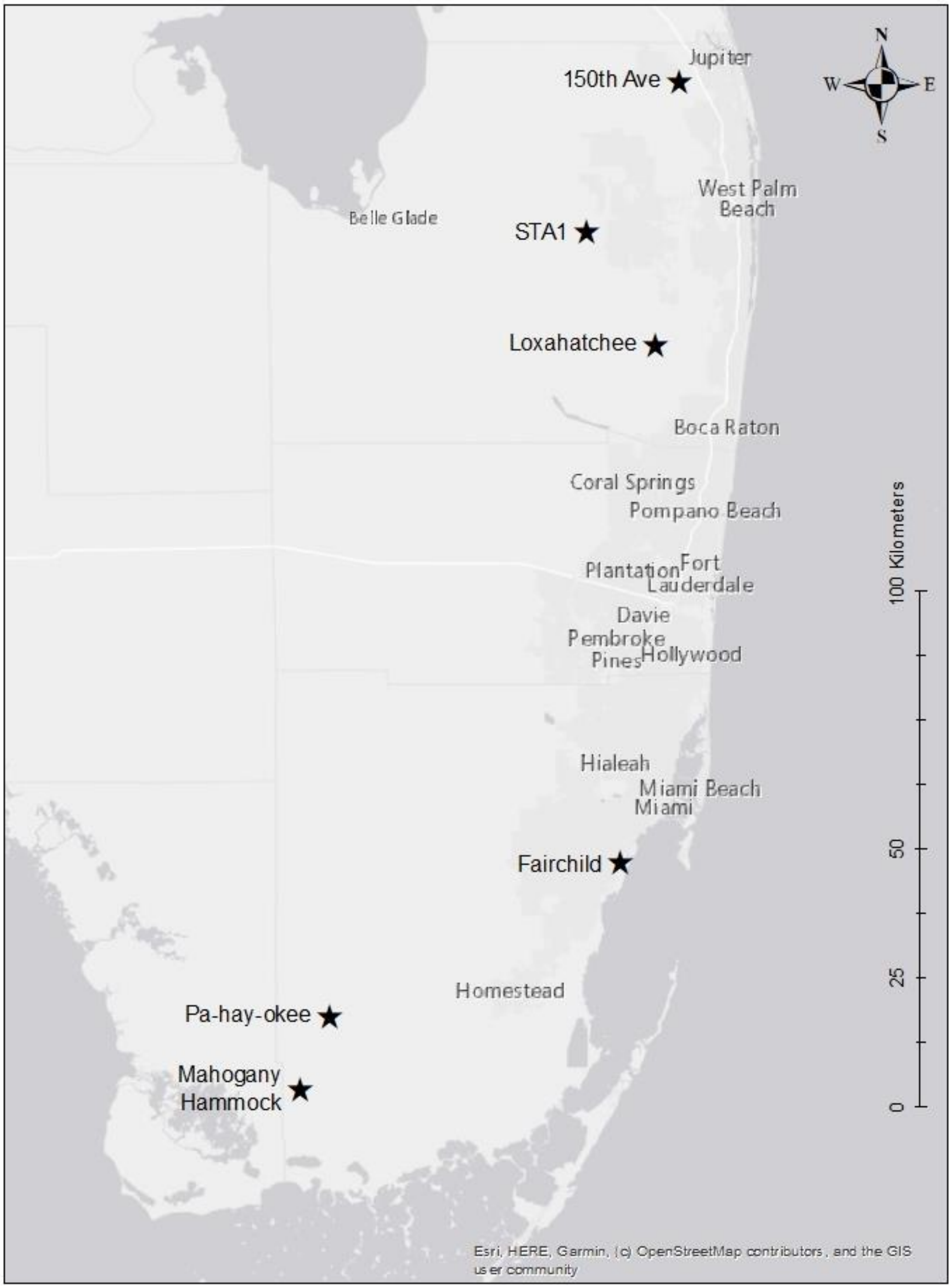


Figure 2

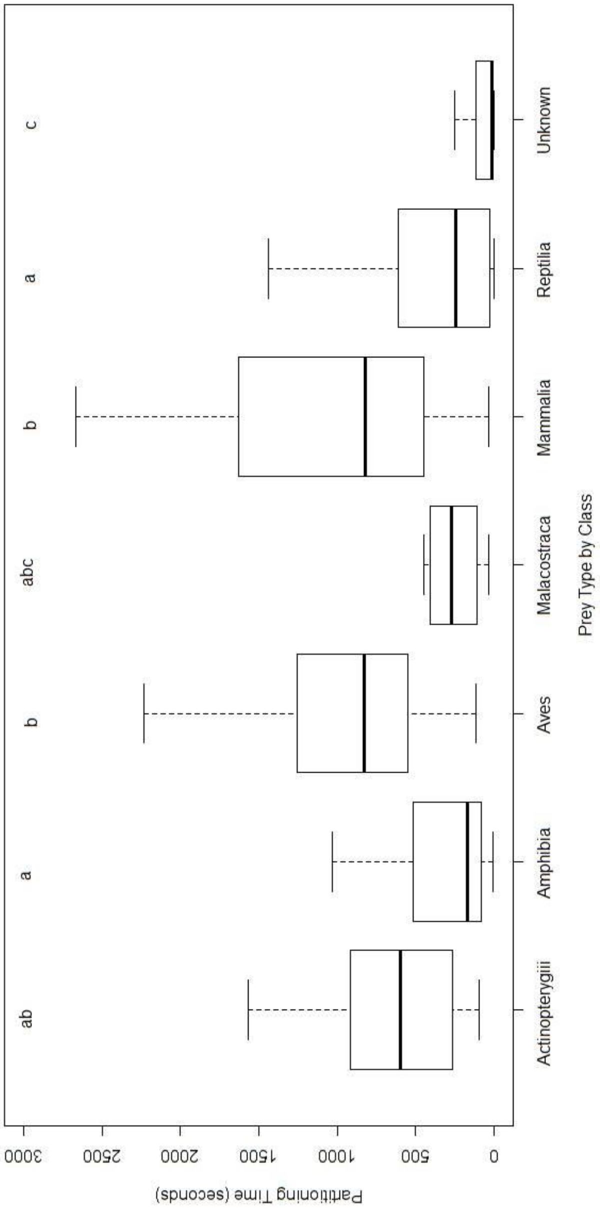

Partitioning Time (seconds)
0
500
1000
1500
2000
2500
3000
ab
a
b
abc
b
a
c
Actinopterygiii
Amphibia
Aves
Malacostraca
Mammalia
Reptilia
Unknown
Prey Type by Class

