PUBLIC MOTIVATIONS FOR RESOURCE PROVISIONING AND PHYSIOLOGICAL IMPACTS ON WHITE IBIS (*EUDOCIMUS ALBUS*) IN URBAN SOUTH FLORIDA

by

SHANNON ELIZABETH CURRY

(Under the Direction of Sonia M. Hernandez)

ABSTRACT

Human activities including supplemental feeding substantially impact wildlife. In South Florida, wetland birds including American white ibis increasingly forage in urban habitats where people provide anthropogenic food directly (feeding birds in parks) and indirectly (e.g., landfills, dumpsters). Urban habitat use and food supplementation likely affect ibis health, and ibis presence at urban parks provides opportunities to educate people regarding how their behaviors affect wildlife and public health. We captured white ibis in South Florida urban habitats and assessed diet, stress, and immunity to better understand how supplemental feeding and urban habitat use impact health. We also administered surveys addressing public perceptions of birds and bird feeding to visitors at South Florida urban parks where public bird feeding is common. Stable isotope analysis revealed that urban ibis consumed more anthropogenic foods and less aquatic prey. Isotopic signatures were depleted in δ^{13}C and δ^{15}N with increased surrounding developed land cover, suggesting increased ibis consumption of bread in more developed habitats. Corticosterone was positively correlated with H:L ratios, but no stress parameters were correlated with immune function. Stress and immunity varied considerably overall; however, some birds exhibited immune and stress levels indicative of either adaptation or chronic stress. Some ibis may therefore benefit from urban habitats, while others experience increased stress and suppressed immunity with implications for altered pathogen infection. Park visitors regularly fed birds at home (27%) or parks (60%), and 31% fed birds on the day of the survey. Visitors who fed birds were more interested in birds but varied in their motivations for feeding. Most visitors would stop feeding if birds carry disease, and visitors were generally uncertain if bird feeding benefits birds, and what foods are appropriate. We must educate people with realistic information about disease risk while communicating that public health depends on maintenance of environmental and wildlife health. Improving interactions between urban residents and local wildlife requires obtaining public support for management, which may include improving features of urban areas that support wildlife (e.g., regulating bird feeding), or highlighting the importance of wild habitat conservation or restoration if urban areas increase risks and jeopardize success for wildlife.

INDEX WORDS: urbanization, urban wildlife, white ibis, *Eudocimus albus*, anthropogenic food provisioning, wildlife disease, stress, immunity, corticosterone, bacterial killing, bird feeding, public perceptions, human dimensions, One Health

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DEDICATION

I dedicate this to my grandmother, who reveled vicariously in my stories of adventure. You would have thoroughly enjoyed my accounts of traipsing across (mostly urban) Southeastern lands to catch wildlife for research, and I’m forever grateful I had prior opportunities to fascinate you with epics I acquired while studying in Oxford libraries, frolicking over Irish countryside, sleeping beneath backcountry Arizona stars, and forever pursuing desert sunsets.

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CHAPTER 1

INTRODUCTION

Urban growth and development is occurring rapidly, and substantially alters global ecosystems, with variable impacts for wildlife (Vitousek et al. 1997, Evans et al. 2011, Sol et al. 2014). Some wildlife not traditionally associated with urban environments increasingly use urban areas. This shift likely relates to increased and predictable access to food resources compared to resources available in minimized or degraded native habitats (Evans et al. 2011). Bird feeding in backyards and at urban parks is one source of such resources (Robb et al. 2008, Chapman and Jones 2009), and also provides urban residents with opportunities to observe and interact with wildlife (Jones and Reynolds 2008). While supplemental foods may improve wildlife condition, nutritionally deficient or contaminated foods may negatively affect wildlife health (Bradley and Altizer 2007, Robb et al. 2008, Murray et al. 2015). Urban habitats provide altered exposure to pathogens for wildlife, through environmental contamination and interaction with novel species. Particularly in South Florida, Everglades-associated wading bird species like the white ibis (*Eudocimus albus*) increasingly visit urban areas for food resources. These birds interact regularly with people, who provide supplemental food that may afford increased calories if ibis struggle to find food resources in degraded Everglades habitats. However, ibis in urban Florida have increased risk of infection with pathogens like *Salmonella* spp. that are of wildlife and public health concern (Hernandez et al. 2016). Public contact at urban parks with ibis and other birds, plus contact with railings or tables contaminated with birds' feces, increase likelihood of zoonotic transmission of pathogens like *Salmonella* spp. Therefore, ibis and other wading birds may benefit, but also experience negative health consequences, from use of alternative urban habitats with supplemental food resources. Similarly, people who feed and interact with urban birds or visit urban parks where birds are present may benefit from these interactions, but may also experience increased conflict from risks including zoonotic disease.

In Chapter 2, we review research of birds in urban areas, avian health in the context of human-caused changes, white ibis in urban South Florida as a system in which to explore impacts of urban habitat use and supplemental feeding on avian health, and ways in which people interact with and benefit from urban wildlife—specifically through supplemental bird feeding. In Chapters 3–5 we present results of our research in these areas, and in Chapter 6 we summarize conclusions from our research, offer suggestions for applying our research to management and public education programs, and present avenues for relevant future research.

Study Area

We captured ibis in Palm Beach County, Florida (PBC; 26.650708°, -80.276931°). PBC is a highly developed county located east of parts of the Everglades wetland ecosystem, and the county encompasses multiple land cover types with variable suites of stressors. Ibis numbers have been increasing in PBC for over a decade, primarily in the non-breeding season, and some ibis flocks are present predictably at certain sites (Welch 2016). Based on preliminary observations, we identified seven sites with consistent flocks of ibis (>10 ibis) habituated to human presence sufficiently for capture (see Hernandez et al. 2016). The sites included a zoo, a parking lot, and various urban parks, all of which varied in the availability of anthropogenic food, surrounding land cover type (e.g., wetland, developed), and ibis flock habituation to people.

Sample Collection

We captured ibis using nylon leg lassos at seven sites in PBC just after the breeding season (11 July to 31 August 2013, hereafter "summer," n=68) and at six of seven sites just prior to the following breeding season (December 2013, hereafter "winter," n=24). We did not capture ibis in other seasons, as ibis leave urban parts of PBC during the breeding season. We collected standard morphometric measurements and measured body mass, which we standardized by calculating the residuals after regressing mass by tarsus length (with separate regressions for male and female ibis). In July–August 2013, we attached VHF transmitters to track a subset of ibis for a larger project investigating ibis movement and health (Welch 2016).

We collected fresh feces from captured ibis immediately after defecation, blood at three time points—within 2 minutes of capture, 15 minutes post-capture, and 30 minutes post-capture, and smears from fresh whole blood at one time point (typically at 15 minutes post-capture. All animal capture and handling procedures were approved by the University of Georgia's Institutional Animal Care and Use Committee (AUP#A2011 08-018).

Survey Methods

We developed an on-site survey from questions created specifically for this study and questions adapted from previously published studies (Horvath and Roelans 1991, Fulton et al. 1996), and conducted a pilot test of the survey in winter 2012 (December

20–21). We then removed and reworded several questions as appropriate, resulting in a final survey that took approximately ten minutes to complete and comprised bird feeding behaviors and motivations; general interest in and knowledge of birds; orientations toward birds and wildlife; preferred resources for seeking bird-related information; and socio-demographic characteristics.

We administered the survey at one PBC park in summer 2013 (July 10–30) and winter 2013 (December 9–21) and at another PBC park in summer 2015 (July 8–14) and winter 2015 (December 17–22). These sampling periods accounted for season shifts in residency in South Florida and were also timed to coincide with sampling for the concurrent white ibis study. To control for possible differences in park visitation throughout the day and between weekdays and weekends, we stratified available sampling dates by dividing days into weekday and weekend groups, and dividing daylight hours into three blocks (morning, afternoon, and evening). We then selected sampling sessions randomly from all possible blocks, with sessions for weekday and weekend days selected separately. During each stratified-random sampling session, we approached every other adult visitor (at least 18 years old) present at the park. We allowed participants to complete the survey on their own, or respond to the questions as read by the researcher. All participants consented to the research prior to completing the survey, and all procedures were approved by the University of Georgia’s Institutional Review Board (IRB Project # 2013-10432-0).

Movement and Land Cover Analysis

We tracked a subset of ibis captured in July–August 2013 via radio telemetry from September 2013 to July 2014 at the seven capture sites and along a 104-km pre-set route across urban Palm Beach County (Welch 2016). Ibis are present in urban areas primarily during the non-breeding season; therefore, for this project we excluded breeding season detections. We analyzed non-breeding season (September–February) detections by dividing the number of detections of each ibis in the sampling area (which included both the capture sites and a 0.5-km radius around the pre-set route) by the total number of visits to the sampling area.

We determined land cover types surrounding capture sites in ArcGIS by reclassifying raster data from the 2014 Cooperative Land Cover Map (Florida Fish and Wildlife Conservation Commission and Florida Natural Areas Inventory) into relevant categories, including a combined category for all wetland types, and a combined category for all developed types. We calculated the number of pixels in each land cover category within a 2-km-radius buffer around the center of each capture site, reflecting the average daily foraging area of an urban ibis (Hernandez unpublished data). We then determined the percentage of each land cover category surrounding each capture site by dividing the number of pixels for the category by the total number of pixels in the 2-km-radius buffer.

Stable Isotope Analysis

In Chapter 3, we used stable isotope analysis to assess ibis use of anthropogenic resources in urban Palm Beach County. We determined isotopic ratios of 13/12 carbon and 15/14 nitrogen isotopes in plasma and fecal samples from captured ibis, and from likely diet source items. Our objectives were: to assess the relationship between land cover surrounding different urban capture sites and isotopic ratios; to compare isotopic signatures of ibis foraging at different urban capture sites and between ibis foraging in urban versus wild habitats; and to determine the relative proportions of likely food sources in ibis diets. We also assessed the relationship between isotopic ratios in feces versus plasma to determine the feasibility of using non-invasively collected fecal samples in future diet studies.

Stress and Immune Function

In Chapter 4, we assessed multiple parameters of stress and immunity in ibis captured in urban Palm Beach County. We used assays targeting the hormone corticosterone in plasma and its metabolites in feces, and a bactericidal assay that quantified the capacity of ibis plasma to kill *Escherichia coli* bacteria. We also determined heterophil-to-lymphocyte ratios (H:L ratios) from differential cell counts of whole blood smears. We sought to assess if increased ibis use of urban habitat was correlated with increased stress and suppressed immune function. Overall, we expected ibis with higher corticosterone levels to have lower bactericidal capacity, and that corticosterone levels would be correlated with H:L ratios. We also expected that ibis which spent more time in urban habitats and ibis captured at habitats with greater surrounding developed land would exhibit higher corticosterone levels and reduced bactericidal capacity.

Public Perceptions of Birds and Bird Feeding

In Chapter 5, we conducted public surveys at two PBC urban parks to establish and compare the prevalence of bird feeding activity, and to assess public motivations for feeding and general interest in and knowledge of birds. We compared park visitors who did and did not feed birds to better understand the socio-demographic characteristics and self-reported interest/knowledge of people who engage in bird feeding activity. We also characterized sub-groups of visitors who feed birds, and we expected to find multiple clusters of visitors who feed birds for different reasons and may therefore differ both in socio-demographic characteristics and self-reported levels of interest in and knowledge of birds. Finally, we evaluated future behavior change in visitors that feed birds based on communication of disease risk, and evaluated preferred resources for communication of bird-related information to visitors.

Summary

In Chapter 6, we discuss the general conclusions of our research pertaining to urban ibis diet, stress, and immune function, as well as public bird feeding and perceptions of urban wildlife. We also review larger implications of this research, as well as future goals for our project and important areas for general future research of coupled human-wildlife relationships in the context of urban impacts on wildlife and public health.

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CHAPTER 2

LITERATURE REVIEW

URBAN AVIAN ECOLOGY

Habitat and Community Dynamics

Anthropogenic developed areas include heterogeneous habitats that differ greatly in floral and faunal composition, with implications for wildlife species diversity, density, and behavior. For example, wildlife can access habitats including roads, parking lots, and other impervious surfaces (Kristan et al. 2004, Morgan et al. 2012); various types of maintained lawns and gardens (Lepczyk et al. 2004, Epstein et al. 2007, Lerman and Warren 2011, Lerman et al. 2012, Belaire et al. 2015); urban parks and green spaces (Epstein et al. 2007, Martin et al. 2012, Welch 2016); urban ponds and wetlands, including wastewater and sewage treatment areas (Frederick and McGehee 1994, Ferns and Mudge 2000, McKinney 2010); specific feeding areas, including backyard bird feeders and outdoor cat food (Lepczyk et al. 2004, Theimer et al. 2015); and waste disposal areas including dumpsters, waste bins, compost piles, and landfills (Rumbold et al. 2009, Maciusik et al. 2010, Caron-Beaudoin et al. 2013, Murray et al. 2015a and b, Dolejska et al. 2016). These heterogeneous habitats vary in their suitability for different species, but many offer food resources, shelter, breeding habitat, and features including reduced predation risk and decreased competition for some wildlife species. More highly developed habitats often benefit generalist foragers (including non-native species) with behavioral plasticity and less-stringent habitat requirements, which may out-compete other species (Lepczyk et al. 2004, Shochat et al. 2004 and 2006, Clergeau and Yesou 2006, McKinney 2006, Anderies et al. 2007, Maciusik et al. 2010, Galbraith et al. 2015). Therefore, the wildlife communities that form in urban habitats differ considerably based on the type of habitat, and also differ considerably from wildlife communities in undeveloped areas.

Urban communities in highly developed landscapes often exhibit greater species homogeneity due to over-abundance of more successful species (e.g., Kristan et al. 2004 noted artificially high raven numbers in areas with supplemental feeding), while habitats with intermediate development may support a higher diversity of native species (McKinney 2002, Lerman et al. 2012); see Anderies et al. 2007 for a model explaining observed high density and lower diversity of urban species based on greater resource availability and lowered predation risk. For traditional wildlife, altered species assemblages generate interactions with large numbers of novel species, including non-native and peridomestic species (e.g., ducks at parks), and potentially including novel predators (Lepczyk et al. 2004, Chapman and Jones 2009, Thiemer et al. 2015). Altered hierarchies may exist between individuals and across species, affecting competition and behaviors among individuals, including aggression (toward both other wildlife and people), which can cause injury and substantially affect stress response (Orams 2002, Shochat et al. 2006, Murray et al. 2016). Populations of successful urban exploitive species may increase, and wildlife may congregate at the urban areas where food and water resources are most plentiful (Thiemer et al. 2015, Murray et al. 2016). Therefore, aggregations of urban wildlife are often at unnaturally high densities (e.g., Fedriani et al. 2001, Theimer et al. 2015, Murray et al. 2016), contributing to increased aggression and behavior change, altered stress, and increased pathogen exposure through contact—including with non-native species carrying novel pathogens (Bradley and Altizer 2007, Martin et al. 2010b, Becker et al. 2015—and see Gottdenker et al.'s 2014 review of the various mechanisms affecting urban pathogen transmission dynamics).

Suite of Stressors

The above changes to habitat and community dynamics present novel stressors—and interactions of multiple stressors—to which wildlife must adapt to successfully exploit urban habitats. Aggression and interactions with novel species (including novel predators), plus altered hierarchies and predation risk (including reduced predation risk, or increased risk from novel species—e.g., cats—Lepczyk et al. 2004), may alter stress responses for wildlife (Goymann and Wingfield 2004, Bradley and Altizer 2007). Additional anthropogenic features of urban habitats present novel stressors for wildlife, including aggregation at abnormally high densities, interaction with unfamiliar species, presence of people and their interactions with wildlife (e.g., feeding, chasing), presence of and interactions with vehicles such as cars and boats, and regular noise from cars and other machinery (Ditchkoff et al. 2006, Slabbekoorn and Ripmeester 2007, Thiemer et al. 2015, Murray et al. 2016). Experience of these stressors may lead wildlife to change their behaviors, including in detrimental ways. Wildlife may increasingly tolerate and interact with people—by habituating and becoming aggressive toward people (Orams 2002, Murray et al. 2015a, Thiemer et al. 2015); becoming dependent on supplemental food (Orams 2002); avoiding people and areas where people are present (e.g., wading birds in urban Rhode Island—McKinney et al. 2010); or changing their activities (e.g., altering timing of bird song in noisy areas, or diurnal behavior in diseased urban coyotes;

Slabbekoorn and Ripmeester 2007, Murray et al. 2015b). They may also alter their reactions to stressors, often varying by species with some more likely than others to adapt to human presence. For example, after habituation to tourists, penguins reduced head turns when tourists were present (Walker et al. 2006); chough in Spain habituated to park visitors and reduced flushing distances, but other birds did not similarly adjust (Jimenez et al. 2011); species rather than site best predicted shorebird flight initiation in Australia (Blumenstein et al. 2003); and flight initiation on an urban-rural gradient differed by species in China, with increased tolerance most pronounced in the little egret (Lin et al. 2012).

These behavioral changes may accompany—even reflect—underlying physiological changes, which vary by individual and species. Some wildlife adapt to novel stressors with positive changes to their stress physiology, by initiating a stress response less frequently (Fokidis et al. 2009), or maintaining their stress physiology and continuing to respond acutely to novel stressors while subsequently returning to a normal stress state. Knapp et al. (2013) found no difference in corticosterone levels between iguanas that were fed or not fed by tourists, and Morgan et al. (2012) found neutral and positive responses in nestling and adult jays to roads (Morgan et al. 2012). However, other wildlife experience negative changes to stress physiology through repeated response to novel stressors that can cause them to enter a chronic stress state, in which they allocate more energy toward the stress response than they obtain from their environment, affecting their energy balance and investment in physiological processes. Chronic stress is correlated with decreased condition, reduction in reproductive investment, and suppression of immune function, all of which alter pathogen infection dynamics (Bradley and Altizer 2007, Cyr and Romero 2007, Chavez-Zichinelli et al. 2013, Downs and Stewart 2014). Different species, and even different individuals, react and adapt to environments and their stressors differently, and whether they become chronically stressed may vary considerably based on the situation and the individual personality and stress physiology (Martin et al. 2010, Cockrem 2013).

Food Resources and Movement

One primary reason wildlife use developed and urban habitats despite altered community dynamics and novel stressors is for the increased and consistent food resources some urban habitats offer (e.g., landfills, static bird feeders). Food provides energy necessary for physiological processes, and when energy needs exceed energy intake, wildlife lose allostatic balance and may experience health-related consequences including chronic stress. Anthropogenic resources are often more consistently available; and since less-available and inconsistent resources have been linked to increased and chronic stress, greater and more consistent urban resources may reduce stress and allostatic load for some urban wildlife—though stress reduction may not occur if wildlife forage at an area with the novel stressors discussed previously (Lynn et al. 2003, Kitaysky et al.1999, Fokidis et al. 2012, Neuman-Lee et al. 2015).

The type, availability, and quality of supplemental resources vary across the developed landscape, and some species and individuals are better able to capitalize on them—particularly generalists (for example, gulls, corvids, and coyotes; Kristan et al. 2004, Murray et al. 2015a, Jerzak 2001), more dominant/aggressive individuals, or species with increased behavioral plasticity (Clergeau and Yesou 2006, Anderies et al. 2007, Calle and Gawlik 2011). Some supplemental foods are appropriate for certain species of wildlife (e.g., bird seed for some passerines—Siriwardena et al. 2007, road kill for corvids—Kristan et al. 2004), and the sheer caloric benefit allows some wildlife to reduce their time and energy spent foraging, improving condition and redistributing energy toward self-care, immune function, and breeding activities (Deerenberg et al. 1997, Bradley and Altizer 2007, Fokidis et al. 2008). Greater investment in immune function may mitigate negative impacts of contaminated food and habitat, through improved ability to fight pathogen infection and reduced risk of shedding and environmental contamination or transmission—for example, Fokidis et al. (2008) found lower blood parasitism in urban areas for some avian species. However, other foods may provide calories but be inappropriate and nutritionally deficient for certain wildlife (Heiss et al. 2009, Murray et al. 2015b), may be contaminated with pathogens or toxins that can suppress immune function and other physiological processes (Green et al. 2006, Blanco et al. 2011, Murray et al. 2016), or the environment in which they are accessed may be contaminated (Cizek et al. 1994, Martin et al. 2010, Murray et al. 2016). Knapp et al. 2013 found changes in blood chemistry and haemoparasite prevalence based on supplemental feeding. Heiss et al. (2009) found that rural versus urban crow nestlings were larger with higher protein levels, and when some rural crows had access to supplemental food, their nestlings were smaller than those of rural crows without available supplemental resources. Easy access to poor food can also perpetuate a cycle for less-fit wildlife, whereby they survive but in poor condition because they have constant access to poor quality foods (Murray et al. 2015b). Some species shift from transient or seasonal movements in the wild to increased sedentism in urban areas—at times becoming residential and perhaps dependent on supplemental foods (Orams 2002, Prange et al. 2004, Martin et al. 2012). If infected animals shed increasingly large numbers of pathogens or reduce their movements, some urban areas may be increasingly contaminated, increasing the risk of pathogen exposure and infection (Cizek et al. 1994, Murray et al. 2016).

Fitness and Reproductive Success

Species able to capitalize on energy from urban-associated food resources without adverse hormonal changes or reduced health may benefit from urban areas as a "source" habitat that improves population success through individual fitness and reproductive success (Moore and Hopkins 2009). Chamberlain et al. (2009) review avian productivity in urban habitats, and Robb et al. (2008) review ways in which supplemental bird feeding positively and negatively affects birds, including via altered productivity. Individuals may have better condition, contributing to increased survival (including over-winter survival for some migratory species) and perhaps lower parasite prevalence, and ultimately allowing greater investment in long-term reproduction (Schoech and Bowman 2001, Siriwardena et al. 2007, Fokidis et al. 2008). As Robb et al. (2008) demonstrate in their review, sometimes reproductive success itself may improve in urban habitats through reduced nest predation, and via resource supplementation: birds that nest in urban areas and those that return to wild habitats to breed may benefit from increased overwinter survival of breeding-age adults, earlier onset and longer duration of breeding, and increased egg-laying and nesting effort. Additionally, increased success of nestlings has been tied in some studies to continued and/or increased anthropogenic food availability during breeding season (Robb et al. 2008)—for example, Kristen et al. (2004)

found increased fledging of raven chicks with greater anthropogenic subsidies of trash or roadkill.

However, the consequences of supplemental feeding are often more complicated. Individual fitness and survival may suffer if supplemental foods are poor nutritionally, or if wildlife increasingly encounter toxins or pathogens through consumption of supplements (see previous section). Foraging in anthropogenic areas may increase risk of predation for some species—for example, feral cat predation is a known risk for birds and other wildlife (Lepczyk et al. 2004). Linking supplemental resources to reproductive success is complicated because some species only provide anthropogenic foods to their young in seasons of poor natural food availability (Dorn et al. 2011), and others may consume anthropogenic foods themselves but avoid giving these foods to nestlings, perhaps preferring traditional foods that may be more nutritionally appropriate (Jerzac 2001, Schoech et al. 2004, O'Leary and Jones 2006). Some research demonstrates negative consequences associated with use of supplemental resources, including: reduced egg-laying; reduction in nestling survival, size, and health (Heiss et al. 2009); and increased nest predation for urban breeders (Shochat 2004, Harrison et al. 2010). The earlier onset of breeding in some supplemented birds can put nestlings out of sync with seasonally available food resources, and nestlings may not be more successful after fledging (Schoech and Bowman 2001, Robb et al. 2008). Urban habitats are therefore "sinks" for both wildlife with reduced fitness or reproductive success, or wildlife whose young are unsuccessful.

Overall Health

Urban habitat use can both positively and negatively affect wildlife health, including via aspects discussed above (habitat/food resources; exposure/response to novel stressors, contaminants, and pathogens; energetic input and expenditure related to resources and movement; fitness and reproductive success) (Bradley and Altizer 2007, Martin et al. 2010, Becker et al. 2015). These factors have been correlated often to individual health via assessment of nutrition, stress, immune function, or pathogen prevalence. However, these aspects of individual health are all related within an individual and together contribute to that individual’s health and success—therefore, integrated studies of urban impacts on multiple indices of health are important. Stress responses and immune function are particularly important components of overall health, through their importance in maintaining energy balance, and their role in the dynamics and outcomes of stress- and pathogen-related disease. While urban areas often present novel stressors and facilitate increased pathogen exposure, consistent access to food can reduce chronic stress, and increased energetic input may boost immune function and help individuals fight pathogens (Fokidis et al. 2012). Conversely, decreased nutrition and development of chronic stress may negatively affect physiology and contribute to immunosuppression, increasing the likelihood and intensity of pathogen infection (Romero 2004, Bradley and Altizer 2007, Downs and Stewart 2014, Neuman-Lee et al 2015). Indeed, the outcomes of pathogen infections for wildlife are highly variable based on numerous factors—and food resources are a particularly important factor (Becker et al. 2015). Additionally, since many populations of urban wildlife still traverse the interface of urban and wild habitats, they may transmit pathogens from urban areas back to wild areas, with intra- and inter-specific population-level impacts (Martin et al. 2010, Ramos et al. 2010).

Successful Exploitation

Successful exploitation may not depend exclusively on health; however, decreased health can diminish individual survival and reproductive output, perhaps drawing the line between a “source” versus “sink” habitat for an individual. Wildlife range in their abilities to adapt without health consequences and successfully exploit urban habitats (Chavez-Zichinelli et al. 2013). Commonly studied urban “exploiter” (or synanthropic) species are often generalist foragers with behavioral plasticity—including non-native species—that tolerate the novel stressors of urban areas and capitalize on food resources (Johnston 2001, Luniak 2004, McKinney et al. 2006). These species may still experience negative impacts on health and fitness, but for some exploiters without these negative impacts, urban areas are ultimately “source” habitats that improve individual and population success (Luniak 2004). Many classic urban exploiters are species we commonly associate with cities, including non-native species, which have long been adapted to these environments and do well in highly developed landscapes (e.g., various corvids, pigeons, some song birds, gulls; Jerzak 2001, Johnston 2001, McKinney 2006). Conversely, urban “avoider” species often have specific habitat and foraging requirements that they cannot meet in urban areas, and/or cannot adapt to novel stressors.

Many species fall in between; these urban “adaptors” may use urban areas (perhaps both due to consistent resource availability and wild habitat degradation) but prefer fringe habitats or areas of intermediate development (e.g., suburbs), or they may use urban habitats more sporadically than exploiters, including seasonal use, or supplementation of wild foraging and habitat use (McKinney 2002 and 2006, Calle and Gawlik 2011, Dorn et al. 2011). These species may increasingly be forced into developed areas due to difficulty successfully foraging in natural areas, but there may be large variation in the success of these animals in adapting to novel habitats and stressors, and the trade-offs between more available and consistent food resources with changes in behavior/hierarchies, stress, nutrition, and exposure to contaminants/pathogens may allow some animals to be successful but not others (Fokidis et al. 2008, Chavez-Zichinelli et al. 2013). Even within species, some individuals adapt more successfully than others, including due to personality and flexibility of stress response systems that maintain allostasis. Some of these species are “winners” as described by Shochat (2004) who live on the credit of urban areas with abundant resources, while others may survive and contribute to population numbers, but never achieve the health and fitness necessary to breed and contribute to the population (Shochat 2004). Many urban “adaptors” that are native species less traditionally associated with urban habitats are currently trying to adapt. It is important to understand this process and assess whether the species is truly successful without adverse changes to stress and immune processes—or increased pathogen prevalence—to determine if urban habitats can serve as “sources” rather than “sinks” for these species, which may include species of concern.

AVIAN HEALTH AND DISEASE ECOLOGY

Wildlife Disease Ecology

Introduction to Health and Disease in Wildlife

Wobeser (1997) defines disease in wildlife as "any impairment that interferes with or modifies the performance of normal functions, including responses to environmental factors such as nutrition, toxicants, and climate; infectious agents; inherent or congenital defects; or combinations of these factors." Wobeser considers "disease" a condition that may arise following infection with a pathogen (or exposure to a toxin/contaminant), as determined by numerous factors that continually push and pull wildlife between disease and health, and ultimately mortality and survival (Wobeser 1997). Wobeser highlights that his terminology of "impaired function" versus "illness or death" acknowledges the influence of multiple factors on health; for example, the outcome of exposure to an infectious agent varies, including by sex, age, life-history stage, and co-infection status. Healthy organisms do not exceed their energetic requirements and can successfully maintain normal function despite exposure to contaminants or pathogenic agents. Within an organism, the immune system is critical in preventing disease and maintaining health, as it responds to and neutralizes foreign agents (e.g., contaminants, pathogens). However, the immune system is linked to other physiological processes in the organism, including the endocrine system; hormones—including those released during a stress response—can therefore affect immune response. Additionally, all physiological processes depend on energy, and many rely on specific nutrients. Energy is allocated among these processes; therefore, if an organism has limited energy intake, some processes—including some components of the immune system—may be down-regulated; this contributes to increased risk of infection and exacerbated disease outcomes, but may also protect organisms from immunopathology. Therefore, a healthy organism with enough energy invested in immune defense may be exposed to pathogenic agents without developing “disease” (McEwen and Wingfield 2003, Downs et al. 2014) However, an unhealthy organism with limited energy resources—or an organism responding to a stressor or experiencing an energy-intensive stage (e.g., reproduction)—may down-regulate some aspects of immunity, allowing pathogen infection leading to disease, or may succumb to disease upon co-infection with multiple pathogens (Sheldon and Verhulst 1996, Romero 2004). The variable outcomes of pathogen infection are determined not only by numerous intrinsic factors (e.g., energy, nutrition, and stress), but also by the route and dose of pathogen exposure, co-infection with multiple pathogens, and anthropogenic factors affecting both pathogens and hosts (Bradley and Altizer 2007, Hall and Saito 2008, Boughton et al. 2011). Wildlife disease ecology examines these dynamics at a population level, recognizing that the impacts of pathogen exposure and infection in wildlife in terms of health, fitness, and reproduction can have population- and community-level effects (Sheldon and Verhulst 1996, Wobeser 2006, Martin et al. 2010b).

Anthropogenic Effects on Pathogen Dynamics

Pathogens have normal cycles (e.g., dial, seasonal, annual) and a well-evolved role in wildlife systems—sometimes with population-level significance—and organisms have developed complex immune systems adapted to respond effectively to pathogens (Hall and Saito 2008, Downs and Stewart 2014). However, human activities (e.g., land use change, climate change, introduction of animals) substantially alter the prevalence, distribution, and virulence of pathogens, as well as wildlife immune system function (Daszak et al. 2001, Martin et al. 2010, Gottdenker et al. 2014). For example, people substantially destroy and alter wild habitats: disturbance, fragmentation, and land use change affect pathogen transmission cycles (see Gottdenker et al. 2014 for a review of pertinent literature), and can lead to emergence of infectious diseases significant for public and wildlife health (Patz et al. 2004, Brearley et al. 2012). Global climate change and associated shifts in temperature and rainfall, including shifts due to human activities in urban areas, allow certain pathogens to persist or flourish where previously they could not, affecting pathogen density, virulence, distribution, and seasonality of infection in both wild and urban areas (Bradley and Altizer 2007, Martin et al. 2010).

People transport and alter the distributions of native and non-native wild and domestic animals—including their various pathogens—and introduce them to novel habitats, with positive and negative impacts for native wildlife (Daszak et al. 2001, Martin et al. 2010). Non-native species (including domestic animals) may stress native wildlife and affect immunity, out-compete native wildlife for resources critical in maintenance of immunity and health, infect naïve native wildlife with non-native pathogens, or dilute the prevalence of native pathogens in native wildlife populations by serving as alternate less-suitable hosts for these pathogens (Riley et al. 2004, Alexander and McNutt 2010, Martin et al. 2010). For example, Telfer et al. (2005) found reduced prevalence of *Bartonella* spp. in Irish wood mice after a bank vole invasion. Kopp and Jokela (2007) had similar results from an experiment in which an invasive snail species co-housed with a native snail species diluted pathogen prevalence in the native snail. Millins et al. (2016) found infection in non-native gray squirrels with native *Borellia* strains; however, the authors are unsure what role the gray squirrels play in community pathogen transmission dynamics. More directly, human contamination of landscapes, including through pathogen and toxin runoff, can expose wildlife at higher rates and to novel agents, increasing risk of pathogen infection (Cizek et al. 1994, Bradley and Altizer 2007) and/or cell death and altered hormone and cellular production from toxin exposure (Green et al. 2006, Martin et al. 2010).

People also provide direct and indirect supplemental food to wildlife, both in natural settings via tourism, and throughout urban and suburban areas (Orams 2002, Lepczyk et al. 2004, Jones and Reynolds 2008, Knapp et al. 2013, Murray et al. 2016). Direct and indirect resource provisioning can substantially alter exposure and tolerance of wildlife to pathogenic agents—including by lowering exposure (e.g., Aponte et al. 2014 found lower endoparasite prevalence in gulls consuming anthropogenic foods)—and aggregation at food sources can increase wildlife densities and contact (Dhondt et al. 1998, Bradley and Altizer 2007, Knapp et al. 2013, Becker et al. 2015). All of these changes affect the transmission cycle and course of infection of various pathogens in wildlife, including wildlife in urban areas.

Studies in Wildlife

Assessing disease in wildlife is challenging. We often observe only mortality or survival in wild animals; however, sub-lethal consequences of disease may impact population success more than individual mortality—through diminished reproductive output of seemingly healthy members of a population, and because unhealthy individuals may carry and transmit pathogens of population-level concern (Wobeser 1997). Wildlife may not present clinical signs recognizable as disease; wildlife often die and are quickly consumed or decompose in their (often inaccessible) environment; diseased wildlife may alter their behavior to avoid people; and researchers rarely observe the same animal more than once in the field (Wobeser 2006). Therefore, to better assess disease and understand its causes—including how anthropogenic factors exacerbate infection—researchers should examine various indices of health in seemingly healthy animals. For example, researchers can determine wildlife exposure to and infection with various pathogens, assess baseline levels of stress and induced stress response, and measure the functioning of various immune system components. Numerous studies have addressed these questions separately. Specific to human-altered environments, researchers have investigated urban-associated parasites and pathogens in wildlife (Lawson et al. 2010, Ramos et al. 2010, Dolejska et al. 2016); emerging infectious diseases (Simon et al. 2014, Rulli et al. 2017); pathogen exposure or infection and stress levels across gradients of human development (Chavez-Zichinelli 2010 and 2013, Lehrer et al. 2010, Hamer et al. 2012), or compared between urban and rural or wild areas (Gregoire et al. 2002, Riley et al. 2004); and endocrine and immune function in contaminated landscapes (deSwart et al. 1996, Harms et al. 2010, Jayasena et al. 2011). However, few studies have addressed these questions in the same urban wildlife system, considering the interplay of anthropogenic factors, pathogen dynamics, and individual health.

Therefore, studies of how anthropogenic activity and urban habitat use affect wildlife health and disease must surpass pathogen prevalence assessments by assessing less-overt aspects of health that contribute to disease—including stress response and immune function—in the environmental context (here, including relevant anthropogenic factors). Brearley et al. (2013) suggest studying relationships between stress, immunity, and pathogen dynamics specifically in the context of habitat fragmentation and change. Several years later, Hing et al. (2016) highlight the continued need for additional research of anthropogenic impacts on health parameters, as these are stressors for wildlife and as such can alter and exacerbate infection and disease. Specifically to our research, we seek to assess the role of anthropogenic factors in urban areas (e.g., food resource availability/type, land use type, environmental contamination, inter-specific contact, suite of stressors) in changes to indices of wildlife health (e.g., pathogen prevalence, stress hormone levels and response, immune function).

