THE EFFECTS OF URBANIZATION ON WILDLIFE BEHAVIOR AND HOST-PARASITE DYNAMICS

by

CALI ANN WILSON

(Under the Direction of Sonia Altizer and Richard J. Hall)

ABSTRACT

As natural habitats are lost, wildlife increasingly use urban areas. Urban environments offer novel access to resources, including food intentionally thrown to wildlife in parks. Exploiting these resources can alter wildlife behaviors such as boldness, aggression, and flocking. These behaviors in turn can shape individual exposure and susceptibility to infectious diseases, population-level transmission and the potential for pathogen sharing among urban wildlife, domestic animals, and people. Therefore, understanding the behavioral determinants of parasite transmission and impacts of urbanization on these processes is a central question in disease ecology, with implications for human health and wildlife conservation. My dissertation research quantifies behavioral variation in urban wildlife and explores the consequences of urbanization for wildlife behavior and pathogen dynamics at multiple biological scales, integrating synthetic approaches and field studies. First, I synthesize knowledge of how urbanization influences behavioral variation and parasitism, using behavior-parasitism feedbacks as a guiding framework for wildlife management and shaping future research questions. Next, I use field observations and experiments to quantify behaviors relevant to pathogen transmission in American white ibis, a species which has recently undergone dramatic behavioral and dietary shifts to exploit anthropogenic food sources in urban parks in south Florida. I quantify activity budgets of wild ibis in natural wetlands and urban parks and use experimental feeding trials to quantify how food provisioning influences ibis density. I also examine how human feeding of ibis in urban settings influences aggressive behaviors using fine-scale behavioral analyses of video data. I find that food provisioning increases flock density and aggression frequency, but reduces the time that ibis spend foraging. These behavioral responses could increase exposure to contact-transmitted pathogens but might reduce the transmission of enteric diseases with fecal-oral transmission. Collectively, this work advances knowledge of how human feeding of wildlife in urbanizing landscapes influences their infection risk by altering the behavior of individual animals.

INDEX WORDS: Disease ecology, foraging, urbanization, wildlife, behavioral ecology, American white ibis

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DEDICATION

In loving memory of my mother, Donna M. Wilson.

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CHAPTER 1

INTRODUCTION

Urban areas are expanding at unprecedented rates, with nearly 70% of the world's population expected to live in urban areas by 2050 (United Nations, Department of Economic and Social Affairs, Population Division 2019). Most wildlife species are unable to persist in cities, but some can acclimate and adapt to these human dominated habitats. Food provided unintentionally through dumpsters and landfills, or deliberately through feeding of wildlife for conservation or recreation, creates many opportunities for humans, domestic animals, and wild animals to interact (Cox and Gaston 2018). With almost half of urban US households regularly providing food for birds, wildlife feeding is pervasive and is an important way for people to engage with and learn about wild animals (Robb et al. 2008). Food subsidies can impact animal health, behavior, and species interactions, and can also have undesirable consequences, especially when they facilitate disease transmission (Becker and Hall 2014, Murray et al. 2016, Lawson et al. 2018, Moyers et al. 2018).

For many infectious diseases, individual hosts or host species differ their ability to acquire and transmit pathogens (Woolhouse et al. 1997, Lloyd-Smith et al. 2005). In some cases, hosts with more social contacts or exploratory personality types have a greater risk of encountering and transmitting pathogens. This contact behavior might correlate with other individual-level characteristics, such as stress or immune responses, that determine pathogen shedding (Cohen et al. 2007, Stein 2011). Identifying individuals that contribute disproportionately to transmission, known as superspreaders, is crucial for predicting infection dynamics and managing pathogen outbreaks (Woolhouse et al. 1997, Lloyd-Smith et al. 2005). Importantly, behaviors other than social contact also determine transmission, including feeding behavior and habitat use. Individual-level variation in the use of particular foraging locations could affect exposure to environmentally-acquired pathogens (Amoroso et al. 2019, Paquette et al. 2020). For example, greater exploration and activity levels predict higher ectoparasite abundance in sciurids (Boyer et al. 2010, Bohn et al. 2017), likely due to greater exposure risk.

Behaviors associated with urban habitat use, including feeding on novel resources provided by humans, could increase exposure risk and potential for pathogen spillover between wildlife and humans (Becker and Hall 2014, Becker et al. 2015). For example, feeding wildlife can disproportionately favor bold or aggressive individuals, promote aggregation and aggression around resources (Wright and Gompper 2005, Flint et al. 2016), and foster novel species assemblages (Oro et al. 2013), all of which can increase exposure to pathogens (Dhondt et al. 2005). On the other hand, provisioned animals might spend less time foraging, which might increase time and energy for immune and behavioral defenses (Kaburu et al. 2019a). Because these diverse responses can influence population and landscape-level infection patterns in different ways, studies that integrate multiple levels of biological organization are needed to understand the consequences of human-altered landscapes for wildlife-pathogen interactions.

American white ibis (*Eudocimus albus*) are well suited as a model species to address the goals of this study. They are highly visible, large-bodied, and abundant birds that inhabit coastal sub-tropical habitats. White ibis are wetland feeders that move nomadically to track suitable foraging conditions. Anthropogenic habitats such as lawns provide reliable foraging habitat, bringing ibis into cities where they have learned to exploit anthropogenic food sources, including hand-feeding by humans (Kushlan 2011, Hernandez et al. 2016, Murray et al. 2018). Ibis are infected by pathogens with a range of transmission modes, including those acquired from contaminated food and water while foraging (e.g., *Salmonella spp.* and avian influenza), through close contact with other birds (e.g., feather mites), and parasites that pass through an intermediate host (e.g., parasitic flatworms in snails) (Pence and Bush 1973, Hernandez et al. 2016, Bahnson et al. 2020). Extensive research has been conducted on the health and movement behavior of American white ibis populations in South Florida. Recent studies showed that ibis fed in urban parks are more likely to be infected with *Salmonella spp.*, and have lower body mass, compared to those in natural areas (Hernandez et al. 2016, Murray et al. 2018). However, urban habitat use may actually improve ibis health in some ways; urban ibis were found to have lower ectoparasite burdens (Murray et al. 2018), lower baseline corticosterone levels during post-breeding season, and higher bacterial killing ability against *E. coli* than wetland conspecifics (Cummings et al. 2020b, 2020a). Lastly, movement studies suggest that ibis may become habitat specialists during the non-breeding season, with few individuals frequently moving between urban and wetland habitat types (Teitelbaum et al. 2020a). Together these findings suggest that urbanization and provisioning may offer trade-offs for ibis health and behavior. However, we currently lack fine-scale information on characteristics of individual and flock-level behaviors of ibis and how anthropogenic food provisioning alters these interactions. Understanding these behavior is important for informing public guidelines for wildlife feeding to prevent ibis and other urban birds from becoming nuisance species (Martin et al. 2007) and reduce the changes of pathogen sharing.

My dissertation research investigates how urban environments and anthropogenic food provisioning alter the behavior of urban wildlife in ways that can influence the transmission of infectious diseases. The main goals of this work are to: (i) review and synthesize current literature at the intersection of urbanization, wildlife behavior, and infectious disease (Chapter 2); (ii) assess how American white ibis behavior (*Eudocimus albus*) differs between urban and natural environments (Chapter 3), and (iii) quantify how anthropogenic food provisioning influences behaviors relevant to pathogen transmission, including changes in density and aggressive interactions (Chapters 3 and 4).