Figure 3

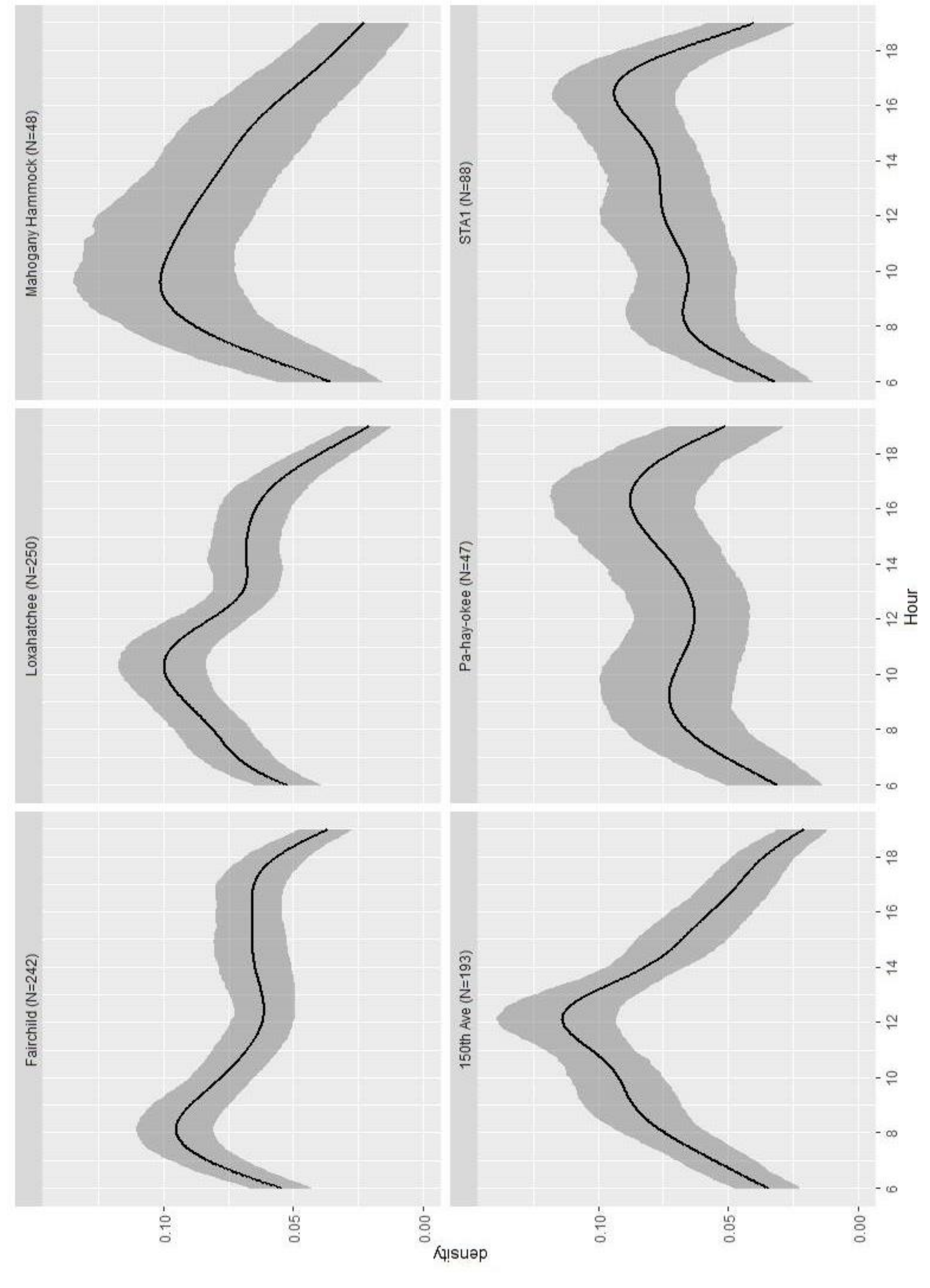
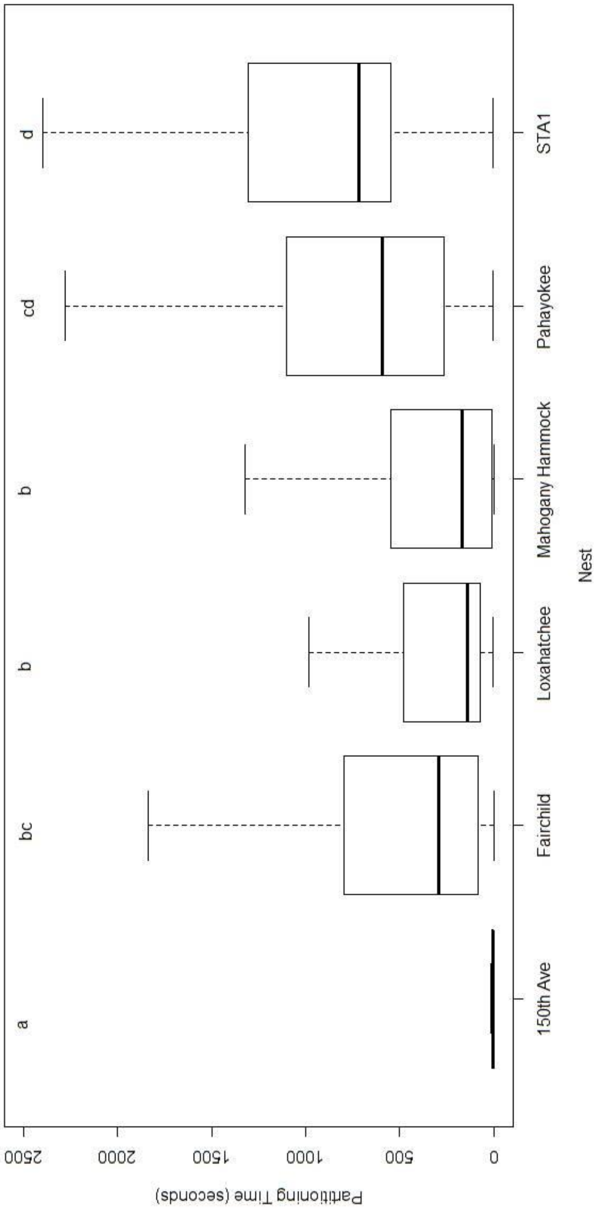

Fairchild (N=242)
Loxahatchee (N=250)
Mahogany Hammock (N=48)
150th Ave (N=193)
Pa-hay-okee (N=47)
STA1 (N=88)
density
0.00
0.05
0.10
Hour
6
8
10
12
14
16
18

Figure 4



a
bc
b
b
cd
d
2500
2000
1500
1000
500
0
Partitioning Time (seconds)
150th Ave
Fairchild
Loxahatchee
Mahogany Hammock
Pahayokee
STA1
Nest

CHAPTER IV

ANTICOAGULANT RODENTICIDE EXPOSURE IN SOUTH FLORIDA RED-SHOULDERED HAWKS

Abstract

In 2008, the United States Environmental Protection Agency imposed new restrictions on the use of anticoagulant rodenticides (ARs), in part because of the risk of secondary poisoning to non-target wildlife such as raptors. Though secondary poisoning of raptors with ARs has been documented for decades, there remain many knowledge gaps, including among species and geographic regions. The present study screened the livers of 74 red-shouldered hawks (*Buteo lineatus*) collected in South Florida. Forty-nine percent of the 74 hawk livers were found to contain at least one AR, a lower frequency than seven out of nine previously published AR studies in raptors in the United States. Brodifacoum and bromadiolone were found in 23 birds (11 birds had both rodenticides), with difethialone found in two birds. Average brodifacoum concentrations were 109 ppb and average bromadiolone concentrations were 35 ppb. A commonly used approximation for the lethal toxicity threshold of ARs in raptors is 100 ppb, which only six of the birds in the present study exceeded. Probabilistic thresholds for the onset of symptoms are estimated to be much lower at 20 ppb, a threshold met by 75% of AR-positive birds in the present study. The present study represents the first formal investigation into AR exposure in a Florida raptor and only the second study to screen red-shouldered hawks, perhaps because they are not common predators of the commensal rodents targeted by ARs. More research is needed into the exposure to ARs in this species throughout its range and the effect of migration on ARs in raptors generally.

Keywords: anticoagulant rodenticide, raptor, Red-shouldered Hawk, Florida

Introduction

In 2008, the United States Environmental Protection Agency (EPA) amended regulations concerning the sale and use of several anticoagulant rodenticides (ARs), restricting the sale of brodifacoum, bromadiolone, difenacoum, and difethialone to pest management professionals and agricultural users only (Murray 2017). These rodenticides, among others, are known as second-generation anticoagulant rodenticides (SGARs) because they were developed beginning in the 1970s after rodents were found to be resistant to first-generation anticoagulant rodenticides (FGARs) (Murray 2011). Both generations of ARs are designed to interrupt the process of blood clotting by inactivating vitamin K epoxide reductase, a necessary liver enzyme (Rattner et al. 2014). Second-generation anticoagulant rodenticides are often 100% lethal to rodents after only a single feeding because of their greater efficiency in binding to this enzyme compared to FGARs, which require multiple feedings to be lethal (Rattner et al. 2014; Murphy 2018). Though death is nearly guaranteed, it can take up to 13 days to kill the rodents during which time they behave in ways that make them easy prey for predators (Hindmarch and Elliot 2018).