Components of Wildlife Health

Pathogen Exposure and Prevalence

Metrics—The most direct way to determine dynamics of disease in wildlife systems is to assess wildlife exposure to and infection with pathogens that cause disease. Exposure to pathogenic agents—including bacteria, viruses, or toxins—activates an organism’s immune system, which comprises innate and adaptive components that target and remove foreign agents, including pathogens (see the following section for a more thorough explanation of the immune system). Infection occurs when a pathogen replicates in an organism’s body, resulting in increased numbers of the pathogen in tissues, and shedding of viral or bacterial material in body fluids (e.g., saliva, feces). Researchers can assess current infection by detecting and culturing the etiologic agent from tissues in which is it likely present (e.g., saliva, feces, blood, liver, brain—the optimal tissue varies by pathogen and host), and they can detect the presence of a pathogenic agent in an organism’s tissue by looking for specific sequences of its DNA via polymerase chain reaction (PCR) in these samples. However, PCR detection is typically not informative in apparently healthy animals, but is best applied in clinically diseased animals with likely high levels of pathogenic agent in their tissues. The immune system produces antibodies targeted at specific pathogens, and immune cells remember pathogens to which they have responded to more quickly identify and respond to the same pathogen in the future. Therefore, the presence of antibodies during and persistence of antibodies after infection allows researchers to assess wildlife antibody titers via numerous assay techniques to determine exposure to and previous infection with various pathogens.

Studies in Wildlife—Studies have documented considerable anthropogenic effects on infection dynamics in wildlife by assessing pathogen prevalence in human-modified landscapes, including cities; by surveying for multiple pathogens or focusing on a pathogen of concern; or by comparing pathogen prevalence between altered and non-altered landscapes, or along gradients of human development. Alexander and McNutt (2010) found that human activities including changes in numbers and distribution of domestic animals altered exposure to and distribution of pathogens in endangered African dogs. Knapp et al. (2013) compared iguanas in unvisited areas and areas visited by tourists providing supplemental food, finding higher endoparasite prevalence in tourist-visited iguanas likely related to increased iguana densities in visited areas. Jimenez et al. (2011) found lower prevalence of parasites in choughs at tourist-visited sites in Spain. Lehrer et al. (2010) found a positive relationship between *Toxoplasma gondii* antibodies in woodchucks and degree of urbanization along a gradient in Illinois, which reflects increasing overlap in more urban areas between woodchucks and cats (the definitive host for *T. gondii*). Hamer et al. (2012) similarly found increased prevalence of antibodies to

West Nile Virus with increasing urbanization. Murray et al. (2015) observed mange in urban coyotes that used more developed areas, consumed less protein, and had increased home ranges and daytime activity compared to urban coyotes without mange. Fokidis et al. (2008) found lower blood parasitism in urban birds—particularly in one species—but also higher leukocyte counts and heterophil-to-lymphocyte ratios for some urban birds, ultimately highlighting a likely interplay between immunity, infection risk, and availability of food resources in determining how well certain birds adapt to urban habitats.

For urban wildlife, it can also be informative to specifically assess urban-associated pathogens (e.g., *Salmonella* spp., *Escherichia coli*) or contact-associated pathogens (e.g., avian influenza and paramyxoviruses for wild birds in contact with ducks at urban parks). Cizek et al. (1994) and Hernandez et al. (2016) examined *Salmonella* spp. prevalence based on landscape factors; Cizek et al. found a relationship between environmental contamination and wild bird infection, and Hernandez et al. found increased infection in habitats with more open-developed and less natural land. Lawson et al. (2010) investigated long-term *Salmonella* spp. infections in birds present at human gardens, noting that supplemental feeding likely plays some role in many infections. Ramos et al. (2010) found *Salmonella* spp. and *Campylobacter* spp. infection in gull chicks on the Iberian coast, with a higher prevalence of *Campylobacter* spp. in gulls foraging predominantly on refuse, and evidence that some gulls may serve as carriers of both bacteria. Epstein et al. (2007) suggested that urban Australian white ibis pose risks to livestock and public health through contact-associated pathogen transmission, based on culture and antibody titers of various pathogens of avian, human, and livestock concern (including Avian influenza virus, *Salmonella* spp., Newcastle disease virus, and *Haemoproteus* sp.).

Diet and Nutrition

Diet and Health—Diet is critical to wildlife health, as wildlife require adequate caloric intake and specific nutrients (e.g., vitamins and minerals, fatty acids) to maintain essential and nonessential physiological processes. Supplemental anthropogenic foods may not provide appropriate nutrients for wildlife and may themselves be contaminated with toxins or pathogens to which wildlife can be exposed (see previous section, and reviews including Becker et al. 2015 and Murray et al. 2016). Therefore, knowing what foods wildlife consume helps us understand if they are likely experiencing diet-related health consequences. Ezenwa (2004) linked reduced ability to cope with parasite infection during droughts to low-quality diet (reduced protein) in wild bovids—wildlife consuming anthropogenic foods that are poorer-quality and lower in protein compared to traditional foods may experience similar consequences. Van Hemert et al. (2012) used stable isotope analysis to link chickadee diet to beak deformities, finding that chickadees with deformities consumed foods depleted in nitrogen and more variable in carbon than chickadees without deformities, though altered diet likely reflected rather than caused deformity. Knapp et al. (2013) linked tourism and associated supplemental feeding to changes in blood chemistry parameters that could have long-term physiological impacts.

Metrics of Diet—Diet can be determined through techniques including foraging observation (Malmborg and Willson 1988, Frederick and Bildstein 1994); gut, esophageal, regurgitant, or fecal contents analysis (Kristan et al. 2004, Ferns and Mudge 2000, Dorn et al. 2011, Calle and Gawlik 2012, Boyle et al. 2014); stable isotope analysis

(Robb et al. 2011, Murray et al. 2015b); or combinations of techniques (Auman et al. 2011, Caron-Beaudoin et al. 2013, Aponte et al. 2014). Isotope analysis is advantageous for wildlife species that travel widely and may forage in areas inaccessible and unknown to researchers, and to assess diet over a longer time period. Assessing diet via traditional methods—including analysis of food remains or gut contents—can over- and under-quantify certain diet items, and such techniques often require capturing and euthanizing individuals (Frederick and Bildstein 1994, Auman et al. 2011, Weiser and Powell 2011). Such analyses also reflect recently consumed foods, rather than all foods consumed over several days prior to capture, or all foods consumed longer-term. Stable isotope analysis both allows holistic assessment of ibis short- and long-term diet (varying by tissue sampled), and offers the possibility of non-invasive diet assessment from fecal samples (Hobson and Clark 1992, Kelly 2000, Weiser and Powell 2011, Blumenthal et al. 2012).

Stable Isotope Analysis—Isotopic ratios in wildlife tissues reflect those of the foods wildlife consume and assimilate (DeNiro and Epstein 1978 and 1981). Photosynthetic pathways determine the ratios of 13/12 carbon (δ^{13}C) isotopes in plants, and corn and marine plants are more enriched in 13/12 C than terrestrial and freshwater plants. Therefore, processed anthropogenic foods high in corn and corn syrup are enriched in 13/12C (Jahren and Kraft 2008). Ratios of 15/14 nitrogen (δ^{15}N) change predictably by trophic level as 15N is preferentially assimilated in tissues of consumers. The timing of isotopic assimilation from diet sources varies by tissues, which have different turnover rates—for example, plasma generally reflects short-term diet over several days (Hobson and Clark 1992 and 1993, Podlesak et al. 2005). The enrichment of C and N between diet and a consumer (trophic enrichment factor [TEF]) varies by species, diet, and tissue (DeNiro and Epstein 1978 and 1981); however, standard TEFs are commonly used in the literature, and a recently developed model calculates species-specific TEFs based on enrichment factors of species with similar habitat associations (Healy et al. 2016). Isotopic ratios of an organism's feces likely directly reflect dietary components un-enriched by assimilation in tissue (Hwang et al. 2007, Blumenthal et al. 2012). Therefore, analysis of relative $\delta^{13}C$ and $\delta^{15}N$ ratios in wildlife tissues corrected with TEFs can reveal the trophic level ($\delta^{15}N$) and type ($\delta^{13}C$) of foraging (Kelly 2000). Various tissues can be used to assess short-term diet, including plasma (reflecting diets within 1 to 4 days in ibis) and feces (likely more representative of ratios in actual diet) (Hobson and Clark 1993, Podlesak et al. 2005, Hwang et al. 2007). Feces are additionally valuable as they can be obtained from free-living wildlife without the necessity of capturing the animals.

Studies in Wildlife— Stable isotope analyses have been used extensively to determine wildlife diets (Newsome et al. 2010, Lemons et al. 2011, Murray et al. 2015), including avian diets (Hobson 1986, Kelly 2000, Inger et al. 2006 and 2008). Several studies have examined isotopic ratios in feces (Podlesak et al. 2005, Hwang et al. 2007, Varo and Amat 2008, Blumenthal et al. 2012). Stable isotope ellipse-based niche analyses allow comparison of diets across groups, and stable isotope mixing models determine contributions of likely food sources to an individual's diet (Parnell et al. 2010, Jackson et al. 2011). Recent studies have applied stable isotope analysis to wildlife in urban systems. Robb et al. (2011) identified use of human-provided supplemental food by blue tits via stable isotope analysis, and Auman et al. (2011) found differences in isotopic signatures between urban and non-urban silver gulls. Murray et al. (2015) assessed diet in urban coyotes via isotopic ratios in conjunction with movement analysis, and Caron-Beaudoin et al. (2013) tied movement of urban gulls to consumption of anthropogenic foods. However, studies have not yet addressed ibis diet with urban habitat use.

Baseline Stress and Stress Response

Basics of Endocrinology—Organisms respond to perceived stressors through hierarchical physiological processes. The hypothalamic-pituitary-adrenal (HPA) axis is critical in the vertebrate stress response and controls secretion of glucocorticoid stress hormones (typically cortisol or corticosterone, dependent on species). Upon perception of a stressor, the hypothalamus in the brain releases adrenocorticotropic hormone (ACTH), which travels to and stimulates the pituitary gland to release corticotropin-releasing hormone (CRH). CRH then circulates through the bloodstream and binds to receptors in the adrenal gland, stimulating production and secretion of glucocorticoid stress hormone (e.g., corticosterone in birds). Corticosterone then travels through the blood and binds to receptors in the body, signaling organs and cells to initiate physiological processes that help the animal respond effectively to a stressor (e.g., mobilization of energy via gluconeogensis) (Romero 2004, Sheriff et al. 2011). While corticosterone directly stimulates gluconeogenesis and therefore mediates energy distribution and allocation, it is also a chemical messenger that up- and down-regulates various physiological processes (e.g., reproduction, behavior) (McEwen and Wingfield 2010, Wilcoxen et al. 2011, Neuman-Lee et al. 2015). Hormones reach peak levels in the blood typically between 15 and 30 minutes, and once hormone levels reach a certain concentration in the brain, the hypothalamus ceases hormone production through the negative feedback loop, and the animal returns to a baseline level of circulating corticosterone—typically within 60–90 minutes (Romero 2004, Sheriff et al. 2011). Additional physiological processes work in concert with corticosterone and the HPA axis to allow organisms to effectively respond to stressors, including catecholamine hormones (epinephrine and norepinephrine) integral to the fight or flight response (McEwen and Wingfield 2003).

Allostasis and Chronic Stress—Response to stressors via corticosterone and other hormone release is normal and not indicative of disease. Organisms with adequate energy intake can distribute energy toward the stress response without negative consequences, and the hormonal response of wildlife to normal events are well-documented, including fluctuations in response by time of day, season, life-history stage, sex, and age. The term “allostasis” explains “normal” stress responses in the context of fluctuating environmental conditions, avoiding ambiguous and often misused terms like “stress” and “homeostasis” (McEwen and Wingfield 2010). McEwen and Wingfield (2010) define allostasis as homeostasis, plus anticipation of demands from changes in life-history stage (e.g., reproduction, molt, migration), plus additional costs of less-predictable factors (e.g., parasite load and disease, social status, injury). An organism can maintain allostasis while diverting energy toward an acute stress response related to predictable events, and even unpredictable environmental factors (e.g., adverse weather), as long as the organism has sufficient access to energetic resources and does not expend more energy than it acquires (see McEwen and Wingfield 2003 and 2010 for more detailed descriptions). This acute stress response enhances some immune system components, perhaps mobilizing them to respond to the threat of a stressor (Schmidt et al. 2015). However—particularly when an animal encounters unpredictable stressors, or continued and frequent stressors—the organism may experience prolonged acute stress response, and/or the energy of the stress response may increase the animal's allostatic load, resulting in a state of chronic stress.

Chronically stressed animals may experience continuous activation of the HPA axis response and cessation of negative feedback loop function. These animals therefore may constantly release corticosterone, but with dampened sensitivity to acute stressors and reduced magnitude of response following perception of an acute stressor (indicative of reduced ability of adrenal tissue to secrete corticosterone). Excess energy diverted toward continual HPA axis activation cannot be used for other processes; diversion of energy, plus the role of corticosterone as a mediator in various physiological processes, means chronic stress has numerous deleterious effects—for example, suppression of breeding and other hormones, immunity, and digestion; stress-related disease; and long-term effects such as reduced feather growth or replacement (Romero 2004, Cyr et al. 2007, Butler et al. 2009, DesRochers 2009). However, some organisms may dampen the HPA axis before reaching chronic stress, perhaps to avoid immune suppression and pathogenicity related to chronic stress. Cyr et al. (2007) found support for this after conducting an experiment with captive European starlings in which they induced chronic stress but did not observe immune suppression. However, adult females under the chronic stress protocol had lower baseline corticosterone levels (Cyr and Romero 2007).

Metrics of Stress—Stress is often measured through quantification of glucocorticoid hormones before and during a stress response, typically via immunoassay (See Sheriff et al. 2011 for a thorough review of tissues, assays, and caveats for corticosterone studies in wildlife). Baseline stress is commonly measured via levels of corticosterone in plasma; when samples are collected within three minutes of capture, this indicates the level of circulating stress hormone in the organism prior to the stress response induced by capture and handling (Angelier et al. 2010). Ecologists debate interpretation of free versus total corticosterone (corticosterone travels through the blood both freely and bound to corticosteroid binding globulin (CBG), which may fluctuate differentially from free hormone), though most ecologists follow the free-cort hypothesis and believe that for their purposes, free corticosterone is the most relevant measure. However, bound corticosterone can still be biologically active, and cleaving can occur that liberates bound corticosterone (See Sheriff et al. 2011 for a full discussion of pros and cons of measuring free versus bound corticosterone). Some corticosterone from the bloodstream is metabolized and excreted; therefore, longer-term baseline stress can be measured via levels of corticosterone hormone metabolites in feces, which cross-react with assays targeted at corticosterone, and can be reliably measured with standard immunoassays once extraction and assay protocols are validated for a species (Mostl et al. 2005, Palme et al. 2005). This type of analysis indicates corticosterone metabolized and excreted during the animal's intestinal transit time, which varies by species and ranges 2–24 hours for various birds (Palme et al. 2005). Fecal samples are best collected and frozen soon after defecation, and once frozen can be maintained with stability for extended periods of time prior to analysis (Herring and Gawlik 2002, Mostl et al. 2005).

The stress response is often measured in laboratory/experimental settings via standard stress-challenge protocols that include administration of corticosterone hormone (Khan and Robert 2013) or administration of ACTH to stimulate corticosterone production (Nilsson et al. 2008); these studies often later administer dexamethasone to assess the function of the negative feedback loop (MacDougall-Shackleton et al. 2013).

In the field, some researchers use pellets or other implants (Cote et al. 2006, Almasi et al. 2009) or noninvasive means (Breuner et al. 1998) to release corticosterone into the blood stream prior to sampling—again often requiring holding animals for an extended period of time. However, researchers have established use of standard capture and handling protocols in the field as an inherent stress challenge, which does not require holding animals for an extended time (e.g., Cockrem and Silverin 2002, Romero 2012, Grunst et al. 2014). Following this protocol, samples collected at a set point after capture (often 15 or 30 minutes) indicate induced stress, or the peak HPA axis response to the stressor of capture.

In addition to measurements of hormones including corticosterone, differential counts of white blood cells quantify the numbers and ratio of heterophils to lymphocytes (H:L ratio) in the blood. During stress, including following infection or injury, more heterophils are often released into the peripheral circulation as lymphocytes are redistributed outside of circulation; therefore, the ratio of heterophils to lymphocytes in the blood increases (Davis et al. 2008). Researchers also measure stress more generally by quantifying wildlife responses to stressors, assumed to indicate underlying changes in stress physiology. For example, studies have used avian flight initiation distance and scores of wildlife habituation toward people as metrics of wildlife perception of human presence/approach as a stressor (Walker et al. 2006, Jimenez et al. 2011, Clucas and Marzluff 2012, Lin et al. 2012).

Studies in Wildlife—Studies have documented variation in baseline and induced stress in wildlife—including by sex, age, life-history stage (e.g., molt, breeding), and individual phenotype/personality—with varying results. Metrics of stress including H:L ratios may respond differently based on pathogen infection, as demonstrated through increased relative heterophil production by house finches infected with *Mycoplasma gallisepticum* versus those with no infection (Fratto et al. 2014). Baseline and induced corticosterone is generally lower in older individuals, though some studies have documented otherwise, perhaps due to population selection favoring older individuals with more robust stress responses (Wilcoxen et al. 2011). Kitaysky et al. (1999) found increased baseline and induced corticosterone through the breeding season. Romero et al. (2008) experimentally found considerable variation in individual baseline corticosterone across time; while relative levels between birds were consistent at night, relative daytime levels changed based on length of day and during molt. Studies have found high variation between—but lower variation within—individuals. Ouyang et al. (2011) found repeatable baseline corticosterone levels in superb starlings within but not across seasons and years, and non-repeatable induced corticosterone levels; however, Cockrem and Silverin (2002) found greater repeatability of peak than baseline corticosterone in great tits, also finding individual differences in the timing of peak responses, with some at 10 and others at 30 minutes post-capture. Some evidence suggests the HPA axis and its responsiveness is developed early in life (i.e., maternal HPA responses, and early life exposure to stressors, can "program" the HPA axis), and varies by personality or coping style, which may also be developed in early life stages (Cyr and Romero 2007, Schoech et al. 2011, Cockrem 2013). Stress physiology may also be somewhat plastic, allowing some individuals to adjust in new environments, somewhat dependent on "personality" and phenotypic plasticity (more research is necessary regarding the persistence and adaptation of phenotypes) (Martin 2009, Ouyang et al. 2011, Schoech et al. 2011, Cockrem 2013).

Pertinent to urban ecology and altered stressors and inter-specific interactions for wildlife in urban areas, some studies have investigated impacts on stress of status and hierarchy, tourism, and habituation to people and novel stressors. Other studies specifically address urban impacts on endocrine response by compare populations along gradients of urbanization or between urban and non-urban (or disturbed and non-disturbed) areas. Results reveal wide variation in stress responses, as highlighted in the Bonier (2012) review of urban avian endocrine research. Knapp et al. (2013) found no differences in baseline or induced stress levels in iguanas at tourist visited and non-visited areas. They suggest the unexpected lack of difference relates to food availability, as other studies have not differentiated between fed and unfed populations. They also suggest hormonal adaptation in the visited iguana group. Berger et al. (2005) found higher glucocorticoid levels (and suppressed immune function) in territorial male iguanas during the breeding season. Vleck et al. (2000) found several instances of higher heterophil-to-lymphocyte ratios related to visible injury in breeding penguins that lost their territory. Jimenez et al. (2011) found adaptation in two chough species to tourist-visited areas via reduced flushing behavior and lower fecal glucocorticoid metabolite levels; however, they note that other species present in the area did not similarly adapt. Walker et al. (2006) found lower corticosterone response (suggesting reduced adrenocortical tissue ability to secrete corticosterone) in penguins in a tourist-visited (vs. non tourist-visited) area, and also noted rapid habituation of penguins in non-visited areas to humans (measured via corticosterone and head turns). Atwell et al. (2012) used corticosterone levels to assess adaptation after urbanization, finding changes in stress responses in a recently urbanized versus wild population of dark-eyed juncos. Chavez-

Zichinelli et al. (2013) found differences in the ability of avian species to adapt to urban habitats; towhees exhibited chronic stress, but inca doves adapted well. Clucas and Marzluff (2012) found increased flight initiation distances of birds along an urban-rural gradient (suggesting greater habituation in urban areas). Fokidis et al. (2009) found similar baseline corticosterone in urban versus rural birds but higher total corticosterone response in urban birds, variable by life history stage (e.g., breeding, molt)—though free corticosterone differed less than total. They also found some species-specific effects and noted less variability between life stages in urban birds, suggesting that predictable resources available to these birds may reduce their need to vary HPA responsiveness across life-history stages. Chavez-Zichinelli et al. (2010) assessed fecal corticosterone in house sparrows across three land uses (urban, suburban, and industrial), finding variation in stress and immunoglobulin within all land use types, suggesting some birds in all land use types were stressed and some were not. However, results from the industrial land use type showed correlation of high fecal corticosterone with low immunoglobulin, suggesting some birds in this land use type may be responding poorly to stressors.

Many studies have examined how food stress or availability of supplemental foods affects stress hormones, which is relevant to understanding impacts of altered resource availability in anthropogenic habitats. Kitaysky et al. (1999) compared birds in breeding colonies with and without food restrictions and found that baseline and induced corticosterone rose during the breeding season in both colonies, but baseline corticosterone was higher and induced corticosterone lower for birds in the food-restricted colony. Lynn et al. (2003) found short-term increases in total corticosterone, and long-term increases in free corticosterone, in food-stressed birds. Schoech et al.

(2004 and 2007) conducted studies with the Florida scrub-jay comparing suburban birds (with access to supplemental food), wild birds given ad libitum high protein/high fat food, wild birds given ad libitum low protein/high fat food, and wild birds with no access to supplemental food. In 2004, they found the lowest corticosterone levels in suburban birds, followed by birds with access to high protein/high fat foods, followed by birds with access to low protein/high fat foods—all of which were lower than corticosterone levels in wild birds without supplemental food access. Jays with access to supplemental food bred earlier, possibly due to the relationship of consistent and available food and nutrients to corticosterone levels. Suburban birds had lower baseline and higher induced corticosterone than all other groups, and the authors suggest the lack of differences between the three non-suburban wild bird groups may relate to greater natural food availability that year due to favorable environmental conditions. Vleck et al. (2000) found that breeding penguins only exhibited higher corticosterone levels during prolonged fasting when the fast exceeded 50 days—which was well beyond normal fasting length for most of the birds, and likely was the point at which penguins exhausted their stored energy reserves.

Immune Function

Basics of Immunology—The immune system is composed of numerous components that react to and remove foreign invaders including pathogens (see Demas et al. 2011 and Downs and Stewart 2014 for overviews of the immune response relevant to wildlife research). The immune system is comprised of an innate and an adaptive arm, each of which employ humoral and cell-mediated components. Innate immunity is always present and is not pathogen-specific: the physical barriers of skin and mucous membranes always act as immune defenders, and cells involved in the inflammatory response act upon recognition of a foreign agent to neutralize invaders at or near the site of entry; for example, mast cells release histamine that operates at a local level, and macrophages and other cells mark and kill invaders via phagocytosis. Adaptive immune responses are activated after the immune system recognizes a particular threat; these include the antibody response, in which cells retain memory of specific pathogens and upon re-exposure can more quickly recognize and produce antibodies to neutralize the pathogen. Different immune system components have different purposes, so immune responses vary based on the type of foreign invader (i.e., the same immune arms will not be activated at the same level for every type of threat) (Adamo 2004, Boughton et al. 2011, Demas et al. 2011). Additionally, components of immunity may be invested in differentially and up- and down-regulated based on energy resources, circulating stress hormones, environmental factors, and even basic individual variation (Adamo 2004, Forsman et al. 2008, Boughton et al. 2011).

Ecoimmunology—Ecological immunology (or ecoimmunology) recognizes that individual variation in ecological and environmental challenges (e.g., resource availability, parasite infection) influences trade-offs in allocating energy toward immune function and other processes (including reproduction) (French et al. 2009, Boughton et al. 2011, Demas et al. 2011). Ecoimmunology studies often incorporate assessment of stress, which is affected by individual ecological and environmental challenges (see previous section) and directly impacts immune function. Stress is typically linked to immunosuppression, but some studies have related increased circulating corticosterone to enhancement of specific immune system components, and acute stress may enhance, but chronic stress suppress, some immune components (Schmidt et al. 2015). Martin 2007 notes that during unpredictable stressful events, increased immune sensitivity to glucocorticoids can allow the heightened HPA axis response to enhance immune function and effectively react to the event. Buehler et al. (2008) found enhancement of some immune system components and suppression of others in red knots following capture and handling, but also found that among the affected immune components, some responded more quickly than others to the stress of capture and handling. Matson et al. (2006) and Millet et al. (2007) found diminished innate bactericidal capacity against *E. coli* in multiple avian species, related to increased corticosterone post-capture. Stier et al. (2009) found that corticosterone reduced antibody production (cell-mediated immunity) but not constitutive innate immunity. The authors also found reduced growth and reduced resistance to oxidative stress with higher corticosterone, hypothesizing that birds suppress the humoral immune response during stress to avoid immunopathology and related tissue damage. Martin et al. (2005) similarly suggest that birds in areas with greater pathogen risk (e.g., tropics) may keep glucocorticoid hormone levels low to ensure enhanced immune function, and their comparison of tropical and New Jersey birds supported this hypothesis. While trade-offs between physiological processes including immunity are often thought of in terms of energy, Svensson et al. (1998) found suppressed humoral immune function (via lowered antibody production) related to cold stress, but found no support that energy explained the trade-off. Rubenstein et al. (2008) found reduced plasma bactericidal ability in tropical superb starlings in the driest year within a seasonally changing but unpredictable environment; increased prolactin correlated to higher bactericidal capacity, but the authors did not find the expected negative correlation between corticosterone and bactericidal capacity. They therefore suggest that prolactin plays a role in mediating immune function of superb starlings based on environmental change, and while corticosterone may also play a role, it may be more complicated, or may be more associated with social dynamics, or differ from expected results in temperate birds.

Metrics of Immune Function—Numerous techniques have been developed and employed to better quantify and assess the arms of the immune system in wildlife. While heterophil-to-lymphocyte ratios are often applied to stress studies, quantification of these plus other white blood cells (i.e., eosinophils, basophils, monocytes) can reveal changes in the production and distribution of immune cells during stress events and upon exposure to pathogenic agents (Demas et al. 2011). Various assays assess components of immune ability (e.g., phagocytocis by macrophage action, inflammatory response, antibody production, bactericidal action) (for discussion and use of various assays, see Millet et al. 2007, Buehler et al. 2008, and Demas et al. 2011). Many of these assays are best employed in laboratory settings on captive wildlife or on free-living populations available for repeated sampling (e.g., birds in nest boxes). At minimum, most assays require holding animals overnight to assess immune response. For example, the PHA skin test, which assesses innate immunity via the magnitude of swelling response after subcutaneous phytohemagglutinin injection, requires observation at a set point after injection (Berger 2005, Martin et al. 2005, Forsman et al. 2008, Schmidt et al. 2015). Some tests inject animals with benign antigen or vaccinate them to assess antibody response, sometimes before exposing them to challenges (e.g., a stress challenge) to determine how the challenge affects antibody production; however, this requires resampling the same individual (Svensson et al. 1998, Forsman et al. 2008, Butler et al. 2009, Stier et al. 2009).

For free-living wildlife captured once, cell counts can be performed on blood smears, and some tests of innate immunity can be performed on properly stored blood samples—for example, phagocytosis assays and the bactericidal assay are widely employed on whole blood and plasma in the field, and plasma frozen at -80°C (Tieleman et al. 2005, Matson et al. 2006, Millet et al. 2007, Girard et al. 2008, Hing et al. 2016). When performed on plasma, the bactericidal assay assesses the individual's ability to fight off a non-specific foreign invader by quantifying the ability of complement proteins to kill bacterial colonies. Matson et al. (2006) compared bactericidal ability of avian whole blood and plasma against *Escherichia coli* (non-pathogenic strain 8739) and found similar killing ability by tissue type; therefore, the immune mechanism primarily responsible for killing this strain of *E. coli* is complement proteins present in both whole blood and plasma (rather than cellular responses only present in whole blood)—this was later confirmed by Millet et al. (2007).

Studies in Wildlife—Numerous studies with varying results have investigated impacts of sex, age, species, corticosterone levels, and land use on different immune function metrics, of which a subset of studies investigated immune function in the context of urban environments or anthropogenic effects. Berger et al. (2005) found suppressed PHA in territorial male iguanas during the breeding season, and Pap et al. (2010) found changes to multiple immune indices in birds throughout an annual cycle. Cyr et al. (2007) found that dampened stress responses in captive starlings were not correlated to immune suppression as measured by T-cell mitogen challenge. Butler et al. (2009) simulated chronic stress by administering low levels of corticosterone to kestrel nestlings for one week; they found no short-term changes but longer-term enhancement of PHA, suggesting chronic early-life stress affects immune development. Schmidt et al. (2015) exposed sparrows to either corticosterone treatment or food restriction; they found reduced PHA in males of both treatments but no effect in females. Martin et al. (2005) found lower baseline and dampened induced corticosterone in tropical versus northern (New Jersey) birds, but no changes to PHA—suggesting possible immune system insensitivity to glucocorticoids in tropical birds. Chavez-Zichinelli et al. (2010) examined house sparrow fecal corticosterone and immunoglobulin levels in three land use classes and found considerable variation in all land uses; based on a negative relationship between corticosterone and immunoglobulin in industrial areas, they suggest some birds in these areas experience high levels of stress and correlated suppressed immune function.

Tieleman et al. (2005) first used the bactericidal assay to compare bacterial killing ability across avian species with different natural history traits and found high variability by species. Matson et al. (2006) documented considerable variability in killing ability across avian species. Millet et al. (2007) also found species variation in bacterial killing, plus diminished killing with prolonged capture and handling stress. Tieleman (2010) examined age-and sex-effects and repeatability of bactericidal capacity; they found repeatable killing ability within individuals, no sex differences, and higher killing in older birds between the ages of 1 and 7 years. Schmidt et al. (2015) exposed sparrows to corticosterone treatment or food restriction and found sex-specific effects on immune function. Females had no changes by either treatment to killing of either *E. coli* or

Candida albicans, while males treated with corticosterone had lower *E. coli* and higher *C. albicans* killing than males with food restrictions or controls. Rubenstein et al. (2008) found the lowest bacterial killing ability in birds in the driest of four years, with no relationship to corticosterone but a positive relationship to prolactin, suggesting mediation of bacterial killing by prolactin rather than corticosterone. Girard et al. (2011) assessed bactericidal capacity against *Staphylococcus aureus* and found lower killing in male passerine birds, variability by species, and no relationship between age and bacterial killing, suggesting innate immune function may reach adult performance more quickly than adaptive immune function and reduce age-related variation. They also documented lower bacterial killing for birds with chewing lice, which contrasts with Fratto et al. (2014), who found a non-significant trend of increased bactericidal capacity in birds with *Mycoplasma gallisepticum* infection that was maintained during handling stress.

Bacterial killing (and other immune function assays) can be challenging at best—and uninformative at worst—when interpreted alone (Adamo 2004, Demas et al. 2011, Hing et al. 2016). However, when examined in conjunction with assessment of other immune components and physiological parameters, they can help better understand individual tradeoffs in immunity and ways in which other processes like diet, stress hormone levels, and pathogen infection influence immune function. Additionally, while assessment of immunity via bactericidal capacity has been used in varying ecological contexts for a variety of species, it has less often been applied to birds in developed or urban areas, so outcomes in urban birds are less predictable. Girard et al. (2011) conducted their study with suburban birds. Schmidt et al. (2017) assessed bactericidal capacity over six years in agricultural areas, finding increased killing in more intensively farmed areas. However, in general the bactericidal capacity of wildlife in anthropogenic habitats including urban areas is less well understood.

Integrative Studies of Urban Wildlife Health

Few studies integrate all of these features to assess overall how habitat features and food resources in urban environments affect the overall health of adapting species. Substantial research exists both on the relationship between stress and immune function (generally demonstrating immunosuppressive effects of increased corticosterone and chronic stress) and the relationship between pathogen infection and stress, or pathogen infection and immune components. However, this research also reveals complexities in these relationships, which may change or disappear based on species and situation, and may have thresholds above and below which correlations do not exist (see previous section). Fewer studies have investigated the relationship between stress and immune function in the context of pathogen infection, beyond noting that immune suppression plays a role in infection. The outcome of pathogen infection is highly dependent on immune function and therefore dependent on numerous less-direct factors including stress and nutrition—therefore, incorporating measures of diet, stress, and immunity in studies of pathogen prevalence is critical.

In non-urban wildlife, research has focused on features of habitat use and movement patterns, diet and changes in condition, altered pathogen prevalence, and changes to stress physiology and immune defense. Moore and Hopkins (2009) developed a theoretical framework to tie physiological function (e.g., hormones, immunity, energetics) to performance and ultimate reproductive success, emphasizing that interactions and trade-offs exist within and between various physiological functions.

Sheldon and Verhulst (1996) discuss some of the general trade-offs organisms make with pathogen prevalence and immunity (and other energetic pressures). Becker et al. (2014) modeled published data of feral cats and feline leukemia to show that food provisioning changes survival and fecundity, contact rates, and immune function—leading to increased pathogen transmission at low and high, but not intermediate, levels of provisioning. Hing et al. (2016) integrated pathogen prevalence, fecal glucocorticoid hormone levels, and immune function (via phagocytic activity) in studies of the endangered Australian woylie; neither stress hormone levels nor phagocytic ability affected infection status, but a negative relationship between stress hormone levels and phagocytic ability was present in infected woylie, suggesting stress-related immunosuppression may occur in actively infected individuals. Burgeon et al. (2010) looked at the relationship between energy, stress and immunity in captive-bred mallards.

Many current urban-adapting species are less studied in general in these novel habitats, in part because they are not classically associated with such urban habitats—and studies of shifts in diet/nutrition, habitat use, stress and stress response, and immune function for such species are particularly lacking. However, the initial changes and long-term responses of these species to urban habitats may differ considerably from those of more often researched urban-associated species (e.g., coyotes, raccoons, crows, gulls). Studies have examined changes as non-native species expand their range, but less often address native species that expand into urban habitats; research has addressed shifts for species including Australian white ibis, sacred ibis, and white storks in Europe (Clergeau and Yesou 2006, Kruszyk and Ciach 2010), and wading birds in urban wetlands

(McKinney 2010). However, these studies rarely integrate assessment of multiple physiological parameters related to anthropogenic habitat use.

Several studies do serve as models in their integration of health parameters, at times in the context of urban-adapting species and their altered movement and habitat use. Auman et al. (2011) and Caron-Beaudoin et al. (2013) studied gulls, an urban-adapted species, but tied movement to anthropogenic resource consumption in urban areas. Fratto et al. (2014) found that presence of *Mycoplasma gallisepticum* infection in house finches buffered immune suppression (via H:L ratios and bactericidal capacity) during stress. Jimenez et al. (2011) measured behavioral changes, fecal glucocorticoid metabolites, and prevalence of multiple parasites to assess the capacity of wild chough to adapt to human tourism. The authors found reduced flushing distance, lower levels of glucocorticoid metabolites, and lower pathogen prevalence and pathogen species richness in choughs at tourist-visited sites, suggesting these birds can successfully adapt to anthropogenic areas, and may benefit via improved health. Fokidis et al. (2008) assessed blood parasites and cell counts in urban birds, mentioning how the interplay of food, immunity, and risk of parasite infection affect birds' adaptive success. These types of integrated health studies that examine factors associated with multiple parameters of health (i.e., impacts of anthropogenic resource consumption and movement shifts on stress, immune function, and pathogen prevalence) should be conducted with recent urban adaptive species to assess impacts and inform better urban habitat management and species conservation.