In Chapter 2, I synthesize previously published work that examines urbanization and wildlife behavior, including foraging behavior, movement behavior, mating and rearing of offspring, and conspecific interactions. I explore the consequences for host-parasite dynamics by altering behavior-infection feedbacks and variation among individuals in their ability to acquire and transmit pathogens. I then explore the implications for pathogen-sharing with domestic animals and people, and how leveraging understanding of urban wildlife behavior can shape wildlife management and disease surveillance in cities. I conclude by highlighting knowledge gaps and priorities for future work, including an urgent need for studies that examine the consequences of urban wildlife behaviors for host-pathogen evolution.

Chapters 3 and 4 focus on the behavior of American White Ibis, nomadic wetland birds that have recently become habituated to taking human-provided food in urban parks in south Florida. In Chapter 3, I use observational field data from urban and natural sites, and experimental feeding trials, to explore how food provisioning affects ibis behaviors relevant to parasite transmission. I first ask whether there are immediate, short-term effects of provisioning on ibis density by experimentally feeding ibis flocks, using video recordings to observe interactions while being provisioned, and observational focal follows to observe interactions while not being fed. I find that ibis flock densities more than double during short intervals when birds are actively provisioned with food. I then ask whether these effects of provisioning on behavior are detectable on longer time scales, by conducting focal observations of ibis and comparing behavior across urban parks with different levels of provisioning activity. Results show that foraging time decreases with flock size and provisioning levels. Lastly, I compare ibis behavior in wetland sites (with no provisioning) against provisioned urban sites to examine long-term changes in activity budgets and find minimal overall differences in behaviors measured here. The results of Chapter 3 provide insight into how human-provided food impacts behavior at multiple scales and is crucial for predicting changes in the transmission of pathogens and understanding how urbanization impacts wildlife health.

Given that results in Chapter 3 show that anthropogenic food provisioning drastically altered ibis density, I extend this work in Chapter 4 to examine how provisioning influences individual social interactions among ibis, namely aggressive interactions. To do this, I compare aggression observed in ibis foraging on natural substrates in urban areas to aggression observed while ibis were actively being provisioned with human-provided food. I find that active provisioning increases the frequency of aggressive interactions and the proportion of birds in a flock observed being aggressive. Next, I capitalize on fine-scale video data to explore drivers of individual variation in aggression in birds being actively fed. For each focal bird in the flock being fed, I calculate two metrics of conspecific density (flock-level and local density around focal birds) and the focal bird's average distance from the food source. I find that the interaction between distance from anthropogenic food and conspecific density (either flock or local) are the best predictors of aggression in urban ibis. These results suggest even short-duration provisioning in wildlife increases the frequency of aggressive behaviors which could have important consequences for wildlife health and pathogen exposure, and lead to human-wildlife conflict.

Importantly, my dissertation work expands on recent efforts to understand how urbanization impacts wildlife ecology by identifying how individual variation in behaviors relevant to exposure and susceptibility to infectious disease are modified in urban environments. My empirical work that focused on a recently urbanized wading bird provides much-needed empirical quantification of how short-duration hand-feeding of wildlife in parks increases conspecific density and aggression frequency, and suggests that ephemeral aggregations at feeding events could be critical for pathogen transmission in urban-habituated wildlife. My dissertation uses a range of methods (i.e., statistical modeling, literature review, observational and experimental field data) and considers multiple scales of biological observation to examine urban wildlife ecology. This work advances understanding of wildlife responses to urbanization and demonstrates that anthropogenic food provisioning can have complex effects on infectious disease dynamics through its effects on animal behavior.

CHAPTER 2

WILDLIFE BEHAVIOR AND PATHOGEN DYNAMICS IN AN URBANIZING WORLD[1]

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Abstract

More than half of the earth's human population now lives in urban areas, which account for a growing fraction of the earth's land cover. Wildlife that use urban habitats often show behaviors that allow them to exploit food and other resources available in cities, and tolerate urban stressors. Selection for behaviors that improve success in urban environments can alter the transmission of infectious diseases, in part by changing within- and among-species contacts, movement patterns, and susceptibility to infection. These changes can alter the population-level and spatial spread of infection and can also exacerbate individual differences in behavior in ways that lead to superspreading. Given increased reliance of wildlife on cities in areas where natural habitat has been degraded, and the frequency of human-wildlife contact in cities, urban wildlife play a growing role in the emergence of zoonotic pathogens. Thus, understanding the links between animal behavior and parasite ecology in urban environments is critical both for managing public health risks and for supporting species conservation. Here we synthesize recent findings of how urbanization alters diverse components of wildlife behavior, including foraging, movement, and social interactions. We also consider behavior-infection feedbacks and how variation among individuals predicts their ability to acquire and transmit pathogens. We then explore the implications for pathogen-sharing with domestic animals and people, and how an understanding of urban wildlife behavior can shape wildlife management and disease surveillance in cities. We conclude by highlighting knowledge gaps and priorities for future work, including an urgent need for studies that examine the consequences of urban wildlife behaviors for host-pathogen evolution.

Introduction

Urbanization is a pervasive component of global environmental change that can have far-reaching consequences for wildlife ecology (Simkin et al. 2022). As natural habitats are lost and degraded, urban areas increasingly serve as refuges for wildlife. Although some species benefit from milder climates and novel resources offered by urban areas, accessing these benefits exposes wildlife to stressors including noise and light pollution, contaminants, novel species interactions and elevated mortality through collisions with human structures or traffic (Longcore and Rich 2004, Andrade et al. 2021, Farnsworth et al. 2024). As urban areas continue to expand around the globe, understanding the ecological and evolutionary mechanisms through which wildlife persist in these novel environments is critical for urban planners and conservation practitioners to create livable cities for both humans and wildlife (Egerer and Buchholz 2021).

One way that wildlife can adapt or acclimate urban areas is by modifying their behavior (Lowry et al. 2013). Natural behaviors such as individual learning and social cognition can diminish or change in frequencies, and new behaviors can arise (Lee and Thornton 2021). Some changes (e.g., flight initiation distance) can develop within hours and others (e.g., new behavioral syndromes) respond over longer timescales and can lead to evolutionary change (Ritzel and Gallo 2020). In addition to directional shifts in the mean frequency of a behavior exhibited in a population, selective pressures in urban areas could enhance or reduce intraspecific variation in behavior (Thompson et al. 2022). Behavioral traits can determine which individuals can successfully inhabit urban areas. For some species, bold or neophilic individuals can better exploit urban resources (e.g., Australian water dragons Sprau and Dingemanse 2017, Baxter-Gilbert and Whiting 2019, Baxter-Gilbert et al. 2021). Moreover, urban habitat use can decouple behaviors such as boldness and aggression (i.e. behavioral syndromes, Bókony et al. 2012). Although behaviors associated with city-living are well documented across wildlife species, studies that assess their ecological impacts for species interactions are crucially needed.