The risk of secondary poisoning to predatory wildlife species was part of the rationale used by the EPA to restrict the sale of these rodenticides in 2008 (Erickson and Urban 2004). Raptors are one such taxon exposed to ARs through their diet (Erickson and Urban 2004). Once poisoned prey is consumed, ARs are quickly filtered out of the blood and stored for long periods of time in the liver (Gómez-Ramírez et al. 2012). Therefore, most investigations of AR exposure in raptors screen the livers of deceased birds rather than any tissue from living birds (Kwasnoski et al. 2019). Studies of this nature frequently find a large proportion of sampled birds have been exposed to ARs (Table 1).

Though the risk of ARs to wild raptors has been documented since the 1980s, much of the basic science surrounding this risk remains unknown (Merson et al. 1984; Erickson and Urban 2004). The few experimental feeding studies that have been conducted on captive raptors using FGARs (Rattner et al. 2012) and SGARs (Newton et al. 1990) show wide individual- and species- level variability in both lethal and sublethal effects from equal doses of rodenticides. Attempts to link rodenticide poisoning to antemortem symptoms at wildlife rehabilitation hospitals also remains elusive, with some individuals displaying vague symptoms (such as depression, shock, and in some cases hemorrhage) and other AR-poisoned individuals presenting as asymptomatic (Murray 2017).

Studies investigating raptors in the wild face many complicating factors. Anticoagulant rodenticides have been detected in the livers of deceased raptors from Massachusetts (Murray 2011; Murray 2017), New York (Stone et al. 2003), New Jersey (Stansley et al. 2014), California (Gabriel et al. 2018), Virginia (Hegdal and Colvin 1988), Kentucky (Slankard et al. 2019), and North Carolina (Weir et al. 2018), which leaves many areas of the United States uninvestigated. The delayed onset of symptoms can lead to a bird being recovered several miles away from the source of the toxicant or many hundreds of miles away during migration (Herring et al. 2017). Even closely related resident raptor species in the same location have shown different rates of exposure (Gabriel et al. 2018). Rodents in the diet is thought to pose a greater risk to raptors than other prey species, which would put rodent specialists living near urban or agricultural areas at greatest risk (Geduhn et al. 2016). However, recent literature has found several exceptions to the expectation that rodents are the greater risk to raptors (Gabriel et al. 2018; Lettoof et al. 2020).

To supplement the growing literature documenting the risk of ARs to raptors, the livers of red-shouldered hawks (*Buteo lineatus*, RSHAs) admitted to three wildlife hospitals in south Florida were screened. My study represents only the second investigation into AR exposure in the RSHA species (Weir et al. 2018) and the first AR study of any raptor in Florida.

Methods

Between January 2017 and January 2020, I collected red-shouldered hawk carcasses along with their medical records from three local wildlife hospitals: South Florida Wildlife Center in Hollywood, Pelican Harbor Seabird Station in Miami, and Busch Wildlife Sanctuary in Jupiter. No animals were euthanized for the purposes of the study; all animals either died in care or were humanely euthanized because of grave prognoses. Antemortem symptoms were recorded from the medical records when available. Three additional carcasses were donated to the project from members of the public (one roadkill, one window strike, and one unknown). I categorized age using plumage characteristics as follows: hatch years (HY) had 100% juvenile plumage regardless of time of year, second years (SY) were those with any mix of juvenile and adult plumage, and after hatch year (AHY) birds were those with 100% adult plumage. The HYs and SYs were then collapsed into a combined subadult category, while AHYs were considered adults. All carcasses of this species were included in the study, regardless of age, time of year, or antemortem symptoms.

Livers were screened for nine ARs (brodifacoum, bromadiolone, chlorphacinone, coumachlor, dicoumarol, difenacoum, difethialone, diphacinone, and warfarin) at the Iowa State University Veterinary Diagnostic Laboratory (Ames, IA). All samples were run using liquid chromatography combined with triple quadrupole mass spectormetry (LC-MS/MS) following Smith et al. (2017). Livers were homogenized and extracted in 10% (v/v) methanol in acetonitrile in a ratio of 1-g sample to 6 mL of extraction solvent with a solid phase extraction clean-up prior to analysis. The first third of my samples were run on a Waters Quattro Premier XE (Waters Corporation, MA, USA) and the remaining samples were run on a Thermo Fisher Scientific TSQ Altis (Thermo Fisher Scientific, PA, USA). The reporting limit for the Waters instrument was 5 parts per billion (ppb) for all nine ARs and the reporting limits for the Thermo Scientific instrument were as follows: brodifacoum 10 ppb, bromadiolone 5 ppb, chlophacinone 10 ppb, coumachlor 2 ppb, dicoumarol 5 ppb, difenacoum 2 ppb, difethialone 25 ppb, diphacinone 10 ppb, and warfarin 2 ppb. Trace amounts were not considered positive findings in this study and are therefore not reported. Chi-squared tests were used to determine whether the age of the bird was independent of AR presence in the liver. Fisher’s exact tests were used to determine whether year or month of admittance was independent of AR presence in the liver.

Results

Of the 74 red-shouldered hawk livers screened for rodenticides, 36 had detectable levels of at least one rodenticide (48.6%). Two-thirds of AR-positive cases contained only one AR (11 brodifacoum, 12 bromadiolone, and one diftethialone) while the remaining third contained two ARs (11 brodifacoum and bromadiolone, one brodifacoum and difethialone). No FGARs were detected in the study. When present above the detection limit, the average concentration in parts per billion (ppb) ± standard deviation of each rodenticide alone and in combination are listed in Table 2. Across all cases positive for brodifacoum, the average concentration was 109 ± 181 ppb and across all cases positive for bromadiolone, the average concentration was 35 ± 57 ppb. Concentrations ranged from 10.3 to 707 ppb for brodifacoum and from 5 to 282.4 ppb for bromadiolone.

Ninety-four percent of all carcasses were collected between September and February (though three birds did not have dates). No relationship was found between AR presence in the liver and year (Fisher's exact test, p=0.11) or month (Fisher's exact test, p=0.16). Thirty-seven medical records noted the address where the birds were found. No geographic pattern was detected (Fig. 1). Of the 65 medical records that noted the time of death, 11 were euthanized for grave prognoses, 47 died within 24 hours of admittance, and the remaining 7 died within four days of entering the hospital. Consequently, antemortem symptom notes were often sparse, but the most frequently noted symptoms were depressed mentation and no blink, which were present in equal numbers of AR-positive birds and AR-negative birds (Table 3). A Chi-squared test revealed AR-positive birds varied by age using both the three-tiered age classification (X^2=12.52, df=2,p=0.002) and the two-tiered age classification (X^2=10.51, df=1,p=0.001). Thirty-nine percent of HY birds, 32% of SY birds, and 81% of AHY birds had at least one AR in their livers.

Discussion

The prevalence of AR-positive birds is lower in this study (49%) than many recent investigations into AR exposure in raptors (Table 1), though the exclusion of trace findings makes this a conservative figure. This could be because most other investigations have not included RSHAs. RSHAs are often associated with wetland or riparian habitats throughout their range, which may reduce the amount of time spent foraging in urban and agricultural landscapes, where AR use is heaviest (Bosakowski and Smith 1997). Moreover, RSHAs may have a wider prey base than raptor species more commonly screened for ARs, such as owls, thereby further reducing their risk (Strobel and Boal 2010). Small mammals make up a minority of the RSHA diet across much of their range (Strobel and Boal 2010), with commensal rodents making up a small percentage of their mammalian prey (Jacobs and Jacobs 2002). Reptiles and amphibians are often important prey items for RSHAs (Strobel and Boal 2010). One recent study found urban reptiles with high frequencies of exposure to ARs (Lettoof et al. 2020). In fact, reptiles may carry higher concentrations of ARs in their livers than mammals and birds due to their slower metabolisms (Lettoof et al. 2020). Wild amphibians have not yet been tested for AR exposure (Lettoof et al. 2020).