WHITE IBIS IN URBAN SOUTH FLORIDA

Traditional Ecology of White Ibis

The American white ibis (*Eudocimus albus*) is a semi-nomadic wading bird in the order Pelecaniformes, family Threskiornithidae (Heath et al. 2009). In the United States, white ibis rely on southeastern wetlands for aquatic prey—including crayfish, fiddler crabs, other invertebrates, small fish, and frogs (Kushlan 1979, Heath et al. 2009, Boyle et al. 2014). Many ibis in the United States forage widely in the Florida Everglades ecosystem, moving nomadically between habitats, as water levels and prey availability fluctuate from anthropogenic hydrological shifts, wet-dry seasonal cycles, and inter-annual variability in rainfall (Gawlik 2002, Frederick et al. 2008, Beerens et al. 2011, Lantz et al. 2011, Herring and Gawlik 2012). White ibis also depend on the Everglades for suitable breeding habitat and locate many of their large annual breeding colonies in this ecosystem.

Over the 20th century, the Florida Everglades ecosystem was substantially altered and degraded, and decreased in size by approximately 50%. This degradation and loss occurred after habitat destruction and hydrologic changes resulting from anthropogenic wetland draining, development, contamination, and non-native species introductions (Davis and Ogden 1994, Crozier and Gawlik 2003). Everglades loss and degradation caused considerable declines in the populations of multiple wading bird species; annual numbers of white ibis nests declined by 87% between 1903 and 2001 (Crozier and Gawlik 2003), and the bird is now a Florida Species of Special Concern (Heath et al. 2009). White ibis breeding numbers are currently used as an indicator for Everglades restoration, because ibis populations depend so highly on prey availability due to hydrologic factors and so will likely respond directly to active hydrologic management/restoration, and because ibis are aesthetically pleasing to the public and their relationship to wetland health is easily understood (Kushlan 1997, Crozier and Gawlik 2003, Frederick et al. 2008).

White Ibis Urban Shifts

Ibis are generalist foragers and have been previously documented in anthropogenic areas and/or foraging for anthropogenic foods, including at wastewater treatment ponds and landfills (Frederick and McGehee 1994, Rumbold et al. 2009). Ibis have also been documented supplementing food for their nestlings with anthropogenic foods in years of poor resource availability (Dorn et al. 2011, Boyle et al. 2014) and foraging on terrestrial prey from lawns in the non-breeding season (Heath et al. 2009). However, only within the past 10–20 years have larger numbers of ibis been noted spending more time in cities. Ibis are increasingly observed foraging in various environments, including at: urban lawns and water bodies where they likely consume various terrestrial invertebrates, dumpsters and landfills where they consume anthropogenic foods, and urban parks where they consume human handouts, such as bread commonly provided to ducks (Chapman and Jones 2009, Hernandez et al. 2016, Welch 2016). Urban sites exist within a heterogeneous landscape and differ considerably in food resources available to ibis, both due to variation in the surrounding land cover type (e.g., wetland vs. developed), and human influence (e.g., direct bird feeding, presence of trash). Therefore, birds may forage differently across and within sites, with some ibis consuming greater amounts of human handouts (e.g., bread, chips) than others. Ibis in urban areas, when compared to their wild counterparts, experience prolonged aggregation at high densities, exposure to a novel suite of stressors (e.g., large groups of people, cars, noise), and altered behavior including habituation—even sometimes aggression—toward people (personal observation). Ibis also interact closely with novel species common at urban habitats such as parks and landfills, including muscovy ducks (*Cairina moschata*), American pekin ducks (*Anas platyrhynchos*), and laughing gulls (*Leucophaeus atricilla*).

Prior to our research, no studies have quantified changes in ibis movement, habitat use, and diet in urban areas, or determined if ibis exhibit features of successful urban adaptation. A concurrent study established high fidelity of some ibis to a landfill located next to a breeding site that has been used by ibis for at least three decades (Rumbold et al. 2009, Welch 2016). We predict that American white ibis capitalize on the consistent food available at more urban locations by shifting from nomadic foraging on aquatic wetland prey to sedentary behavior, exhibiting fidelity to urban sites where they may consume increasing amounts of anthropogenic foods relative to their wild counterparts.

Increased urban site fidelity and exploitation of urban foods may lead some ibis to be successful urban adaptors, though this has not been established conclusively, and it remains to be determined if the calories in supplemental foods improve ibis health, or if certain nutritionally deficient foods negatively affect ibis health and preclude successful adaptation. Ibis likely encounter various novel pathogens at varying rates across urban habitats—from contact with novel species and environmental exposure—and have a documented high prevalence of *Salmonella* spp. (Hernandez et al. 2016). Therefore, if some birds experience chronic stress that pushes them out of allostatic balance, they may experience immunosuppression with implications for their ability to fight off pathogens, and the negative effects of this may ultimately outweigh the benefits they gain from increased access to food resources. Conversely, if some birds adapt to urban habitats and experience no change to or reduced stress response, the increased access to food resources may help them better invest in immune function and increase their lifetime productivity.

Urbanization of Similar Species

While research has not yet addressed American white ibis urban habitat use and health implications, research of several taxonomically related species provides valuable information and a model for studying ibis response to urbanization. The white stork (*Ciconia ciconia*), a wading bird in the order Ciconiiformes, recently shifted its foraging and movement patterns in central Europe and the Iberian peninsula (specifically, Portugal), and some storks capitalize on resources available at landfills and abandon former migratory behavior in favor of fidelity to these areas, including during the breeding season (Kruszyk and Ciach 2010, Gilbert et al. 2016). This shift may relate to human development and reduction of suitable habitat for foraging, which likely has also led to substantial declines in white stork populations (Kruszyk and Ciach 2010). Individuals of a species more closely related to white ibis—the African sacred ibis (*Threskiornis aethiopicus*)—have been successfully expanding into parts of developed Europe after escaping from zoos and being introduced outside of their traditional range, seemingly because the birds are generalist foragers and have behavioral plasticity allowing them to adapt to novel environments (Clergeau and Yesou 2006). This species was also documented in the Florida Everglades, and prior to its elimination through aggressive management, the species was demonstrated to have consumed anthropogenic foods, both primarily and as supplements (Calle and Gawlik 2011).

The Australian ibis, also closely related to the American white ibis, followed a trajectory that seems familiar now with the American counterpart. Notably in comparison to American ibis and Everglades habitat degradation, Australian ibis experienced loss of wetland habitats due to anthropogenic activities and extensive droughts, and though their populations have increased and expanded in urban areas, they have also likely been pushed out of and experienced declines in parts of their traditional range (Ross 2004, Martin et al. 2010). Some Australian ibis now exhibit characteristics of an urban adaptor in their fidelity to urban foraging sites (Martin et al. 2012) and shifts toward foraging and anthropogenic food consumption at landfills and urban parks (Martin et al. 2011). Large numbers of ibis breed in and alongside urban areas, often on natural islands in proximity to landfills and residential areas, and some of ibis likely migrate into these urban locations seasonally for this purpose (Martin et al. 2010 and 2011). Australian white ibis have been documented to carry various pathogens of concern to livestock and public health (Ross 2004, Epstein et al. 2007), and they are managed as pests due to increased numbers—including at large (and noisy and messy) breeding colonies alongside residential areas—habituation to people, noise and nuisance, and public risk including from disease and air strikes (Epstein et al. 2007, Martin et al. 2007, Martin et al. 2011).

Relevant White Ibis Research

Previous studies have established American white ibis diet and movement patterns in natural ecosystems including the Florida everglades. Kushlan et al. (1979) extensively documented natural foraging. Later, Dorn et al. (2011) documented adult ibis use of anthropogenic resources for provisioning nestlings, and Boyle et al. (2014) found similar ibis diets. Various studies confirm ibis as highly nomadic birds that move widely based on the suitability of foraging habitat (Heath et al. 2009, Beerens et al. 2011, Lantz et al. 2011). Research has not investigated American white ibis movement and habitat use in urban areas until this project (see Welch 2016 for more details). However, research on the related Australian ibis demonstrated one-way daily movements up to 35 km, multi-day nomadism of 40–50 km in urban birds, and high long-term fidelity to urban habitats in birds initially captured in urban areas (Martin et al. 2011, Martin et al. 2012).

Previous studies investigated American white ibis stress levels and prevalence of various pathogens in non-urban contexts, and determined prevalence of various pathogens for taxonomically related species in urban contexts. Epstein et al. (2007) conducted a study with Australian white ibis across urban areas of the prevalence of several pathogens of concern for wildlife, livestock, and public health. However, other studies of pathogen prevalence or health metrics including stress and immune function are lacking for white ibis or any related species in anthropogenic habitats. Some research has been conducted with wild or wild caught white ibis from the Everglades pertaining to stress responses via heat shock proteins and corticosterone hormone in plasma and feces. Adams et al. (2009) conducted a captive experiment with nestlings from the Everglades, in which the birds were dosed with methylmercury (an endocrine-disrupting contaminant present in the ecosystem with known effects on ibis) to assess their hormonal response, including corticosterone, via fecal samples. Heath et al. (2003) measured hormones (including corticosterone) in wild adult white ibis. Relevant to our research, both studies validated the use of their extraction protocols and radioimmunoassay techniques for quantification of corticosterone in plasma and corticosterone metabolites in feces, allowing our research to confidently follow the same procedures for white ibis tissues (Mostl et al. 2005). Herring and Gawlik (2012) investigated stress levels via fecal corticosterone, plasma corticosterone, and heat shock proteins in wild ibis related to mercury levels and variation in environmental condition. This study used an enzyme immunoassay and therefore is not directly comparable with the Adams et al. (2009) and Health et al. (2003) studies; however, it provides some additional understanding of wild ibis stress physiology.

Decades of pathogen studies have demonstrated ibis susceptibility to infection with various pathogenic agents, which largely do not affect adult ibis at a population level. However, some pathogens are of particular concern in this system for ibis and other wading bird species—especially as ibis have regular intra- and inter-specific interactions at nightly roosts and densely occupied communal breeding areas, and may frequently traverse the urban-wild interface. While many pathogens documented to infect ibis either rarely cause adult ibis mortalities or are not a population-level concern for the species (e.g., *Clostridium botulinum*, Eastern Equine Encephalitis), they may have less direct population-level impacts through transmission to more susceptible species, and to naive nestlings (Phalen et al. 2010). In urban areas, similarly to birds including gulls, ibis may serve as carriers that move pathogens—including urban-associated pathogens (e.g., *Salmonella* spp.)—between habitats, increase environmental contamination at certain habitats, and transmit pathogens of human health concern to the public through close proximity to people and contamination of public areas (Ross 2004, Epstein et al. 2007, Ramos et al. 2009, Hernandez et al. 2016).

Wading birds including ibis can carry avian influenza viruses, paramyxoviruses, and bacteria in the genus *Chlamydia*, none of which are documented as a concern for the species (Friend and Franson 1999, Kaleta and Taday 2003, Epstein et al. 2007). However, large paramyxovirus mortalities have been noted in cormorants (Kuiken 1999), which interact with ibis in the wild. Urban wading birds may also contribute to the transmission cycle because of increased exposure and infection from interacting with or being in environments contaminated by known reservoirs of these pathogens (Anseriformes and Charadriiformes) (Kaleta and Taday 2003, Stallknecht 2003, Epstein et al. 2007). Ibis can carry haemosporidian blood parasites (including genera *Plasmodium*, *Haemoproteus*, and *Leucocytozoon*), which can cause disease and mortality in susceptible individuals including nestlings (Friend and Franson 1999). These parasites also infect related species including the threatened American wood stork (which are often proximal to white ibis in large, dense nestling colonies). Wild and urban ibis are documented shedding *Salmonella* spp. at comparatively high rates (Hernandez et al. 2016), likely acquiring the bacteria from contaminated environments and possibly transmitting it to other environments or wildlife, similarly to the urban transmission cycle in other species (Epstein et al. 1997, Ramos et al. 2009).

Theories for Urban Ibis

Urban ibis in South Florida afford an ideal system to study how a food- and habitat-motivated shift in wildlife habitat use affects health through altered stress and immune function, and if such alterations are tied to increased or decreased pathogen infection risk. Ibis consume anthropogenic resources of varying quantity and quality across the developed landscapes of urban Palm Beach County. These birds may alter their movement patterns and behaviors, exhibiting higher site fidelity and reduced daily foraging areas, and becoming habituated to people. Such ibis encounter varying novel species and spend much of their time in unnaturally dense aggregations. Through intra- and inter-specific contact, plus foraging in contaminated landscapes, ibis likely encounter novel pathogens at altered rates and intensities. Therefore, we expect changes to ibis health (including stress, immunity, and pathogen prevalence) based on their use of habitats in urban Palm Beach County. The implications of diminished health are significant. Most ibis continue to forage and breed in natural areas; therefore, ibis could transmit pathogens to conspecifics (including naïve nestlings) or other species (including species of concern such as wood storks). Ibis breeding numbers have declined significantly and could be negatively impacted both by diminished adult health and infection-related poor nestling survival. Ibis also use areas in close or direct proximity to people, so they may present a threat to public health through pathogen transmission and behavioral change related to resource consumption and habituation.

PUBLIC PERCEPTIONS AND BIRD FEEDING

Globally, wildlife not traditionally associated with urban environments increasingly use urban areas. This shift likely relates to increased and predictable access to food resources compared to resources available in minimized or degraded native habitats (Evans et al. 2011). Backyard bird feeding is one source of such resources. Backyard bird feeding is a common activity worldwide (Jones and Reynolds 2008, Reynolds et al. 2017). Based on the 2011 census, 73% of households in the United States (U.S.) feed birds (USFWS 2011). The activity of feeding birds in public urban parks (often various domestic, peridomestic, and wild ducks, among other species) has not been well quantified and is generally less studied than backyard bird feeding. However, this common activity likely impacts a considerable number of birds globally (though the practice is concentrated in certain areas), and may be engaged in more than backyard feeding by families and people with less general interest in birds (Oost 2004, Chapman and Jones 2009, Reynolds et al. 2017). Backyard bird feeding typically targets songbirds and related species and may benefit these birds in various ways, including through increased calories that may particularly improve survival during harsh winter months (see Amrhein et al. 2004 and Robb et al. 2008 for reviews of how supplemental feeding impacts birds). The activity is officially encouraged by some organizations (e.g., the Cornell Lab of Ornithology in the U.S.) and guidelines are published about how to practice feeding correctly (i.e., providing nutritious foods like seed mixtures or suet with calories, protein, and fat similar to what birds would normally consume) (Jones and Reynolds 2008, Robb et al. 2008). Despite documented benefits, there are known drawbacks to supplemental feeding. In practice, birds at backyard feeding stations may receive less-nutritious foods like bread—which is carbohydrate-rich and protein-poor (Rollinson et al. 2003, Galbraith et al. 2015), and birds fed in parks are often provided such foods (Chapman and Jones 2009, Hernandez et al. 2016). Increased caloric intake from supplemental food may boost immune function and reduce intensity of infection. However, consumption of foods inappropriate nutritionally may compromise immune function and increase pathogen infection risk (Bradley and Altizer 2007). Some pathogens cause recognized feeder-associated diseases in birds—e.g., bacterial diseases like salmonellosis and conjunctivitis, which are transmitted via contact with contaminated saliva or feces (Bradley and Altizer 2007, Benskin et al. 2009, Lawson et al. 2014, Reynolds et al. 2017). Exposure to such pathogens is altered at bird feeding stations due to increased densities, contact rates, and contamination of surfaces (Robb et al. 2008, Reynolds et al. 2017). This is often cited in reference to backyard bird feeding (Lawson et al. 2014); however, altered pathogen transmission also occurs at supplemental feeding areas in public parks (Epstein et al. 2007, Hernandez et al. 2016).

The activity of bird feeding also provides potential benefits and drawbacks for people. As the percentage of people living in urban and sub-urban areas increases, bird feeding and associated activities like watching birds may allow urban residents to connect to nature and experience contact with wildlife (Jones and Reynolds 2008, Belaire et al. 2015, Reynolds et al. 2017). Belaire et al. (2015) found that urban residents overall valued birds in the neighborhood, but derived increased benefits when they perceived higher diversity of bird species. Dallimer et al. (2012) also found psychological benefits associated with perceived diversity of birds, and a recent study correlated increased afternoon bird song with lower levels of depression, anxiety, and stress (Cox et al. 2017).

Several studies examined public motivations for backyard bird feeding, and found that people clearly derive personal benefits from the activity. However, their motivations for bird feeding can be plural, extensive, and sometimes complex. For example, Horvath and Roelans (1991) found that people fed birds primarily for personal motivation—including for aesthetic value and because birds appreciate the food, but also for entertainment and to share positive experiences with other people—but not as much from a sense of duty or to escape their problems. Ishigame and Baxter (2007) found some similar personal reasons for feeding birds, but also found charity-inspired motivations (such as to provide birds with more food). Galbraith et al. (2015) found that personal motivations were most common (e.g., for pleasure, to dispose of bread, to attract wildlife, and to a lesser extent to benefit children), but people also fed to benefit birds or ecosystems, and to atone or give back. Galbraith found only a small percentage of people that fed birds in backyards for the benefit of children. But Oost (2004) found that most wildlife feeding in public places took place in groups or families. Moore et al. (1997) as cited by Oost (2004) found a lesser motivation of feeding wildlife for children's benefit or education. Surprisingly few studies have quantified bird-feeding activity in urban parks (see Chapman and Jones 2009 for one example), and to our knowledge none have specifically assessed motivations for bird feeding in parks. A notable documented difference in bird feeding at parks is that it seems to be an overall more social activity (Oost 2004, Chapman and Jones 2009), and this suggests that motivations may differ, at least for some people. The presence of birds in urban parks may therefore provide a unique opportunity for people who may not feed birds at home and may be less interested in birds overall to connect to nature and wildlife (which may be increasingly important in urban areas). Cox and

Gaston (2015) showed that increased knowledge of species names enhanced benefits for people of interacting with birds, so improving the knowledge of people who feed birds may similarly increase the benefit they gain from watching and feeding birds. Ishigame and Baxter (2007) found the most common reason people did not feed birds was not lack of interest, but belief that feeding birds did not promote their welfare. Therefore, increased knowledge of birds may also improve interactions for people that do not feed birds but maintain interest in them.

Conversely, bird feeding in parks may generate conflicts between birds and people. Soulsbury and White (2015) review ways in which urban wildlife conflict with people, including aggression, nuisance, property damage, and disease. These potential conflicts are relevant to urban birds—the Australian white ibis provides an excellent example of a species that is perceived negatively in urban habitats because of noise, nuisance, aggression, and disease risk (Epstein et al. 2007, Martin et al. 2012). In general, birds at supplemental feeding areas exist in denser and larger aggregations than flocks in wildland areas (see Murray et al. 2015's meta-analysis). They can become habituated toward people, and associate people with food, leading to aggression. Additionally, birds in urban parks often contribute to mess through feces (Epstein et al. 2007, Hernandez et al. 2016). This was the most significant conflict urban residents surveyed by Belaire et al. (2015) experienced with birds, though the conflict was minor. Altered pathogen transmission dynamics in urban birds can increase risk for urban residents—indeed, human cases of salmonellosis have been linked to *Salmonella* spp. infection in both garden-feeding birds (Lawson et al. 2014) and birds supplemented at parks (Hernandez et al. 2016). *Salmonella* spp. infection occurs from contact with saliva or feces, and at parks people can be easily exposed to these pathogens from contact with birds' feces left on picnic tables, railings, and other surfaces (Hernandez et al. 2016). Additionally, the risk of serious infection from *Salmonella* spp. is significant for children and older people with less-developed or suppressed immune systems—both of which groups are commonly observed feeding birds in parks. Altered pathogen transmission is also a risk for any urban-associated bird, which may encounter pathogens from foraging in contaminated urban landscapes (*Salmonella* spp.), and through contact with species that commonly carry certain pathogens (e.g., ducks and avian influenza virus). Therefore, urban birds present at parks can carry pathogens that can be transmitted to other birds, wildlife, domestic animals, and people—and the dynamics of transmission are certainly altered by supplemental feeding that brings birds to contaminated areas, leads to higher densities, and creates opportunities for inter-specific interactions. However, the threats to environmental, wildlife, and human health that exist could be mitigated through better public behaviors with respect to supplemental feeding.

Despite potential conflicts, some research has shown that positive experiences with wildlife and nature help insulate against development of negative public perceptions based on minor conflicts with wildlife (Charles and Linklater 2015). Understanding why people feed birds and how their knowledge, awareness, and interest correlates to the activity is important to promote co-existence, and to educate people regarding impacts of bird feeding and potential disease transmission risk without compromising their support of urban wildlife. The "One Health" paradigm assumes that wildlife, human, and environmental health are intimately linked (Decker et al. 2010). Following this paradigm, public education that healthy wildlife equate to healthy environments and healthy people will encourage public behaviors that promote wildlife (and environmental and public) health—even among people who would not change their behavior solely to protect wildlife health. Absolute prohibition of feeding birds would reduce risks to avian and public health. However, it would negate benefits of the activity for people and remove a critical opportunity to promote nature and wildlife conservation (Galbraith et al. 2015). And some research suggests that prohibition of feeding does not substantially impact the prevalence of the activity (Jones and Reynolds 2008). If people are positively motivated to feed birds—and interested in interacting with and learning more about birds—we may achieve better compliance and overall stewardship by improving rather than eliminating public interactions with wild birds. For example, managers can provide or encourage provision of more nutritionally appropriate foods, or suggest alternative ways to interact with birds that do not involve direct contact (e.g., bird watching). However, any message seeking to change public behavior—particularly one conveying risks of pathogen transmission to the public—must be sensitive to public reception and seek not to unnecessarily frighten people, but to encourage realistic behavior change while maintaining public appreciation and support for urban wildlife (Decker et al. 2010). Studies such as that conducted by Needham et al. (2004) introduce knowledge of wildlife disease to understand risk perception. However, communicating such information to the public regarding disease that affects public health may be counterproductive unless adequate educational resources exist to ensure people understand the risk realistically, and to ensure continued public support for urban wildlife.

Effective framing and dissemination of messaging to improve public knowledge and awareness of realistic risk requires identifying the public's preferred media types, and ultimately implementing and evaluating outreach strategies. Galbraith et al. (2015) found a lack of knowledge of whether supplemental feeding is good or bad for birds. Mallick and Driessen (2003) found that signage about feeding at national parks in Tasmania was effective in that it minimally changed minds, but more often reinforced existing beliefs. However, Oost (2004) saw continued active wildlife feeding in national parks alongside signs that banned feeding. More appropriate to supplemental feeding in urban areas, Clark et al. (2015) experimentally placed signs in parking lots about feeding gulls, and found that the addition of signs changed some but not all people's behavior, and this behavior change was not sufficient to actually reduce the numbers of gulls present. If people are motivated by a desire to help birds, then they should change their behavior in ways that would actually benefit birds—including by altering or stopping their engagement in supplemental feeding. However, this likely will require educational outreach to address likely gaps in public knowledge and understanding of links between public behaviors and bird health. Ishigame and Baxter (2007) found a lack of basic knowledge among bird feeders in their study of the effects of feeding on birds, and the authors expect that feeding will continue as-is unless the bird feeders are able to obtain information grounded in scientific study. While outreach efforts based on scientific evidence may improve public knowledge and increase conservation ethics, this should be established through research, as the links between public interest in birds, bird feeding, and actual conservation ethic are unclear (Jones and Reynolds 2008).

In South Florida, the assemblages of birds at urban parks often include doves, pigeons, a select group of other passerines, and both peridomestic and wild ducks and geese (Hernandez et al. 2016, personal observation). However, recently various

Everglades-associated wading bird species are regularly documented in urban areas. Some of these species are highly specialized (e.g., snail-consuming limpkin (*Aramus guarauna*). Others—notably the American white ibis (*Eudocimus albus*), but also the wood stork (*Mycteria americana*) and the black-crowned night-heron (*Nycticorax nycticorax*)—join flocks of ducks and accept, or even beg for, human handouts like bread (personal observation). The presence of these birds offers a unique opportunity for people to see, interact with, and learn about wetland birds. Bird feeding by the public may provide a vehicle through which to educate people on the importance of and conservation concerns related to the Florida Everglades ecosystem, and establish or reinforce positive views of urban wildlife. However, to capitalize on this opportunity for conservation education, we must ensure that most urban South Florida residents do not begin to view birds like white ibis as pests. In contrast, the Australian white ibis is now managed as a pest and largely not tolerated by urban residents, which makes conservation education with the species more challenging. To avoid this situation with American ibis, we must maintain a positive relationship between the birds and people, in which the birds do not create undue mess, noise, aggression, and pathogen risk (which may mean minimizing bird feeding, regulating what is fed, or even banning feeding at some parks). Currently, official stances on bird feeding differ by country and are not always clearly expressed to the public (Jones and Reynolds 2008). This inconsistency likely contributes to public confusion about whether bird feeding is appropriate. However, signs are appearing at urban parks across the U.S. banning feeding, or banning feeding of foods like bread, crackers, or popcorn. These signs may be effective in changing some local behavior, but official regulation of bird feeding may be the best way to obtain compliance and ensure consistent educational messages for the public. We may succeed in capitalizing on public interest to address knowledge gaps, and encourage people to engage in more conservation-minded behaviors (e.g., feeding birds better foods, or watching vs. feeding birds). Our ultimate goal is to improve public understanding of how changes in their current bird-feeding behavior may be important for preserving avian and public health.

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CHAPTER 3

WHITE IBIS (*EUDOCIMUS ALBUS*) USE OF ANTHROPOGENIC RESOURCES IN URBAN SOUTH FLORIDA ASSESSED VIA STABLE ISOTOPE RATIOS[1]

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[1] Curry, S. E., Murray, M. H., Welch, C. N., Cooper, R. J., and Hernandez, S. M. To be submitted to *Ibis*.

INTRODUCTION

Urban growth and development has substantially altered global ecosystems, including through destruction and alteration of wildlife habitat (Vitousek et al. 1997). While wildlife species respond differently, species diversity is lower in urban areas (McKinney 2006, Evans et al. 2011); however, some species increasingly exploit urban areas, which offer more reliable food resources via direct and indirect human provisioning (e.g., landfills, dumpsters, lawns, supplemental feeding) (Lepczyk et al. 2004, Luniak 2004, Jones and Reynolds 2008, Chamberlain et al. 2009, Evans et al. 2011, Sol et al. 2014). Wildlife species with some common natural history traits—often including a generalist diet—are documented adapting to urban areas and exploiting anthropogenic resources (including common urban-associated species like corvids and house sparrows) (Jerzak 2001, Johnston 2001, McKinney 2006, Evans et al. 2011, Sol et al. 2014). Similarly, some species experiencing traditional habitat loss and degradation may be able to capitalize on urban anthropogenic resources—if they can adapt to novel habitats, species assemblages, predation risk, suites of stressors, and pathogen exposure.

Wildlife use urban habitats because of reliable food resources. However, species reliant on anthropogenic resources may experience health consequences related to anthropogenic resource quality. Anthropogenic resources can be nutritionally deficient for some species, and resources and habitats may be contaminated, negatively affecting fitness and immune function (Ezenwa 2004, Green et al. 2006, Heiss et al. 2009, Murray et al. 2015 and 2016). However, anthropogenic resources provide increased and more predictable caloric input, allowing reduced expenditure of energy on foraging. Therefore, individuals may improve condition, fitness, and survival (Schoech and Bowman 2001, Kristan et al. 2004, Siriwardena et al. 2007, Chamberlain et al. 2009, Newsome et al. 2010), and redistribute excess energy toward activities including self-care, breeding, and immune function (Deerenberg et al. 1997, Bradley and Altizer 2007, Fokidis et al. 2008). Greater investment in immune function can improve ability to fight pathogen infection and mitigate negative impacts of foraging in contaminated urban habitats. Outcomes of pathogen infection for urban wildlife vary based on factors including increased densities at feeding sites, increased inter- and intra-specific contact, and altered exposure to stressors, pathogens, or contaminants—however, supplemental feeding both affects these factors and is an important direct component in pathogen infection dynamics (Bradley and Altizer 2007, Gottdenker et al. 2014, Becker et al. 2015, Murray et al. 2016).

Individuals successfully adapted to urban habitats likely contribute to population success; however, those unable to cope with negative impacts of urban habitat and anthropogenic resource use may compromise species success, including because these individuals may not contribute to the population, and those with compromised immune function are more likely to be infected with and transmit various pathogens of wildlife (and public) concern (Shochat 2004, Newsome et al. 2010). Many species recently observed in urban habitats (e.g., San Joaquin kit fox [*Vulpes macrotis mutica*], American white ibis [*Eudocimus albus*]) are native species of some conservation concern that may increasingly use urban areas as wild habitat loss and degradation progresses. These species are less traditionally associated with and studied in urban contexts. Yet understanding their ultimate failure or success in urban adaptation requires understanding how urban habitat use affects their health, which requires assessing the degree and type of their anthropogenic resource exploitation (Newsome et al. 2010, Becker et al. 2015).

White ibis are semi-nomadic wading birds that rely on wetlands in the southeastern United States for aquatic prey (e.g., crayfish, fiddler crabs, small fish) (Kushlan 1979, Heath et al. 2009, Boyle et al. 2014). Ibis forage widely in the Florida Everglades ecosystem, moving nomadically between habitats as prey availability fluctuates due to wetland management regimes, wet-dry seasonal cycles, and inter-annual variability in rainfall (Gawlik 2002, Frederick et al. 2008, Beerens et al. 2011, Lantz et al. 2011, Herring and Gawlik 2012). Twentieth century habitat destruction and anthropogenic hydrologic changes led to a roughly 50% decline in Everglades habitat, significantly impacting wading bird populations. Ibis—now a Florida Species of Special Concern—experienced an 87% decline in breeding pairs from 1903 to 2001 (Davis and Ogden 1994, Crozier and Gawlik 2003). Ibis are currently an indicator species for Everglades restoration, because they depend heavily on aquatic prey that responds to active hydrologic management and restoration—and this relationship to wetland health is easily understood by the public (Kushlan 1997, Crozier and Gawlik 2003, Frederick et al. 2008, Heath et al. 2009).

Ibis are generalist foragers and have been documented foraging in anthropogenic areas including landfills, and occasionally wastewater treatment wetlands (Frederick and McGehee 1994, Rumbold et al. 2009, Welch 2016). Ibis also provide anthropogenic supplements to their nestlings in years of poor resource availability (Dorn et al. 2011, Boyle et al. 2014) and forage on terrestrial prey from maintained lawns in the non-breeding season (Heath et al. 2009). Within the past 10–20 years, larger numbers of ibis been observed foraging in urban areas, including urban lawns and golf courses with water bodies, dumpsters and landfills, and urban parks where they consume human handouts—

often bread commonly provided to ducks (Chapman and Jones 2009, Hernandez et al. 2016, Welch 2016). A concurrent study was the first to investigate movement patterns of white ibis in urban areas (Welch 2016), and we predict that some ibis capitalize on the consistent food available at urban locations by shifting from nomadic foraging on aquatic wetland prey to sedentary behavior, exhibiting fidelity to urban sites where they may consume increasing amounts of anthropogenic foods relative to their wild counterparts. This trajectory is similar to that of the related Australian white ibis (*Threskiornis molucca*), a likely urban adaptor with reduced daily movements, shifts in habitat use toward urban sites including landfills, and anthropogenic diet—which have led members of that species to exclusively forage and breed in urban areas (Epstein et al. 2007, Smith and Munro 2010, Martin et al. 2011, Martin et al. 2012). American white ibis have not been documented breeding in urban areas, likely due to lack of suitable habitat. However, large numbers of ibis breed alongside a landfill at the edge of urban habitats (Rumbold et al. 2009, Welch 2016).

Urban habitats differ in land cover (e.g., wetland vs. developed) and human activities (e.g., direct bird feeding, presence of trash), both of which influence the foods available to ibis. Therefore, birds may forage differently across and within sites, with some ibis consuming greater amounts of direct and indirect human handouts (e.g., bread, corn chips, dog food, refuse) than others. Determining if ibis successfully adapt—based on exploitation of anthropogenic resources with no health or fitness consequences—requires establishing the extent to which such resources are actually exploited. Additionally, understanding the components of urban ibis diet is important, to tie certain foods to changes in ibis health.

The diet of ibis in wetland habitats has been assessed through foraging observation and bolus contents analysis for adult birds and through bolus contents and stable isotope analyses for nestlings (Kushlan 1979, Dorn et al. 2011, Bryan et al. 2012, Boyle et al. 2014). Bolus contents analysis reflects recently consumed foods and can over- and under-quantify certain items. For ibis, which daily use urban habitats with differing resources, stable isotope analysis offers advantages through assessment of diet over a longer period of time (variable by tissue sampled—e.g., several days for plasma) combined with assessment of short-term diet via analysis of noninvasively collected fecal samples (Hobson and Clark 1992, Kelly 2000, Weiser and Powell 2011, Blumenthal et al. 2012).

Isotopic ratios in wildlife tissues reflect those of the foods wildlife consume and assimilate (DeNiro and Epstein 1978 and 1981). Photosynthetic pathways determine the ratios of 13/12 carbon (C) isotopes in plants, and corn and marine plants are enriched in 13/12 C compared to terrestrial and freshwater plants. Therefore, processed anthropogenic foods high in corn and corn syrup are enriched in 13/12 C (Jahren and Kraft 2008). Ratios of 15/14 nitrogen (N) change predictably by trophic level as 15 N is preferentially assimilated in tissues of consumers. The timing of isotopic assimilation from diet sources varies by tissues, which have different turnover rates—for example, plasma generally reflects short-term diet over several days (Hobson and Clark 1992 and 1993, Podlesak et al. 2005). The enrichment of C and N between diet and a consumer (trophic enrichment factor [TEF]) varies by species, diet, and tissue (DeNiro and Epstein 1978 and 1981); however, standard TEFs are commonly used in the literature, and a recently developed model calculates species-specific TEFs based on enrichment factors of species with similar habitat associations (Healy et al. 2016). Isotopic ratios of an organism's feces likely directly reflect dietary components un-enriched by assimilation in tissue (Hwang et al. 2007, Blumenthal et al. 2012). Therefore, analysis of relative $\delta^{13}C$ and $\delta^{15}N$ ratios in wildlife tissues corrected with TEFs can reveal the trophic level ($\delta^{15}N$) and type ($\delta^{13}C$) of foraging (Kelly 2000).

Stable isotope analyses have been used extensively to determine wildlife diets (Newsome et al. 2010, Murray et al. 2015, Lemons et al. 2011), including avian diets (Hobson 1986, Kelly 2000, Inger et al. 2006, 2008). Several studies have examined isotopic ratios in feces (Podlesak et al. 2005, Hwang et al. 2007, Varo and Amat 2008, Blumenthal et al. 2012). Stable isotope ellipse-based niche analyses allow comparison of diets across groups, and stable isotope mixing models determine contributions of likely food sources to an individual's diet (Parnell et al. 2010, Jackson et al. 2011). Pertinent to our research, recent studies have applied stable isotope analysis to wildlife in urban systems. Robb et al. (2011) identified use of human-provided supplemental food by blue tits via stable isotope analysis, and Auman et al. (2011) found differences in isotopic signatures between urban and non-urban silver gulls. Murray et al. (2015) assessed diet in urban coyotes via isotopic ratios in conjunction with movement analysis, and Caron-Beaudoin et al. (2013) tied movement of urban gulls to consumption of anthropogenic foods. However, studies have not yet addressed white ibis diet with urban habitat use.