Behaviors associated with urban living can alter wildlife-parasite interactions, with a growing number of case studies highlighting how changes in host exposure and susceptibility scale up to influence population level outcomes (Bradley and Altizer 2007, Table 2.1). For example, aggregation at urban roosting or feeding sites in birds can increase exposure to infectious disease (Dhondt et al. 2007). On the other hand, ingestion of toxicants that reduce movement capacity, or frequent anthropogenic disturbance, could reduce exposure to infection (Murray and Sánchez 2021). Studying parasitism through a behavioral lens is vital because traits such as boldness or aggression could make some individuals disproportionately likely to acquire and transmit pathogens (i.e., act as superspreaders of infection, see Box 2.1) (Keiser et al. 2016, Araujo et al. 2016). Moreover, feedbacks between behavior and infection in urban areas could ramp up population-level transmission: for example, stable urban resources could attract large numbers of hosts and thus increase transmission of parasites, and costs of infection that impede movement could prevent hosts from escaping urban sites, potentially leading to the formation of heavily-infected urban resident populations (Satterfield et al. 2015, 2016, Majewska et al. 2019, Teitelbaum et al. 2022). Such research is especially timely since interactions between wildlife, domesticated animals and people in urbanized environments are a key driver of zoonotic pathogen spillover (Plowright et al. 2011, Hassell et al. 2017). Thus, identifying wildlife behaviors that exacerbate risks of pathogen-sharing could be vital for efforts to anticipate and prevent disease emergence.

The goals of this review are to illustrate multiple mechanisms through which behavioral responses to urbanization influence host-pathogen dynamics and their wider implications for urban wildlife conservation and human health. We structure our review by first exploring how urbanization modifies behaviors relating to foraging, movement, social interactions, mating and offspring-rearing, and their consequences for parasite exposure, immune defense, and onward transmission of infectious diseases. Next, we discuss the ways in which these behavioral modifications can impact both human and wildlife health. We conclude by considering how urban habitats can be managed to minimize behavioral changes that increase infection risk, and identifying needs for future work.

Foraging behavior: easy meals, simplified diets, and exposure to toxicants

Resource distribution and stressors in cities can alter wildlife activity patterns (e.g., Berger et al. 2020), with consequences for foraging and anti-parasite defenses. The relative abundance, spatial and seasonal reliability of urban resources such as backyard bird-feeders and trash could reduce search times for successful foraging (Liker and Bókony 2009, Sol et al. 2011), and increase time spent on anti-parasite behavioral defenses such as grooming, or allocation of energy to immune defenses (Kaburu et al. 2019a). For example, American white ibis (*Eudocimus albus*) that consume human-provided foods in parks have lower ectoparasite scores than those in natural wetlands, suggesting a trade-off between time spent foraging versus preening (Murray et al. 2018).

Urban environments can act as a refuge from predators ('safe-habitat hypothesis', Møller 2012), allowing some species to devote less time to antipredator/vigilance behaviors (Mccleery 2009) and more to feeding and anti-parasite defense. On the other hand, predictable anthropogenic food at urban sites (e.g., dumpsters, urban parks) can increase exposure to pathogens through more intensive space use and aggregation within and among wildlife species (Oro et al. 2013). This can increase both conspecific and heterospecific contacts, and allow environmentally persistent pathogens to build up around food sources (Palmer and Whipple 2006, Dhondt et al. 2007, Jurinović et al. 2014, Atterby et al. 2016). In other cases, however, frequent pathogen exposure at sites with human-provided food could serve to immunize individuals against infection if pathogen build-up is slow (Leon and Hawley 2017).

The quality of provisioned food available relative to natural diets is important in determining the effects on wildlife physiological condition and susceptibility to, or tolerance of, infection (Adelman and Hawley 2017, Lawson et al. 2018, Moyers et al. 2018). Easy access to high quality anthropogenic food, such as seeds provided through backyard bird-feeding, could reduce individual susceptibility (and therefore population-level transmission) in times when natural food sources are limited, for example, during winter in high latitude regions (Siriwardena et al. 2007). Alternatively, high food quality could allow hosts to maintain regular activity patterns and reduce the expression of sickness behaviors, such as self-isolation; such behavioral tolerance of infection could increase contacts between infected and uninfected hosts and increase transmission (Stephenson and Adelman 2022). Other anthropogenic food, such as bread that is commonly fed to waterbirds in parks, is poor quality resulting in malnutrition (Bernat-

Ponce et al. 2023), dampened immune responses (Cummings et al. 2020a), or increased time and energy spent foraging to meet nutritional requirements (Jarrett et al. 2020). This could increase susceptibility to infection or elevate mortality from infection for individuals whose diet consists of a large amount of anthropogenic food, with opposing consequences for population-level transmission (Coop and Kyriazakis 2001, Ezenwa 2004, Knapp et al. 2013).

Exposure to contaminants through urban foraging can increase wildlife susceptibility to infection (Blanco et al. 2017) and infection-related mortality across trophic levels; for example, anticoagulant rodenticides used to control urban rodent populations impact infection risk in rodents and their predators (Lemus et al. 2011, Murray and Sánchez 2021) and predict mange-related mortality in bobcats (Serieys et al. 2018). Alternatively, contaminant exposure associated with urban foraging can reduce infection through immune priming (Pölkki et al. 2012, Prüter et al. 2018) or direct lethal effects of toxicants on the pathogen (Hanlon and Parris 2012). Interestingly, infected individuals may be drawn to contaminated areas (e.g., landfills, rodenticide bait stations) if these areas provide easy food or shelter. This can reduce disease transmission if contaminated areas isolate infected individuals or increase mortality, similar to migratory culling (Altizer et al. 2011, Sánchez et al. 2020).

Wildlife movement patterns and urban pathogen spread

Urbanization can reduce long-distance movement behavior through a variety of mechanisms (Withey and Marzluff 2005, Altizer et al. 2011, Tucker et al. 2018, Richardson et al. 2021). Urban environments can attract and trap wildlife moving through the wider landscape; for example, artificial light at night in cities is associated with higher stopover density of birds and can increase migratory dropout and building collisions (Horton et al. 2023). Stable temperatures, seasonally reliable food and fewer predators can reduce cues for departure from urban habitats (Bradley and Altizer 2007), while physical barriers in urban environments, such as roads and tall building can discourage or prevent movement (Shepard et al. 2008). This loss or reduction of long-distance movements in urban habitats can have cascading effects on wildlife infection risk (Satterfield et al. 2018).

Long-distance migratory behavior shapes host susceptibility and exposure to infectious agents in ways that influence population-level transmission (Altizer et al. 2011). In turn, infection can influence an individual's capacity to successfully migrate; therefore, understanding the mechanisms underlying these feedbacks allows us to predict how urbanization will disrupt these linkages. Since the energetic costs of migration can make individuals more susceptible to infection (Owen and Moore 2008, Becker et al. 2020), stable urban resources that reduce migration could allow animals to reallocate resources from needs associated with migration to immune function and resistance to infection. Consistent with this hypothesis, innate immune function was higher in residents than migrant in common blackbirds (*Turdus merula*) (Eikenaar and Hegemann 2016), a partially migratory species in which urban resources predict increased residency.

Because infected animals can have difficulty migrating long distances, migration can lower infection prevalence by removing infected animals from the population, a phenomenon known as migratory culling (Bradley and Altizer 2005, Slowinski et al. 2018). Conditions favoring urban residency can therefore lead to higher prevalence of infection in residents in partially migratory populations, as observed in monarch butterflies (*Danaus plexippus*). Human-planted non-native milkweed (concentrated in urban and suburban gardens) permits the formation of year-round resident monarch populations that become heavily infected by the protozoan parasite *Ophryocystis elektroscirrha* in the southern US (Satterfield et al. 2015, Majewska et al. 2019, Majewska and Altizer 2019).