RSHAs are considered the diurnal analogue of the barred owl (*Strix varia*) just as red-tailed hawks (*Buteo jamaicensis*) are considered the diurnal analogue of great horned owls (*Bubo virginianus*) (Dykstra et al. 2012, Thomas et al. 2011). The only other AR study to include RSHAs thus far found a similar rate of exposure in RSHAs (82% of 11 birds) and barred owls (75% of 8 birds) (Weir et al. 2018). This finding may indicate that RSHAs are exposed at similar rates as the barred owls included in previous studies (40%

of barred owls were AR-positive in northern California, Gabriel et al. 2018; 88% in Massachusetts, Murray 2017; 92% in western Canada, Albert et al. 2010). Because RSHAs often live at the confluence of aquatic and terrestrial habitats, they may be at risk from contaminants from both habitats and, therefore, useful as sentinel species for both terrestrial and aquatic toxicants (Weir et al. 2018).

A commonly used rough approximation for the lethal toxicity threshold of ARs in raptors is 0.1 mg/kg (100 ppb), which only six of the birds in this study exceeded (Stansley et al. 2014, Lettoof et al. 2020). Probabilistic thresholds for the onset of symptoms were estimated to begin much lower at 0.02 mg/kg (20 ppb) in great horned owls (Thomas et al. 2011), a threshold met by 27 birds (75% of AR-positive birds) in this study. However, the contribution of ARs to the deaths of the birds in this study cannot be determined because pre- and post-mortem examinations were conducted without thorough notations of AR-specific symptoms. The most common symptoms noted in the medical records examined for this study were vague and non-prescriptive (depressed mentation, no blink, death within 24 hours of admittance) and found in equal numbers of AR-positive birds and AR-negative birds (Table 3). Other ailments that could cause these symptoms, such as disease or non-AR toxins, were not investigated.

Most studies examining AR exposure in raptors find brodifacoum most frequently and bromadiolone in a minority of cases (Stone et al. 2003, Stansley et al. 2014, Murray 2017, Weir et al. 2018). This study found brodifacoum and bromadiolone in an equal number of cases, similar to Huang et al. (2016) and Lettoof et al. (2020). This study also found a smaller percentage of birds with more than one AR in their liver (33% of AR-positive birds) than others (66% in Murray 2017). Brodifacoum, bromadiolone, and difethialone differ in their chemical structure, palatability, and in their typical formulation in commercial products (Erickson and Urban 2004, Murphy 2018). Sales and patterns of use are considered confidential business information (Elliot et al. 2016) and only some states require annual reports of AR use from pest management professionals (Murray 2017). Florida is not one of them, though the state wildlife agency has recently reported ARs to be a conservation concern for the state's bald eagles (van Deventer et al. 2017).

Adult birds were found to have been exposed to ARs more frequently than juvenile birds in this study, which is in line with findings from other studies (Murray 2011, Huang et al. 2016). Nearly all carcasses were collected between September and February. This seasonal pattern introduces another confounding factor left unexamined in this study, namely the presence of migratory RSHAs in the study area. South Florida has its own subspecies of RSHA, which is distinguished from other subspecies by its noticeably paler adult plumage (Jacobs and Jacobs 2002). Generally, RSHAs in northern states have been found to eat more mammals while those in southern states eat more amphibians and reptiles (Strobel et al. 2010). The local subspecies tends to follow that pattern (unpublished data). RSHAs of both plumages were noted anecdotally in this study, though juvenile birds were difficult to distinguish. Even if subspecies had been tracked in this study, it would be impossible to know whether the ARs detected in the birds had been consumed locally or carried with them during migration (Herring et al. 2017, Kwasnoski et al. 2019). Moreover, migration may be a factor in a raptor's sensitivity to ARs, either through evolutionary selection for a higher tolerance for environmental toxicants (Rainio et al. 2012) or through metabolism of the liver during migration (Table 5.5 in Newton 2010). More study is needed to investigate AR-exposure in more non-target wildlife taxa, how migration interacts with AR exposure, and the extent to which RSHAs are exposed to ARs throughout their range.

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Table 1 Summary table of selected previous raptor rodenticide liver studies in the United States. ARs detected in less than 5% of cases were not included in this table

Citation	Location	N	Species tested	Overall % AR-positive	ARs detected in order of frequency with concentration data
Stone et al. 2003	NY	265	19 species of raptors	49%	Brodifacoum, 84%, 180 ppb (mean) Bromadiolone, 22%, 310 ppb (mean)
Murray 2011	MA	161	RTHA, EASO, BDOW, GHOW	86%	Brodifacoum, 99%, 12 ppb (median)
Stansley et al. 2014	NJ	127	RTHA, GHOW	82%	Brodifacoum, 75%, 72.5 ppb (geometric mean) Bromadiolone, 24%, 106 ppb
Murray 2017	MA	94	RTHA, EASO, BDOW, GHOW	96%	Brodifacoum, 99%, 0.11 ppb (median) Difethialone, 50%, trace Bromadiolone, 46%, trace Difenacoum, 9%, trace
van Deventer et al. 2017	FL	33	BAEA	82%	Brodifacoum, 82%, trace Bromadiolone, 30%, trace Difethialone, 18%, trace Difenacoum, 15%, trace
Weir et al. 2018	NC	44	10 species of raptors	66%	Brodifacoum, 61%, 55.8 ug/kg (mean)
Gabriel et al. 2018	CA	94	BDOW, STOC	55%	Brodifacoum, 93%, trace Bromadiolone, 22%, trace
Slankard et al. 2019	KY	48	BNOW	33%	Brodifacoum, 88%, trace Bromadiolone, 38%, trace
Wiens et al. 2019	OR, WA	40	BDOW	48%	Brodifacoum, 89%, trace Bromadiolone, 11%, trace Difethialone, 11%, trace Warfarin, 5%, trace

Table 2 Summary table of AR findings in the livers of 74 red-shouldered hawks (*Buteo lineatus*) in South Florida

Findings	N	μ ±SD (ppb)
No rodenticides detected	38	
Brodifacoum	11	230 ± 152
Bromadiolone	12	28.2 ± 20.6
Difethialone	1	20.8
Brodifacoum and bromadiolone	11	39.7 ± 16, 41.8 ± 81.3
Brodifacoum and difethialone	1	461.1, 35.7
Total	74	