We assessed anthropogenic resource use of individual adult and subadult ibis in urban South Florida, by assessing $\delta^{13}C$ and $\delta^{15}N$ isotopic ratios in ibis plasma and feces across different types of urban habitats, and we compared $\delta^{13}C$ and $\delta^{15}N$ ratios in feces between urban and non-urban ibis. We expected $\delta^{13}C$ in plasma to be similar to $\delta^{13}C$ in feces for each bird, assuming individual birds foraged similarly day-to-day. Because feces do not reflect assimilated isotopes as plasma does, we expected $\delta^{15}N$ in feces to be depleted relative to plasma and aligned with $\delta^{15}N$ in dietary sources. We predicted that ibis detected by telemetry more frequently in urban habitats (and therefore likely foraging more frequently in urban habitats) would have isotopic signatures more enriched in carbon and depleted in nitrogen than those detected less frequently. We expected isotopic signatures of birds captured at different types of urban sites (e.g., park, zoo, parking lot) to differ, including by foraging breadth (niche width), reflecting differing types and diversity of foraging opportunities. Further, we predicted that the isotopic signatures of birds captured at urban sites with less surrounding wetland or greater surrounding developed land—and, importantly, more supplemental feeding by the general public—would incorporate a higher percentage of anthropogenic foods versus freshwater prey.

METHODS

Study Area

We captured ibis in Palm Beach County, Florida (PBC; 26.650708°, -80.276931°). PBC is a highly developed county located east of parts of the Everglades wetland ecosystem, and the county encompasses multiple land cover types with variable suites of stressors. Ibis numbers have been increasing in PBC for over a decade, primarily in the non-breeding season, and some ibis flocks are present predictably at certain sites (Welch 2016). Based on preliminary observations, we identified seven sites with consistent flocks of ibis (>10 ibis) habituated to human presence sufficiently for capture (see Hernandez et al. 2016). The sites included a zoo, a parking lot, and various urban parks, all of which varied in the availability of anthropogenic food and surrounding land cover type (e.g., wetland, developed; see Figure 3.1 for map of capture sites and Table 3.1 for a summary of site features).

White Ibis Capture and Sample Collection

We captured ibis using nylon leg lassos at seven sites in PBC just after the breeding season (11 July to 31 August 2013, hereafter “summer,” n=68) and at six of seven sites just prior to the following breeding season (December 2013, hereafter “winter,” n=24). We did not capture ibis in other seasons, as ibis leave urban parts of PBC during the breeding season. We collected standard morphometric measurements and measured body mass, which we standardized by calculating the residuals after regressing mass by tarsus length (with separate regressions for male and female ibis). We determined sex by extracting DNA from 10 µl whole blood with a Qiagen DNeasy blood extraction kit (Qiagen, Valencia, CA, USA) following the manufacturer’s protocol. We then used 2550F/2718R primers to distinguish between male and female ibis (Fridolfsson and Ellegren 1999, Ong and Vellayan 2008). In July–August 2013, we attached VHF transmitters to track a subset of ibis for a larger project investigating ibis movement and health (Welch 2016). Upon capture and when not undergoing sample collection, we held birds in individual bags. We released all birds within 60 minutes of capture.

To measure fecal stable isotope ratios, we collected fresh feces from captured ibis in bullet tubes immediately after defecation, placed samples in a cooler with frozen gel packs, and froze samples at -20°C when field processing was complete (within six hours). To measure plasma stable isotope ratios, we obtained blood samples from the jugular or tibiotarsal vein with 21–25 gauge needles, and collected all blood samples in individual heparinized tubes. We stored samples in a cooler with frozen gel packs and centrifuged all blood samples within four hours of collection for 10 minutes at 3,500 g to separate the plasma fraction, which we immediately froze at -20°C. To establish isotopic ratios for dietary sources, we collected and froze samples of known wetland and anthropogenic foods, which we augmented with values obtained from published literature (see Table 2 for a description of all dietary source items). For comparison, we also assessed isotopic ratios in adult and nestling ibis feces collected from non-urban sites, including ibis nesting colonies, a prairie surrounded by rural and agricultural lands, and a landfill on the outskirts of PBC. We obtained and stored fresh feces from individual ibis at these sites between 2013 and 2015, as described above. We transported all frozen samples to the University of Georgia (UGA) and maintained samples at -20°C until analysis. All animal capture and handling procedures were approved by the UGA Institutional Animal Care and Use Committee (AUP#A2011 08-018).

Stable Isotope Analysis

We dried all fecal, plasma, and prey samples for a minimum of 48 hours, after which we pulverized plasma samples and select prey items with a micro-spatula and homogenized fecal samples and remaining prey items with a ball-mill grinder. We measured and weighed 1.5 mg of each sample into tin capsules and determined carbon and nitrogen isotopic ratios with a continuous-flow isotope mass spectrometer (Thermo Finnigan Delta V [Bremen, Germany]) coupled to a CHN (Carlo Erba NA1500 [Milan Italy] with a Thermo Finnigan Conflo III interface [Bremen, Germany]). All analyses were completed at the UGA Stable Isotope Ecology Laboratory (Center for Applied Isotope Studies, University of Georgia, Athens, Georgia). We included standard materials with known isotopic ratios between every 12 samples for calibration and drift compensation. Following laboratory standards, we obtained ratios of carbon and nitrogen stable isotopes for ibis feces and plasma expressed in conventional delta (δ) notation, as parts per thousand (‰) for the ratio of carbon to the international standard PeeDee Belemnite ($\delta^{13}C$) and the ratio of nitrogen to the international standard atmospheric air ($\delta^{15}N$). We also obtained carbon and nitrogen isotopic ratios values for natural and anthropogenic food items, which we compiled a priori into six categories based on known ibis foraging behavior and similar isotopic signatures (see Table 3.2 for a description of categories and food items).

Movement and Land Cover Analysis

We tracked a subset of ibis captured in July–August 2013 via radio telemetry from September 2013 to July 2014 at the seven capture sites and along a 104-km pre-set route across urban PBC (Welch 2016). Ibis are present in urban areas primarily during the non-breeding season; therefore, for this project we excluded breeding season detections. We analyzed non-breeding season (September–February) detections by dividing the number of detections of each ibis in the sampling area (which included both the capture sites and a 0.5-km radius around the pre-set route) by the total number of visits to the sampling area.

We determined land cover types surrounding capture sites in ArcGIS by reclassifying raster data from the 2014 Cooperative Land Cover Map (Florida Fish and Wildlife Conservation Commission and Florida Natural Areas Inventory) into relevant categories, including a combined category for all wetland types, and a combined category for all developed types. We calculated the number of pixels in each land cover category within a 2-km-radius buffer around the center of each capture site, reflecting the average daily foraging area of an urban ibis (Hernandez unpublished data). We then determined the percentage of each land cover category surrounding each capture site by dividing the number of pixels for the category by the total number of pixels in the 2-km-radius buffer.

Statistical Analysis

We determined correlations between all $\delta^{13}C$ and $\delta^{15}N$ isotopic ratios and season, sex, age, and standardized mass with *t*-tests and linear models. We evaluated correlation between ibis isotopic signatures and frequency of detection in urban areas with a linear model for a subset of ibis tracked via telemetry. We determined if isotopic ratios in plasma reflect those in feces via linear models with isotopic ratios for paired ibis plasma and feces. We compared isotopic values across sites with ANOVA and examined dietary niche width across sites by comparing the area of Bayesian ellipses calculated for each site with the package SIBER in Program R. We determined relative proportions of diet categories in ibis samples with Bayesian stable isotope mixing models with the SIAR package in R. For plasma mixing models, we input trophic enrichment factors calculated with the SIDER package in R, based on Bayesian models of blood TEFs for other birds with similar habitat associations ($\delta^{13}C$: 1.52 ± 1.09; $\delta^{15}N$: 3.53 ± 0.79). For feces mixing models, we did not include enrichment factors. We ran all statistics in Program R (version 3.3.2, R Core Team 2016).

RESULTS

We determined $\delta^{13}C$ and $\delta^{15}N$ from ibis plasma and feces at seven urban sites in summer and winter 2013 (plasma n=81; fecal n=73; paired plasma and fecal n=62). We determined $\delta^{13}C$ and $\delta^{15}N$ from ibis feces at non-urban sites from 2013–2015 (Landfill: n=33; prairie park: n= 23; Everglades nesting colonies: n=49), and from 20 reference diet items in six categories. Plasma and feces were enriched in $\delta^{13}C$ and $\delta^{15}N$ in summer compared to winter 2013, with significant enrichment for plasma $\delta^{13}C$ (Welch's *t*-test: $t_{33.83}=2.71$, $p=0.01$; Summer mean=-20.26‰, Winter mean=-21.59‰) and plasma $\delta^{15}N$ (Welch's *t*-test: $t_{41.39}=2.14$, $p<0.04$; Summer mean=7.89‰, Winter mean=7.44‰). Isotopic ratios were not correlated with sex, age, or standardized mass.

Relationship Between Feces and Plasma

Ratios of $\delta^{13}C$ and $\delta^{15}N$ in feces and plasma were positively correlated (Carbon: $F_{1,60}=39.17$, $R^2=0.40$, $p<0.01$; Nitrogen: $F_{1,60}=6.58$, $R^2=0.10$, $p=0.013$; Figure 3.2). Compared to plasma, feces were slightly enriched in $\delta^{13}C$ (Paired *t*-test: $t_{61}=1.67$, $p=0.0502$; mean difference 0.56‰) and substantially depleted in $\delta^{15}N$ (Paired *t*-test: $t_{61}=21.92$, $p<0.01$; mean difference 5.08‰).

Urban Habitats and Site Differences

Non-breeding season urban detections of 28 tracked ibis (September–February) ranged 0.00% to 98.08% (mean=45.42%, SD=34.43%). Detections were negatively correlated with $\delta^{13}C$ in plasma ($F_{1,22}= 4.16$, $R^2= 0.16$, $p=0.05$; Figure 3.3). Plasma and fecal $\delta^{13}C$ were negatively correlated with percent developed land surrounding the capture site (Plasma $F_{1,79}=8.47$, $R^2=0.10$, $p<0.01$; Feces $F_{1,70}=8.57$, $R^2=0.11$, $p<0.01$); Figure 3.4). Fecal $\delta^{15}N$ was negatively correlated with percent surrounding developed land ($F_{1,70}=8.47$, $R^2=0.11$, $p<0.01$) and positively correlated with percent surrounding wetland ($F_{1,70}=7.04$, $R^2=0.09$, $p<0.01$).

Ratios of $\delta^{13}C$ and $\delta^{15}N$ in plasma and feces did not differ significantly between most capture sites; however, plasma $\delta^{13}C$ at JB differed from LW ($p<0.01$) and DP ($p<0.05$) ($F_{6,74}=3.36$, $p<0.01$); plasma $\delta^{15}N$ at LW differed from ICP ($p=0.05$) and PV

(0.05) ($F_{6,74}=2.58$, p=0.025); and fecal $\delta^{15}N$ at ICP differed from JB ($p<0.01$) ($F_{6,65}=2.78$, p=0.018). Two sites had comparatively small plasma SIBER ellipse areas that overlapped with ellipses of other sites but not each other (PP=0.71‰^{2} and LC=1.63‰^{2}). One site had a comparatively large plasma SIBER ellipse width that extended past the ellipse extents of other sites (LW=6.83‰^{2}) (Figures 3.4 and 3.5). Most fecal SIBER ellipses overlapped; however, two sites had larger ellipse areas that extended past the ellipse extents of other sites (PV=17.20‰^{2}, JB=18.44‰^{2}). The nestling ellipse was substantially depleted in $\delta^{13}C$ and only overlapped with one site (PV); the landfill ellipse was comparatively enriched in $\delta^{15}N$ but overlapped with several sites; the prairie ellipse was comparatively depleted in $\delta^{15}N$ but overlapped with several sites. See Figure 3.6 for ellipse areas by site.

Capture Sites and Diet Proportions

Proportions of source categories in feces were similar across urban sites, but differed from reference values of wild nestling ibis, which consumed 90% aquatic prey (see Figure 3.8). Feces of ibis collected at the landfill had more similar proportions of all categories than feces of ibis from other sites. JB feces had a slightly higher proportion of corn-based foods than other categories, and prairie feces had the greatest proportion of bread. Bread also was the highest proportion in feces from all urban sites except JB. When proportions of the six categories were combined into natural or anthropogenic foods, all urban sites and the prairie had higher proportions of anthropogenic foods; the landfill had a higher proportion of natural foods; and the nestlings had more than twice the proportion of natural foods. Proportions in plasma were also similar across sites, with overall higher proportions of bread and freshwater invertebrates (see Figure 3.8). LW plasma had a higher proportion of fish and JB a higher proportion of saltmarsh invertebrates than other sites. See Figure 3.7 for isotopic signatures in relation to source signatures, and Figure 3.8 for proportions of sources in ibis samples divided by capture sites.

DISCUSSION

Diets of adult and nestling white ibis have been established in various wetland habitats via observation, bolus analysis, and stable isotope analysis of feathers (Dorn et al. 2011, Boyle et al. 2014, Kushlan1979, Bryan et al. 2012). This study was first to assess fecal and plasma $\delta^{13}C$ and $\delta^{15}N$ in ibis, and to assess diet and document $\delta^{13}C$ and $\delta^{15}N$ signatures for ibis in urban habitats. We were unable to compare plasma isotopic signatures of ibis captured in urban versus wild habitats. However, fecal isotopic signatures of urban ibis differed from fecal isotopic signatures of ibis in agricultural and natural habitats. Ibis at PV had signatures slightly overlapping those of nestling ibis, which presumably consume primarily crayfish and freshwater invertebrates due to salt intolerance (Bildstein et al. 1991, Heath et al. 2009)—though see Bryan et al. 2012, who found that coastal nestlings had feathers unexpectedly enriched in $\delta^{13}C$. However, most urban ibis feces were enriched in $\delta^{13}C$ compared to nestling feces, and depleted in $\delta^{13}C$ and $\delta^{15}N$ compared to typical saltmarsh prey. Therefore, our results suggest PBC ibis rely less on freshwater and/or saltmarsh aquatic prey than has been described for wild ibis in previous studies. Overall, plasma and feces were enriched in both $\delta^{13}C$ and $\delta^{15}N$ in summer. Our sampling occurred just after the ibis breeding season, at a time when birds often disperse widely from large wetland breeding colonies (Bildstein 1991), and when fewer people visit and feed birds at urban sites (personal observation). Therefore, depletion of ibis feces and plasma in winter may reflect increased access to bread from human provisioning, and increased or more exclusive use of urban habitats compared to summer.

We confirmed from paired plasma and fecal samples that the ratio of $\delta^{13}C$ in ibis plasma reflects that in feces, suggesting use of noninvasively collected fecal samples may be appropriate for studying short-term diet in this and likely other species via $\delta^{13}C$. Feces were depleted in $\delta^{15}N$ compared to plasma, though not by a predictable amount. Fecal $\delta^{15}N$ was similar to that in reference diet samples; likely isotopic ratios in feces reflect dietary components unassimilated in tissue and are therefore not enriched compared to diet, as is plasma (Blumenthal et al. 2012 and other mammalian studies had similar findings, as did Podlesak et al. 2005 with birds—but see Hwang et al. 2007 and Varo and Amat 2008). The rarity of fecal isotopic analysis in wildlife dietary studies may relate to confusion about what results represent; while our results suggest that feces are valuable for isotopic analysis, we acknowledge issues cited in other studies (e.g., differential excretion of dietary components, digestive physiology and efficiency; Podlesak et al. 2005, Varo and Amat 2008). Feces may be best in isotopic studies that compare populations with likely greater variation (e.g., our comparison of urban to nestling, prairie, and landfill ibis), or to track dietary stability or change (see Podlesak et al. 2005). Studies with feces will be particularly important when noninvasive sampling is preferable (e.g., with endangered or elusive species).

We expected tissues of ibis from sites with greater surrounding developed land to be enriched in $\delta^{13}C$, reflecting consumption of anthropogenic foods (e.g., refuse, corn-based foods). However, we found depleted $\delta^{15}N$ and $\delta^{13}C$ in plasma of ibis from sites with greater surrounding developed land. The isotopic signature of bread (wheat-based) is depleted in δ^{13}C, which may explain the depleted signatures of ibis foraging in more developed areas with more access to parks where people commonly feed birds bread. Additionally, ibis foraging in certain developed areas may have access to small ponds that could provide freshwater invertebrates similarly depleted in δ^{13}C. We also found depleted δ^{15}N in feces of ibis from sites with greater surrounding developed land, and enriched δ^{15}N in feces of ibis from sites with greater surrounding wetland. Caron-Beaudoin et al. (2013) theorized anthropogenic food consumption in gulls with depleted δ^{15}N signatures but similar δ^{13}C signatures compared to other gulls, as δ^{15}N signatures are lower in anthropogenic than natural foods.

Overall, ibis varied considerably in their urban habitat detection, consistent with previous studies that have shown wide variation in individual ibis foraging and movement (Bildstein 1991). Depleted δ^{13}C signatures of PBC ibis plasma correlate to increased urban habitat detection. However, when this relationship is examined by site, it only persists for one site—ICP—at which ibis do consume a comparatively high amount of bread (personal observation). Ibis detected frequently at ICP could rely more on human-provisioned bread, while ibis detected frequently at other urban sites could have greater access to more δ^{13}C enriched anthropogenic foods, including refuse from trashcans and dumpsters. Determining differential availability of these resources requires fine-scale spatial analysis beyond the resolution of our land cover analysis, and may be best assessed through digitization of aerial photographs, or with a discrete study quantifying the availability of these resources.

While δ^{13}C and δ^{15}N signatures were similar at most urban sites, we found some variation likely related to differences in the availability of supplemental foods at and in areas surrounding the capture site. Ibis at LC and PP had reduced plasma ellipse areas. Ellipse areas for LC and PP feces were larger than plasma but among the smallest of fecal ellipses across capture sites. Perhaps resources are comparatively restricted at these sites: for example, ibis at LC (the zoopark) likely eat similar foods, and ibis at PP (the parking lot) have reduced options, while ibis at an urban park may eat various terrestrial foods and supplement with a variety of anthropogenic foods. In general, ellipse areas were much larger for feces than plasma at all sites, and assimilated plasma δ^{13}C and δ^{15}N differed from short-term fecal δ^{13}C and δ^{15}N in some ibis. These differences between feces and plasma are important to understand. Variation in food resources available at one site across multiple days may cause changes in plasma isotopic ratios even for an ibis with high site fidelity, which will complicate use of isotopic ratios to determine if an ibis forages at one or multiple sites. Differences in fecal and plasma signatures may also relate to differential assimilation of certain dietary components—ibis may forage on resources with a wide array of isotopic signatures but not equally assimilate all dietary components. SIBER analyses are robust to small sample sizes, but may perform best with sample sizes over 10; therefore, the small sample sizes at several of our sites may have affected our ellipse calculations.

SIAR mixing model results demonstrate consumption of a wide variety of food resources, including clear use of anthropogenic resources and likely continued consumption of traditional prey items by PBC ibis. Proportions of diet sources in feces were similar for birds at most urban sites, with freshwater invertebrates and bread as the highest categories at most sites. Proportions in feces from all urban sites were distinct from nestlings, shown to consume >70% freshwater invertebrates. Proportions of diet sources in plasma were also similar across sites, though small differences in modeled proportions included greater consumption of fish by ibis at LW, and greater consumption of saltmarsh invertebrates by ibis at JB. These differences may reflect foraging by some birds captured at LW and JB at different—perhaps non-urban—sites offering increased access to fish and saltmarsh prey, respectively—or may reflect daily changes in the resources available at a site. Our crayfish source signatures were comparatively depleted in δ^{15}N compared to literature-reported freshwater crayfish, which may have artificially elevated the proportion of freshwater invertebrates in the diet of birds captured at urban sites. SIAR mixing models also depend on source inputs: as comprehensive assessment of dietary sources for a generalist species is difficult, our source inputs may not fully encompass the range of ibis foraging.

The anthropogenic foods ibis typically access in urban areas may not be appropriate and could compromise ibis health; these foods are often nutritionally poor (e.g., white bread), and are low in protein compared to saltmarsh invertebrates and fish, and compared to literature-reported freshwater crayfish (our crayfish source signatures were comparatively depleted in δ^{15}N). We did not find signatures consistent with a diet of exclusively corn-based foods. However, we did see evidence of significant consumption of bread and some consumption of refuse. Ibis may continue to supplement anthropogenic resources with natural prey like freshwater invertebrates and may therefore buffer direct impacts from nutrient deficiency. However, anthropogenic resources such as refuse accessed at dumpsters and landfills may be contaminated by toxins and pathogens. Evans et al. (2011) note considerable differences in the responses of avian individuals and species to urban habitats. Ibis, given their documented variation in foraging, may also vary in their use of anthropogenic resources and ability to adapt successfully to urban habitats. Ibis have documented exposure to pathogens including *Salmonella* spp., avian influenza viruses, and paramyxoviruses at urban habitats, both through environmental exposure (Hernandez et al. 2016) and inter-specific contact (Hernandez unpublished data). Therefore, any urban habitat use and consumption of nutritionally poor anthropogenic resources—despite potential increased caloric intake—may compromise ibis condition and immune function, facilitating infection and transmission of various pathogens, both to other ibis and to naïve individuals, including nestlings during the breeding season. Our future research will correlate isotopic signatures with health parameters to better understand if ibis are successfully exploiting urban resources, or if consumption of poor-quality foods including bread combined with use of urban habitats with novel stress and pathogen exposure has consequences for ibis health.

In SIAR mixing models, we assumed no enrichment in feces and used biologically relevant trophic enrichment factors modeled from known values of white ibis feathers and blood of similar species. However, our use of unconfirmed values may have impacted our models. The relationship between isotopic ratios in ibis diet, feces, and plasma should be confirmed through validation tests that also establish enrichment factors (similar to Podlesak et al. 2005, and Mizutani et al. 1992 for ibis feathers). Future research should directly compare diets of ibis in multiple urban, agricultural, and wild habitats in the same season, also assessing additional tissues to evaluate longer-term diet. Multi-season and multi-year studies would be beneficial, as hydrologic cycles vary greatly in Florida, and the likelihood of anthropogenic food supplementation by ibis has been documented to vary based on wetland conditions (Dorn et al. 2011). Therefore, determining how important urban habitats are for species conservation will require understanding multi-year habitat use and how diets are impacted by wetland conditions. Telemetry tracking allowed us to detect ibis at urban and known natural sites; however, we could not reliably determine where ibis foraged outside of these areas. Therefore, use of GPS and satellite-based tracking technology would be helpful to better quantify overall ibis foraging habitat use beyond just known areas. To discern between consumption of freshwater invertebrates and bread, observational studies that directly quantify ibis consumption of anthropogenic foods—such as bread—at urban sites would be valuable.

In conclusion, we determined that isotopic ratios of carbon and nitrogen in plasma resemble but are not identical to isotopic ratios in feces. In general, we found slight enrichment of carbon and substantial enrichment of nitrogen in plasma compared to feces. We postulate that variation in isotopic ratios between plasma and feces reflects variation in diets consumed over a period of days (i.e., less variation between tissues indicates more similar day-to-day diet, and vice versa) and some variation in assimilation and excretion of certain food items. Therefore, feces are useful for dietary studies—particularly as a non-invasive technique—but likely are most useful when comparing likely-different populations, or when combined with analysis of additional tissues (e.g., plasma). Additionally, examining habitat use by tracking individuals can better contextualize both fecal and plasma isotopic ratios. We found that overall, ibis captured at urban sites likely foraged similarly (based on overlapping isotopic signatures at most sites). However, within the subset of ibis for which we calculated urban detection, ibis detected more often in urban habitats had different isotopic signatures that generally reflected increased consumption of bread or freshwater invertebrates rather than corn-based foods or saltmarsh invertebrates. Based on telemetry results, we suggest these signatures reflect consumption of bread or freshwater invertebrates available in urban habitats, as these birds forage more frequently in urban areas and therefore are less likely to have access to natural foods. Overall, we found evidence in plasma and feces for ibis consumption of anthropogenic foods, particularly compared to the likely natural diet of nestling ibis. Seasonal differences in isotopic signatures may reflect increased consumption of anthropogenic foods in winter, suggesting ibis dependence on urban habitats varies by season and urban habitats may be more critical during certain periods within a year. Understanding the extent to which species of conservation concern rely on and can adapt to urban habitats is critical, particularly because these species often do not adjust well to urban habitats and are at the greatest risk of population decline and extinction. Our project is a valuable new direction for the field of urban wildlife ecology in its application of dietary and movement analysis to better understanding urban impacts on wildlife health.

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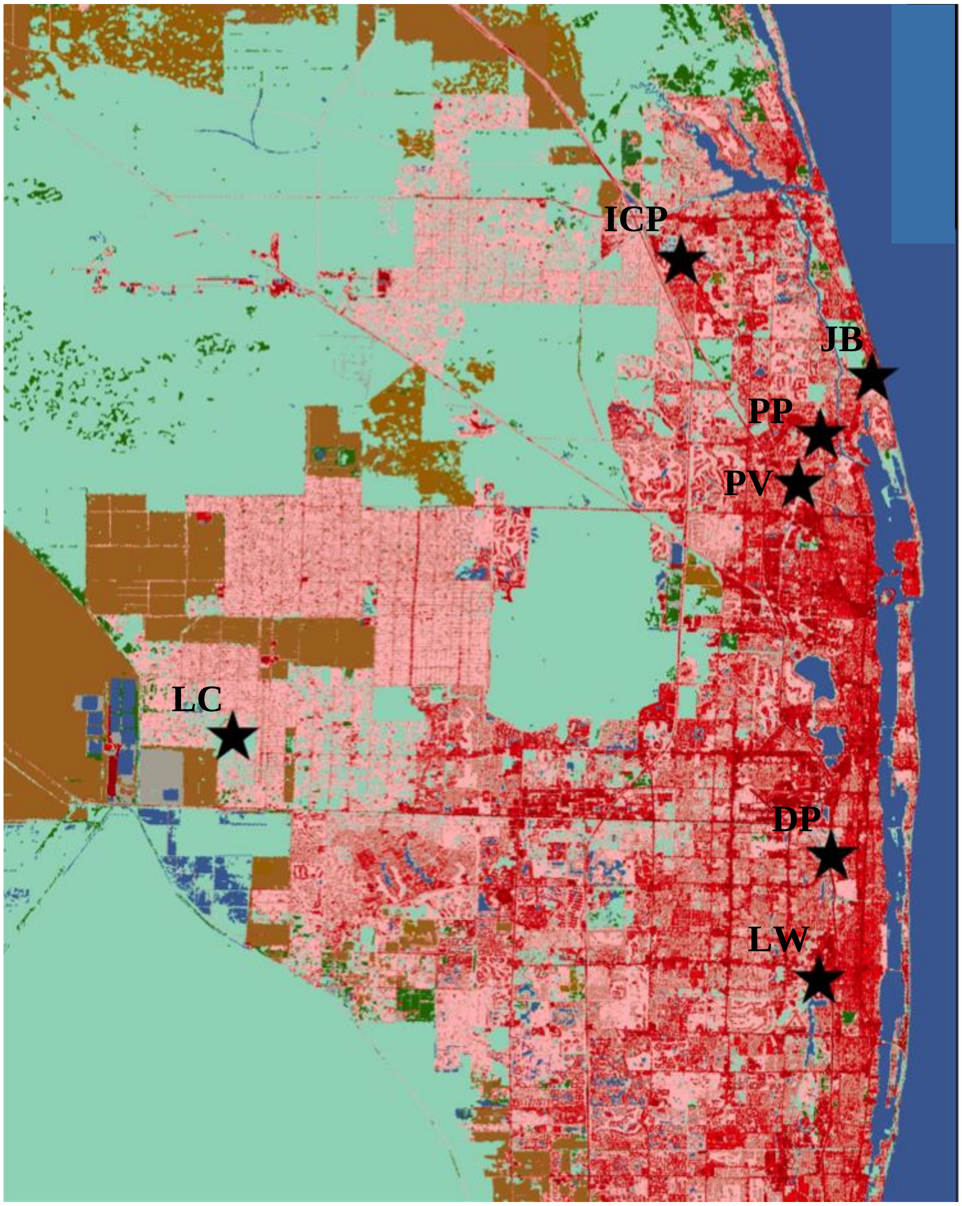

Figure 3.1. Map of Palm Beach County, Florida depicting white ibis capture site locations (stars), names (alpha codes), and surrounding land use (blue—water; green—freshwater wetland; brown—agricultural; pink to red—gradient of developed).

Table 3.1. Characteristics of seven white ibis capture sites (all located in Palm Beach County, Florida). [Dev—developed; Wet—freshwater wetland; Urb. Det.—urban detection; P—plasma; F—feces]

Code	Name	Type	Dec. Degrees	%Dev.[1]	%Wet.[1]	Urb. Det.	Samples
DP	Dreher Park	Urban Park	N26.66440 W080.06952	93.92	0.00	47.67%	14 (P) 15 (F)
ICP	Indian Creek Park	Urban Park	N26.91688 W080.13370	87.95	0.72	44.49%	15 (P) 9 (F)
JB	Juno Beach (Pelican Lake)	Urban Park	N26.86768 W080.05270	44.02	2.56	23.27%	12 (P) 14 (F)
LC	Lion Country Safari	Zoological Park	N26.71398 W080.32359	61.2	4.51	56.15%	9 (P) 8 (F)
LW	Lake Worth (John Prince Park)	Urban Park	N26.60966 W080.07731	87.98	1.10	57.56%	13 (P) 13 (F)
PP	Promenade Plaza	Parking Lot and Apartment Complex	N26.82189 W080.08375	93.34	0	46.69%	6 (P) 6 (F)
PV	Prosperity Oaks Village	Retirement Home and Pond	N26.84317 W080.07451	83.77	1.58	42.10%	11 (P) 8 (F)

[1] Calculated at a 2-km radius surrounding the site

Table 3.2. Mean and standard deviation of stable δ^{13}C and δ^{15}N isotope values (‰) for compiled reference diet categories (including values obtained from published literature), including the items included in each category.

			δ^{13}C (‰)		δ^{15}N (‰)	
Type	**Category**	**Items**	**Mean**	**± SD**	**Mean**	**± SD**
Natural	Freshwater Invertebrates	crayfish[1,2]; water beetle[1]; dragonfly nymph[1]	-26.67	± 1.30	3.51	± 1.21
	Saltmarsh Invertebrates	fiddler crab[1]; sand flea[1]	-15.80	± 0.71	6.09	± 0.52
	Fish	flagfish[2] ; Eastern mosquitofish[2]; golden topminnow[2]	-27.75	± 0.33	6.09	± 0.52
Anthro-pogenic	Bread	white bread[1,3]; wheat bread[1]; white flour baked buns[1,4]	-25.03	± 0.72	2.87	± 0.90
	Refuse	dog food[1]; chicken nugget[1]; chicken[5]; beef[5]; turkey[3]; pork[3]	-18.29	± 2.00	3.57	± 1.30
	Corn-based	Yellow corn chip[1]; white corn chip[1]; Flamin' hot Cheetos[1]	-13.15	± 0.81	3.10	± 0.65

[1] Our analysis; [2] Sargeant et al. 2010; [3] Nash et al. 2012; [4] Bostic et al. 2015; [5] Jahren and Kraft 2008

Table 3.3. Mean ratios of δ^{13}C and δ^{15}N for ibis fecal and plasma samples, divided by capture site.

	Feces				**Plasma**			
	δ^{13}C (‰)		δ^{15}N (‰)		δ^{13}C (‰)		δ^{15}N (‰)	
Site	**Mean**	**± SD**	**Mean**	**± SD**	**Mean**	**± SD**	**Mean**	**± SD**
DP	-21.24	± 2.74	2.41	± 0.98	-21.18	± 2.18	7.88	± 0.83
ICP	-21.91	± 2.94	1.24	± 1.09	-20.76	± 2.33	7.56	± 0.61
JB	-18.72	± 3.80	3.73	± 2.85	-18.75	± 2.30	7.56	± 0.67
LC	-21.13	± 2.50	3.66	± 1.21	-21.02	± 0.71	7.85	± 0.94
LW	-21.90	± 2.02	2.96	± 1.78	-21.88	± 1.88	8.64	± 1.75
PP	-22.02	± 2.25	2.35	± 0.89	-19.72	± 0.94	7.26	± 0.28
PV	-20.85	± 5.13	1.93	± 1.11	-19.72	± 2.36	7.46	± 0.52

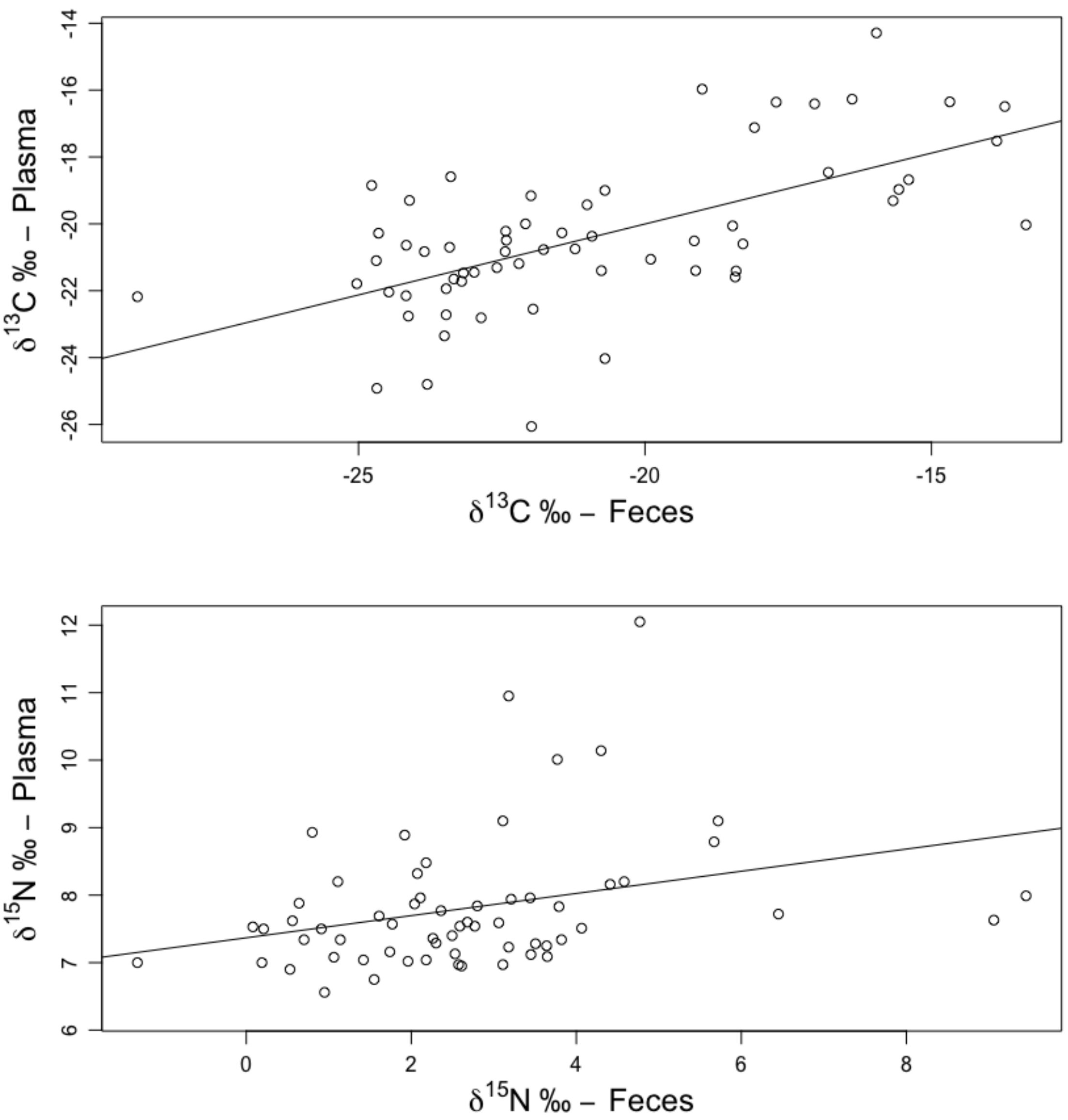

Figure 3.2. Relationship between $\delta^{13}C$ (top) and $\delta^{15}N$ (bottom) ratios in ibis plasma and feces.