Pathogen sharing between urban residents and migrants can further erode the benefits of migration for pathogen avoidance: in a modeling study of partial migration in songbirds, urban-induced residency led to a higher proportion of infected migrants departing shared breeding sites, with high levels of migratory culling substantially reducing migrant population size (Brown and Hall 2018). Alternatively, positive feedbacks between elevated transmission risk at aggregated urban resources, and reduced probability of migrating while infected, could reduce landscape-level pathogen spread between urban residents and non-urban migrants. In historically nomadic species, urban site fidelity is predicted to reduce outbreak frequency of Hendra virus in flying-foxes (*Pteropus spp.*) (Plowright et al. 2011, see Box 2.2) and *Salmonella spp.* in American white ibis (*E. albus*) (Teitelbaum et al. 2022).

Importantly, reduced dispersal of animals in urban areas can reduce gene flow, with implications for susceptibility to infection and population-level infection risk (Kennedy and Ward 2003, Epps et al. 2007, Balkenhol and Waits 2009, Jha 2015, Johnson and Munshi-South 2017, Becker et al. 2018, Miles et al. 2019). For example, genetic analysis of white-footed mice found along an urban to rural gradient found higher levels of inbreeding (Richardson et al. 2021) and an inverse relationship between urbanization and several metrics of genetic diversity among urban dwelling mice (Munshi-South et al. 2016). Reduced genetic diversity has been shown to increase susceptibility to infection for a number of wildlife species (O'Brien and Evermann 1988, Spielman et al. 2004, King and Lively 2012), in part because genetic diversity ensures that at least some favorable resistance alleles are present to allow the host population to cope with debilitating diseases. This is often seen in endangered species with low population numbers (e.g., Tasmanian devils and the transmissible cancer Devil Facial Tumor Disease, Miller et al. 2011)). Consequently, reduced movement that subdivides populations could produce higher prevalence in urban areas and lower prevalence in non-urban areas.

Parasites, mating signals, and costs of rearing offspring

Urbanization impacts the expression and perception of mating signals such as mating calls and coloration (reviewed in Heinen-Kay et al. 2021, Cronin et al. 2022) which could alter host-pathogen dynamics via immune investment or conspecific interactions. For example, some birds increase their song volume in response to noise pollution (Dowling et al. 2012). The increase in song volume can compromise vocal performance and subsequently lower mating opportunities in urban environments (Luther et al. 2016), which in turn could lead to a loss of MHC diversity that increases susceptibility to parasitism (Kurtz et al. 2004, Sommer 2005), or population declines that reduce host availability for parasites. Alternatively, changes to mating signals that promote extra-pair paternity in urban environments could increase variation in immunity and reduce parasite loads within broods (Møller et al. 2004, Grinkov et al. 2018, Pipoly et al. 2019). Parasite infection can also impact animal calls, including bird song complexity (Spencer et al. 2005) and frog calls (Halfwerk et al. 2019). Therefore, infection history that limits an individual's ability to modify their signals in noisy environments could subsequently affect sexual selection.

Sexual signals such as songs and colors are often honest indicators of infection or susceptibility to infection (Hamilton and Zuk 1982). If altered expression of these signals in urban environment decouples signal quality from infection status, this could influence exposure risk of mates and offspring, as well as impeding selection for pathogen resistance. Honest signals might even be reversed in urban settings if sick animals in cities shift their energetic investment to maximize reproduction, termed 'terminal ornamental investment' (Hutton and McGraw 2016, Sykes et al. 2021). For example, urban house finches (*Haemorhous mexicanus*) infected with coccidia had larger patches of carotenoid coloration (Sykes et al. 2021).

Trade-offs between territoriality and parental care in some species may be decoupled in urban environments, and the physiological changes underlying these behavioral modifications can differentially impact offspring susceptibility to infection. Aggression is energetically costly and can limit investment in parental care in natural settings when resources are limited (Badyaev and Hill 2002). One study of urban song sparrows showed that males increased both aggression and nest visitation relative to rural birds, and had higher fledgling success, suggesting that ready access to resources in urban environment alleviates these tradeoffs and improves offspring condition (Lane et al. 2023).

Urbanization changes the types of materials available for nesting animals to use when building nests, and incorporating anthropogenic resources into nesting can either lower or increase parasitism. For example, cigarette butts in bird nests can protect against ectoparasites, potentially representing a novel mechanism of self-medication via nicotine (Suárez-Rodríguez et al. 2013). White storks living in close proximity to urban landfills have been documented using plastic to insulate nests (Jagiello et al. 2020). Offspring can consume the plastic which is detrimental to their health (Lavers et al. 2014) and affect both exposure to chemicals in the plastic and infectious agents on the plastic and susceptibility to other infectious diseases (Ormsby et al. 2024).

Urbanization impacts on parental provisioning behaviors also influence parasitism in offspring. Human activity in urban areas can disrupt the regular feeding of nestlings by parents, leading to lower breeding success (Glądalski et al. 2016) and potentially higher risk of parasitism if nestlings are in poor body condition. Additionally, the food parents provide their offspring in urban environments can impact offspring health in opposing directions. Urban supplemental diets could improve offspring success by mitigating the negative effects of parasitism (Knutie 2020) or could be toxic if parents are consuming contaminated foods (Sriram et al. 2022).

Conspecific interactions: more social in the city

Urbanization alters conspecific interactions through a variety of mechanisms which can subsequently impact social dynamics and individual health. Stable and predictable food resources can allow urban habitats to support higher densities of wildlife, leading to more frequent aggressive interactions, especially if individuals attracted to urban areas have aggressive/bold phenotypes (Tuomainen and Candolin 2011). For example, urban Cuban rock iguanas (*Cyclura nubila*) exhibited more aggressive interactions per capita, and more male-male but fewer male-female interactions (Lacy and Martins 2003). In urban song sparrows (*Melospiza melodia*), food subsidy predicted higher territorial aggression (Foltz et al. 2015). While aggression could increase parasite transmission through higher contact rates, improved fitness associated with resource acquisition could moderate the impacts of infection. For example, aggression predicts higher feline immunodeficiency virus infection in urban male feral cats; the fact that older cats also show higher infection rates suggests these animals can tolerate infection (Courchamp et al. 1998). Positive associations between aggression and fitness in urban environments could therefore favor the transmission of parasites that manipulate host aggressive and exploratory behavior for their onward transmission, such as *Toxoplasma gondii*, for which human and wildlife infections are more common in urban than non-urban habitats (Barros et al. 2018, Morais et al. 2021).

Anthropogenic factors could influence social behavior of urban wildlife through means other than food availability. For example, urban macaques (*Macaca mulatta*) groom in shorter bouts when they interact with people more frequently (Kaburu et al. 2019b). Grooming directly removes ectoparasites, but allogrooming could increase the transmission of directly transmitted parasites via direct contact between individuals. Similarly, the use human-built structures, such as human houses, overpasses, or sewers, by wildlife can also alter conspecific contact. For example, some bat species use spaces in ceilings and between beams and walls in human-built structures as roosts (Fenton et al. 1994). These human-build structures appear to sustain larger colonies than natural roosts and the use of these structures can alter bat-bat and bat-human contact (Vivier and van der Merwe 2007, Lunn et al. 2023).