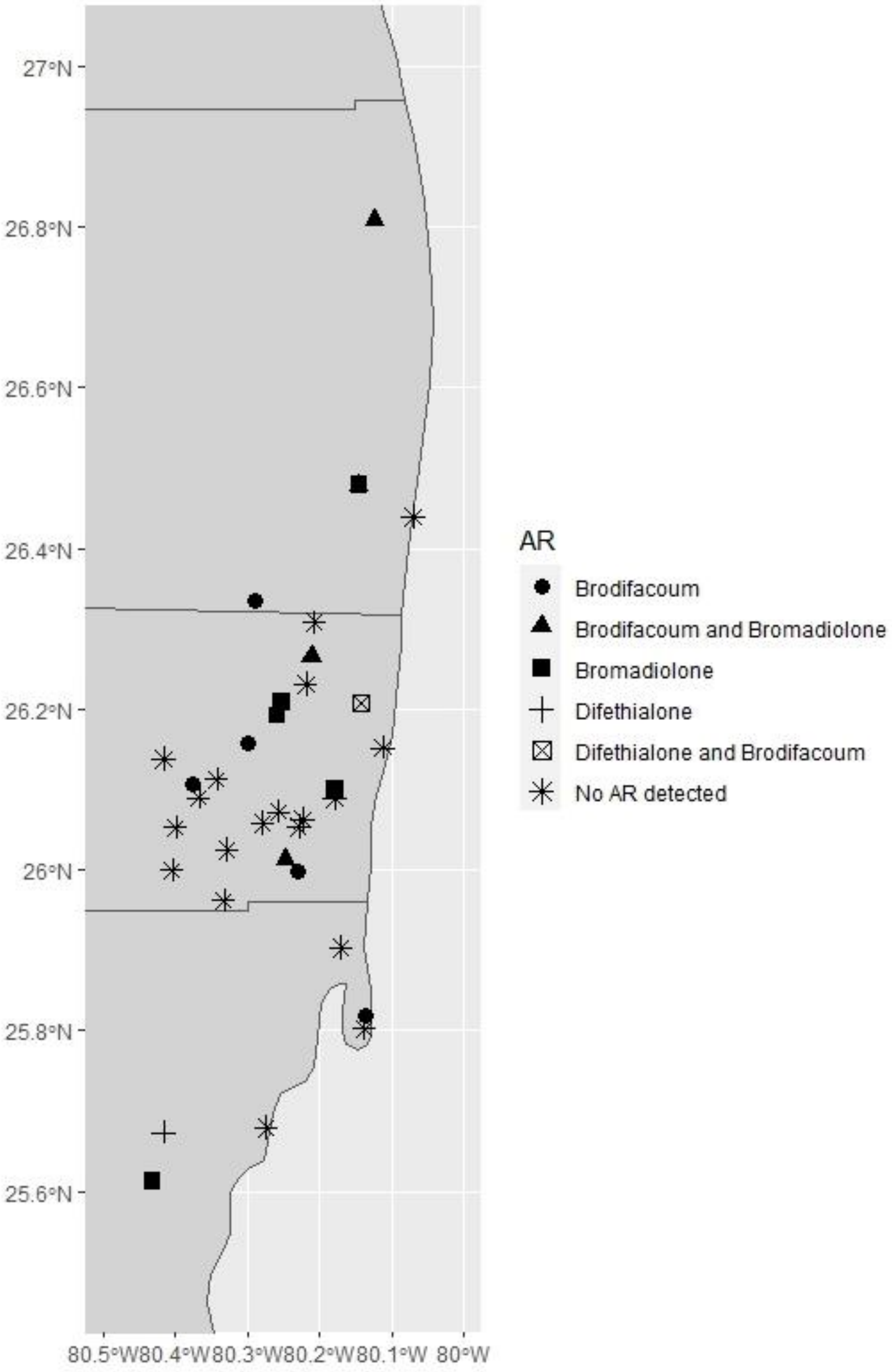
Table 3 Symptoms noted in patients from the South Florida Wildlife Center. The top three rows are AR symptoms noted in Murray (2011).

Symptom from birds that died of unknown causes	Clean birds	AR birds
Depressed (i.e. head hanging, unable to stand. Not due to trauma)	18	21
Anemia/Hypoproteinemia	1	1
Excessive bleeding/poor capillary refill time		3
No blink [swollen eyelids]	15 [2]	13 [1]
Dyspneic	3	5
High blood Creatine Kinase	1	1
Very low blood pressure		1
High WBC	2	
Very high blood pressure	1	
Total birds with antemortem symptoms	20	22

Figure Captions

Fig. 1 AR cases that came in with an address

Figure 1


27°N
26.8°N
26.6°N
26.4°N
26.2°N
26°N
25.8°N
25.6°N
80.5°W
80.4°W
80.3°W
80.2°W
80.1°W
80°W
AR
● Brodifacoum
▲ Brodifacoum and Bromadiolone
■ Bromadiolone
+ Difethialone
☒ Difethialone and Brodifacoum
✳ No AR detected

CHAPTER V

REDUCED GENETIC DIVERSITY IN THE SOUTH FLORIDA SUBSPECIES OF RED-SHOULDERED HAWKS

Abstract

Birds are under-represented in the landscape genetics literature. This field of study could be especially useful for providing insight into the population dynamics of avian predators, which are often cryptic and highly mobile over large territories. The Red-shouldered Hawk (*Buteo lineatus extimus*) is the most abundant hawk in southern Florida with unique phenotypic and behavioral characteristics compared to its conspecifics elsewhere in the United States. In this study, we quantified the genetic diversity of *B. l. extimus* in three South Florida counties at nine microsatellite loci. We detected a recent bottleneck within this population, high F_{IS} levels, and a significant degree of relatedness among individuals despite no known relatives being included in our sampling scheme. No isolation-by-distance was detected among the birds sampled. Though this hawk remains numerically abundant, the reduced genetic diversity found in this study may inhibit this unique subspecies' ability to adapt to the rapidly changing environment in South Florida.

Key words: subspecies, genetic diversity, urban

Introduction

Predators are frequently chosen to be the focus of conservation efforts both for their charisma and their functional role in their environments (Sergio et al. 2006). Predators may regulate prey populations (Thirgood et al. 2000, Luna et al. 2020) and they may change the behavior of consumers by creating a landscape of fear (Atkins et al. 2017). By studying predators, researchers can gain insights into a variety of ecosystem conditions and processes such as those maintaining biodiversity (Sergio et al. 2006), the presence of toxins (Lodenius and Solonen 2013), the prevalence of disease (Boal et al. 1998), and more. But studies of predators can be especially challenging considering the large territories predators maintain, the cryptic and/or dangerous nature of these species, and their naturally lower abundance in the environment compared to many prey species (Donázar et al. 2016).

Genetics has become a popular tool in the study of predators because a single sampling event can provide insight into the population dynamics of a species of conservation concern more efficiently than traditional monitoring methods (Booms et al. 2011). A limited number of samples may provide sufficient information to address conservation questions (Hale et al. 2012). Genetic sampling can be non-invasive and may not even require the researcher to encounter the animal (Martínez-Cruz and Camarena 2018).

Birds have received less genetic study than would be expected based on their abundance (Kozakiewicz et al. 2018). Because they are capable of flight, researchers assume their movements, and therefore their gene flow, are less restricted by landscape features (Kozakiewicz et al. 2018). Low levels of effective dispersal can maintain genetic connectivity between geographically separated populations (Robertson et al. 2018). But genetics can also provide insight into population dynamics over much longer timescales than would be captured by studying the movements of individuals today (Garcia et al. 2011). For example, genetic investigations of raptors have found bottleneck events that coincide with the rapid human population growth in North America over the last two centuries (Hull et al. 2008a, Hull et al. 2008b). The reduced genetic diversity after a bottleneck event is a conservation concern because high levels of diversity allow for a species to adapt to a dynamic environment (Martínez-Cruz 2011).

Florida is home to many unique subspecies of birds (Eo et al. 2010, Barrowclough et al. 2019). This is because it remained unglaciated during the last glacial maximum 18,000 years ago (Eo et al. 2010, Barrowclough et al. 2019). Animal populations inhabiting the Florida peninsula today remain somewhat reproductively isolated from the rest of their conspecifics across the rest of the continental United States, which maintains their unique phenotypic characteristics (Eo et al. 2010, Barrowclough et al. 2019). However, Florida is especially vulnerable to two of the top threats to birds this century: anthropogenic land use changes and climate change (Reece et al. 2013, Rosenberg et al. 2019). In South Florida especially, the human population has quintupled in the last fifty years, which has necessitated a concurrent increase in urbanization (Nijman and Clery 2015). Many South Florida counties enacted development boundaries that constrain urban development to the east in order to protect state and federal wetlands to the west (Nijman and Clery 2015).

The Red-shouldered Hawk is the most abundant hawk species in Florida (Toland 2003). In South Florida, it can fill the ecological niche of the avian top predator because larger raptors are less abundant in this region (eBird 2020). The Red-shouldered Hawks of southern Florida (*Buteo lineatus extimus*) are paler and smaller than Red-shouldered Hawks elsewhere (Jacobs and Jacobs 2002). They live in open wetlands more often than conspecifics in more northern states where riparian forests are their preferred habitats (Morrison et al. 2007) and consume different prey species than Red-shouldered Hawks in other states (unpublished data). *B. l. extimus* might be expected to have a smaller population size than other *B. l.* subspecies because it is restricted to the southern half of Florida (Barrowclough et al. 2019). Many peninsular populations have naturally lower genetic diversity because of their reproductive isolation and reduced population size (Battisti 2014).