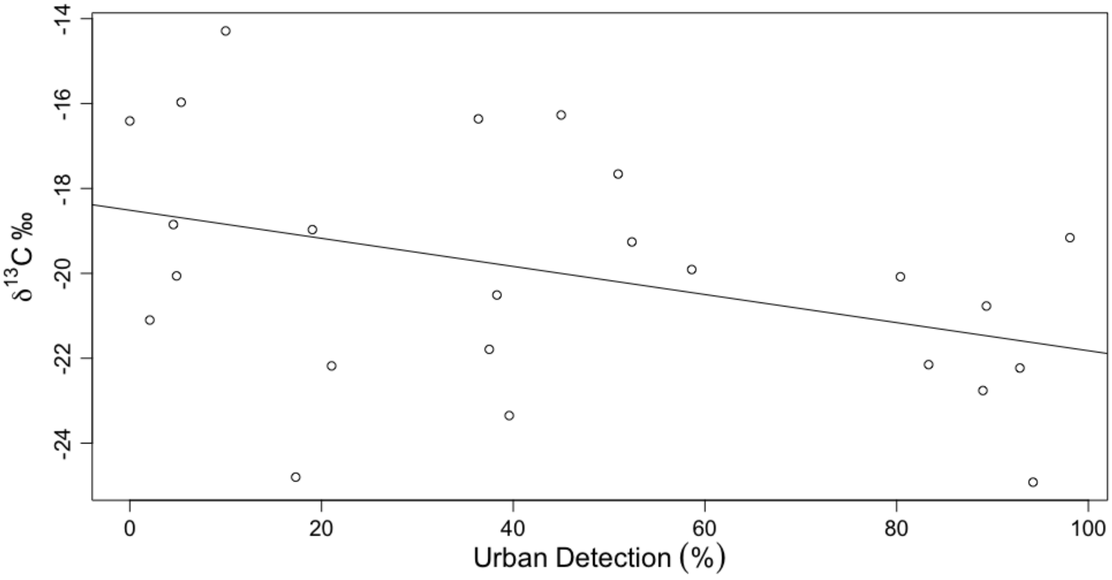

Figure 3.3. Relationship between δ^{13}C in ibis plasma and percent detection of ibis in urban areas.

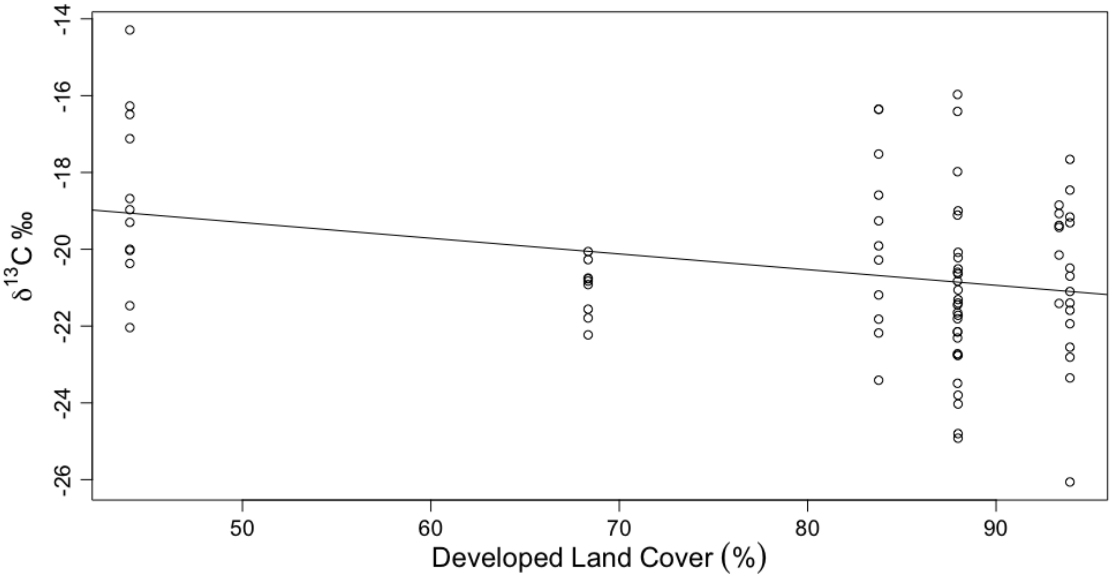

Figure 3.4. Relationship between δ^{13}C in plasma and percent developed land cover at a 2-km radius around the capture site.

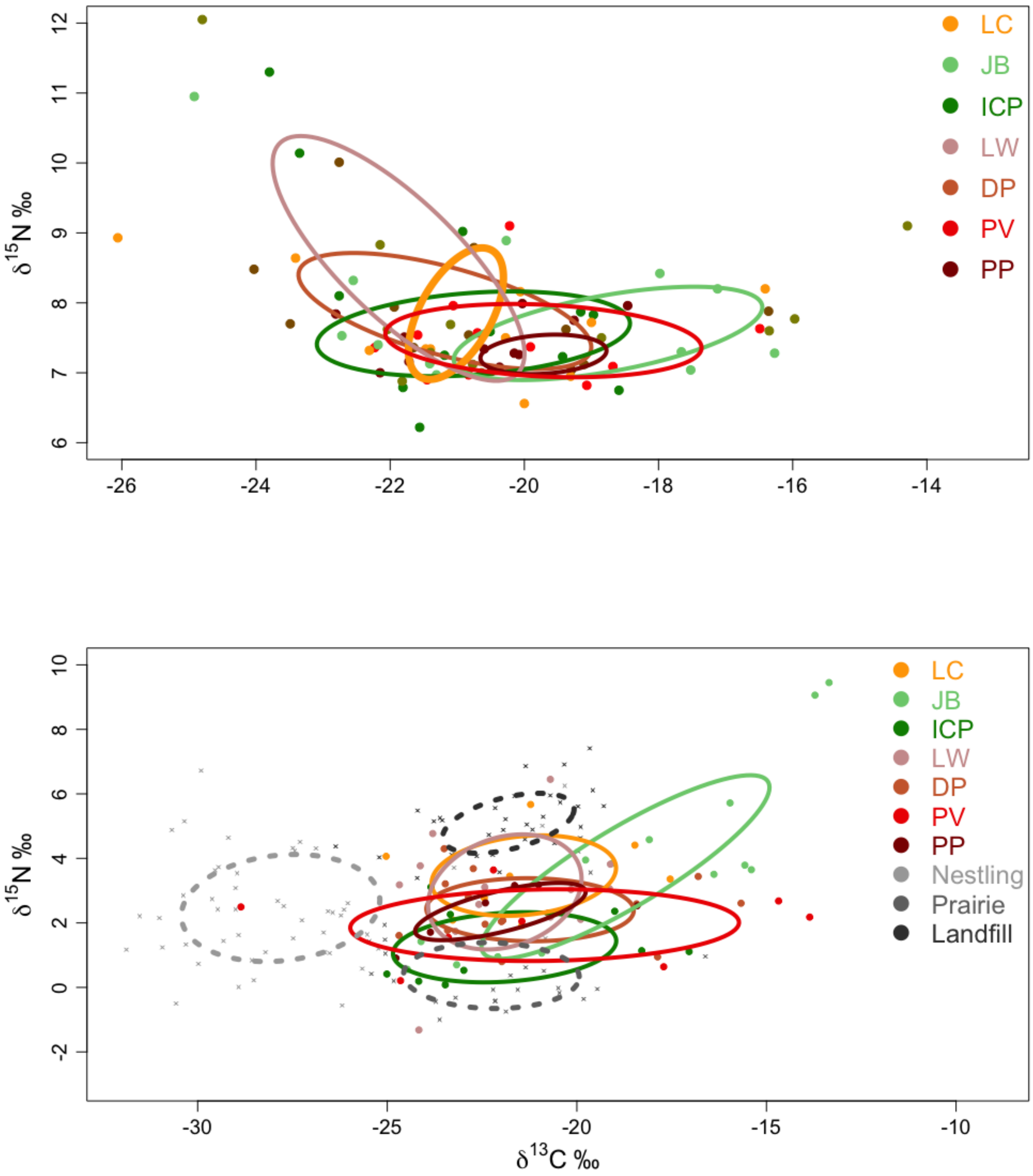

Figure 3.5. SIBER stable isotope standard ellipses for δ^{13}C and δ^{15}N in ibis plasma (top) and feces (bottom) by capture site, calculated to contain 40% of the data points for each site and corrected for small sample sizes.

Table 3.4. SIBER Bayesian ellipse areas for ibis fecal and plasma samples at each capture site (calculated to contain 40% of the data points for each site), including fecal samples for three reference sites, and the ratio of fecal to plasma ellipse areas.

Site	**Feces**	**Plasma**	**Feces : Plasma**
DP	7.98	4.38	1.82
ICP	9.40	4.23	2.22
JB	18.44	3.86	4.78
LC	8.35	1.63	5.13
LW	10.55	6.83	1.54
PP	4.39	0.71	6.14
PV	17.20	3.56	4.84
Nestling	13.78456	---	---
Prairie	7.772203	---	---
Landfill	4.612996	---	---

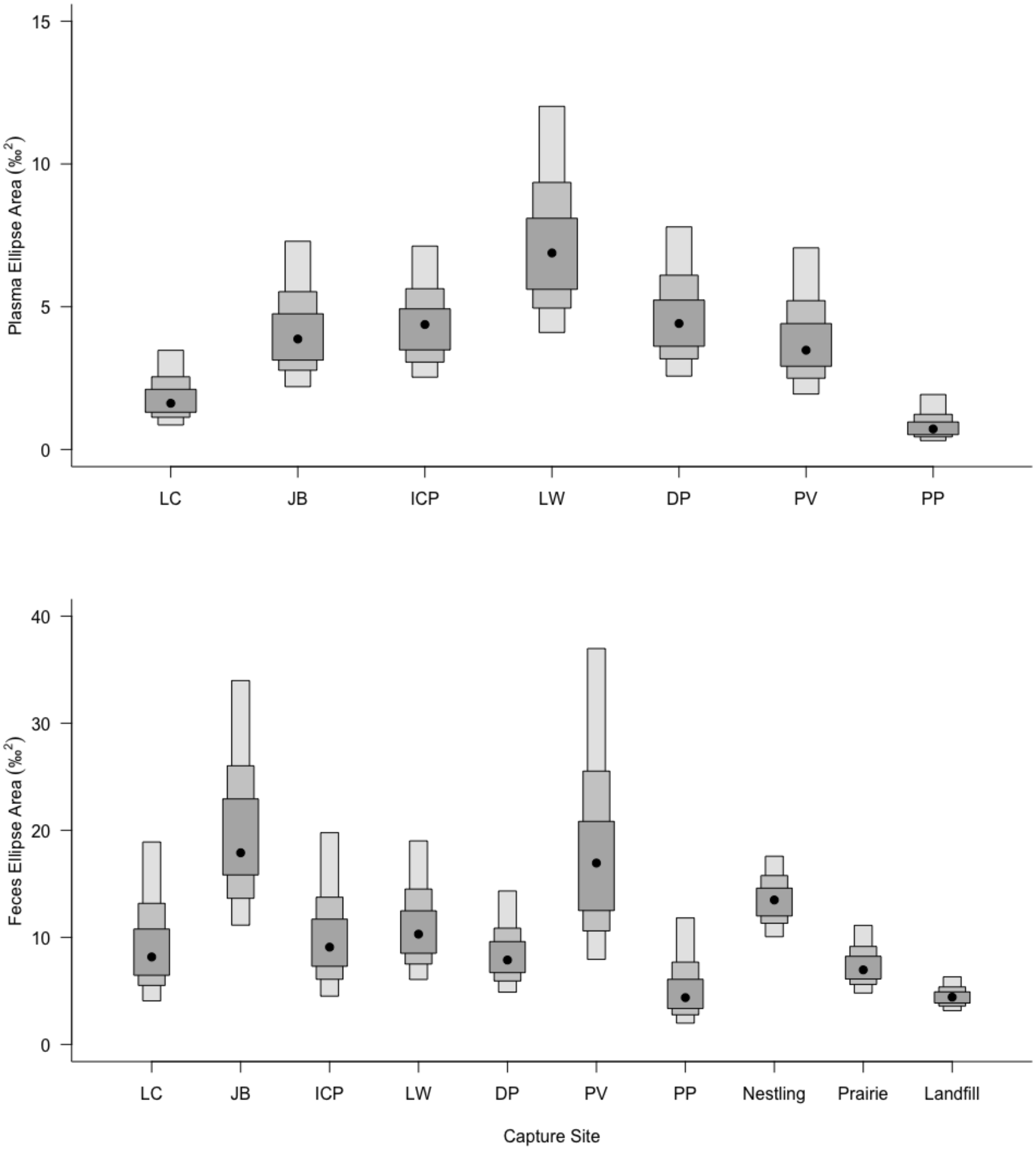

Figure 3.6. SIBER Bayesian ellipse areas for ibis plasma (top) and feces (bottom) at each capture site (including fecal samples for three reference sites), with means (black dots), and 99%, 95%, and 50% credible intervals.

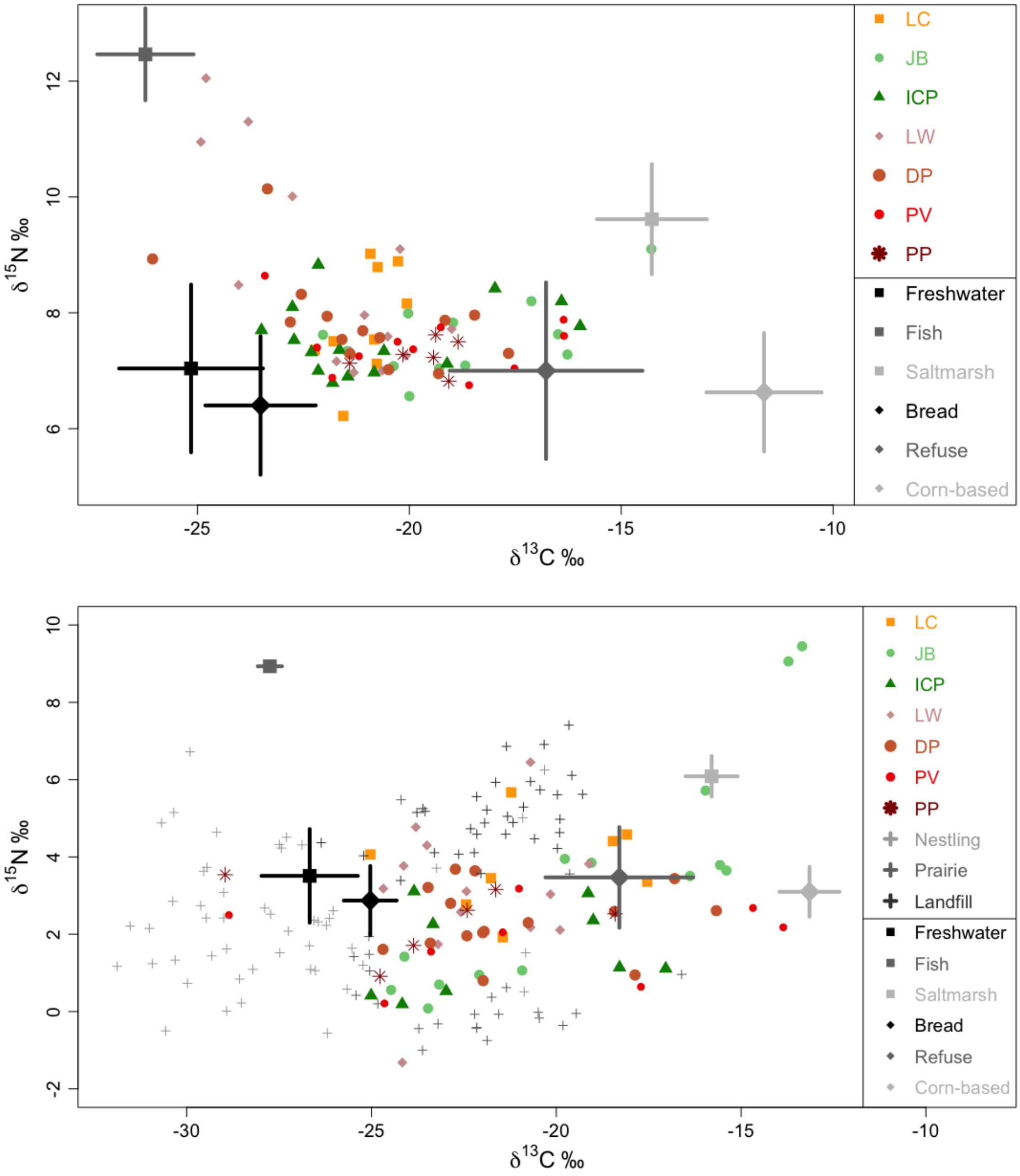

Figure 3.7. Isotopic signatures of ibis plasma (top) and feces (bottom) with unique color-symbol combinations for capture sites, including fecal signatures for three reference sites. Signatures of diet source items in six categories are shown with means ± standard deviation; squares show natural and diamonds show anthropogenic diet source categories.

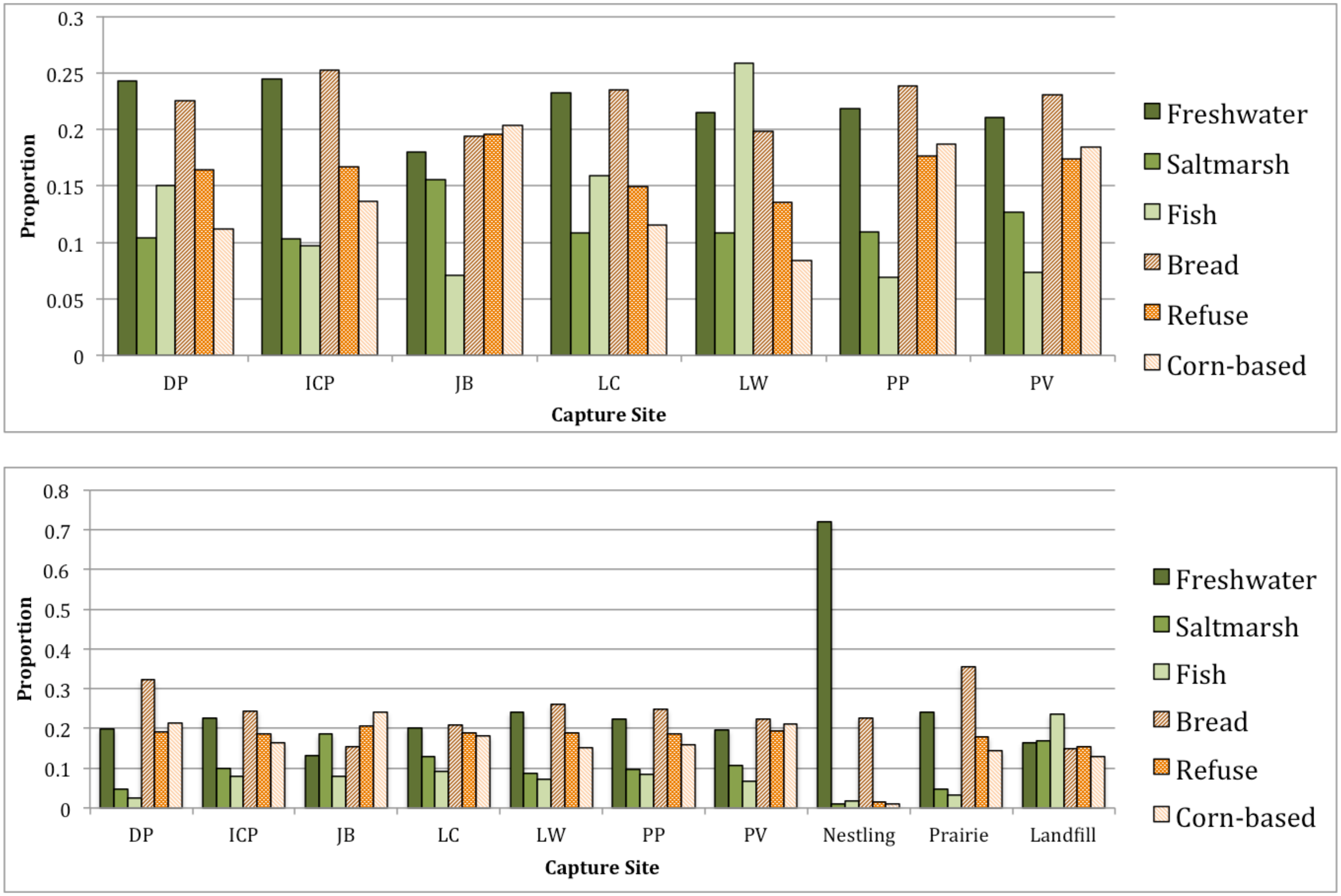

Figure 3.8. Posterior means of proportions of six diet source categories (green—natural foods; orange—anthropogenic foods) determined with SIAR mixing models, shown by capture site for ibis plasma (top), and feces including reference groups (bottom).

CHAPTER 4

INFLUENCE OF URBAN HABITAT USE ON STRESS AND IMMUNE FUNCTION OF WHITE IBIS (*EUDOCIMUS ALBUS*) IN SOUTH FLORIDA[2]

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[2] Curry, S. E., Navara, K. J., Welch, C. N., Becker, D. J., Cooper, R. J., Yabsley, M. J., and Hernandez, S. M. To be submitted to *General and Comparative Endocrinology*.

INTRODUCTION

Urban growth and development substantially alters global ecosystems, with variable impacts for wildlife (Vitousek et al. 1997, Evans et al. 2011, Sol et al. 2014). Some respond to habitat alteration by increasingly exploiting urban areas with reliable food resources. For example, ravens feed their nestlings roadkill (Kristan et al. 2004); urban coyotes exploit dumpsters and compost piles (Murray et al. 2015a and b); wild birds use supplemental feeders (Lepczyk et al. 2004, Jones and Reynolds 2008); wading birds consume human handouts in parks (Epstein et al. 2007, Hernandez et al. 2016); and various species forage on refuse at landfills (Caron-Beaudoin et al. 2013, Dolejska et al. 2016). Urban-associated species have some common traits that facilitate adaptation and exploitation of anthropogenic resources, including broad diet/habitat requirements and behavioral plasticity (Luniak 2004, McKinney 2006, Evans et al. 2011, Sol et al. 2014)—for example, non-native house sparrows and corvids (e.g., magpies) are well-documented urban exploiters (Jerzak 2001, Marzluff 2001). Some species recently observed in urban habitats (e.g., San Joaquin kit fox [*Vulpes macrotis mutica*]—Newsome et al. 2010) are native species of conservation concern that may increasingly rely on urban areas as wild habitat loss and degradation progresses. These less urban-associated species may similarly capitalize on urban anthropogenic resources if their foraging and habitat requirements are met and they can adapt to urban stressors without adverse health effects.

Compared to wildlife in natural areas, urban wildlife experience altered: inter- and intra-specific interactions (Goymann and Wingfield 2004, Bradley and Altizer 2007); predation risk (Lepczyk et al. 2004); densities (Bradley and Altizer 2007, Murray et al. 2016); and interactions with people (e.g., feeding, chasing) and vehicles (e.g., cars and boats) (Ditchkoff et al. 2006, Slabbekoorn and Ripmeester 2007, Murray et al. 2016). Organisms respond to perceived stressors (including those aforementioned) via the adrenocortical stress response. In all vertebrates, the stress response is partially controlled by the hypothalamic-pituitary-adrenal (HPA) axis, which initiates corticosterone hormone release and triggers gluconeogenesis and mediation of other physiological processes (Romero 2004, McEwen and Wingfield 2010, Sheriff et al. 2011). The ratio of heterophils to lymphocytes in blood (H:L ratio) also increases following stress, due to increased release of heterophils into peripheral circulation and redistribution of lymphocytes outside of circulation (Davis et al. 2008). Perception of stressors may lead some wildlife to adjust their habitat use and activities, by avoiding urban areas where people are present (McKinney et al. 2010) or changing the timing of activities (e.g., altering bird song—Slabbekoorn and Ripmeester 2007). Other wildlife may adjust behaviorally and habituate to perceived stressors. For example, as tourist visits increased, penguins reduced the number of head turns toward tourists (Walker et al. 2006), and some species of birds reduced their flushing distance in the presence of people (Blumenstein et al. 2003, Jimenez et al. 2011, Lin et al. 2012).

Urban wildlife exhibit wide variation in physiological stress responses (see Bonier's 2012 review for urban birds). Some adapt to urban or disturbed areas and subsequently respond less frequently or less intensely to perceived stressors. For example, Morgan et al. (2012) found neutral and positive responses in nestling and adult jays to roads. Other wildlife may continually respond to stressors and ultimately experience chronic stress via prolonged HPA axis activation (Martin et al. 2010, Cockrem 2013), resulting in increased levels of circulating corticosterone due to impaired function of the negative feedback loop that halts corticosterone production when a stressor is no longer present (Chavez-Zichinelli et al. 2013, Downs and Stewart 2014). Persistent exposure to chronic stress may also lead to lower levels of corticosterone (Cyr and Romero 2007a and 2007b), perhaps from reduced HPA axis sensitivity meant to lower risk of pathology associated with elevated corticosterone. Corticosterone affects immune function, and some immune components are differentially enhanced or suppressed during a stress response (Adamo 2004, Boughton et al. 2011, Demas et al. 2011). Buehler et al. (2008) found variable effects of handling stress on red knot immune components, and Stier et al. (2009) found that corticosterone reduced adaptive but not innate immunity. Bactericidal capacity is a common metric of innate immunity used to assess the ability of cell-mediated and humoral immune components to non-specifically target and kill pathogenic agents. Matson et al. (2006), Millet et al. (2007), and Schmidt et al. (2015) found diminished innate bactericidal capacity against *E. coli* related to increased corticosterone levels. However, Fratto et al. (2014) found that *Mycoplasma gallisepticum* infection in house finches buffered suppression of bactericidal capacity during stress. Short-term suppression and enhancement of immune components during stress can be beneficial. However, chronic stress can lead to long-term detrimental immunosuppression.

Numerous factors influence pathogen infection for urban wildlife, including resource quality, density at supplemental feeding sites, inter- and intra-specific contact, and exposure pathogens or contaminants (Bradley and Altizer 2007, Becker et al. 2015, Murray et al. 2016). Exploitation of more predictable anthropogenic resources may allow allocation of additional energy toward immunity (Deerenberg et al. 1997, Fokidis et al.

2008). However, anthropogenic resources vary widely in quality. Some are appropriate for certain species—for example, raven chicks with greater access to anthropogenic trash or roadkill had increased fledging success (Kristen et al. 2004). However, other resources are nutritionally deficient—for example, rural crow nestlings supplemented with lower-protein foods were smaller (Heiss et al. 2009). Pathogen exposure may increase for wildlife in urban areas, from consumption of contaminated foods (e.g., toxin exposure in vultures—Green et al. 2006) in contaminated habitats (e.g., relationship between *Salmonella* spp. contamination of birds and their environment—Cizek et al. 1994) with altered intra- and inter-specific interactions (e.g., *Toxoplasma gondii* exposure of urban woodchucks in habitats with cats (the definitive host)—Lehrer et al. 2010). These factors impact pathogen exposure and infection, but the outcomes of infection vary considerably. Murray et al. (2015b) observed mange in urban coyotes that used more developed areas, consumed less protein, and had increased home ranges and daytime activity. Knapp et al. (2013) found higher endoparasite prevalence in iguanas provided supplemental food, likely related to increased iguana densities. Fokidis et al. (2008) found lower blood parasitism but higher heterophil-to-lymphocyte ratios in some urban birds, highlighting likely interplay between immunity, infection risk, and availability of food resources in successful adaptation to urban habitats. Stress is likely critical in predicting ultimate outcomes of pathogen infection for urban wildlife, particularly through its role in mediating immunity.

The American white ibis (*Eudocimus albus*) is ideal to study how urban habitat use impacts stress and immune function in less urban-associated species. White ibis are semi-nomadic wading birds that rely on wetlands in the southeastern United States for aquatic prey (e.g., crayfish, fiddler crabs, small fish) (Kushlan 1979, Heath et al. 2009). Ibis forage widely in the Florida Everglades ecosystem, moving nomadically between habitats as prey availability fluctuates due to wetland management regimes, wet-dry seasonal cycles, and inter-annual variability in rainfall (Gawlik 2002, Frederick et al. 2008, Beerens et al. 2011, Lantz et al. 2011). Twentieth century habitat destruction and anthropogenic hydrologic changes led to a ~50% decline in Everglades habitat, significantly impacting wading bird populations. Ibis—now a Florida Species of Special Concern—experienced an 87% decline in breeding pairs from 1903 to 2001 (Davis and Ogden 1994, Crozier and Gawlik 2003). Ibis are currently an indicator species for Everglades restoration, because they depend heavily on aquatic prey that responds to hydrologic management/restoration—and this relationship to wetland health is easily understood by the public (Kushlan 1997, Crozier and Gawlik 2003, Frederick et al. 2008, Heath et al. 2009).

Ibis have been documented for decades foraging on maintained lawns (Heath et al. 2009) and at landfills (Rumbold et al. 2009). However, within the past 10–20 years ibis have become abundant on golf courses, urban lawns, dumpsters, landfills, and specifically at urban parks where they consume human handouts—often bread commonly provided to ducks (Chapman and Jones 2009, Hernandez et al. 2016, Welch 2016). A concurrent study was the first to describe the movements of white ibis in urban areas. That study found that some ibis capitalized on consistent food available at urban locations by shifting from nomadic foraging on aquatic wetland prey to sedentary behavior, exhibiting fidelity to urban sites with anthropogenic foods (Welch 2016). The trajectory of the American white ibis toward becoming a fully urbanized bird is similar to that of the related Australian white ibis (*Threskiornis molucca*). The Australian ibis is an urban adaptor with reduced daily movements, regular use of urban sites including landfills, and a largely anthropogenic diet—a subset of the population now exclusively forages and breeds in urban areas (Epstein et al. 2007, Martin et al. 2011 and 2012). For American white ibis, urban habitats differ in land cover (e.g., wetland vs. developed), and human impacts (e.g., direct bird feeding, presence of trash, human presence), which influence ibis exposure to stressors and pathogens. Ibis likely vary in their frequency of urban habitat use and may therefore be exposed and respond to urban stressors at differing extents. Ultimately, establishing how urban habitat use affects ibis stress response and immune function is a first step towards determining if ibis will successfully adapt to exploiting anthropogenic resources in urban habitats without adverse health effects.

We hypothesized that increased use by white ibis of more urban habitats in South Florida would be associated with increased stress levels and suppressed immune function. We measured five attributes of stress and immunity in individual ibis: baseline fecal corticosterone; baseline plasma corticosterone; induced plasma corticosterone; H:L ratios; and plasma bactericidal capacity. Specifically, we expected that: (1) ibis with higher corticosterone would have lower bactericidal capacity; (2) ibis that spent more time in urban habitats would have increased corticosterone and reduced bactericidal capacity; and (3) ibis captured at habitats with greater surrounding developed land would have increased corticosterone and lower bactericidal capacity.

METHODS

Study Area

We captured ibis in Palm Beach County, Florida (PBC; 26.650708°, -80.276931°). PBC is a highly developed county located east of parts of the Everglades wetland ecosystem, and the county encompasses multiple land cover types with variable suites of stressors. Ibis numbers have been increasing in PBC for over a decade, primarily in the non-breeding season, and some ibis flocks are present predictably at certain sites (Welch 2016). Based on preliminary observations, we identified seven sites with consistent flocks of ibis (>10 ibis) habituated to human presence sufficiently for capture (see Hernandez et al. 2016). The sites included a zoo, a parking lot, and various urban parks, all of which varied in the availability of anthropogenic food, surrounding land cover type (e.g., wetland, developed), and ibis flock habituation to people (see Figure 4.1 for map of capture sites and Table 4.1 for a summary of site features).

Capture and Sample Collection

We captured ibis using nylon leg lassos at seven sites in PBC just after the breeding season (11 July to 31 August 2013, hereafter “summer,” n=68) and at six of seven sites just prior to the following breeding season (December 2013, hereafter “winter,” n=24). We did not capture ibis in other seasons, as ibis leave urban parts of PBC during the breeding season. We collected standard morphometric measurements and measured body mass, which we standardized by calculating the residuals after regressing mass by tarsus length (with separate regressions for male and female ibis). We determined sex by extracting DNA from 10 µl whole blood with a Qiagen DNeasy blood extraction kit (Qiagen, Valencia, CA, USA) following the manufacturer’s protocol. We then used 2550F/2718R primers to distinguish between male and female ibis (Fridolfsson and Ellegren 1999, Ong and Vellayan 2008). In July–August 2013, we attached VHF transmitters to track a subset of ibis for a larger project investigating ibis movement and health (Welch 2016). Upon capture and when not undergoing sample collection, we held birds in individual bags. We released all birds within 60 minutes of capture.

For fecal corticosterone analysis, we collected fresh feces from captured ibis immediately after defecation, placed samples in bullet tubes in a cooler with frozen gel packs, and froze samples at -20°C when field processing was complete (within six hours). For all other analyses, we obtained blood samples from the jugular or tibiotarsal veins with 21–25 gauge needles. We collected blood at three time points—within 2 minutes of capture, 15 minutes post-capture, and 30 minutes post-capture. We never collected more than 1% of the bird's mass in total blood volume to avoid detrimental effects from blood collection. We prepared smears from fresh whole blood at one time point (typically at 15 minutes post-capture), which we air-dried and fixed with methanol on the same day and stored in dry boxes until later processing. We collected all remaining blood in individual heparinized tubes. We stored blood samples in a cooler with frozen gel packs and centrifuged all blood samples within four hours of collection for 10 minutes at 3,500g to separate the plasma fraction and create aliquots for each sample. We immediately placed aliquots for bactericidal assays in liquid nitrogen and froze aliquots for corticosterone analyses at -20°C. We transported all frozen samples to the University of Georgia (UGA) and maintained samples at -80°C (aliquots for bactericidal assays) and -20°C (aliquots for corticosterone analyses) until analysis. All animal capture and handling procedures were approved by the University of Georgia's Institutional Animal Care and Use Committee (AUP#A2011 08-018).

Fecal Corticosterone Analysis

We collected feces to measure corticosterone metabolites, reflecting baseline stress across the time of intestinal transit—e.g., one to three hours for white ibis (Mostl et al. 2005, Palme et al. 2005, Adams et a. 2009). We maintained freshly frozen feces at -20°C as per Herring and Gawlik (2012) and subsequently dried individual fecal samples for at least 48 hours. We extracted 0.05 g of each fecal sample with 8 ml of 95% ethanol. We vortexed for 30 minutes then centrifuged at 2,500 rpm for 15 minutes, after which we decanted 6 ml supernatant into glass culture tubes and evaporated supernatant in a fume hood for at least two days. We determined levels of corticosterone metabolites with a ^{125}I Double-Antibody radioimmunoassay kit (MP Biomedicals, Santa Ana, CA, USA) following the manufacturer's protocol. This kit has been previously validated for white ibis feces (Adams et al. 2009).