Mitigating human health risks and supporting urban wildlife conservation

Pathogen sharing between people, domestic animals, and wildlife:

Urban wildlife interact directly and indirectly with humans and domestic animals. This presents challenges for public health because some urban wildlife, such as flying-foxes (Box 2.2) and rodents, harbor a variety of zoonotic diseases, and because people are more likely to come into close contact with wildlife in urban areas. Examples of human exposure to pathogens from urban-living wildlife include West Nile virus (a mosquito-borne virus amplified by birds) (Talbot et al. 2019), Hendra virus (harbored by flying foxes and uses horses and dogs as bridge hosts) (Playford et al. 2010), and *Borrelia burgdorferi*, the causative agent of Lyme Disease (a tick-borne disease with urban animals serving as maintenance hosts) (Heylen et al. 2019). Urban environments can select for more bold and aggressive animals (Lapiedra et al. 2017, Baxter-Gilbert et al. 2019, 2021), which can lead to more frequent direct interactions between these individuals and humans. For example, black kites (*Milvus migrans*) in urban areas of Japan attack humans for their food (Galbreath et al. 2014). If aggression also predicts infection status, these individuals might contribute disproportionately to zoonotic spillover risk.

From the opposite direction, humans and domesticated animals can introduce novel pathogens into wildlife populations, with devastating consequences for wildlife health. For example, canine distemper virus (CDV) introduced into free-ranging lions, likely attributed to viral spillover from local high density domestic dog populations, contributed to severe declines in lion populations, with one epidemic killing ~30% of lions in the Serengeti Ecological Region (Roelke-Parker et al. 1996, Carpenter et al. 1998, Viana et al. 2015). Some species, such as American white ibis (*E. albus*), can become acclimated to and specialize on using urban parks for foraging and other activities (Teitelbaum et al. 2020b). These parks offer higher contact rates with people who actively feed the birds, and contact with water sources contaminated with sewage and domesticated animal waste, thus potentially exposing the birds to generalist pathogens such as *Salmonella spp.* (Hernandez et al. 2016, Murray et al. 2018). While mathematical models predict that specializing on urban habitats can slow the spread of pathogens acquired by wildlife into natural habitats (Teitelbaum et al. 2022), they also point to the pivotal role of individuals that readily switch between urban and non-urban habitats in moving pathogens from domestic into wild hosts.

Human-wildlife interactions in urban environments present ample opportunity for bidirectional pathogen sharing between species. For example, white-tailed deer (*Odocoileus virginianus*) in close proximity to humans have become infected with SARS-CoV-2 from multiple distinct human-deer transmission events (Hale et al. 2022). The virus is able to circulate within free-ranging deer populations, suggesting that white-tailed deer could serve as wildlife reservoirs of SARS-CoV, and viral variants originating in deer have been shown spill back over into humans (Feng et al. 2023). While many studies have explored the roles of human behavior and wildlife behavior in the circulation of zoonotic pathogens within species (Bidaisee et al. 2013, Craft 2015, Hirsch et al. 2016, Yadana et al. 2023), studies that simultaneously quantify behaviors of people and wildlife that lead to risky human-wildlife contact are urgently needed (Table 2.1).

Recommendations for management:

As urban areas continue to expand and human-wildlife interactions become more frequent and widespread, conservationists and urban planners could be increasingly tasked with managing infection risk for humans and wildlife. One possible solution is restoring and protecting natural or nonurban environments to keep wildlife out of cities, as habitat loss and food shortages can drive wildlife into urban areas (Eby et al. 2023). However, keeping wildlife out of cities is impractical in most situations, and urban areas provide important habitat when natural habitats are degraded or destroyed (McKinney 2008). Therefore, designing urban areas in ways that meet the needs of both humans and wildlife while also mitigating behavioral changes that increase infection risk is crucial. Urban space planners can focus on creating wildlife-friendly spaces that maintain natural and infection-avoiding behaviors urban wildlife, while simultaneously reducing exposure risk (Combs et al. 2022).

When designing wildlife-inclusive spaces, one way to limit deleterious behavioral changes associated with infection risk is to consider the entire life-cycle of the focal species (Apfelbeck et al. 2020) to preserve natural behaviors. Anthropogenic food sources or ornamental plants that modify natural movements of wildlife should be properly managed to minimize impacts on urban wildlife ecology. For example, proper waste management can prevent aggregation around food resources and the consumption of anthropogenic food (Barrett et al. 2014). For monarch butterflies, cutting back non-native tropical milkweed (*Asclepias curassavica*) in pollinator gardens in the winter can help preserve natural migration behavior and reduce infection risk (Satterfield et al. 2015, 2016). Similarly, while it may be impossible to fully eliminate anthropogenic food sources, minimizing access to anthropogenic food can promote natural behaviors. For example, urban red-winged Starlings (*Onychognathus morio*) on a university campus with fluctuating periods of human presence modified their behavior to spend more time foraging on natural food sources when students were absent and food outlets were closed (Stofberg et al. 2019). This suggests that even short-term changes in the availability of human-provided food can encourage wildlife to consume natural food sources when available, mitigating physiological effects of poor-quality anthropogenic food and subsequent effects on susceptibility and infection risk. These approaches for limiting deleterious behavioral changes in urban wildlife will require a combination of public outreach and education to change human behavior, including signage and public service announcements, and the potential enforcement of penalties or other disincentives.

In some cases, habitat managers can use existing knowledge of behavioral phenotypes in wildlife populations to their advantage. Some researchers (see Honda et al. 2018) argue in support of ‘personality management’ instead of population management to mitigate disease risk in these highly populated urban areas by selectively culling the most bold individuals and select for shy individuals that are less likely to interact with humans. This can minimize human-wildlife interactions to prevent disease transmission between humans, wildlife, and domestic species. Similar principles can be applied to populations that are vaccinated or treated for infectious diseases (e.g., Rushmore et al. 2014) to reduce disease prevalence within urban populations where vaccines are distributed to individuals that are most likely to interact with others. A combination of these approaches should be considered when managing infection risk for humans and wildlife in urban areas.

Future priorities for behavior-parasitism research in urban environments

Empirical studies that simultaneously examine animal behavior and parasitism in cities and suburbs are crucially needed to identify drivers of pathogen exposure and better predict future infection risk. Given that parasite infection (or risk of parasite exposure) can also influence the behavior of both uninfected and infected individuals (Behringer et al. 2006), research that explores urbanization as a driver or disruptor of behavior-parasitism feedbacks could yield critical insights into wildlife disease and zoonotic exposure risk in human-dominated landscapes (summarized in Table 2.2). These studies will be enhanced by technological advances for tracking and analysis of animal movements, remote monitoring of wildlife physiological processes (heart rate, body temperature, stress), and pathogen detection and diagnostics.

We advocate for field studies of behavior-infection linkages along gradients of urbanization, combined with multi-factorial experiments that manipulate multiple aspects of the urban environments, to understand the mechanisms underlying associations between parasitism and behavior. Such empirical research can in turn inform the development of mathematical models that explore the consequences of urbanization on behavior and parasitism over ecological and evolutionary timescales. Work is especially needed to examine the evolutionary consequences of urbanization on behavior-parasitism feedbacks, including how pathogens evolve in response to wildlife behavioral changes in cities. Another important question involves identifying human and wildlife behavioral attributes that influence interspecific contact and spillover risk, and how human perceptions of infection risk from urban wildlife influence attitudes towards urban wildlife conservation.

A better understanding of how multi-species interactions (e.g., community ecology) change in response to urban wildlife behavior is crucial for understanding the dynamics of multi-host pathogens, which disproportionately account for emerging infectious diseases worldwide. Similarly, cities might support novel species assemblages of wildlife and change host community composition and even host microbiome composition in ways that can enhance the spread of some pathogens and limit the transmission of others. Taking a broad view of the diverse ways in which urbanization using a variety of tools and host systems will allow future studies to further our understanding of the ways in which urbanization impacts wildlife behavior and the transmission of infectious diseases.