Hull et al. (2008b) detected a bottleneck in the *B. l. elegans* subspecies in California, which they attributed to urbanization over the last 200 years. In this study, we set out to quantify the genetic diversity of *B. l. extimus* in three South Florida counties. We also investigated whether this population is panmictic or if spatial genetic structuring could be detected, either through isolation by distance or across the urban development boundaries.

Methods

Samples used in this study were collected from two sources. Blood samples (<0.5 cc) were taken from chicks and adults during banding activity at active nests in Palm Beach, Broward, and Miami-Dade counties. Blood was stored on FTA cards (Whatman Bioscience) at room temperature in the lab until DNA extraction. Red-shouldered Hawk carcasses were collected from three wildlife rehabilitation hospitals in the study area as part of an anticoagulant rodenticide study. Muscle samples were taken from these birds and stored frozen at -4° C until DNA extraction.

DNA was extracted from FTA cards and muscle tissue using DNEasy Blood and Tissue Kit (Qiagen). Nine microsatellite loci from Hull et al. (2007) were chosen for analysis: B220, D107, D123, D207, D220, D223, D234, D310, and D324. Fluorescently-labeled primers for nine microsatellite loci were attached to extracted DNA using PCR in 10 µL volumes containing 5.5 µL distilled water, 1 µL DNA, 2 µL 5x reaction buffer (Promega), 1 µL MgCl2, 0.1 µL each forward and reverse primers, 0.2 µL dNTP, and 0.1 µL Taq polymerase. Thermal cycling parameters from Hull et al. (2007) were used. PCR products were then run through a 3130xl DNA Analyzer (Applied Biosystems, Inc) and scored using GeneMarker software (SoftGenetics, State College, PA).

Because carcasses may have included Red-shouldered Hawks of other subspecies that migrated into the study area, a cluster analysis in STRUCTURE version 2.3.4 (Pritchard et al. 2000) was conducted to determine if all birds sampled for this study could be considered a single population. For the STRUCTURE analysis, we tested K=1-5 with 15 replicates each using a burn-in period of 10,000 and a run length of 100,000 iterations. Birds known to be of the *B. l. extimus* subspecies were also tested separately from birds of uncertain subspecies in GeneAlEx version 6.5 (Peakall and Smouse 2012) to determine if differentiation existed between the two groups. Loci were then tested for deviations from Hardy-Weinberg Equilibrium (HWE) and linkage disequilibrium in GENEPOP version 4.2 (Raymond and Rousset 1995). The Weir and Cockerham (1984) estimate of F_{IS} were calculated in GENEPOP. MICROCHECKER (van Oosterhout et al. 2004) was used to test for scoring errors and null alleles. Measures of genetic diversity, such as number of alleles (N_A), observed (H_o) and expected (H_e) heterozygosity, were calculated in GeneAlEx. Effective population size was calculated using NeEstimator version 2.1 (Do et al. 2014). ML-RELATE was used to estimate relatedness between all pairs of individuals included in the dataset, which included no related individuals to our knowledge (Kalinowski et al. 2006). Individuals were also labeled as urban or exurban depending on their collection location and F_{ST} values were calculated in GeneAlex to determine if differentiation could be detected between urban and exurban birds. A Mantel test in GeneAlex was used to test for isolation by distance. We tested for a bottleneck using the one-tailed Wilcoxon sign-rank test for heterozygote excess in program BOTTLENECK version 1.2.02 (Piry et al. 1999) using the infinite allele and two-phase models. Means are reported with their standard deviations.

Results

Nine loci were amplified for 49 birds (22 known to be *B. l. extimus* and 27 of uncertain subspecies). The only missing information was four loci for one bird of unknown subspecies (Table 1). The STRUCTURE analysis showed strong support for K=1 (Fig. 1) and F_{ST} between known Florida birds and birds of unknown origin was very low (0.018). Therefore, all subsequent analyses were conducted on all 49 birds together. Six of the nine loci deviated from HWE, all exhibiting an excess of homozygotes (Table 1). There was no evidence of any linkage disequilibrium. MICROCHECKER found evidence of possible null alleles at six loci: D123, D207, D220, D223, D234, D310, and D324. After a test of HWE using MICROCHECKER-adjusted allele frequencies, four loci were still found to be out of HWE: D107, D123, D310, and D324.

The number of alleles at each locus ranged from 8 to 26 (μ=15 ± 6.5). Observed heterozygosity was 0.65 ± 0.21. F_{IS} values were greater than zero at six loci: D123, D207, D220, D223, D310, and D324 (Table 1). Rare alleles (frequency <5%) ranged from 12.5%-77% (μ=39%) of the alleles at a locus. Effective population size was estimated to be 198 (95% CI=132-373). ML-RELATE found 96 of 1,128 possible pairings (8.5%) to be related at least at the level of half-siblings, which is greater than would be expected by chance alone (5%). The F_{ST} value between birds sampled from exurban areas and birds sampled from urban areas was very low (F_{ST}=0.023). The Mantel test was not significant for isolation by distance (P=0.38, Fig. 2). The BOTTLENECK analysis did find evidence of a recent bottleneck under both the infinite allele model (P<0.001) and the two-phase model (P=0.019).

Discussion

The birds sampled in this study did not meet the assumptions of HWE. This could be caused by the presence of null alleles at D207, D220, and D223 which were flagged by MICROCHECKER, but entered HWE when tested with adjusted allele frequencies. However, these loci have been tested on Red-shouldered Hawks before with no evidence of null alleles (Hull et al. 2008b). Therefore, the HWE deviations in this study are unlikely to be caused by null alleles.

F_{IS} values should be close to zero in a randomly mating population (Morinha et al. 2016). F_{IS} values were greater than zero at six loci (Table 1), possibly indicating inbreeding. Inbreeding is to be expected in a population that has experienced a genetic bottleneck. The BOTTLENECK software tests for a genetic bottleneck by testing to see if expected heterozygosity (H_e=1-$\sum q_i^2$ where q_i is the frequency of each allele) is greater than H_{eq} (the amount of heterozygosity simulated based on the number of alleles) (Piry et al. 1999). Because a bottleneck was detected using my data, there was greater H_e than expected based on the number of alleles, or said another way, the amount of H_e in my data would need a larger number of alleles to be simulated by the software.

Alleles are lost more quickly in a bottleneck event than heterozygosity (Piry et al. 1999). This can be seen in Table 2. When the Hull et al. (2008b) data are subset to examine just the eight loci also used in this study, we find that genetic diversity of Florida Red-shouldered Hawks (both heterozygosity [H_e=0.86] and number of alleles [N_A=13.9]) is intermediate between California (which also had a bottleneck detected, H_e=0.79, N_A=8.3) and eastern Red-shouldered Hawk populations (H_e=0.88, N_A=15.3). The percent of alleles lost is greater than the percent heterozygosity lost for both California and Florida birds. Both Red-shouldered Hawks and Swainson's Hawks in California experienced bottleneck events within the last 200 years, which coincides with human population growth in that state (Hull et al. 2008a, Hull et al. 2008b).

Southern Florida has a more recent history of development. The human population in the three counties studied here has quintupled in the last 50 years and is still one of the fastest growing metropolises in the nation (Nijman and Clery 2013). The original Everglades ecosystem has been reduced by half over the last hundred years and even protected areas have very different plant communities today due to drastic anthropogenic changes to the flow of water across the landscape (Bernhardt and Willard 2009). Though the Red-shouldered Hawk is currently the most abundant hawk in the state of Florida and is not considered to be a conservation concern, recent genetic investigations suggest the *B. l. extimus* subspecies could be considered a genetically distinct species (Barrowclough et al. 2019). This study found evidence for a bottleneck within this subspecies, a significant amount of relatedness among presumably unrelated individuals, and highly positive F_{IS} values due to an excess of homozygotes. Birds with high homozygosity have been found to suffer numerous fitness consequences including reduced hatching success (Blomqvist et al. 2010) and reduced likelihood of survival to adulthood (Doyle et al. 2016). The effective population size estimate is not cause for concern as there is often more than an order of magnitude difference between N_e and N and the estimate calculated here falls well within estimates calculated for numerous species of least concern (Doyle et al. 2016). However, it would be interesting to know the effective population size of the California and eastern US populations for comparison because elevated F_{IS} values can also result from genetic drift operating on small effective population sizes (Brown et al. 2013).