Plasma Corticosterone Analysis

We collected plasma at three time points to measure circulating corticosterone. Plasma corticosterone levels up to 3 minutes following a stressor reflect the baseline stress state of the organism (Angelier et al. 2010); whereas plasma corticosterone levels at a set point following a stressor (typically 15–30 minutes in birds) reflect the magnitude of the stress response (see Cockrem and Silverin 2002, Romero 2012, Grunst et al. 2014). To facilitate comparison with Health et al. (2003)'s previous research on white ibis, we quantified plasma corticosterone with an in-house radioimmunoassay, following methods described by Wingfield and Farner (1975) and Etches (1976). Briefly, we added a small amount of tritiated hormone (1,000 cpm) to each 50 µl plasma sample for later calculation of recovery efficiency, after which we twice extracted corticosterone from each 50 µl sample using 3 ml of diethyl ether. We snap-froze samples, collected supernatant in a fresh tube, and evaporated supernatant in a fume hood for at least two days. We re-suspended plasma samples in 300 µl of phosphate buffered saline (PBS) gel and added duplicate aliquots of 100 µl to assay tubes. We used an additional 50-µl sample to determine extraction efficiencies. We added 50 µl of tritiated hormone (approximately 10,000 cpm) and 50 µl of rabbit-derived anti-corticosterone antibody (MP Biomedicals, Solon, OH USA, cat#07-120016) to each assay tube and to additional tubes containing a graduated curve of corticosterone. We then incubated all assay tubes for 18 hours, after which we added 500 µl of a solution containing dextran-coated charcoal to each tube. We incubated tubes for 10 minutes and centrifuged tubes at 4,500 rpm for 10 minutes to separate bound and free fractions. We decanted supernatant into scintillation vials and counted radioactivity after adding 4 ml of scintillation fluid. We corrected the final concentration for each sample with its individual extraction recovery percentage.

For analyses, we excluded corticosterone results for ibis that fell outside of our ranges for each time point. Therefore, we only included samples collected at 0–2 minutes after capture, 13–20 minutes after capture, and 27–37 minutes after capture. We calculated corticosterone levels at the 15- and 30-minute time points as the value at the respective time point minus the baseline corticosterone level for that bird.

Bacterial Killing Analysis

We used the bacterial killing assay (BKA) to assess innate immunity by determining the ability of plasma humoral components (i.e., complement proteins) to kill bacterial colonies (bactericidal capacity). We quantified bactericidal capacity of ibis plasma against *Escherichia coli* (*E. coli*; strain ATCC 8739) following Matson et al. (2006), with minor modifications. Specifically, we diluted *E. coli* bacterial stock with phosphate buffered saline to achieve ~600 colony-forming units (CFUs) per 10 µl. We diluted 50 µl of each ibis plasma sample in 150 µl CO2-independent media enriched with 4 mM L-glutamine. We then combined 10 µl of the bacterial dilution with 140 µl of each blood dilution. We also combined 10 µl of the bacterial dilution with 140 µl of CO2-independent media enriched with 4 mM L-glutamine, as positive controls with ~200 CFUs per 50 µl. We vortexed all plasma-bacteria combinations and let sit for 60 minutes, following which we plated 50 µl of each onto tryptic soy agar plates. We incubated all plates at 37°C for 16 hours then counted the number of CFUs per plate. We calculated BKA for each sample as 1 – (CFU of sample / mean CFU of positive controls). We primarily assessed bactericidal capacity from blood collected at the 15-minute time point; however, we substituted results from the 30-minute time point for several birds with missing results (as our BKA results at 15 and 30 minutes did not significantly differ).

Differential Cell Counts

We recorded the number of heterophils, lymphocytes, monocytes, eosinophils, and basophils out of 100 leukocytes from Wright-Giemsa stained blood smears under 1,000 x magnification (oil immersion), and we calculated the ratio of heterophils to lymphocytes (H:L ratio) as a measure of chronic stress and inflammation (Davis et al. 2008).

Movement and Land Cover Analysis

We tracked a subset of ibis captured in July–August 2013 via radio telemetry from September 2013 to July 2014 at the seven capture sites and along a 104-km pre-set route across urban PBC (Welch 2016). Ibis are present in urban areas primarily during the non-breeding season; therefore, for this project we excluded breeding season detections. We analyzed non-breeding season (September–February) detections by dividing the number of detections of each ibis in the sampling area (which included both the capture sites and a 0.5-km radius around the pre-set route) by the total number of visits to the sampling area.

We determined land cover types surrounding capture sites in ArcGIS by reclassifying raster data from the 2014 Cooperative Land Cover Map (Florida Fish and Wildlife Conservation Commission and Florida Natural Areas Inventory) into relevant categories, including a combined category for all wetland types, and a combined category for all developed types. We calculated the number of pixels in each land cover category within a 2-km-radius buffer around the center of each capture site, reflecting the average daily foraging area of an urban ibis (Hernandez unpublished data). We then determined the percentage of each land cover category surrounding each capture site by dividing the number of pixels for the category by the total number of pixels in the 2-km-radius buffer.

Statistical Analysis

To improve normality (Shapiro Wilk's test) and homogeneity of variance (Bartlett's test), we square root transformed plasma corticosterone results at capture and 30-minutes post-capture, log transformed fecal corticosterone metabolite levels and H:L ratios, and arcsin transformed BKA and urban detections. We determined correlations between corticosterone levels, H:L ratios, and bactericidal capacity with season, time of day, sex, age, and standardized mass using Welch's *t*-tests and linear regressions. We compared corticosterone, bactericidal capacity, and H:L ratios across all capture sites with analysis of variance (ANOVA). For a subset of birds tracked via VHF telemetry, we assessed the relationship between percentage of urban habitat use and corticosterone, bactericidal capacity, and H:L ratios using linear regressions. We performed all statistical analyses in Program R (version 3.3.2, R Core Team 2016). Results are presented as means ± standard deviation (SD).

RESULTS

We determined baseline corticosterone (plasma level at capture or PCORT-A [0–2 minutes]; mean=1.51±1.17ng/mL, n=66). We calculated the change in plasma corticosterone after 15 minutes of handling (plasma level 15 minutes post-capture or PCORT-B [13–22 minutes] minus PCORT-A; mean=18.75±8.94 ng/mL, n=55). We calculated the change in plasma corticosterone after 30 minutes of handling (plasma level 30 minutes post-capture or PCORT-C [27–37 minutes] minus PCORT-A; mean=13.95±7.79 ng/mL, n=42). We determined corticosterone metabolites in fecal samples (FCORT; mean=2.34±3.64 µg/g, n=75), bactericidal capacity in plasma (BKA; mean=41.93±25.63%, n=68), and whole-blood H:L ratios at one time point (H:L; mean=0.44±0.28, n=83). Table 4.2 presents summary statistics for all metrics.

General Findings

FCORT declined by date of capture ($F_{1,73}=37.74$, $R^2=0.34$, $p<0.001$) and was higher in summer compared to winter 2013 (Welch's *t*-test: $t_{65.06}=5.37$, $p<0.001$). BKA declined by date of capture ($F_{1,66}=5.99$, $R^2=0.08$, $p=0.017$) and was higher in summer compared to winter 2013 (Welch's *t*-test: $t_{41.37}=2.28$, $p<0.03$). Standardized mass declined by date of capture ($F_{1,90}=6.28$, $R^2=0.07$, $p=0.014$) and was higher in summer compared to winter 2013 (Welch's *t*-test: $t_{41.37}=2.28$, $p<0.03$). H:L declined by standardized mass ($F_{1,81}=4.11$, $R^2=0.05$, $p<0.05$), but the relationship was no longer significant when we controlled for date. We found no other significant correlations with date of capture, season, sex, age, or standardized mass.

Plasma Corticosterone Response

Plasma corticosterone increased for all ibis between capture (PCORT-A) and the 15-minute time point (PCORT-B) (Paired *t*-test: $t_{80.78}=-17.66$, $p<0.01$; Figure 4.2). Plasma corticosterone decreased overall between the 15- and 30-minute time points (Paired *t*-test: $t_{133.98}=3.65$, $p<0.01$; Figure 4.2)—though corticosterone continued to increase for 17 of 58 ibis. Corticosterone remained higher at 30 minutes than 0–2 minutes (Paired *t*-test: $t_{59.35}=-13.62$, $p<0.01$; Figure 4.2). PCORT-A and PCORT-B were significantly positively correlated ($F_{1,53}=14.57$, $R^2=0.22$, $p<0.001$; Figure 4.3), as were PCORT-B and PCORT-C ($F_{1,40}=6.02$, $R^2=0.13$, $p<0.02$; Figure 4.3). However, PCORT-A and PCORT-C were not significantly correlated.

Relationship Between Stress Parameters and Innate Immunity

PCORT-A and PCORT-B were positively correlated with H:L ratios (PCORT-A: $F_{1,58}=15.55$, $R^2=0.21$, $p<0.001$; PCORT-B: $F_{1,51}=5.45$, $R^2=0.10$, $p=0.024$; Figure 4.4), but PCORT-C was not. FCORT was not correlated with PCORT-A, -B, or -C but was positively correlated with H:L ratios in summer 2013 (July–August) ($F_{1,43}=9.86$, $R^2=0.19$, $p<0.01$). No parameters were significantly correlated with BKA.

Stress and Immunity by Urban Fidelity

Non-breeding season urban detections of 28 tracked ibis (September–February) ranged from 0.00% to 98.08% (Mean=45.42%, SD=34.43%). Overall, detections were positively correlated with fecal corticosterone ($F_{1,20}$= 4.365, R^2= 0.18, $p<0.05$; Figure 4.4), a relationship that remained significant when we controlled for date of capture ($F_{2,19}$= 11.23, R^2= 0.54, $p<0.04$). Percent urban detection was not correlated with BKA, H:L, or PCORT at any time point.

Stress and Immunity by Capture Site and Features

No parameters differed significantly by capture site (see Tables 4.3 and 4.4 for summary statistics by site), or by percent developed land cover or percent freshwater wetland land cover surrounding the capture site. Ibis at PP had the highest bactericidal capacity with the lowest variability of all capture sites. Ibis at LC had the highest average fecal corticosterone, and one ibis with extremely high fecal corticosterone was captured at LW. On average, ibis at LC had the lowest PCORT at both 15 and 30 minutes post-capture (Figure 4.2).

DISCUSSION

We found that urban habitat use impacted stress, through higher levels of fecal corticosterone metabolites in ibis detected more frequently in urban areas, even after we controlled for the influence of capture date. Plasma corticosterone levels were not similarly correlated to urban detection. FCORT reflects cumulative stress hormone release and metabolism over several hours, while PCORT reflects circulating stress hormone at the time of sampling. Higher FCORT in ibis that spend more time in urban areas likely reflects an increased number of stress responses in these birds, suggesting features of urban habitats act as stressors for these individuals. Our measurements of stress in the birds tracked with telemetry were taken in summer (July–August 2013) and pre-date our assessment of urban habitat use. Ibis come to urban PBC after the breeding season, beginning primarily in July, and then are present to varying degrees in urban habitats until prior to the following breeding season (around February). Therefore, while some birds may have been in urban areas for weeks or days prior to capture, others may have come to PBC just prior to capture. It is possible that the ibis later detected more frequently in urban habitats were able to adapt to perceived stressors and later reduce the number of stress responses, reflected in lowered FCORT over the season. Jimenez et al. (2011) found lower fecal corticosterone in habituated chough at tourist versus non-tourist sites. While re-capturing ibis in this system is challenging, it would be valuable to track the change in stress hormones over time to better understand if increased urban habitat use is associated with adaptation in stress response for these birds. We made periodic efforts to track ibis to other locations and are reasonably confident that ibis detected more frequently in our study likely do spend more time in urban habitats; however, some ibis may have used urban areas outside of our tracking areas and therefore evaded detection.

We observed seasonal differences in FCORT, which declined significantly based on the date of ibis capture, and reached levels similar to those of ibis in winter by August 20. While PCORT was not significantly higher in summer, we did observe the highest PCORT values in summer (not necessarily from the individuals with higher fecal corticosterone). We began capturing ibis on July 11, when most birds were likely finished with breeding activities; however, some ibis could feasibly have still been invested in nestling care. Corticosterone has not been assessed in free-living white ibis following the breeding season. However, Heath et al. (2003) found increasing plasma corticosterone over the breeding season in female white ibis, and hormone concentrations were similar in both males and females at the end of the breeding season. Similarly, Kitaysky et al. (1999) found increased baseline and induced corticosterone in penguins (a species with bi-parental care) through the breeding season. Food stress from increased rainfall and prey dispersal in summer may also contribute to higher corticosterone in the summer. Increased ibis use of consistent anthropogenic food in the non-breeding season may mitigate food stress and contribute to lower FCORT levels observed in winter. The bird with the highest FCORT was a male in summer that had a diet consistent with non-urban foods, and had very high plasma baseline and low induced corticosterone. Possibly this bird was chronically stressed, due to breeding season, food stress, failure to adapt to urban habitats, or some combination of these factors.

We did not find other significant differences in stress or immune function parameters by urban detection, capture site, or surrounding land cover. This may relate to high variation in ibis movement and habitat use, or to differences in ibis exposure to stressors both across and within urban sites. In general, individual ibis in natural habitats vary substantially in movement patterns (Bildstein 1991, Beerens et al. 2011). While ibis in urban areas use an average foraging area of 1.67 km, this can range from small daily foraging areas to complete nomadism (Hernandez unpublished data). We captured birds just following the breeding season and began monitoring movement in September. During the breeding season, ibis are largely not present in urban PBC; however, birds begin returning to urban areas in July. Therefore, some ibis may have shifted their movement after sampling toward increased urban habitat use between the time of sampling and the beginning of our tracking.

Several PBC capture sites were associated with differences in ibis corticosterone, perhaps because of unique features present at these sites. Ibis captured at LC had some of the highest FCORT and lowest PCORT-B levels. LC is a zoo where birds encounter unusual stressors and are exposed to people in pulses throughout the day, including large groups of children in school groups. Ibis at DP exhibited wide variation in all parameters, perhaps related to some birds using the nearby zoo. DP is located near a zoo, and our observations plus reports from zoo personnel of banded birds indicate some ibis captured at DP also spend time at that zoo. Walker et al. (2005) found penguins in areas with tourist visitation had lower corticosterone response, and they demonstrated that these birds had reduced ability to secrete corticosterone. LC birds with such low responses (PCORT-B) could also have reduced sensitivity, indicative either of progression toward adaptation, or of chronic stress (Rich and Romero 2005). Chavez-Zichinelli et al. (2010) assessed fecal corticosterone in house sparrows across three land uses (urban, suburban, and industrial) and found variation in corticosterone and immunoglobulin levels within all land use types, suggesting some birds in all land use types were stressed and some were not. However, results from the industrial land use type showed a significant correlation between high fecal corticosterone and low immunoglobulin concentration, suggesting some birds in this land use type may be responding poorly to stressors. Similarly, some ibis at LC with high FCORT may be responding poorly to the unique stressors present at the zoo, while others respond positively or experience no changes.

The stressors ibis are exposed to across and within sites, as well as what individual ibis perceive as stressors, likely vary. Ibis with lower corticosterone responses may be better adapted to urban habitats. However, while lower induced corticosterone may be adaptive, we believe there is a threshold of induced corticosterone below which ibis may be chronically stressed with reduced ability to respond effectively to stressors. Levels of physiological parameters indicative of chronic stress have not been established and may not exist as discrete predictable points—instead, looking at changes in parameters within an individual after exposure to chronic stress may be best to determine the magnitude and direction of change (Dickens and Romero 2013). While recapturing free-living ibis is challenging, this would help elucidate those thresholds for this species. Additionally, HPA axis sensitivity has been documented to vary by individual and phenotype; therefore, ibis likely respond somewhat differently to the same environment. Some evidence suggests HPA axis responsiveness is developed early in life (i.e., maternal HPA responses, and early life exposure to stressors, can “program” the HPA axis), and varies by personality or coping style, which may also be developed in early life stages (Cyr and Romero 2007, Schoech et al. 2011, Cockrem 2013). Stress physiology may also be somewhat plastic, allowing some individuals to adjust in new environments, somewhat dependent on “personality” and phenotypic plasticity (more research is necessary regarding the persistence and adaptation of phenotypes) (Martin 2009, Ouyang et al. 2011, Schoech et al. 2011, Cockrem 2013). Behavioral tests (including exploratory behavior in novel areas) can reveal underlying personality differences, which have been linked to differences in HPA axis response. While we could not conduct similar tests under our field protocol, they would be valuable to better understand some unexplained variation in stress parameters.

The timing of the HPA axis response varies by species and has not been previously established for white ibis. Many avian species reach peak corticosterone circulation 15 or 30 minutes after the stress of capture (Atwell et al. 2012, Cockrem 2013). All ibis in our study mounted a stress response in which corticosterone levels increased during capture and handling; most ibis reached peak corticosterone levels at the 15-minute time point and experienced a subsequent decline by the 30-minute time point. One ibis with an extremely low response did reach corticosterone levels lower at 30 minutes than at capture; however, no other ibis had returned to baseline levels by the 30-minute time point. We were therefore unable to completely document the return to baseline in our animals or calculate the total amount of circulating corticosterone during the stress response. It is unsafe to hold ibis in a subtropical climate long enough to obtain samples after 30 minutes in the field. If ibis can be held safely past 60 minutes, or sampled in a climate-controlled facility or laboratory setting, it would be valuable to collect blood samples >30 minutes post-capture to document the time it takes ibis to return to baseline corticosterone levels and therefore better calculate the total amount of corticosterone released by each bird. It would also be valuable to conduct a standard challenge to look at corticosterone response and negative feedback function, and to assess changes in HPA axis sensitivity that may occur during chronic stress.

We found several significant relationships between our metrics of stress and immune function. Plasma corticosterone at 15 minutes related positively to baseline plasma corticosterone, demonstrating that birds with higher baseline circulating corticosterone had a higher corticosterone response. Ibis baseline and induced corticosterone related positively to H:L ratios, confirming previous findings with birds (Vleck et al. 2000, Davis 2005) that suggest increased release of heterophils into and redistribution of lymphocytes out of blood occurs in concert with corticosterone release in response to a stressor. H:L ratios respond more slowly to stressors than corticosterone (Vleck et al. 2000, Davis 2005), so they may be unchanged from baseline at our 15 minute time point. While it merits validation, H:L ratios obtained from blood collected >3 minutes post-capture may be sufficient to assess baseline stress when obtaining an initial blood sample is difficult. We found no relationship between fecal corticosterone metabolites and baseline or induced plasma corticosterone. Fecal samples integrate corticosterone released over a period of hours and as such may reflect multiple responses to stressors, while plasma corticosterone relates to the current stress state of the bird.

We did not observe significant changes in BKA over our three sampling periods, during 30 total minutes of capture and handling. We therefore primarily used BKA results from the 15-minute time point, but justified supplementing values from 30-minute samples when 15-minute samples were missing. We also did not see any individual relationships between stress and BKA for plasma or fecal corticosterone. Generally, studies of birds find no effect or a suppressive effect of corticosterone on BKA, depending on species (Matson et al. 2006). One study found enhanced BKA soon after capture and another found suppressed BKA after 30 minutes of handling (Millet et al. 2007); however, BKA suppression was not documented until 60 minutes after the stress of capture for some tropical bird species (Matson et al. 2006) and was not seen at all for red knots (Buehler et al. 2008). Ibis may not experience stress-related suppression of

BKA. Or perhaps we missed an initial increase prior to 15-minutes after capture, or did not detect a later suppression because we were unable to collect samples past 30 minutes.

BKA assesses one aspect of the innate immune system by determining the ability of plasma humoral components (i.e., complement proteins) to kill bacteria (Tieleman et al. 2005, Matson et al. 2006, Millet et al. 2007). However, innate immunity is multifaceted and employs numerous cell-mediated and humoral components to non-specifically target and kill pathogenic agents. Additionally, adaptive immunity employs numerous components to target and kill specific pathogenic agents (Downs and Stewart 2014). We could not hold birds long enough in the field to conduct assays of other immune components. However, assessment of components additional to BKA would be beneficial, as these components respond differently both to corticosterone and pathogen infection (Stier et al. 2009, Forsman et al. 2008). Multiple studies have shown that pathogen infection alters the interactions between stress and immune function (Brooks and Mateo 2013, Fratto et al. 2014, Hing et al. 2016). Girard et al. (2011) found lower BKA in birds with more chewing lice. However, Fratto et al. (2014) found that bacterial infection buffered stress-related suppression of innate immunity. One study found reduced BKA with parasitic and viral infections—while BKA is likely not involved directly in fighting such infections, perhaps energy is diverted from BKA and invested in the adaptive immune response. Some ibis in our study likely have current infection with or prior exposure to parasitic, viral, or bacterial agents, which may affect BKA. We chose to challenge ibis with a strain of non-pathogenic *E. coli* to which they would likely not have prior exposure. However, ibis innate immunity likely responds differently to pathogenic bacteria (as found by Millet et al. 2007), and other types of bacteria, so assessing innate immune response to other pathogens including those ibis are more likely to encounter (e.g., *Salmonella* spp.) would be valuable.

Brearley et al. (2013) suggested studying relationships between stress, immunity, and pathogen dynamics in the context of habitat fragmentation and change. Hing et al. (2016) assessed these relationships in a non-anthropogenic system, but highlight that anthropogenic factors can be stressors for wildlife and as such can alter and exacerbate infection and disease. We were not able to directly assess the relationship between stress, immunity, and infection in white ibis. However, urban ibis have a documented high prevalence of *Salmonella* spp. (Hernandez et al. 2016) as well as high prevalence of haemoparasite infection and antibodies to avian influenza virus and paramyxoviruses (Coker 2015, Hernandez unpublished data). Future research should strive to tie stress and immune function to pathogen prevalence in individuals, examining the factors that alter stress and immunity and therefore impact risk and intensity of infection and disease. Ibis respond to seasonal and anthropogenic shifts in prey availability related to hydrology, so multi-season and -year studies would better disentangle impacts of these fluctuations from impacts of urban habitat use on health. Because ibis have such variable habitat use, and the stressors present in urban areas may vary so widely at a fine scale, GPS tracking and more comprehensive quantification of stressors would likely help better explain variation in stress and immune function parameters. We were unable to capture ibis in wild habitats for this study, and an ongoing study reveals that the link between urban or wild capture site and habitat use is not always clear. However, a comparison between ibis that use primarily wild versus primarily urban habitats is critical to understanding whether urban habitat use is positive or negative for the species.

Prior studies established white ibis stress physiology in wild contexts, primarily in the breeding season. As it is inappropriate to compare results obtained with different laboratory methodology, we restricted our comparisons to two studies that followed the same assay protocols. Heath et al. (2003) determined corticosterone in wild adult ibis plasma through the breeding season, and Adams et al. (2009) quantified corticosterone metabolites in feces from wild-caught juvenile ibis raised in an aviary. While many of our baseline plasma values are in the range of those published by Heath et al. (2003), our maximum values and averages exceed the published values, and our highest value is more than three times the highest published value. Corticosterone has not been assessed in ibis after the breeding season, but for other species with similar breeding activity, corticosterone levels are highest during breeding (Kitaysky et al. 1999). Therefore our non-breeding values may be even higher comparatively. Many of our fecal corticosterone values are in the range of values published by Adams et al. (2009) (including for ibis exposed to methylmercury); however, we noted several extremely high values from our ibis captured in summer. We also found significantly higher overall fecal corticosterone in summer (corresponding to a time just after the breeding season) compared to winter (prior to the pre-breeding season), consistent with Adams et al.'s (2009) findings for control and high-mercury dosed ibis (but not low- and medium-dosed ibis) between July and December. Therefore, while corticosterone levels of some PBC ibis are similar to their counterparts in wild or captive settings, other PBC ibis release far more corticosterone, perhaps related to urban habitat use.

Ibis may be a good candidate for adaptation, given the success of the taxonomically related white ibis in urban Australian and sacred ibis in urban Europe

(Clergeau and Yesou 2006, Martin et al. 2011 and 2012). Ibis are food restricted, so if urban habitats offer predictable resources in times of scarcity in wetland habitats, the birds are likely to capitalize on them. Indeed we detected several ibis exclusively in urban habitats, suggesting these birds are quite reliant on such areas for food. Ibis may have the capacity to adapt, even to the point of experiencing changes to stress physiology that mitigate the negative impacts of corticosterone. However, different species, and even different individuals, react and adapt to environments and their stressors differently, and whether they become chronically stressed may vary considerably based on the situation and the individual personality and stress physiology (Martin et al. 2010, Cockrem 2013). While adaptation of some ibis may support the conclusion that urban habitats contribute to population success, some birds may not be able to adapt and may experience sublethal effects that influence their survival or reproductive fitness, ultimately affecting population success (Shochat 2004). Additionally, the negative impact of even a few increasingly stressed and immunocompromised birds could outweigh any benefits through risk that these individuals will more likely be infected with and transmit pathogens, both in urban areas and to naïve nestlings and possibly other species in the wild (Phalen et al. 2010), as ibis traverse the urban-wild interface and return to natural areas to breed (Ramos et al. 2010, Martin et al. 2010a, Hernandez et al. 2016). Often species of concern are not present or are present in lower numbers in urban areas, and it is critical for conservation to understand if these species may be able to adapt, but also if adapted species are at increased risk of pathogen transmission that outweighs benefits of urban habitat use. Therefore, we ultimately must identify birds that frequently use urban sites but have not adapted and reduced stress response, and may have moved into periods of repeated stress response and chronic stress with consequences for increased pathogen infection and transmission.

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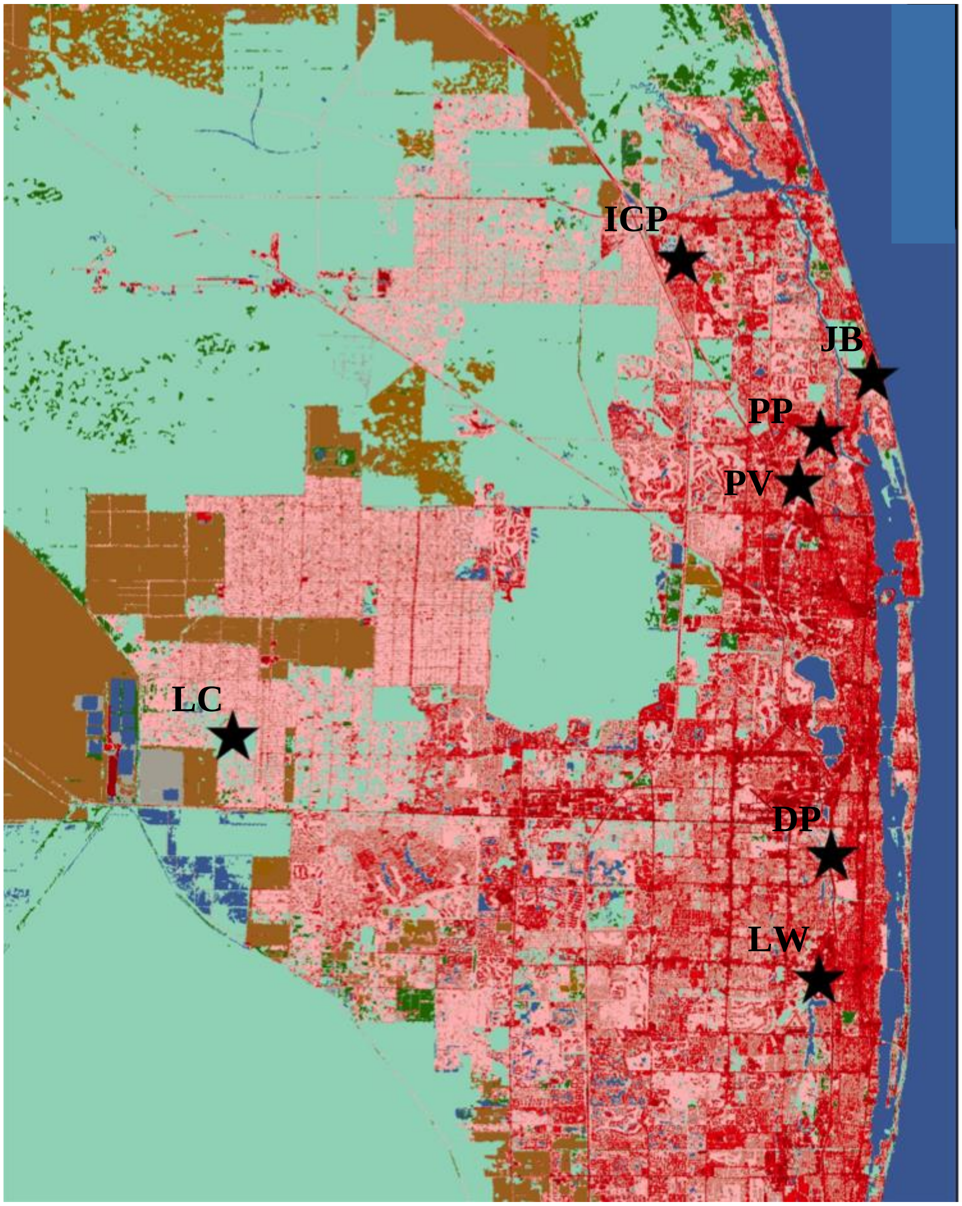

Figure 4.1. Map of Palm Beach County, Florida depicting white ibis capture site locations (stars), names (alpha codes), and surrounding land use (blue—water; green—freshwater wetland; brown—agricultural; pink to red—gradient of developed).

Table 4.1. Characteristics of seven white ibis capture sites (all sites located in Palm Beach County, Florida). [Dev—developed; Wet—freshwater wetland; Urb. Det.—urban detection]

Code	Name	Type	Dec. Degrees	%Dev.[1]	%Wet.[1]	Urb. Det.
DP	Dreher Park	Urban Park	N26.66440 W080.06952	93.92	0.00	47.67%
ICP	Indian Creek Park	Urban Park	N26.91688 W080.13370	87.95	0.72	44.49%
JB	Juno Beach (Pelican Lake)	Urban Park	N26.86768 W080.05270	44.02	2.56	23.27%
LC	Lion Country Safari	Zoological Park	N26.71398 W080.32359	61.2	4.51	56.15%
LW	Lake Worth (John Prince Park)	Urban Park	N26.60966 W080.07731	87.98	1.10	57.56%
PP	Promenade Plaza	Parking Lot and Apartment Complex	N26.82189 W080.08375	93.34	0	46.69%
PV	Prosperity Oaks Village	Retirement Home and Pond	N26.84317 W080.07451	83.77	1.58	42.10%

[1] Calculated at a 2-km radius surrounding the site

Table 4.2. Summary statistics of stress and immune function parameters for all ibis captured in PBC in 2013, including minimum (Min), maximum (Max), mean, standard deviation (SD), and sample size (N).

Parameter	Min	Max	Mean	± SD	N
PCORT-A (0–2 min.)	0.12	5.63	1.51	± 1.17	66
PCORT-B (15 min.–0 min.)	0.13	41.88	18.75	± 8.94	55
PCORT-C (30 min.–0 min.)	0	42.24	13.95	± 7.79	42
FCORT	0.25	26.50	2.34	± 3.64	75
BKA	0.00	0.88	0.4193	± 25.63	68
H:L Ratio	0.10	1.74	0.44	± 0.28	83

Table 4.3. Summary statistics of plasma corticosterone (PCORT; ng/mL) by capture site, including mean, standard deviation (SD) and sample size (N) for PCORT-A (baseline PCORT 0–2 minutes post-capture), PCORT-B (PCORT at 15 minutes post-capture minus PCORT-A), and PCORT-C (PCORT at 30 minutes post-capture minus PCORT-A).

	PCORT-A			**PCORT-B**			**PCORT-C**		
Site	**Mean**	**± SD**	**N**	**Mean**	**± SD**	**N**	**Mean**	**± SD**	**N**
DP	1.13	± 0.70	11	16.11	± 10.01	10	10.94	± 8.71	8
ICP	1.70	± 1.13	11	18.41	± 5.65	9	16.41	± 9.01	6
JB	1.96	± 1.32	10	23.33	± 10.82	9	15.31	± 7.04	6
LC	1.11	± 1.07	7	12.33	± 7.22	6	10.80	± 1.44	4
LW	1.48	± 1.15	10	23.30	± 11.79	8	16.95	± 12.79	6
PP	1.44	± 1.21	8	19.07	± 3.97	5	13.51	± 2.65	4
PV	1.69	± 1.62	9	17.31	± 5.82	8	13.66	± 5.93	8

Table 4.4. Summary statistics of fecal corticosterone (FCORT; µg/g), heterophil-to-lymphocyte ratios (H:L), and bactericidal capacity (BKA, %) by capture site, including mean, standard deviation (SD), and sample size (N).

	FCORT			**BKA**			**H:L**		
Site	**Mean**	**± SD**	**N**	**Mean**	**± SD**	**N**	**Mean**	**± SD**	**N**
DP	1.97	± 1.80	15	28.25	± 24.01	12	0.38	± 0.20	16
ICP	1.48	± 1.59	9	51.09	± 17.81	11	0.31	± 0.11	12
JB	1.97	± 1.77	14	42.82	± 25.02	11	0.48	± 0.28	13
LC	3.77	± 4.63	8	34.63	± 29.68	8	0.44	± 0.25	10
LW	3.17	± 7.09	13	47.23	± 28.14	13	0.61	± 0.43	14
PP	2.29	± 2.74	7	64.25	± 13.57	4	0.45	± 0.31	6
PV	1.98	± 2.25	9	36.78	± 26.96	9	0.37	± 0.20	12

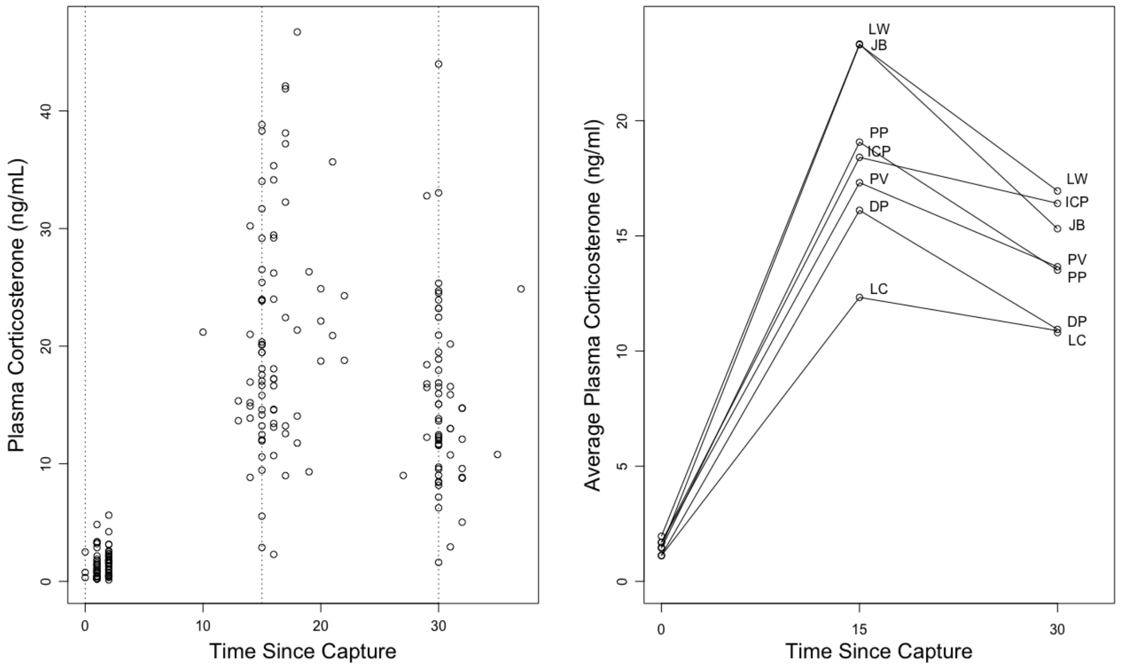

Figure 4.2. Left: White ibis plasma corticosterone at baseline (0–2 minutes) and during capture/handling (13–22 minutes and 27–37 minutes after capture). Right: Average white ibis plasma corticosterone by capture site at three time points (baseline, 15, and 30 minutes post-capture).