Acknowledgements

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Tables, Boxes, and Figures:

Box 2.1. Behavioral variation and behavior-infection feedbacks as a framework for understanding wildlife disease in urban environments

Individual variation in fixed components of animal personality, such as exploration and boldness, and context-dependent expression of behaviors, such as movement and foraging decisions, can lead to heterogeneity in the ability to acquire and transmit pathogens (host competence for infection) (Dizney and Dearing 2013, Ezenwa et al. 2016). In turn, the infection status of individuals (or perception of infection risk) can influence the expression of behaviors relevant to transmission, leading to reinforcing or regulating feedbacks that determine population-level infection outcomes (Hawley and Ezenwa 2022). Understanding how components of urban environments, from food subsidies to artificial light, noise, or contaminant pollution, influence behavioral variation and infection-behavior feedbacks, is a useful framework for studying the drivers and consequences of infectious diseases in urban wildlife.

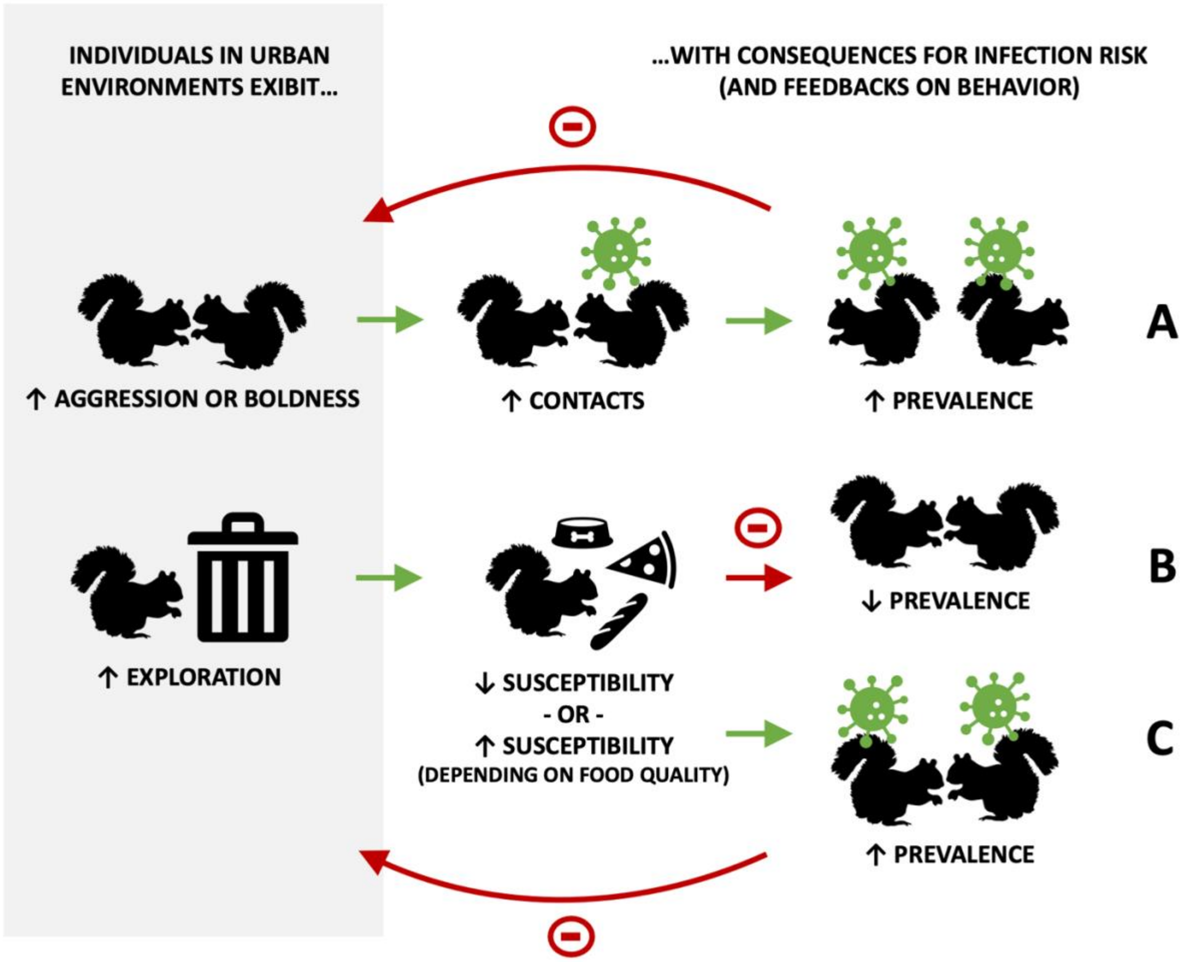


Figure 2.1 Schematic showing how urbanization influences the frequency of behavioral types (left column), the implications for components of transmission (middle column) and the consequences for infection prevalence in urban (relative to non-urban populations) (right column). The red arrows indicate how urbanization could alter how infection influences the expression of behaviors, resulting in feedbacks that influence transmission patterns. Letters A-C correspond to pathways by which urbanization influences the bidirectional relationship between behavior and infection.

First, urbanization can alter behavioral variation and the relative importance of focal individuals in contributing to infection transmission. For example, urban environments can favor animals exhibiting behavioral syndromes that allow successful exploitation of novel anthropogenic resources, resulting in a higher proportion of bold, exploratory, aggressive individuals (Lapiedra et al. 2017, Baxter-Gilbert et al. 2019, 2021). Since anthropogenic food sources are often provided at predictable locations, this can lead to crowding and more frequent aggressive interactions that promote transmission of close-contact transmitted pathogens (see Figure 2.1 pathway A). Alternatively, if access to resources decouples behavioral syndromes, reducing the expression of aggressive behaviors, or if those individuals able to exploit anthropogenic food receive nutritional benefits that improve immunity, selection for exploratory individuals in urban environments could reduce pathogen transmission (see Figure 2.1 pathway B).

Second, urbanization could also how infection influences behaviors relevant to transmission. In natural environments, infection behaviors such as self-isolation can decouple behavioral syndromes if sick individuals are less aggressive or less exploratory (Poulin 2013, Hawley et al. 2021). However, access to urban resources could alter the expression of such sickness behaviors with implications for transmission. For example, lethargy induced by infection is associated with infected house finches to spending more time at bird feeders, increasing their contributions to transmission at feeding stations (see Figure 2.1 pathway C; Adelman and Hawley 2017). Similarly, if animals with access to urban resources better tolerate infection, they might be less likely to express transmission-reducing behaviors such as isolation, potentially increasing transmission (Henschen and Adelman 2019). More studies are needed to understand how urbanization alters infection-behavior feedbacks.

Box 2.2. Australian flying-foxes as a case study of behavioral changes and pathogen transmission in urban environments

A well-studied example in which urbanization alters animal behavior with consequences for local and regional infection dynamics involves Australian flying-foxes (*Pteropus spp.*) and Hendra virus. Pteropus bats are reservoir hosts for numerous highly pathogenic viruses of human health concern (Mackenzie et al. 2003, Hayman et al. 2013), including Hendra virus (Field et al. 2001), which is a morbillivirus that causes mild infections in bats but is highly lethal to horses and humans. Since use of urban sites brings bats into close proximity to humans and horses, creating more opportunities for viral spillover events (Plowright et al. 2011), understanding the mechanisms underlying urban flying fox behaviors relevant to transmission is crucial to designing management strategies.