Though Red-shouldered Hawks in South Florida are equally productive in urban and exurban areas (unpublished data), more work is needed to determine habitat availability and the population growth rate throughout its range. Two Breeding Bird Atlases have been conducted in Florida, the first from 1986 to 1991 and the second from 2011 to 2016 (Breeding 2020). Confirmed Red-shouldered Hawk breeding activity declined by 38% between the two surveys in the tri-county study area examined here (from 42 records to 26 records) despite the greater sampling effort in the latter survey (Breeding 2020). Reduced breeding activity is not the only cause for concern in this subspecies; fifty percent of Red-shouldered Hawks sampled in this region have been exposed to anticoagulant rodenticides (unpublished data).

Reduced opportunities for breeding due to development, novel sources of mortality associated with urbanization, and the unknown impact of climate change could combine with the reduced genetic fitness found in this study leading to population declines of this subspecies. Future work should compare the measures of genetic diversity found here to museum specimens collected prior to human development in the region to quantify exactly how much genetic diversity has been lost.

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Figure Captions

Figure 1 Plot showing the results of the STRUCTURE analysis.

Figure 2. Plot of paired genetic distances and geographic distances.

Figure 1

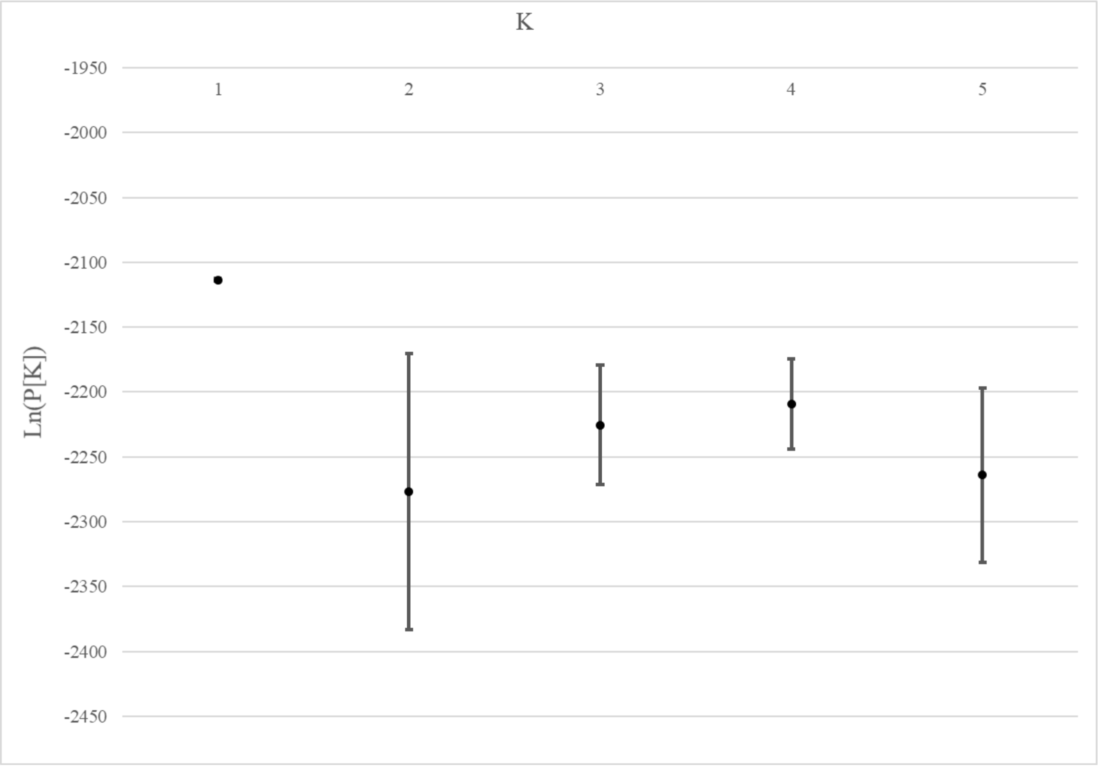
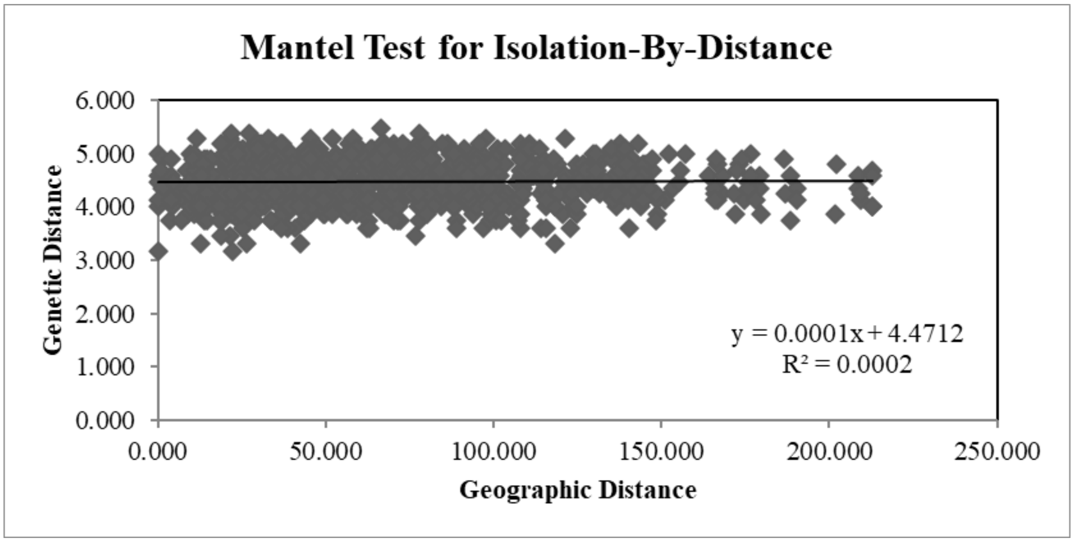

K
-1950
-2000
-2050
-2100
-2150
-2200
-2250
-2300
-2350
-2400
-2450
1
2
3
4
5
Ln(P[K])

Figure 2


Mantel Test for Isolation-By-Distance
Genetic Distance
6.000
5.000
4.000
3.000
2.000
1.000
0.000
0.000
50.000
100.000
150.000
200.000
250.000
Geographic Distance
y = 0.0001x + 4.4712
R² = 0.0002

Tables

Table 1 Measures of genetic diversity. Rare alleles were defined as having a frequency < 5%.

Locus	N	N_A	Rare alleles	HW p-value	H_o	H_e	F_{IS}
B220	49	8	1	0.8907	0.837	0.802	-0.033
D107	49	13	4	0.0195	0.878	0.884	0.018
D123	48	26	20	<0.0001	0.458	0.931	0.515
D207	48	19	13	<0.0001	0.354	0.906	0.616
D220	49	11	5	0.0672	0.612	0.762	0.206
D223	49	9	2	<0.0001	0.429	0.828	0.490
D234	48	11	3	0.9136	0.917	0.865	-0.05
D310	49	14	4	<0.0001	0.714	0.895	0.212
D324	48	24	16	<0.0001	0.646	0.935	0.319

Table 2 Measures of genetic diversity compared to the comparable loci in Hull et al. 2008b.