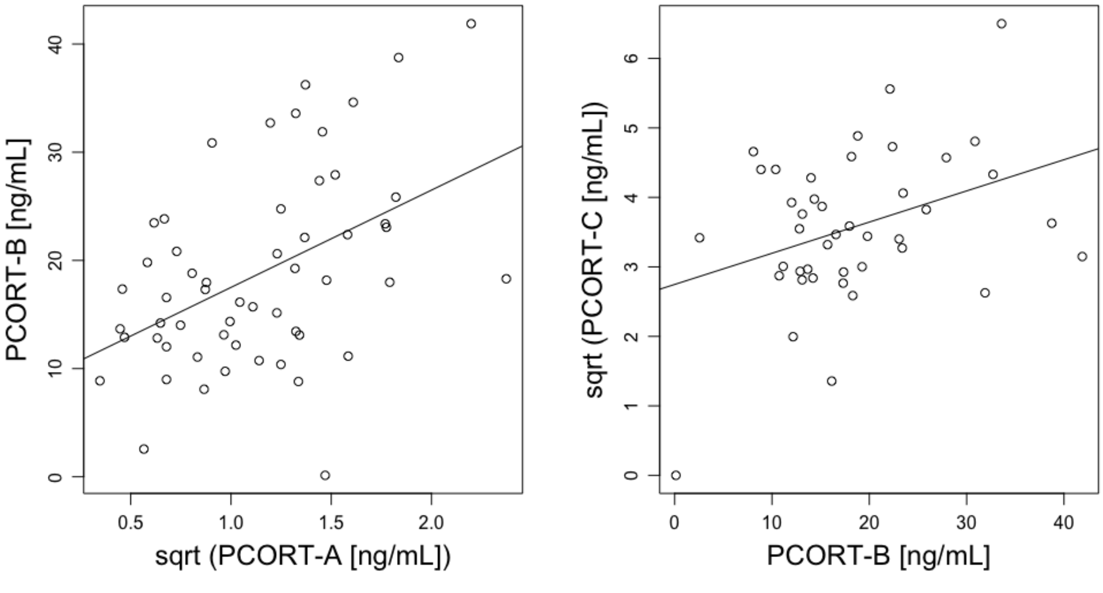

Figure 4.3. Left: White ibis with higher plasma corticosterone at capture (PCORT-A) have higher corticosterone 15 minutes post-capture (PCORT-B; R^2=0.22, p<0.01). Right: White ibis with higher plasma corticosterone 15 minutes post-capture (PCORT-B) have higher corticosterone 30 minutes post-capture (PCORT-C; R^2=0.22, p<0.01).

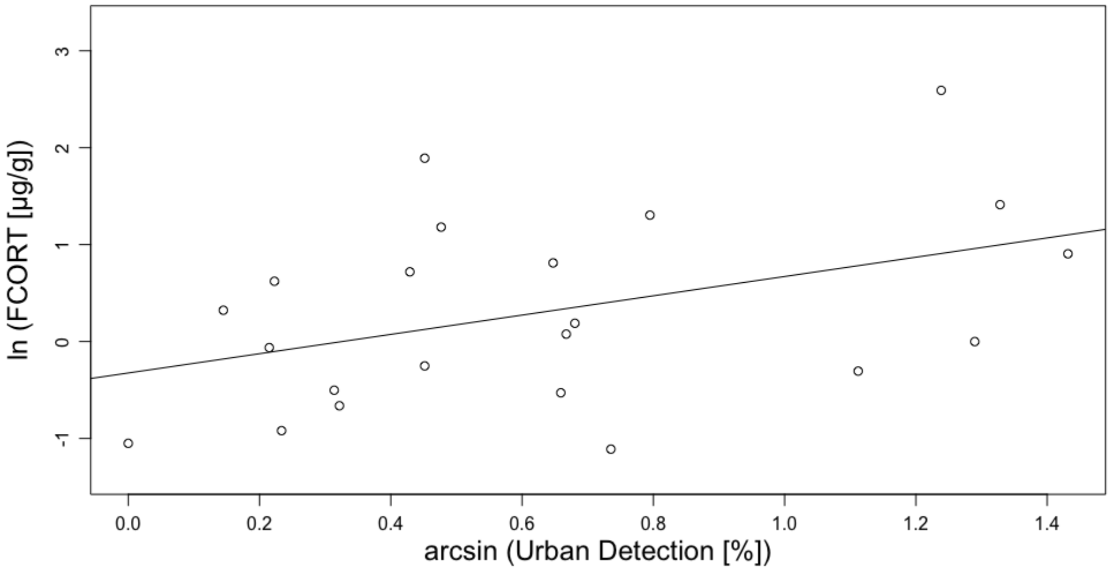

Figure 4.4. White ibis fecal corticosterone (FCORT) by percent urban detection, showing a significant positive relationship (R^2= 0.18, p<0.05).

CHAPTER 5

PUBLIC MOTIVATIONS FOR FEEDING BIRDS AT SOUTH FLORIDA URBAN PARKS AND IMPLICATIONS FOR DISEASE RISK COMMUNICATION[3]

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[3] Curry, S. E., Larson, L. L., Green, G. T., and Hernandez, S. M. To be submitted to *Landscape and Urban Planning*.

INTRODUCTION

Backyard bird feeding is a common activity worldwide (Jones and Reynolds 2008, Reynolds et al. 2017). Based on the 2011 census, 73% of households in the United States (U.S.) feed birds (USFWS 2011). Backyard bird feeding typically targets songbirds and related species and may benefit these birds in various ways, such as providing increased calories that may particularly improve survival during harsh winter months (see Amrhein et al. 2004 and Robb et al. 2008 for reviews of how supplemental feeding impacts birds). The activity is officially encouraged by some organizations (e.g., the Cornell Lab of Ornithology in the U.S.) and guidelines are published about how to practice feeding correctly (i.e., providing nutritious foods like seed mixtures or suet with calories, protein, and fat similar to what birds would normally consume) (Jones and Reynolds 2008, Robb et al. 2008). Despite documented benefits to feeding, there are some known drawbacks. These drawbacks include increased spread of certain pathogens related to the increased densities, contact rates, and contamination of surfaces at supplemental feeding stations (Robb et al. 2008, Reynolds et al. 2017). Some of these pathogens cause recognized feeder-associated diseases in birds—e.g., bacterial diseases like salmonellosis and conjunctivitis, which are transmitted via contact with contaminated saliva or feces (Bradley and Altizer 2007, Benskin et al. 2009, Lawson et al. 2014, Reynolds et al. 2017). However, increased caloric intake from supplemental food may boost immune function and reduce intensity of infection—in fact, supplemental feeding has been encouraged during some outbreaks.

The activity of feeding birds in public urban parks (which often include various domestic, peridomestic, and wild ducks, among other species) has not been adequately examined and is less studied than backyard bird feeding. However, this activity is common and likely impacts a considerable number of birds globally (though the practice is concentrated in certain areas), and may be an activity engaged in more than backyard feeding by families and people with less general interest in birds (Oost 2004, Chapman and Jones 2009, Reynolds et al. 2017). In practice, birds at backyard feeding stations may receive less-nutritious foods like bread—which is carbohydrate-rich and protein-poor (Rollinson et al. 2003, Galbraith et al. 2015), and birds fed in parks are often provided such foods (Chapman and Jones 2009, Hernandez et al. 2016). Consumption of foods inappropriate nutritionally may compromise immune function and increase risk of pathogen infection (Bradley and Altizer 2007). While altered prevalence of such diseases is often cited in reference to backyard bird feeding (Lawson et al. 2014), altered pathogen transmission also occurs at supplemental feeding areas in public parks (Epstein et al. 2007, Hernandez et al. 2016).

The activity of bird feeding also provides potential benefits and drawbacks for people. As the percentage of people living in urban and sub-urban areas increases, bird feeding and associated activities like watching birds may allow urban residents to better connect to nature and experience contact with wildlife (Jones and Reynolds 2008, Belaire et al. 2015, Reynolds et al. 2017). Belaire et al. (2015) found that urban residents overall valued birds in the neighborhood, but derived increased benefits when they perceived higher diversity of bird species. Dallimer et al. (2012) also found psychological benefits associated with perceived diversity of birds, and a recent study correlated increased afternoon bird song with lower levels of depression, anxiety, and stress (Cox et al. 2017). Several studies examined public motivations for backyard bird feeding, and found that people clearly derive personal benefits from the activity. However, their motivations for bird feeding can be plural, extensive, and sometimes complex. For example, Horvath and Roelans (1991) found that people fed birds primarily for personal motivation—including for aesthetic value and because birds appreciate the food, but also in part for entertainment and to share positive experiences with other people—but not as much from a sense of duty or to escape their problems. Ishigame and Baxter (2007) found some similar personal reasons for feeding birds, but also found charity-inspired motivations (such as to provide birds with more food). Galbraith et al. (2015) found that personal motivations were most common (e.g., for pleasure, to dispose of bread, to attract wildlife, and to a lesser extent to benefit children), but people also fed to benefit birds or ecosystems, and to atone or give back. Surprisingly few studies have quantified bird-feeding activity in urban parks (see Chapman and Jones 2009 for one example), and to our knowledge none have specifically assessed motivations for bird feeding in parks. A notable documented difference in bird feeding at parks is that it seems to be an overall more social activity (Oost 2004, Chapman and Jones 2009), and this suggests that motivations may differ, at least for some people.

The presence of birds in urban parks may therefore provide a unique opportunity for people who may not feed birds at home and may be less interested in birds overall to connect to nature and wildlife (which may be increasingly important in urban areas). Conversely, feeding birds in parks may create potential conflicts between birds and people. Soulsbury and White (2015) review ways in which urban wildlife conflict with people, including aggression, nuisance, property damage, and disease. These potential conflicts are relevant to urban birds—the Australian white ibis (*Threskiornis molucca*) provides an excellent example of a species that is perceived negatively in urban habitats because of noise, nuisance, aggression, and disease risk (Epstein et al. 2007, Martin et al. 2012). In general, birds at supplemental feeding areas exist in denser and larger aggregations than flocks in wildland areas (see Murray et al. 2015's meta-analysis). These birds can become habituated toward people, and associate people with food, leading to aggression. Additionally, birds in urban parks often contribute to mess through feces (Epstein et al. 2007, Hernandez et al. 2016), which was the most significant conflict urban residents surveyed by Belaire et al. (2015) experienced with birds—though the conflict was minor. Altered pathogen transmission dynamics in urban birds can increase risk for urban residents—indeed, human cases of salmonellosis have been linked to *Salmonella* spp. infection in both garden-feeding birds (Lawson et al. 2014) and birds supplemented at parks (Hernandez et al. 2016). Despite potential conflicts, some research has shown that positive experiences with wildlife and nature help insulate against development of negative public perceptions based on minor conflicts (Charles and Linklater 2015).

Attitudes toward wildlife, interest in birds, and motivations for feeding birds are all linked to the action of feeding birds. Therefore, understanding why people feed birds and how their knowledge, awareness, and interest correlates to the activity is important to promote co-existence, and to educate people of the impacts of bird feeding and potential disease transmission risk without compromising their support of urban wildlife. Particularly for wildlife encountering degradation and loss of their traditional habitat, urban areas may provide alternative habitat critical for population success. The "One Health" paradigm assumes that wildlife, human, and environmental health are intimately linked (Decker et al. 2010). Following this paradigm, public education that healthy wildlife equate to healthy environments and healthy people will encourage public behaviors that promote wildlife (and environmental and public) health—even among people who would not change their behavior solely to protect wildlife health. Absolute prohibition of feeding birds would reduce risks to avian and public health. However, it would also negate benefits to people from the activity, and remove a critical opportunity to promote conservation of wildlife and nature (Galbraith et al. 2015). And some research suggests that prohibition of bird feeding does not have much impact on the prevalence of the activity (Jones and Reynolds 2008). If people are positively motivated to feed birds—and interested in interacting with and learning more about birds—we may achieve stronger compliance and overall stewardship by improving rather than eliminating public interactions with wild birds. For example, managers could provide or encourage provision of more nutritionally appropriate foods, or suggest alternative ways to interact with birds that do not involve direct contact (e.g., bird watching). However, any message seeking to change public behavior—and particularly conveying the risk of pathogen transmission to the public—must be sensitive to public reception and seek not to unnecessarily frighten people, but to encourage realistic behavior change while maintaining public appreciation and support for urban wildlife (Decker et al. 2010).

Globally, wildlife not traditionally associated with urban environments increasingly use urban areas. This shift likely relates to increased and more predictable access to food resources compared to resources available in minimized or degraded native habitats (Evans et al. 2011). In South Florida, the assemblages of birds at urban parks often include doves, pigeons, and several other passerines, and both peridomestic and wild ducks and geese (Hernandez et al. 2016). However, recently various Everglades-associated wading bird species are regularly documented in urban areas. Some of these species are highly specialized (e.g. snail-consuming limpkin (*Aramus guarauna*). Others—notably the American white ibis (*Eudocimus albus*), but also the wood stork (*Mycteria americana*) and the black-crowned night-heron (*Nycticorax nycticorax*)—join flocks of ducks and accept, or even beg for, human handouts like bread (personal observation). The presence of these birds provides an ideal opportunity for city residents to see, think about, connect to, and presumably learn about surrounding natural environments, such as the Everglades, and hopefully appreciate the importance of urban spaces for wildlife conservation, including how this relates to proper feeding.

However, potential exists for conflict between people and birds at these parks. Ibis particularly visit urban parks in large aggregations, can be habituated and aggressive toward people, and generate considerable mess through deposition of feces on sidewalks and picnic tables (Hernandez et al. 2016, personal observation). Ibis have also been documented to carry pathogens of concern for other wildlife, domestic animal, and public health (e.g., *Salmonella* spp., avian influenza viruses; Epstein et al. 2007, Hernandez et al. 2016). Ibis and urban-associated species commonly fed in urban parks likely encounter these pathogens from foraging in contaminated urban landscapes (*Salmonella* spp.), and through contact with species that commonly carry certain pathogens (e.g., ducks and avian influenza virus). Therefore, the birds at South Florida urban parks do carry pathogens that can be transmitted to other birds, wildlife, domestic animals, and people—and the dynamics of transmission are certainly altered by supplemental feeding that brings birds to contaminated areas, leads to higher densities, and creates opportunities for inter-specific interactions. However, the threats to environmental, wildlife, and human health that exist could be mitigated through improved public behaviors with respect to supplemental feeding.

We established and compared the prevalence of bird-feeding activity at urban parks in South Florida. We also assessed the general self-reported levels of interest in and awareness of birds for all park visitors, and motivations for feeding birds at urban parks for people who engaged in the activity. Specifically, we characterized sub-groups of people who feed birds based on similarities in their motivations for feeding birds, and we compared these sub-groups to people who do not feed birds with respect to interest in birds, self-reported knowledge of birds, general value orientations toward birds and wildlife, and socio-demographic attributes. We also assessed if any of the sub-groups of people who feed birds would respond differently based on disease risk scenarios (i.e., would they stop feeding birds in the future if birds carry a disease that affects other birds, wildlife, domestic animals, or people). Finally, to better identify strategies for positively influencing behavior of people who feed birds in the future, we determined if general visitors and sub-groups of people who feed birds have different communication preferences (e.g., do some prefer to receive information about birds via the Internet more than brochures?).

METHODS

Study Area

This study was conducted at two urban parks in Palm Beach County, a highly developed county east of parts of the Everglades wetland ecosystem. Juno Beach or Pelican Lake Park (hereafter, “JB”) is a park with a small lake surrounded by a walking trail and green space along the trail. Indian Creek Park (hereafter, “ICP”) has a small pond and a playground, and green space with picnic tables and ball courts. These two parks were among seven sites at which we monitored urban white ibis diet, stress, immune function, and movement for a concurrent study. This research augmented the white ibis diet study to tie together public motivations for behaviors that likely influence ibis natural history. Therefore, we selected JB and ICP from the seven sites used in that study based on the presence of regular human visitors and frequent public bird feeding at both parks. The two sites differ in numbers of visitors, motivation for visiting the park, size of the ibis flock, and degree of bird feeding, most of which also differ by season. We previously documented a high prevalence of *Salmonella* spp. at both parks, suggesting pathogen transmission risk is elevated in birds at these sites, and likely between birds and people (particularly of concern for elderly and young with less-robust immune systems).

Survey

We developed an on-site survey from questions created specifically for this study and questions adapted from previously published studies (Horvath and Roelans 1991, Fulton et al. 1996), and conducted a pilot test of the survey at JB and ICP in winter 2012 (December 20–21). Following the pilot test, we used principle axis factoring to confirm that questions addressed underlying constructs, and we used Cronbach’s alpha to assess internal reliability of items for each construct. We removed questions that lowered overall alpha values or did not contribute to an overall alpha value of at least 0.7. We also removed and reworded several questions that were problematic for respondents during the pilot test. The final survey took approximately 10 minutes to complete and comprised seven primary categories, discussed below in the order they appeared in the survey.

The first three survey categories addressed bird feeding behaviors and motivations. One category used yes/no, closed-ended, and open-ended questions to evaluate participation in recreational activities, including bird feeding. Six of the questions in this category pertained to recreational activities at the park (number of visits to the park in past year, primary reason for park visit on the day of the survey, if they fed birds or not, how many birds they fed, if they brought children or not, and if the children fed birds). Two questions pertained to activities in general (if they keep a home bird feeder, and if they feed birds in general). A second category assessed motivations for feeding birds with six questions asked on a five-point likert scale, where 1= "Strongly Disagree" and 5= "Strongly Agree" (e.g., "I feed wild birds to be closer to nature"). Participants could check "I don't feed wild birds" as an alternate response. We later reduced these six questions to two categories: feeding birds for personal benefit (four items) and feeding birds for birds' benefit (two items). A third category assessed future bird-feeding behavior based on five disease risk scenarios, using five questions asked on a five-point likert scale, where 1= "Very Unlikely" and 5= "Very Likely" to stop feeding birds given the scenario (i.e., "I would stop feeding wild birds in the future if wild birds carry a disease that affects BLANK," in which the blank included "wild birds," "wild birds and other wildlife," "domestic animals," "people," or "wildlife, domestic animals, and people"). Participants could check "I don't feed wild birds" as an alternate response.

The fourth, fifth, and sixth survey categories addressed general interest in and knowledge of birds, orientations toward birds and wildlife, and preferred resources for seeking bird-related information. One category assessed interest in and knowledge of birds with eight questions on a five-point likert scale, where 1= "Strongly Disagree" and

5= “Strongly Agree” (e.g., “I intentionally watch wild birds,” “I know the species names of wild birds I see”). We later reduced these eight questions to two categories: interest in birds (two items) and knowledge of birds (six items). A second category used check-all questions to ask which of seven types of resources participants would use in the future to obtain more information about birds (brochure, signs at the park, email newsletter, Internet, workshop, field guide, or staff member at the park). A third category assessed value orientations toward wildlife using six questions on a five-point likert scale, where 1= “Strongly Disagree” and 5= “Strongly Agree” (e.g., “Birds should have similar rights to those of humans,” “I feel a strong connection to wildlife”). We later removed two items, and then reduced the remaining four items to two categories: belief in wildlife rights (two items) and connection to wildlife (two items).

The seventh category included six closed- and open-ended questions pertaining to socio-demographic characteristics, including census-type questions (gender, age, highest completed level of education, total household income before taxes, and state plus zip code of primary residence) as well as questions specific to the study site (residence status in South Florida [non-resident, seasonal, or year-round] and number of years residing in South Florida). Independently of the survey, we collected anecdotal data pertinent to bird feeding at the park by recording comments made by participants to the researcher regarding bird feeding.

Data Collection

We administered the survey at JB in summer 2013 (July 10–30) and winter 2013 (December 9–21) and at ICP in summer 2015 (July 8–14) and winter 2015 (December 17–22). These sampling periods accounted for season shifts in residency in South Florida and were also timed to coincide with sampling for the concurrent white ibis study. To control for possible differences in park visitation throughout the day and between weekdays and weekends, we stratified available sampling dates by dividing days into weekday and weekend groups, and dividing daylight hours into three blocks (morning, afternoon, and evening). We then selected sampling sessions randomly from all possible blocks, with sessions for weekday and weekend days selected separately. During each stratified-random sampling session, we approached every other adult visitor (at least 18 years old) present at the park. We allowed participants to complete the survey on their own, or respond to the questions as read by the researcher. Multiple entry points exist at JB, but use of the park is restricted to areas around a circular walking trail. Therefore, we walked along the trail and intercepted every other person we encountered. One entrance is primarily used at ICP; therefore, we approached visitors as they arrived and asked them to return the survey when they left as an exit survey. We were also able to see and approach the smaller number of visitors that arrived from other areas to ICP. We did not approach anyone wearing headphones, talking on the phone, biking, or running, as we considered these visitors unavailable and therefore not part of the study population. All participants consented to the research prior to completing the survey, and all procedures were approved by the University of Georgia's Institutional Review Board (IRB Project # 2013-10432-0).

Statistical Analysis

We used principle axis factoring to reduce questions with multiple items to meaningful categories (as described above). We retained all factors with eigenvalues of at least 1.0 and retained all items with factor loadings of at least 0.4 following oblique rotation. We assessed internal reliability of these categories with Cronbach's alpha (>2 items; items with alpha >0.7 retained) or Spearman's rho (2 or fewer items) (see Appendix A, Tables A.1–A.4 for scores). We used a two-step cluster analysis with log-likelihood and Bayesian Information Criterion, as per Sharp et al. (2011) and Larson et al. (2016) to identify types of feeders based on similar responses to bird-feeding motivational statements (collapsed from a five- to three-point scale).

We calculated the average scores across the items in four reduced factors (interest in birds, knowledge of birds, belief in wildlife rights, and connection to wildlife). We used these averages plus questions about bird feeding activity and socio-demographic variables to compare between people who did and did not feed birds, and across motivational clusters, with Chi Square tests, Welch's *t*-tests and analysis of variance (ANOVA), with Bonferroni corrections for multiple comparisons. We report results as percentages or means ± standard deviation, and note significant relationships at an alpha level of 0.05. We completed all statistical analyses in SPSS (IBM v. 24).

RESULTS

Characteristics of Park Visitors

We surveyed 352 visitors to JB (2013, n=171) and ICP (2015, n=181) in summer (n=206) and winter (n=146) seasons, with a 66.49% response rate (JB=61.73% and ICP=73.86%). Visitors were primarily female (60.29%), older (18–89, mean 46.45±16.26), well-educated (73.3% with at least a college degree), affluent (40.2% made > $75,000), and most were year-round residents (84.3%). Visitors at ICP compared to JB were younger (t (311.94) = 10.45, p<0.001), had lower incomes (χ^2 (4) = 10.91, p=0.028), were more likely year-round residents (χ^2 (2) = 18.31, p<0.001), and were more likely to have visited with children on the day of the survey (χ^2 (1) = 19.77, p<0.001). We did not find any other significant differences between socio-demographic variables by season or park.

Bird Feeding at the Parks

Overall, 59.66% of visitors (n=210) fed birds in general, and 31.25% (n=110) fed birds during their park visit on the day of the survey. Fewer visitors came to the park primarily to feed birds (18.5%, n=37/200). At the time of the survey, 26.88% of park visitors maintained a home bird feeder (n=93/346). More visitors to ICP feed birds in general than visitors to JB (χ^2 (1) = 17.12, p<0.001).

Characteristics of Bird-Feeding Visitors

Visitors who fed birds were overall younger (*t* (344) = -2.40, p=0.017), had not completed as high a degree of education (χ^2 (2) = 7.51, p=0.023), and had lower incomes (χ^2 (5) = 11.37, p=0.044). Visitors who fed birds did not differ from visitors who did not feed birds in any other socio-demographic variables. Visitors who fed birds more often visited the park on the day of the survey with children (χ^2 (1) = 19.77, p<0.001) and had a lower number of visits to the park over the past year than visitors who did not feed birds (Welch's *t* (179.7) = 3.60, p<0.001). Visitors who fed birds more likely maintained a bird feeder at their residence (χ^2 (1) = 12.18, p<0.001), had higher levels of interest in birds (Welch's *t* (252.27) = -2.11, p=0.036), and more strongly agreed that birds and wildlife should have rights equal to humans (*t* (343) = -2.37, p=0.018).

Motivations for Feeding Birds

Two-step cluster analysis based on participant responses to bird-feeding motivational questions (n=200) identified three groups of visitors with similar motivations for bird feeding. These clusters correspond to visitors who (1) overall enjoy feeding birds but feed more for personal reasons than to help birds [hereafter, "Enthusiasts," n=71], (2) overall enjoy feeding birds but feed more because birds need food [hereafter, "Stewards," n=60], and (3) do not enjoy feeding birds as highly and feed more for personal reasons than to help birds [hereafter, "Passives," n=69]. We included visitors who do not feed birds as a fourth group for comparisons [hereafter, "Non-feeders," n=141]. Table 3 summarizes motivations across the three clusters.

Stewards had lower educational levels than Enthusiasts, Passives, and Non-feeders (χ^2 (6) = 17.54, p=0.007), but no other socio-demographic variables were significant predictors of cluster membership. Stewards and Enthusiasts were more likely than Passives to have fed birds during their visit on the day of the survey (χ^2 (3) = 87.25, p<0.001), and Stewards had most likely visited the park on the day of the survey primarily to feed birds (χ^2 (3) = 42.63, p<0.001). Stewards and Enthusiasts were more likely to maintain a bird feeder at their residence than Passives, but all bird feeder groups were more likely to have a home feeder than Non-feeders (χ^2 (3) = 12.87, p=0.005). Non-feeders had the highest number of visits to the park in the past year, and Passives had the lowest (F (3,159.27) = 7.42, p<0.001). All groups more likely visited the park on the day of the survey with children compared to Non-feeders, but Enthusiasts and Passives were most likely to visit with children (χ^2 (3) = 18.35, p<0.001).

Stewards and Enthusiasts had the highest interest in birds (F (3,330) = 7.04, p<0.001) and self-reported knowledge of birds (F (3,331) = 2.97, p=0.032), followed by Non-feeders, with Passives having the lowest interest and self-reported knowledge. Stewards and Enthusiasts had the highest beliefs in bird and wildlife rights, followed by

Passives, all of which were higher than Non-feeders ($F(3,332) = 5.07$, $p=0.002$). Non-feeders had the highest connection to birds and wildlife, and Enthusiasts had the lowest ($F(3,332) = 8.97$, $p<0.001$).

Disease Risk and Communication Preferences

Most visitors said they would likely or very likely stop feeding birds if they carried disease, whether that was disease transmissible to other birds (70.7% likely or very likely), birds and other wildlife (72.6% likely or very likely), domestic animals (76.1% likely or very likely), people (82.3% likely or very likely), or wildlife, domestic animals, and people together (81.9% likely or very likely). However, significantly more Stewards said they were “very unlikely” and significantly more Enthusiasts said they were “unlikely” to stop feeding if disease was transmissible to domestic animals ($\chi^2(8) = 19.26$, $p=0.014$) or people ($\chi^2(8) = 21.38$, $p=0.006$). Overall, Passives were most likely to stop feeding birds, followed by Enthusiasts and then Stewards.

Visitors would most likely use the Internet (60.5%), signs at the park (44.8%), or brochures (40.5%) to obtain more information about birds. Fewer visitors would use a staff member at the site (31.0%) or a field guide (29.5%). Very few visitors would take advantage of a workshop (11.0%) or email newsletter (8.6%). Preferred communication resources did not differ significantly between visitors who in general did or did not feed birds. However, among sub-groups of visitors who fed birds, Enthusiasts would most likely use brochures ($\chi^2(2) = 17.44$, $p=0.024$) and Passives would least likely use a field guide ($\chi^2(2) = 6.38$, $p=0.041$). See Figure 5.2 for percentages of each sub-group that would use each resource type.

Qualitative Results

Some visitors expressed uncertainty about the rules for feeding birds at the park, if feeding birds is okay in general, and if bread is unhealthy to feed birds (21 people, or 10% of the people who feed birds). Other visitors were more certain about the impacts of feeding and told us they do not feed birds because of this, citing reasons including negative effects on bird health, that birds will become dependent on supplemented food, increased aggression in birds that are fed, and that the numbers of birds increase and birds begin to follow people begging for food. In between these groups, some visitors like to feed birds when they know what to feed them, but sometimes are unsure about appropriate foods. Several of these visitors expressed desire for better information on what to feed birds. Some visitors who do not feed birds bread described what they feed instead (including sprout bread with peanuts, corn, “scratch,” and popcorn).

Several visitors told us why they no longer feed birds. Multiple visitors know now that feeding birds is bad, so either they no longer feed, or they feed squirrels or fish instead. Other visitors expressed concern about aggression from the birds at the park. Some of these visitors were never bird feeders, but others stopped feeding birds after they or their children were chased or bit by the birds. A few of these visitors asked if our research would help get bird feeding stopped at the park.

Other visitors expressed why they value bird feeding beyond the motivations addressed in the survey. One visitor sometimes gives birds the food they are eating themselves, as the birds deserve some of what they have. One visitor feeds birds only after it rains, when they need food more and beg for it. Another visitor feeds primarily to dispose of stale bread. One visitor commented that so many people feed birds old, even moldy, bread—instead, this person buys fresh bread every time they feed birds, expressing that if a person will not eat the bread, why should the birds eat it? Another visitor feeds in part because they believe we are all part of a system like the human body, and if any part of the system stops working, all parts suffer. Several visitors expressed that they do not generally feed birds, but on occasion feed with their children or grandhildren. Others do not feed in South Florida but feed birds at a seasonal residence elsewhere, or in places where they feel birds more need the food.

DISCUSSION

Our research differed from other studies that only addressed the behavior of and motivations for bird feeding activity in backyards or private gardens (Horvath and Roelans 1991, Ishigame and Baxter 2007, Cox and Gaston 2016), or at wildland parks (Oost 2004). We conducted this research at urban parks, and while we asked if participants maintained a home bird feeder, we specified that visitors should answer survey questions about birds considering those birds present at the public park where the survey was completed. At both JB and ICP, such birds primarily included ducks, grackles, gulls (in the winter), and white ibis. We quantified bird feeding in summer and winter of 2013 at JB, and summer and winter of 2015 at ICP. As we followed the same procedures at both parks in our sampling design (similar dates, stratified random sampling across times of day and days of week), we feel confident in our comparison of the rates of feeding across parks. We documented a higher prevalence of bird feeding at ICP than at JB. More visitors to ICP came to the park to use the playground, and more visitors to JB came to exercise, so perhaps ICP is more common as a location for bird feeding. The flock of birds is also larger at ICP. Because more people that feed birds visit the parks with children, it may also be that with more children visiting ICP, more bird feeding also occurs. Overall, we likely underestimated the prevalence of bird feeding, suggesting the activity is quite prevalent and may be on par with estimates of backyard bird feeding in the U.S. (73%, USFWS 2011) as well as the United Kingdom and Australia (likely at least 50%, Reynolds et al. 2017).

Characteristics of Bird-Feeding Visitors

Visitors who fed birds in general had lower levels of education, lower income, and were younger in age. This contrasts to findings of studies with people who feed birds in their backyard, who are predominantly female and older (Bjerke and Ostdahl 2004, Lepczyk et al. 2004, Galbraith et al. 2015). Perhaps these differences relate to increased bird feeding at parks by younger people in family groups. Among all visitors, those that feed birds have greater self-reported interest in birds and belief that birds and wildlife should have similar rights to those of humans. Visitors also more likely have a bird feeder at their residence—though many respondents anecdotally stated they would like to have a home feeder but live in a building where that is not allowed, which likely confounds fully demonstrating the relationship between the behaviors of home bird feeding and bird feeding in parks. The people who feed birds do not have a similarly higher level of self-reported knowledge of birds. However, we may be able to capitalize on their interest to address knowledge gaps, and encourage them to engage in more conservation-minded behaviors (e.g., feeding birds better foods, or watching instead of feeding birds). Cox and Gaston (2015) showed that increased knowledge of species names enhanced the benefits for people of interacting with birds, so improving the knowledge of people who feed birds may similarly increase the benefit they gain from watching and feeding birds. An important future research question is whether younger people more likely feed birds at these parks, or whether people generally feed birds in parks less often as they age. An additional question is whether later attainment of higher education or increased income leads to reduction in bird feeding behavior. Gabraith et al. (2014) also highlighted these questions as pertinent to the results of their investigation of backyard bird feeding. Lin et al. (2014) found that a nature orientation was the strongest predictor of both time spent outside in a yard and visits to urban parks, so the people present at parks may be those already somewhat inclined toward visits. This may suggest most people feeding birds are of this subset; however, we observe some odd behaviors including people who drive into the parks, dump food, and leave—these people do not visit for the park but come specifically to feed birds. Overall, we feel this may demonstrate some differences in the people who feed birds at parks versus those that feed in backyards, and research should continue to address the gap of knowledge about this subset of bird feeders.

We did not ask questions to understand if people had past trauma or dislike of birds that might impact their interest, perceptions, and activities. Based on conversations with visitors, some in general are not interested in or do not like birds. However, some stopped feeding birds or developed a dislike of birds based on a past experience of conflict with birds. For instance, several visitors used to feed birds at the park with their children, but they stopped after the birds either chased or tried to bite their child. These negative interactions are concerning, because provisioning of food leads to increasingly habituated and food-driven birds at these parks, with aggressive behaviors and lower avoidance of people. If the activity by which people connect to birds ultimately changes their interaction with birds and removes their support of birds, then we should encourage another activity that preserves positive interactions and support. However, many visitors may have the same experiences but do not grow to dislike or cease feeding the birds.

Motivations for Feeding Birds

We asked visitors if they agreed with six statements regarding their motivations for bird feeding. Overall, these statements aligned with two general categories: feeding birds for personal reasons (i.e., relaxation, entertainment, connection to nature) and feeding to benefit birds (because birds need food, and to help the environment). These categories are consistent with several other studies of motivations for backyard feeding, including that more people in our study fed for personal reasons than to benefit birds. Our six closed-ended questions regarding motivations for bird feeding were developed based on the range of common responses provided during our pilot test to an open-ended question about why respondents feed birds. This closed-ended format was best for our context, which relied on short-duration intercept surveys. However, some people struggled to articulate why they feed and had reasons outside of these six motivations. Other studies have used open-ended questions, but they may not be sufficient to truly understand the range of motivations for bird feeding. Employing a different method such as longer interviews specifically with bird feeders may be effective to get a more complete sense of overall motivations, particularly as some lay outside of the more commonly cited ones. However, using the set categories for our survey allowed us to look at broad differences in general motivations of bird feeders. Respondents clustered into three overall groups based on these broad motivations for feeding birds, which we called “Enthusiast,” “Stewardship,” and “Passive” feeders.

Enthusiast and Stewardship feeders had similarly high levels of interest in, connection to, and attitudes toward birds compared with Passives feeders and non-feeders. Both groups overall enjoyed feeding birds, but Enthusiasts fed slightly more for personal reasons than to benefit birds, while Stewards more highly agreed that they feed birds because birds need food. Passive feeders did not as highly enjoy feeding birds for any reasons compared to Enthusiasts and Stewards. Passives fed birds primarily for personal reasons including entertainment and connection to nature, and not to benefit birds.