Urban environments alter roosting and foraging behaviors, with consequences for infection transmission. Urban gardens offer predictable year-round food sources for flying-foxes. Tracking studies comparing foraging and roosting behavior of urban and rural grey-headed flying-foxes (*P. poliocephalus*) have shown that bats exhibit higher site fidelity to urban roosts, and that bats using urban roosts forage over shorter distances (Meade et al. 2021). This results in urban roosts being larger and more permanent than natural roosts (Markus and Hall 2004,

Spectacled Flying-foxes near a backyard in Queensland, Australia. Photo by Noel Preece.

Eby et al. 2014), which is predicted to increase pathogen transmission between roosting bats (Laughlin et al. 2019, Lunn et al. 2021). Further, foraging in urban areas is associated with higher exposure to contaminants such as heavy metals, and higher ectoparasite loads (Sánchez et al. 2022). Sub-lethal effects of contaminant exposure that alter foraging behavior and susceptibility to infection could reinforce feedbacks favoring urban roost fidelity and high transmission (Sánchez et al. 2020), motivating additional research on how infection status and contaminant loads alter foraging preferences and movement capacity.

Urban foraging preference and site fidelity can reduce the frequency of long-distance nomadic movements, with opposing outcomes for infection spread and outbreak potential. Mathematical models suggest that reduced frequency of long-distance movements by individuals could reduce outbreak frequency by reducing spread of the virus among bat camps. However, reduced connectivity of bat populations arising from limited movements increases the time between outbreaks; waning immunity in previously infected animals can then increase susceptibility to Hendra virus in these populations and lead to larger outbreaks following viral reintroduction (Plowright et al. 2011). It remains unknown whether active or prior viral infection influences movement decisions of individuals or collective abandonment of roosts, and how potential tradeoffs between infection and long-distance movement are mediated by access to urban resources; such knowledge can be critical for understanding whether urbanization promotes or inhibits landscape-level spread (Becker et al. 2018).

Leveraging information on drivers of bat behavior in urban areas shows promise for mitigating zoonotic risk in Australia and other regions. Careful work has linked stable urban resources, seasonal food shortages, and natural habitat loss to bat roosting, foraging and nomadic movement behavior and Hendra virus shedding (Plowright et al. 2015, Eby et al. 2023, Baranowski and Bharti 2023). This has led to policy-based recommendations to restore natural bat habitat as a key strategy in recovering natural foraging behaviors and reducing urban colonization by bats and preventing nutritional stress. Technological advances in tracking and biologging are increasing our ability to understand linkages between individual demography status (e.g. age, sex, reproductive status), health (e.g. immunity and infection status) and behavior (e.g. personality, foraging or dispersive movements). Quantifying this individual variation could further optimize outbreak surveillance and monitoring, or interventions targeted at individuals or colonies predicted to contribute disproportionately to spread.

Table 2.1. Examples and mechanisms illustrating how behavioral changes associated with urbanization can influence host-parasite dynamics in a diverse array of host and parasite taxa. Photo credits: Black-tufted marmoset photo by Luiz Carlos Rocha (CC-BY 2.0), Wood frog photo by Memer15151 on Wikimedia Commons (CC BY-SA 4.0), American white ibis and monarch butterfly photos by Cali Wilson.

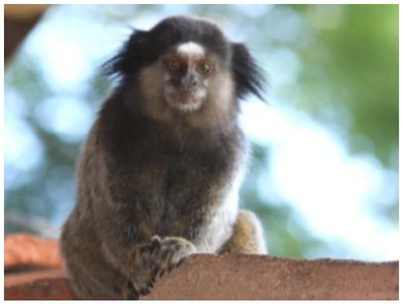
	Host and parasite(s)	Behavioral change(s) due to urbanization	Implications for infection risk
	Black-tufted marmoset (*Callithrix penicillata*) and *Leptospira interrogans*	Urban marmosets descend to the ground more frequently while searching for food in urban environments where they beg for food from humans (Duarte et al. 2012) and come in contact with sewage overflow and other contaminants (Wilson et al. 2021).	Zoonotic diseases (including *L. interrogans*) have caused severe pathology and mortality in urban black-tufted marmosets (Wilson et al. 2021, Sousa et al. 2023).
	Wood frog (*Lithobates sylvaticus*) and trematodes (*Ribeiroia ondatrae* and *Echinostoma trivolvis*)	Wood frog larvae exposed to road salt in urban areas had reduced anti-parasite behaviors (i.e., they did not increase activity in the presence of trematode cercariae which is an effective way to reduce infection) (Milotic et al. 2017).	Trematode infection was highest in Wood frogs exposed to medium and high levels of road salt (Milotic et al. 2017).
	American white ibis (*Eudocimus albus*) and *Salmonella spp.*	Ibis consume anthropogenic foods sometimes directly from the hands of humans (Hernandez et al. 2016, Murray et al. 2018) and provisioning correlates with larger flock sizes, higher density of birds and increased aggression events (see Chapters 3 and 4).	Urban ibis have higher prevalence of *Salmonella* (Hernandez et al. 2016).
	Monarch butterfly (*Danaus plexippus*) and *Ophryocystis elektroscirrha* (OE)	The consumption of human-planted non-native milkweed is associated with the formation of resident populations of monarchs that forego their long-distance migrations (Satterfield et al. 2015, Majewska et al. 2019, Majewska and Altizer 2019).	Resident populations are heavily infected with OE. Infection prevalence is higher in non-migratory resident monarch populations (Satterfield et al. 2015)

Table 2.2. Outstanding questions and future research priorities for advancing our understanding on the implications of urban behavioral modifications on infectious disease dynamics.

Evolutionary consequences of urbanization on behavior-parasitism feedbacks

- How is pathogen evolution shaped by host behavioral responses to urbanization?
- Could wildlife behaviors evolve in response to altered pathogen risk in cities?
- How is host and pathogen coevolution in urban environments shaped by animal personality traits?

Integrating human and wildlife behavior at the urban zoonotic interface

- How do behavioral traits of urban wildlife (e.g. tameness) influence human-wildlife interactions and infection risk?
- What attributes of human behavior predict close contact with wildlife in cities?
- How do perceptions of infection risk from urban wildlife influence human use of urban spaces, and attitudes towards urban wildlife conservation?

Urbanization, behavior and communities of microbes and parasites

- How do host behavioral changes in cities influence (or get influenced by) their microbiomes, and how do these influence host susceptibility to infection?
- How does urbanization influence feedbacks between behavior and parasite coinfection?
- Does the behavior of urban wildlife result in a simplification or shift in parasite communities?

Urbanization effects on behavior of vector-borne and complex lifecycle parasites

- How does vector foraging behavior change in response to urbanization? Do these changes align with host behavioral changes or cause mismatches (e.g., in peak activity times)?
- How does urbanization influence parasite manipulation of intermediate hosts? How do dietary shifts in definitive hosts alter exposure to trophically transmitted parasites?

CHAPTER 3

HUMAN-PROVIDED FOOD INCREASES AGGREGATION BUT DOES NOT CHANGE ACTIVITY BUDGETS IN AN URBAN WADING BIRD[2]

[2]Wilson CA, Hernandez SM, Weil JN, Ezenwa VO, Altizer S, Hall RJ.