	CA birds			This study			Eastern birds		
Locus	N_A	% Rare alleles	H_e	N_A	% Rare alleles	H_e	N_A	% Rare alleles	H_e
B220	6	50%	0.71	8	13%	0.80	9	56%	0.80
D107	9	33%	0.81	13	31%	0.88	16	50%	0.90
D123	5	20%	0.64	26	77%	0.93	22	73%	0.91
D207	13	54%	0.87	19	68%	0.91	22	73%	0.93
D220	7	14%	0.83	11	45%	0.76	9	33%	0.86
D223	8	13%	0.82	9	22%	0.83	13	54%	0.86
D234	7	29%	0.79	11	27%	0.87	14	50%	0.86
D310	11	27%	0.87	14	29%	0.9	17	53%	0.92
Average	8.3	30%	0.79	13.9	39%	0.86	15.3	55%	0.88

CHAPTER VI

CONCLUSIONS AND FUTURE DIRECTIONS

Predators serve numerous necessary functions in their ecosystems but are often the first guild to be lost to urbanization (Sergio et al. 2008, Fischer et al. 2012). Raptors are an important exception as they are frequently found in cities across the globe (White et al. 2017). Both urban bird research and raptor research have largely focused on birds in temperate forests in northern latitudes (Marzluff et al. 2001, Buechley et al. 2019). My dissertation provides valuable information on the population dynamics of an urban raptor in a subtropical, wetland-dominated landscape. Though prior urban bird research focused largely on community composition across the urban gradient, my work focused on the demographic and genetic processes within a single species, information necessary to judgements of conservation concern (Marzluff et al. 2001).

Moreover, as much as 40% of prior urban bird research did not provide quantified definitions for the degree of urbanization in their studies and 30% studied only one point on the urban gradient (Marzluff et al. 2001). In Chapter II, I characterized six land cover categories within 500 meters of each nest and found nests across the urban gradient. Percent coverage of each land cover category varied widely across all nests: 0-68% for dense wetland (μ=13% ± 19%), 0-79% for sparse wetland (μ=28% ± 25%), 0-62% for grass (μ=11% ± 13%), 0-38% for water (μ=9% ± 9%), 0-71% for trees (μ=26% ± 21%), and 1-62% for impervious surface (μ=14% ± 15%). Though the likelihood of nest success was not related to land cover proportions. Studies of Red-shouldered Hawks in northern temperate forests often find increasing forest cover to correlate with increased nest success (Dykstra et al. in press) and increased occupancy (Henneman and Anderson 2009). Florida Red-shouldered Hawks are more similar to California Red-shouldered Hawks, which also exhibit no relationship between nest success and land cover variables

(Rottenborn 2000). I did find that despite being the most frequent nesting substrate, nests in palm trees were eight times more likely to fail. Future work should explore why the hawks so often choose to nest in palm trees despite high rates of failure and the ready availability of alternative tree species.

Birds in this study, produced an equal number of fledglings at successful urban nests (2 ± 0.63), successful exurban nests (1.75 ± 0.64 young), and successful nests at the edge of these two categories (1.75 ± 0.46), which could be taken as an encouraging finding in light of South Florida's continuing urbanization. But confirmed Red-shouldered Hawk breeding activity declined by 62% in my tri-county study area between the first Florida Breeding Bird Atlas in 1986-1991 and the most recent Atlas in 2011-2016, despite the greater sampling effort in the latter survey (Breeding 2020). Future work should calculate the remaining breeding habitat availability as well as the rate of habitat loss as South Florida has developed over the last seventy years.

In Chapter III, I examined the amount and identity of prey items fed to chicks by adult Red-shouldered Hawks at both urban and exurban nests. Red-shouldered Hawks in this study had a lower range of prey delivery rates per hour than has been previously reported for this species (Townsend 2006). Red-shouldered Hawk nestlings in Florida grow to a smaller adult size and have less thermoregulatory demand, which may account for the lower prey delivery rates. In fact, nestlings in this study area often appeared to be heat-stressed, spending much of the day panting and moving continuously throughout each day as shade cover shifted with the sun or being shaded by adults when shade cover was unavailable. Future work could examine whether heat stress negatively impacts nestling health or whether available shade plays a role in nest site selection.

Red-shouldered Hawks are known to consume more reptiles and amphibians in the southern portion of their range and more mammals in the northern portion of their range (Strobel and Boal 2010). The Florida birds I studied followed this pattern: 58% of identifiable prey items were reptiles and 18% were amphibians. This proportion differed markedly from other southern populations (except Texas) which consume amphibians primarily and reptiles secondarily (Strobel and Boal 2010). Though mammals and birds were a minority of the items fed, their provisioning times (a proxy for biomass) were significantly larger than the provisioning times of reptiles and amphibians. This study also documents a number of new prey items not previously recorded for Red-shouldered Hawks such as juvenile alligators (*Alligator mississippiensis*), Cuban knight anoles (*Anolis equestris*), and green iguanas (*Iguana iguana*).

Though my sample size was too low to draw broad conclusions, the most urban nest I monitored had the lowest diversity of prey items fed to chicks (Chapter III, Table 2). Thirty percent of the prey items fed to chicks at this nest were of one species: the green iguana. Other nests included in my study also appeared to specialize on locally abundant prey. One nest appeared to feed insects, though this is an assumption based on the numerous unidentifiable items that had provisioning times smaller than 15 seconds. Another nest fed mostly birds, which may be a unique observation for this species (Strobel et al. 2010). Despite the wide variety in their diets, all chicks were successfully fledged from every nest recorded in this study. Future work should expand the sample size studied here and investigate whether the various diets found in South Florida contribute to sub-lethal fitness consequences for chicks, such as immune system activity or parasite loads (Sumasgutner et al. 2018).

In Chapter IV, I screened the livers of Red-shouldered Hawks collected in my tri-county area for anticoagulant rodenticides (ARs). Red-shouldered Hawks have only been included in one prior study of AR exposure in raptors, perhaps because the commensal rodents targeted by ARs are not a typical prey item of this species (Weir et al. 2018). This study found 49% of Red-shouldered Hawks in this study area had been exposed to ARs. It is unknown what proportion of the sampled birds were migrants from northern states or resident South Florida birds. Future work should examine the effect of migration on AR storage in the liver because many bird species experience large changes in the mass of their livers as they burn stored fat to fuel their journey (Newton 2010).

In Chapter V, I examined several measures of genetic diversity in the South Florida subspecies of Red-shouldered Hawk. The number of alleles per locus, heterozygosity, and the proportion of rare alleles in this population were all intermediate between California Red-shouldered Hawks and Red-shouldered Hawks in the eastern United States (Hull et al. 2008). I detected a genetic bottleneck among the birds I studied, as well as F_{IS} values which can be a sign of inbreeding, and numerous pairs that appeared related despite a sampling scheme that included no known related individuals. Red-shouldered Hawks in California were also found to have suffered a genetic bottleneck coinciding with human population growth over the last 200 years in that state (Hull et al. 2008). Florida’s human population growth has occurred over a shorter timeframe and Red-shouldered Hawks in Florida are not reproductively isolated from their conspecifics like California hawks. This may explain why a bottleneck has been detected among the Florida birds, but the measures of genetic diversity are not as reduced as the California birds. Future work should compare museum specimens of South Florida Red-shouldered

Hawks collected before human development exploded in the 1960's to contemporary hawks to identify just how much genetic diversity has been lost.

This study has documented the adaptability of the South Florida subspecies of Red-shouldered Hawks in their diet and nest site selection across a wide gradient of urbanization. However, at the same time, this study has documented reductions in the genetic diversity of this population and a high exposure to a potentially lethal toxin. Conservation efforts are often hampered by a lack of baseline natural history information from before a species becomes threatened or endangered (Kauffman et al. 2003). This work sought to provide such information for South Florida's most abundant hawk and extend the study of urban raptors to the largest subtropical metropolis in the United States.

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VITA

DONNA MARAIN

2009-2011	B.S., Science of Natural and Environmental Systems Law & Society Minor Cornell University Ithaca, NY
2010-2011	NSF Biology Research Fellow Cornell University
2011-2012	Fulbright Fellow Amman, Jordan
2013-2016	Avian Biologist Miami Science Museum Miami, Florida
2019	Mosaics in Science Intern Biscayne National Park Miami, Florida
2015-2020	Ph.D., Biology Certificate in Public Management Florida International University Miami, FL
2018-2022	Co-Chairperson, Local Committee Joint Research Conference of the Raptor Research Foundation & Florida Ornithological Society Fort Lauderdale, Florida