We did not ask if people were motivated to feed birds because of children, but we did ask if they visited the park that day with children, and if those children fed birds. In general, people who fed birds at parks visited more often with children than people who did not feed birds. Passive feeders most likely brought children, who most likely fed birds. So these visitors may more than the other groups feed birds to benefit children, but may not personally be as interested in birds or benefit as much from the activity. While we did not ask on the survey, multiple visitors commented once they completed the survey that they only fed birds at parks for their children's or grandchildren's benefit. Perhaps more bird feeding with children occurs in parks than in backyards. Galbraith found only a small percentage of people that fed in backyards for the benefit of children. But Oost (2004) found that most feeding in public places took place in groups or families. Moore et al. (1997) as cited by Oost (2004) found a lesser motivation of feeding for children's benefit or education. During our pilot test, one respondent said they feed birds “to entertain the kids,” so this motivation as well as the desire to educate children may be an important reason why some visitors to JB and ICP feed birds.

Some visitors may be interested in birds and act from ideals of stewardship, but may either not feed birds, or may not feed birds for the reasons that aligned with the Stewardship feeder group in our study. Some park visitors were quite interested in birds, including engaging in regular bird watching, but they do not feed birds, only feed birds at home, or no longer feed birds because they have learned the activity can have negative consequences for birds. Many visitors expressed uncertainty about whether bird feeding actually helps the environment, and some anecdotally told us they did not think the birds present at the park where they completed the survey needed food. However, one person said they generally do not feed birds, but they do at the park where they completed the survey because the birds there are essentially domesticated and therefore reliant on supplemental food. Therefore, some people may feed birds to help them or atone for human environmental damage, but their motivations may not have aligned with our questions, so they may not have been identified as Stewardship feeders.

Some visitors who do not feed birds told us they do not think feeding is good for the birds in general, or specifically in this context. These people may be interested in birds generally, and invested in helping birds and concerned for their welfare, but they do not see bird feeding as a way to help birds. Interestingly, their motivations for not feeding birds may be similar to the motivations Stewardship feeders have for feeding—and some of the Stewardship feeders were adamant that these birds needed food. Asking if people fed birds in the past, or why they do not feed birds might better identify overall concern for birds and help us better reach the needs of people who are interested in helping birds and both feed and do not feed birds. Ishigame and Baxter (2007) asked this question, and they found that more people do not feed birds for welfare issues than from lack of interest. If this prevalence is similar at JB and ICP, then we may have a large pool of people who are interested in birds and willing to engage in more conservation-minded actions, but who will not be reached with messaging targeted only at bird feeders. Leite et al. (2011) found that while few visitors to a Brazilian urban park fed marmosets, many thought the animals were starving and would support supplemental feeding by management. Perhaps the people who are concerned that birds at our parks need food would be content if managers provided food, which would allow more appropriate types and quantities of feeding.

Disease Risk and Communication Preferences

We found differences in how different types of bird feeders would respond to disease risk in the future, and in the communication preferences of the different bird feeders groups and non-feeders. Most visitors that feed birds would likely or very likely stop feeding given any risk of disease transmission; however, some visitors would not stop. One person even said anecdotally they would continue feeding if they were told they had to stop. Stewardship feeders were least likely to stop feeding overall, particularly for a disease that only affected other birds, other wildlife, or domestic animals, rather than people and all groups. Enthusiast feeders were less likely to stop feeding than Passive feeders, but did not have as substantial a divide based on the type of disease. We do not know why some Stewardship feeders were less likely to stop feeding. Regardless, we need to better communicate to them that feeding birds can increase the risk of disease for birds. If these visitors are motivated by a desire to help birds, then they should change their behavior in ways that would actually benefit birds—including by altering or ceasing their engagement in supplemental feeding. Interviewing these types of bird feeders might be necessary to know if they would continue to feed because they think feeding is important to keep birds healthy, or just because they personally value the activity. There are also instances in which feeding during disease outbreaks can help birds, so we need to better communicate that the value of the activity depends on the context. Interviews may also help us build understanding of the mental process for visitors between enjoying bird feeding and changing behavior to benefit birds.

We also found differences in the preferred resources for communication, which is critical in framing and disseminating educational messages. Stewards were least likely to stop feeding given risk of disease, and are less likely to seek additional information or use educational resources than some other groups. However, Stewards would use the Internet at a similar rate to other groups (61%); therefore this may be the best means of communication with this critical group. Enthusiast feeders are also less likely than Passives to stop feeding if they learn of disease risk; however, Enthusiasts are most likely to use several different resources and so may be easier to reach with education in the form of brochures, signs, and websites. Passives are least likely to use most resources, even compared to Non-feeders; however, they would most likely use signs at the park or the Internet. Implementing management and education may be problematic with Stewards, who have higher levels of interest but less often seek more information, and Passives who have low levels of interest and less often seek more information.

Many visitors may not understand the links between supplementary feeding and bird health, and Stewards and Passives may not take advantage of or benefit from education to explain these links, and may therefore be less compliant with management actions. Many visitors were curious and inquired after completing the survey about whether bird feeding is good for birds, and especially if bread is bad for birds. Galbraith et al. (2015) found a similar lack of knowledge regarding whether supplemental feeding is good or bad for birds. We believe messaging—especially through educational signs, brochures, or websites, based on our survey results—would help these people obtain better information. Motivational clusters do not concentrate at either JB or ICP; therefore, both parks will require implementation of mixed-media messaging, but can likely receive the same combinations of educational materials. Since we found variation in the likely use of resources by different groups of people, hopefully the implementation of messaging using a mixture of media types at both parks will improve effectiveness of educational outreach (e.g., pertaining to future disease risk, how to mitigate conflict with birds, and best-practice bird feeding). However, any interventions should be accompanied with experimental evaluation, to ensure that they actually reach people and help either affirm or establish improved behaviors. Mallick and Driessen (2003) found that signage about feeding at national parks in Tasmania was effective in that it minimally changed minds, but more often reinforced existing beliefs. However, Oost (2004) saw continued active wildlife feeding in national parks alongside signs that banned feeding. More appropriate to supplemental feeding in urban areas, Clark et al. (2015) experimented with placing signs in parking lots regarding feeding gulls, and found that the addition of signs changed some but not all people’s behavior, and this behavior change was not enough to significantly reduce the numbers of gulls present. Based on these mixed findings, signs at our parks may be effective, but we should quantify the effects. If we reduce bird feeding among some people but the behavior continues among others, the reduction may not be enough to mitigate negative impacts. We also worry about removing the opportunity through bird feeding for people to learn about and connect to wildlife and nature, and establish or reinforce positive views of urban wildlife. Perhaps bird feeding at urban parks in South Florida provides a unique opportunity to use an iconic wetland species (e.g., white ibis) as a vehicle to educate urban residents about the Everglades and conservation (Charles and Linklater 2015). Ultimately, our goal is to improve public understanding of how changes in their current bird-feeding behavior may help preserve avian and public health. We also seek to reach non-feeders with messages, as they may be interested in birds, but also are at risk from disease or conflict related to birds.

General Conclusions

The idea of pathogen transmission—particularly that bird feeding can alter risk of pathogen transmission even solely among wildlife—is likely complex for the general public. With limited time and space (we would not have been successful implementing a longer survey in this context), we could not ask more, and we hesitated to be too explicit lest we introduce the idea that birds are a public health risk (while birds do present varying degrees of risk, we did not want people without full understanding to inflate the risk) without having adequate means to then provide education that would ensure people realistically understood the risk. We also did not directly address future behavior change, and the actual likelihood that people would stop feeding birds may differ from their self-report of possible future behavior. However, understanding future behavior as it relates to perception of risk is important in this context and is a valuable future area of research. For instance, Decker et al. (2010) discuss disease risk perception among the general public, and highlight how easily we can lose public support for management and wildlife conservation based on perceptions of public health risk from wildlife. Unlike some studies (e.g., Needham et al. 2004), we did not ask about public knowledge of avian pathogen prevalence and disease risk. So we may not have captured the nuance between people who would or would not stop an activity they enjoy if it was harmful to avian health, and people who will likely lose all support for urban wildlife if they perceive them as a threat. We are very interested in both of these groups, which have enormous roles in urban wildlife conservation and the trajectory of management and policy. While our research of *Salmonella* spp. and other pathogen transmission is with white ibis specifically, the issue of altered pathogen transmission between wildlife and to people also encompasses other species. Other wetland species currently forage at South Florida urban parks and consume bread from people, including wood storks and black crowned night herons. Even among assemblages of ducks more typical of urban parks, risk of pathogen transmission still exists among birds and to people. This is a risk for any urban-associated bird, as they likely are infected from contaminated environments and are vehicles for transmission. *Salmonella* spp. infection occurs from contact with saliva or feces, and at parks people can be easily exposed to such pathogens through contact with birds' feces left on picnic tables, railings, and other surfaces. The risk of serious infection from *Salmonella* spp. is significant for children and older people with less-developed or suppressed immune systems—two groups that commonly engage in bird feeding. Passive feeders more than the other groups included people who least enjoy feeding birds, and who more often visited the park with children, who may be more susceptible.

The presence of wading birds including white ibis at urban South Florida parks offers a unique opportunity for people to see, interact with, and learn about a wetland bird. This opportunity may be a vehicle to educate people regarding the importance of and conservation concerns related to the Florida Everglades ecosystem. However, to capitalize on this opportunity for conservation education, we must ensure that urban South Florida residents do not begin to view ibis as pests. As a contrast, the Australian white ibis is now managed as a pest and largely not tolerated by urban residents, which makes conservation education with the species more challenging. To avoid this situation with American ibis, we must maintain a positive relationship in which the birds do not create undue mess, noise, aggression, and pathogen risk (which may require minimizing bird feeding, regulating what is fed, or even banning feeding at some parks). Currently, official stances on bird feeding differ by country and are not always clearly expressed to the public (Jones and Reynolds 2008). This inconsistency likely contributes to public confusion regarding whether bird feeding is appropriate. Signs are appearing at urban parks across the U.S. banning feeding, or banning feeding of foods like bread, crackers, or popcorn. While these signs may be effective in changing some local behavior, official regulations on bird feeding may be the best way to obtain compliance and ensure educational messages are consistent for the public. Additionally, education should be based on science. Ishigame and Baxter (2007) found a lack of basic knowledge among bird feeders in their study of the effects of feeding on birds, and the authors expect that feeding will continue as-is unless the people feeding birds are able to obtain information grounded in scientific study. Amrhein et al. (2014) noted that most research on supplemental feeding does not specifically address urban birds. Garden experiments would help to establish knowledge that answers for the public the questions of “if, ” “when,” and “for how long” to feed wild birds. While outreach efforts based on scientific evidence may improve public knowledge and increase conservation ethics, this should be established through research, as the links between public interest in birds, bird feeding, and actual conservation ethic are unclear (Jones and Reynolds 2008).

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Table 5.1. Characteristics of visitors who did (**feeder**) and did not (**non-feeder**) feed birds in general, showing mean (µ) or percentage and results of significance tests of differences between feeders and non-feeders (Chi Square or Welch's *t*-test).

Variable	**Non-feeder**	**Feeder**	**Significance**
Interest in birds (*µ*)[a]	3.23	3.48	$t_{252.27}$= -2.11, p=0.036*[b]
Knowledge of birds (*µ*)[a]	2.80	2.91	$t_{257.65}$= -0.89, p=0.374[b]
Belief in wildlife rights (*µ*)[a]	2.98	3.25	t_{343}= -2.37, p=0.018*
Connection to wildlife (*µ*)[a]	3.31	3.40	t_{343}= -.77, p=0.445
Park (*ICP*)	37.9%	60.4%	χ^2 (1) = 17.12, p<0.001*
Season (*summer*)	56.4%	59.9%	χ^2 (1) = 0.42, p=0.517
Number of visits (*µ*)	102.85	40.54	$t_{179.70}$=3.60, p<0.001*[b]
Has home feeder (*yes*)	16.7%	33.7%	χ^2 (1) = 12.18, p<0.001*
Brought children (*yes*)	38.60%	62.70%	χ^2 (1) = 19.77, p<0.001*

[a] Averages across factor, from a scale where 1=Strongly Disagree and 5=Strongly Agree

[b] Corrected for unequal variance

*Denotes significance at α=0.05 with Chi Square test or Welch's *t*-test

Table 5.2. Socio-demographic variables of visitors who did (**feeder**) and did not (**non-feeder**) feed birds in general, showing mean (µ) or percentage and results of significance tests of differences between feeders and non-feeders (Chi Square or Welch's *t*-test).

Variable	**Non-feeder**	**Feeder**	**Significance**
Gender (*female*)	60.4%	64.5%	χ^2 (1) = 0.58, p=0.45
Age (*µ*)	49.02	44.77	t_{344}=2.40, p=0.017*
Highest education (*postgrad*)	30.4%	21.0%	χ^2 (2) = 7.51, p=0.023*
Income (*>$75,000*)	31.4%	23.4%	χ^2 (5) = 11.37, p=0.044*
Residence in S.FL (*year-round*)	84.4%	82.7%	χ^2 (2) = 0.19, p=0.91
Years in South FL (*µ*)	18.00	18.62	t_{345}= -0.34, p=0.732

*Denotes significance at α=0.05 with Chi Square test or Welch's *t*-test

Table 5.3. Average motivations for feeding birds across three clusters ("Steward," "Enthusiast," and "Passive"), including motivations for personal and birds' benefit.

Motivational Statement[a]	**Steward**	**Enthusiast**	**Passive**
Personal Benefit	**4.33**	**4.26**	**2.94**
I enjoy feeding wild birds	4.70	4.56	3.58
I feed wild birds because it relaxes me	4.05	4.07	2.51
I feed wild birds for entertainment	4.13	4.15	2.93
I feed wild birds to be close to nature	4.43	4.25	2.75
Birds' Benefit	**4.42**	**2.59**	**2.21**
I feed wild birds because they need food	4.57	2.49	2.43
I feed wild birds to help the environment	4.25	2.68	1.99

[a] Scale: 1=Strongly Disagree, 5=Strongly Agree

Table 5.4. Characteristics of visitors by bird feeding motivational cluster (including non-feeders), showing mean (μ) or percentage and results of significance tests of differences between clusters (Chi Square or analysis of variance).

Variable	**Non-feeder**	**Stew-ard**	**Enthu-siast**	**Passive**	**Significance Test**
Interest in birds (μ)[a]	3.23	3.69	3.71	3.07	$F_{3,330}=7.04$, $p<0.001$*
Knowledge (μ)[a]	2.81	3.00	3.14	2.68	$F_{3,331}=2.97$, $p=0.032$*
Belief in wildlife rights (μ)[a]	2.98	3.56	3.29	3.01	$F_{3,332}=5.07$, $p=0.002$*
Connect to wildlife (μ)[a]	3.84	3.47	2.95	3.31	$F_{3,332}=8.97$, $p<0.001$*
Season (*summer*)	56.7%	65.0%	59.2%	59.4%	$\chi^2(3) = 1.19$, $p=0.755$
Park (*ICP*)	38.3%	61.7%	54.9%	62.3%	$\chi^2(3)=15.80$, $p=0.001$*
Number of visits (μ)	102.33	52.15	50.21	24.54	$F_{3,159.27}=7.42$, $p<0.001$*
Came to feed birds (*yes*)	---	30.0%	16.9%	10.1%	$\chi^2(3) = 42.63$, $p<0.001$*
Fed birds that day (*yes*)	---	56.7%	57.7%	37.7%	$\chi^2(3) = 87.25$, $p<0.001$*
Has home feeder (*yes*)	16.5%	35.6%	35.7%	29.0%	$\chi^2(3) = 12.87$, $p=0.005$*
Brought children (*yes*)	39.0%	53.3%	62.0%	66.7%	$\chi^2(3) = 18.35$, $p<0.001$*

[a] Averages across factor, from a scale where 1=Strongly Disagree and 5=Strongly Agree

*Denotes significance at α=0.05 with Chi Square test or analysis of variance with Bonferroni correction

Table 5.5. Socio-demographic variables of visitors by bird feeding motivational cluster (including non-feeders), showing mean (μ) or percentage and results of significance tests of differences between clusters (Chi Square or analysis of variance).

Variable	**Non-feeder**	**Stew-ard**	**Enthu-siast**	**Passive**	**Significance Test**
Gender (*female*)	60.0%	65.0%	70.4%	63.8%	$\chi^2(3) = 2.26$, $p=0.52$
Age (μ)	48.86	43.24	46.30	43.80	$F_{3,332}=2.42$, $p=0.066$
Highest education (*postgrad*)	30.2%	8.3%	26.8%	21.7%	$\chi^2(6) = 17.54$, $p=0.007$*
Income (*>$75,000*)	31.2%	18.3%	26.9%	24.6%	$\chi^2(15) = 21.50$, $p=0.122$
Residence in South FL (*year-round*)	84.6%	81.7%	81.4%	83.8%	Not significant
Years in South FL (μ)	17.92	15.87	21.18	18.57	Not significant

*Denotes significance at α=0.05 with Chi Square test or analysis of variance with Bonferroni correction

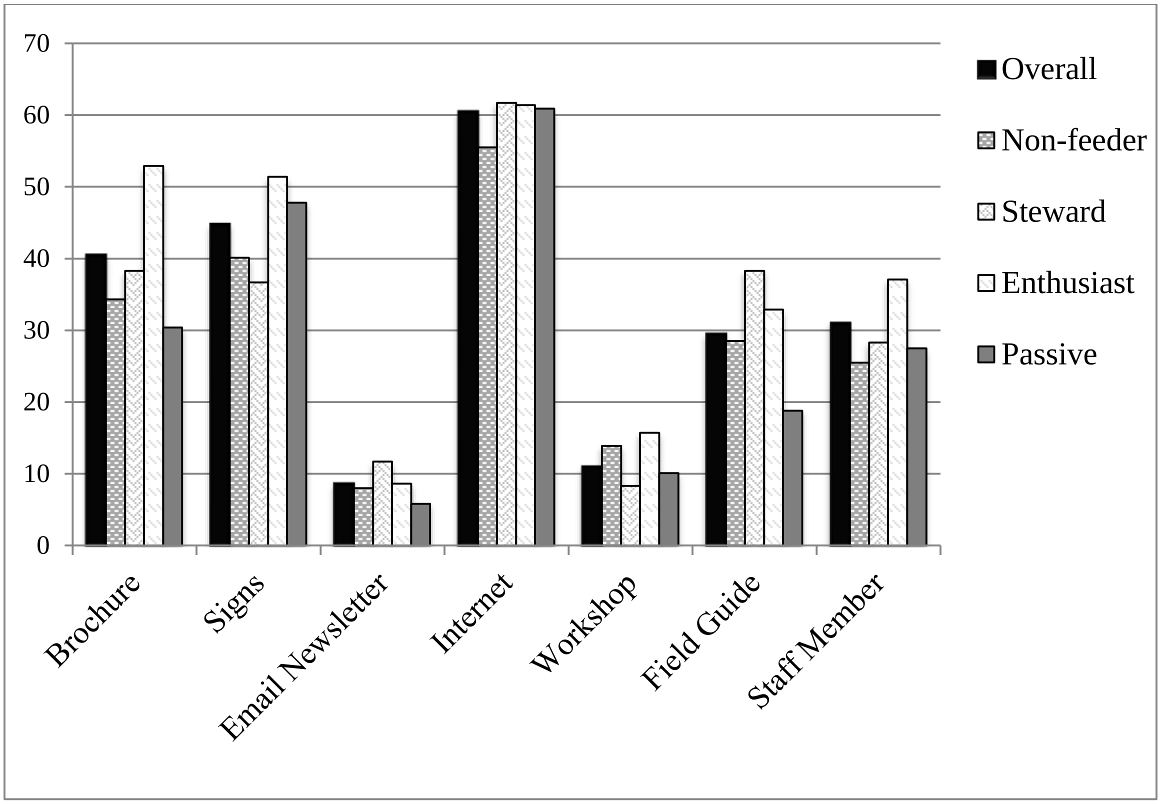

Figure 5.2. Percentage of visitors who would use different educational resources in the future to look up information about birds, including all survey participants (“Overall”) and participants divided by bird-feeding motivational clusters (“Non-feeder,” “Steward,” “Enthusiast,” or “Passive”).

CHAPTER 6

CONCLUSIONS

I sought to better understand how human activities impact the health of birds that use urban habitats, and identify benefits and potential risks for urban residents from the presence of urban birds. Human activities impact wildlife indirectly through urban development, and directly through supplemental bird feeding. In south Florida, wetland birds including the white ibis increasingly forage in urban habitats where people provide food directly (feeding birds in parks) and indirectly (e.g., landfills, dumpsters). Urban habitat use and food supplementation likely affect ibis health, and ibis presence at urban parks provides opportunities to educate people regarding how their behaviors affect avian health, with implications for their own health. In Chapter 2, I reviewed literature pertaining to human-wildlife relationships in urban contexts, specifically addressing urban avian ecology, avian disease ecology, white ibis in urban South Florida, and dynamics of bird feeding and public interactions with birds at South Florida urban parks.

In Chapter 3, I used stable isotope analysis of feces and plasma to determine if urban ibis consume anthropogenic foods, if urban detection or land cover correlates to isotopic signatures, and what proportion of likely source foods was present in each ibis tissue. I found that both plasma and feces were enriched in δ^{13}C and δ^{15}N in summer compared to winter (significantly for plasma). Plasma and fecal samples were significantly correlated in δ^{13}C and δ^{15}N, and feces were substantially depleted in δ^{15}N compared to plasma. Both plasma and fecal δ^{13}C were negatively correlated with developed land cover, and fecal $\delta^{15}N$ was negatively correlated with developed land cover and positively correlated with wetland land cover. Plasma $\delta^{13}C$ and $\delta^{15}N$ and fecal $\delta^{15}N$ differed between several sites, but overall isotopic signatures were not significantly different across urban capture sites. Ellipses surrounding plasma signatures of ibis at PP and LC were relatively small, while the ellipse surrounding plasma signatures of ibis at LW was comparatively large. Ellipses surrounding fecal signatures of ibis at PV and JB were comparatively large. The ellipse surrounding fecal signatures of nestling ibis was depleted in $\delta^{13}C$ and only barely overlapped with PV but no other ellipses; the ellipse surrounding fecal signatures of prairie ibis was depleted in $\delta^{15}N$ and only overlapped with several other ellipses. Nestlings consumed 90% aquatic prey, while other groups consumed similar proportions of prey comprised primarily of bread. Proportions of prey sources in ibis plasma were also similar across sites, with overall highest proportions of bread and freshwater invertebrates. Overall, urban ibis consumed greater proportions of anthropogenic foods and had isotopic signatures that differed from nestlings and ibis foraging at a prairie or landfill, but were similar to each other—however, the breadth of foraging differed by urban capture site based on ellipse areas.

In Chapter 4, I assessed multiple parameters of stress, bactericidal capacity, and H:L ratios in urban ibis. Urban ibis exhibited considerable variation in all parameters. FCORT declined by date and season but increased with urban detection, even when controlling for date. PCORT increased between capture and 15 minutes and generally decreased by 30 minutes; the level at 15 minutes was positively correlated with the baseline level, and the levels at 30 and 15 minutes post-capture were positively correlated with each other. PCORT at baseline and 15 minutes post-capture was positively correlated with H:L ratios, and FCORT was positively correlated with H:L ratios in the summer. No parameters correlated with BKA or differed significantly by site. In general, ibis at PP had the highest BKA, and ibis at LC had the lowest BKA, highest FCORT, and lowest PCORT at 15 and 30 minutes. Despite high variation, some ibis exhibit stress and immune levels indicative of either adaptation or chronic stress.

In Chapter 5, I examined perceptions of urban PBC park visitors toward birds and bird feeding. Park visitors regularly engaged in bird feeding activities at home (27%) or at parks (60%)—including 31% who fed birds at the park on the day of the survey. Visitors who fed birds were younger, had lower incomes and educational attainment, and more likely visited the park with children compared to Non-Feeders. These visitors were more interested in birds with stronger beliefs that wildlife and people should have equal rights. Among visitors who fed birds, three groups emerged based on their motivations for feeding. “Stewards” enjoy feeding birds overall, but slightly more because they believe birds need food. “Enthusiasts” enjoy feeding birds overall, but slightly more for personal reasons (e.g., relaxation, entertainment, connect to nature). “Passives” do not as highly enjoy feeding birds, but feed birds more for personal reasons than to help birds. Passives more likely visited with children than Stewards and Non-Feeders, and had lower interest in and self-reported knowledge of birds than other groups, including Non-Feeders. Passives also had weaker beliefs than Stewards or Enthusiasts that wildlife should have rights equal to those of humans. Interestingly, Non-Feeders felt the strongest connection to wildlife. Most visitors were likely or very likely to stop feeding birds if birds carry disease, regardless of whether the disease affects other birds, wildlife, domestic, animals, or people—however, a small number of visitors were unlikely to stop.

Overall, Passives were most likely to stop feeding, followed by Enthusiasts, and then Stewards. Stewardship feeders and Enthusiast feeders were significantly less likely to stop feeding if a disease only affected domestic animals or people, suggesting a difference in behavior for diseases that affect birds and other wildlife. The most-preferred resources for information about birds were the Internet 61%), signs at the park (45%), or brochures (41%). Preferred resources differed somewhat across types of bird feeding visitors, but did not differ by park; therefore mixed-media educational messages implemented similarly at both parks may be most effective. Overall, many visitors were uncertain if bird feeding benefits birds, and what foods are appropriate to feed. Other visitors are interested in birds but do not engage in bird feeding, suggesting visitors to urban PBC parks encompass broad groups of people who interact with or feed birds in different ways and with different motivations.

We seek to understand if ibis are adapting successfully to urban habitats (as they may require these areas for population success), and determine if specific features of such areas contribute positively or negatively to ibis health. This knowledge will inform more effective management of ibis and other recently urbanized species—whether by improving features of urban areas that support wildlife (e.g., regulating bird feeding), or highlighting the importance of wild habitat conservation or restoration if urban areas increase risk and jeopardize the success of wildlife. Determining successful adaptation for urban ibis is challenging and complex. Captive studies will better validate dietary turnover and assimilation time for the species, to inform robust examination of dietary shifts in urban ibis. The influence of individual personality differences on ibis stress response is also critical, and contributes to the variation in our results. Results from these other areas of research will ideally explain some variation in urban ibis physiology to better elucidate impacts of other relevant features like urban capture sites, and overall inform how well each ibis can adapt successfully to urban habitats. Additional research of ibis fine-scale movement will better establish what habitats ibis use and what percentage of time ibis continue to spend in wild areas. This is central to understanding if diet, stress, and immunity differ for birds that are more “urban” than not, and for determining if any ibis are in fact truly “urban,” or if that distinction is not valid in this ecological system.

People are an integral part of this system—particularly through providing food resources. Therefore, we also must educate the public to gain their support of management, hoping ultimately to improve interactions between urban residents and local wildlife. Short-term, we will implement outreach programs and distribute materials to communicate the results of our white ibis health research, strategies for best-practice bird feeding, and general information about common urban birds. These types of education—as well as the implementation of management plans that regulate bird feeding—will benefit from more in-depth interviews with people who feed birds, and certainly require establishing the efficacy of educational campaigns in promoting positive public behaviors, improving pubic knowledge, and encouraging public stewardship of urban wildlife. Urban birds do present some risk to the public through possible zoonotic disease, and conflicts encompassing noise, mess, and property damage. Therefore, we hope to create and inform education that provides realistic information to the public regarding risk; communicates ways in which public health depends on maintenance of environmental and wildlife health; and ultimately increases management support, urban wildlife stewardship, and conservation ethic among the general public.

APPENDIX A—SURVEY INSTRUMENT (CHAPTER 4)

The University of Georgia
WARNELL
SCHOOL OF FORESTRY & NATURAL RESOURCES

Wild Bird Feeding Survey

Researchers from the University of Georgia are conducting a study to learn about how you interact with wild birds. Your responses to this questionnaire will help us better understand the needs of people who use this site. Your participation is voluntary and your responses are anonymous. <u>In this study "wild birds" are all birds found at this site, including ducks.</u>

<u>Section I.</u> Your Experience Today

1. How many times have you visited THIS site in the <u>past 12 months</u>?

________ visits including today

2. What was the PRIMARY reason for your visit today? ***(Please write response.)***

____

3. Did you or will you feed wild birds <u>during your visit today</u>?

☐ No ☐ Not sure ☐ Yes

3 a. IF you fed wild birds <u>during your visit today</u>, please estimate how many birds you fed. ***(Please check ONE box.)***

☐ 1-25 ☐ 26-50 ☐ 51-75

☐ 76-100 ☐ Over 100

4. Did you bring children with you today? ☐ No ☐ Yes

4 a. If YES, did or will any of those children participate in wild bird feeding today?

☐ No ☐ Not sure ☐ Yes

Section II. Your Wild Bird Feeding Activity

5. Please indicate whether you DISAGREE or AGREE with the following statements concerning wild bird feeding. ***(Circle ONE response for each statement OR check "I don't feed birds".)***

	Strongly Disagree	**Disagree**	**Neutral**	**Agree**	**Strongly Agree**	**I don't feed birds**
I enjoy feeding wild birds.	1	2	3	4	5	☐
I feed wild birds because it relaxes me.	1	2	3	4	5	☐
I feed wild birds for entertainment.	1	2	3	4	5	☐
I feed wild birds to be closer to nature.	1	2	3	4	5	☐
I feed wild birds because they need food.	1	2	3	4	5	☐
I feed wild birds to help the environment.	1	2	3	4	5	☐

6. **How LIKELY would you be to STOP feeding wild birds** in the following scenarios? ***(Circle ONE response for each statement OR check "I don't feed birds".)***

I would STOP feeding wild birds in the future if wild birds:	**Very Unlikely**	**Unlikely**	**Neutral**	**Likely**	**Very Likely**	**I don't feed birds**
Carry a disease that **affects wild birds.**	1	2	3	4	5	☐
Carry a disease that **affects wild birds and other wildlife**.	1	2	3	4	5	☐
Carry a disease that **affects domestic animals.**	1	2	3	4	5	☐
Carry a disease that **affects people**.	1	2	3	4	5	☐
Carry a disease that **affects wildlife, domestic animals, and people**.	1	2	3	4	5	☐

Section III. Your Knowledge Of and Experience With Wild Birds

7. Please indicate whether you DISAGREE or AGREE with the following statements concerning your knowledge of wild birds. ***(Circle ONE response for each statement.)***

	Strongly Disagree	**Disagree**	**Neutral**	**Agree**	**Strongly Agree**
I intentionally watch wild birds.	1	2	3	4	5
I take photographs of wild birds.	1	2	3	4	5
I recognize different types of wild birds.	1	2	3	4	5
I know the species names of wild birds I see.	1	2	3	4	5
I know about wild bird habits and behaviors.	1	2	3	4	5
I know about wild bird biology and natural history.	1	2	3	4	5
I look up species names of wild birds I do not recognize.	1	2	3	4	5
I seek additional information about wild birds.	1	2	3	4	5

8. Which of the following resources would you use to obtain additional information about wild birds? (***Check ALL that apply.)***

☐ Brochure/handout at site
☐ Educational signs at site
☐ Email newsletter
☐ Internet/website
☐ Short workshop/ presentation
☐ Small guide/field book
☐ Staff member at site

9. Please indicate whether you DISAGREE or AGREE with the following statements concerning your attitudes toward wild birds. ***(Circle ONE response for each statement.)***

	Strongly Disagree	**Disagree**	**Neutral**	**Agree**	**Strongly Agree**
Human needs come before the needs of wildlife.	1	2	3	4	5
Birds should have similar rights to those of humans.	1	2	3	4	5
Wildlife should have similar rights to those of humans.	1	2	3	4	5

I feel a strong connection to wild birds.	1	2	3	4	5
I feel a strong connection to wildlife.	1	2	3	4	5
Wildlife should be managed for human benefit.	1	2	3	4	5

Section IV. General Information

10. What is your gender? ☐ Female ☐ Male

11. What is your age? _______ years old

12. What is the highest level of education you have completed? ***(Please check ONE box.)***

☐ some high school
☐ graduated from college or technical school
☐ graduated from high school or GED
☐ postgraduate degree(s)

13. Please indicate your total household income range before taxes last year. ***(Please check ONE box.)***

☐ $25,000 or less
☐ $75,001 to $100,000
☐ $25,001 to $50,000
☐ $100,001 or more
☐ $50,001 to $75,000
☐ Refuse to answer

14. What is your residence status in south Florida? ***(Please check ONE box.)***

☐ Non-resident ☐ Seasonal resident ☐ Year-round resident

15. Approximately how many years have you lived in south Florida? _______ years ***(Please write "0" if non-resident.)***

16. Do you use a bird feeder at your RESIDENCE? ☐ No ☐ Yes

17. Please provide the state and zip code of your primary residence:

____

Thank you again for your time.

APPENDIX B—SUPPLEMENTAL TABLES (CHAPTER 4)

Table A.1. Results of principle axis factor analysis with oblique rotation on bird feeding motivation construct (only including participants who feed birds), revealing sub-constructs of anthropocentric and ecocentric motivations. [α—Cronbach's alpha for construct, ρ—Spearman's rho for construct]

	Pattern Matrix		**Structure Matrix**	
Sub-Construct / Questionnaire Item [a]	**A**	**B**	**A**	**B**
A. Anthropocentric Motivation (α = .820)				
I enjoy feeding wild birds	.694		.709	
I feed wild birds because it relaxes me	.862		.853	
I feed wild birds for entertainment	.711		.678	
I feed wild birds to be close to nature	.677		.730	
B. Ecocentric Motivation (ρ = .647)				
I feed wild birds because they need food		.750		.730
I feed wild birds to help the environment		.864		.903

[a] Scale: 1=Strongly Disagree, 5=Strongly Agree

Table A.2. Results of principle axis factor analysis with oblique rotation on interest and knowledge construct, revealing sub-constructs of interest in and knowledge of birds. [α—Cronbach's alpha for construct, ρ—Spearman's rho for construct]

	Pattern Matrix		Structure Matrix	
Sub-Construct / Questionnaire Item [a]	**A**	**B**	**A**	**B**
A. Interest in Birds / Wildlife (ρ = .535)				
I intentionally watch wild birds		.746	(.466)	.749
I take photographs of wild birds		.677	(.409)	.682
B. Knowledge of Birds (α = .932)				
I recognize different types of wild birds	.627		.769	(.610)
I know the species names of wild birds I see	.863		.875	(.531)
I know about wild bird habits and behaviors	.968		.907	(.470)
I know about wild bird biology and natural history	.891		.832	(.426)
I look up species names of wild birds I do not recognize	.599		.804	(.701)
I seek additional information about wild birds	.549	(.421)	.798	(.745)

[a] Scale: 1=Strongly Disagree, 5=Strongly Agree

Table A.3. Results of principle axis factor analysis with oblique rotation on behavior change construct, confirming one construct. [α—Cronbach's alpha for construct]

Sub-Construct / Questionnaire Item [a]	**Factor Loading**
A. Behavior Change (α = .969)	
STOP feeding if disease affects birds	.900
STOP feeding if disease affects birds/wildlife	.934
STOP feeding if disease affects domestics	.964
STOP feeding if disease affects people	.928
STOP feeding if disease affects all of above	.920

[a] Scale: 1=Very Unlikely, 5=Very Likely

Table A.4. Results of principle axis factor analysis with oblique rotation on the value orientation construct, revealing sub-constructs of belief that wildlife should have equal rights, and feeling of connection to wildlife. [ρ—Spearman's rho for construct]

	Pattern Matrix		**Structure Matrix**	
Sub-Construct / Questionnaire Item [a]	**A**	**B**	**A**	**B**
A. Belief in Wildlife Rights (ρ = .824)				
Birds should have rights similar to those of humans	.911		.920	(.462)
Wildlife should have rights similar to those of humans	.913		.905	(.426)
B. Connection to Wildlife (ρ = .712)				
I feel a strong connection to wild birds		.853	(.440)	.866
I feel a strong connection to wildlife		.854		.843

[a] Scale: 1=Strongly Disagree, 5=Strongly Agree