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Abstract:

In urban areas, animals often aggregate at higher density, move less, and alter their diets to consume anthropogenic food, all of which can affect wildlife health and the transmission of infectious diseases. However, it is unknown whether short-term changes in behavior associated with urban resources scale up to more pervasive long-term behavioral changes across landscape types. In this study, we used observational field data to explore how food provisioning affects behaviors relevant to parasite transmission in American white ibis (*Eudocimus albus*), a waterbird that has recently habituated to urban habitats and anthropogenic food. We found that ibis flock densities more than doubled during short intervals when birds were actively provisioned with food. We then explored activity budgets among urban sites with different levels of provisioning, and found that foraging time decreased with flock size and provisioning levels. Lastly, we compared ibis behavior in more natural wetland sites against urban sites, and found minimal to no differences in behaviors measured here. These results suggest that urbanization and provisioning alter ibis behaviors in ways that could influence for example, exposure to parasites in the short-term, but this has not yet resulted in significant long-term changes in activity budgets. Further studies of how urbanization and intentional feeding influences wildlife behavior can inform management strategies to benefit both wildlife and human health.

Introduction

Urbanization influences wildlife behavior in many ways (Lowry et al. 2013, Sol et al. 2013), including through the availability of supplemental food either provided intentionally through direct feeding of wildlife or unintentionally through, for example leaving refuse available to birds (Oro et al. 2013). The spatial and seasonal reliability of human-provided food can lead animals to alter or abandon natural foraging behaviors, aggregate around supplemental food sources, increase site fidelity, and reduce seasonal and long-distance movements (reviewed in Satterfield et al. 2018). For example, migratory white storks (*Ciconia ciconia*) that naturally feed on invertebrates, fish, amphibians, and small mammals (Antczak et al. 2002, Profus 2006, Ciach and Kruszyk 2010) have formed resident populations in Spain where birds now feed year-round at landfills (Tortosa et al. 1995, Massemin-Challet et al. 2006). Wildlife also aggregate in higher numbers around anthropogenic food subsidies (Hidalgo-Mihart et al. 2006, Aberle et al. 2020), which could increase the frequency of interactions with conspecifics and other species. For example, raccoons (*Procyon lotor*) that are typically solitary, cluster around clumped food resources in experimental feeding plots, leading to higher contact rates between individuals (Wright and Gompper 2005). Supplemental food could also drastically decrease the time animals spend foraging, freeing up time for other activities such as grooming and resting (Agostini et al. 2023). Lastly, habituation to human contact (as facilitated by regular feeding) can increase human-wildlife interactions (Altmann and Muruthi 1988, Orams 2002, Cox and Gaston 2018). Since behavioral changes associated with food provisioning could negatively impact wildlife health and increase human-wildlife conflict, understanding behavioral responses of wildlife to supplemental feeding is crucial for the conservation and management of urban-dwelling wildlife.

Importantly, behavioral responses of wildlife to food subsidies can alter the transmission of pathogens (Bradley and Altizer 2007, Becker et al. 2015, Murray et al.

2016) and increase the risk of pathogen spillover between wildlife and humans (Plowright et al. 2015). Instantaneous responses to food (e.g., increased aggregation around resources) can affect exposure to both close-contact (e.g., respiratory parasites or ectoparasites) and fecal-oral transmitted parasites. For example, higher raccoon contact around experimental food plots increased the prevalence of endoparasites, including raccoon roundworm, *Baylisascaris procyonis* (Wright and Gompper 2005). Changes to activity budgets that alter time spent foraging in urban areas could affect exposure to fecal-oral parasites (Lane et al. 2011). Similarly, decreased time allocated to foraging was shown to increase time spent on behavioral defenses (grooming) in urban rhesus macaques (*Macaca mulatta*) in Bangladesh, potentially reducing ectoparasite loads (Jaman and Huffman 2013). Despite significant progress to date in understanding how human-provided food affects wildlife-pathogen interactions (Sorensen et al. 2014, Becker et al. 2015, Murray et al. 2016), studies are crucially needed to examine behaviors with potentially opposing effects on transmission, and across both shorter and longer timescales - especially in more recently urbanized species that harbor novel parasites of concern to humans or domesticated species.

American white ibis (*Eudocimus albus*) are well-suited for studying the effects of human-provided food on behaviors relevant to parasite transmission. Historically, white ibis foraged on aquatic invertebrates and small fish in natural wetlands (Kushlan 1979). Like other waterbirds, including gulls and ducks, ibis have acclimated to feeding in urban environments and on carbohydrate-rich human-provided food, such as bread. Over the last three decades, ibis have become increasingly common in urban areas in south Florida where they forage in parks, golf courses, and managed wetlands; have habituated to human presence; and are often actively fed and will tolerate hand-feeding (Hernandez et al. 2016, Murray et al. 2018, Kidd-Weaver et al. 2020). Additionally, ibis host a variety of microbes, including those of human health concern, such as avian influenza virus (Bahnson et al. 2020, Christie et al. 2021) and West Nile virus (Silva Seixas et al. 2022). Urban white ibis have been found to have higher prevalence of the enteric bacteria *Salmonella* spp., but lower ectoparasite loads compared to their natural wetland counterparts (Hernandez et al. 2016, Murray et al. 2018). Differences in parasite prevalence and burdens across landscape types might be influenced by differences in ibis behavior due to urbanization and human-provided food. In the wake of a major outbreak of highly pathogenic avian influenza in North America (Bevins et al. 2022, Teitelbaum et al. 2023), it is integral to understand how artificial aggregation of wildlife in urban settings can impact pathogen dynamics.

Here, we used observational field data to explore how food provisioning affects ibis behavior in ways that are relevant to parasite exposure (e.g. contact behavior and foraging) and behavioral defenses against ectoparasites (e.g. grooming). We first asked whether there are immediate, short-term effects of provisioning on ibis density by experimentally feeding ibis flocks. We then asked whether these effects are detectable on longer time scales by conducting focal observations of ibis and comparing behavior across urban parks with different levels of provisioning activity. We hypothesized that birds in larger flocks would spend less time being vigilant and that foraging time would decrease with provisioning frequency. Lastly, we compared ibis behavior in wetland sites (with no provisioning) against provisioned urban sites. We hypothesized that urban birds would spend less time foraging owing to the presence of anthropogenic food, allowing more time for other behaviors such as vigilance or grooming. Exploring the effects of human-provided food on ibis behavior at multiple scales is crucial for predicting changes in the transmission of pathogens, and can help wildlife managers develop appropriate guidelines to maximize benefits and minimize risks to wildlife and people.

Methods

Study sites:

Field data were collected from eight locations in Palm Beach County, Florida (Figure 3.1) classified as either 'urban' or 'natural' sites. In this paper, we followed Teitelbaum et al. (2020) and considered natural habitats to be non-urban habitats that maintain the historical structure and function of local ecosystems, even if these habitats are managed by people. Urban field data were collected from five locations with human-provided food where large numbers of ibis are regularly observed year-round. The five urban sites were separated by a minimum distance of 6 km and four contained water bodies, lawns, and picnic areas. The fifth site was a shopping center parking lot containing a small pond and grass area. Sites differed in average ibis flock size, human visitation frequency, and wildlife feeding frequency. Since ibis using natural areas move nomadically to track water levels suitable for foraging, our natural field data were collected from three wetlands with managed water levels where ibis are reliably encountered.

Behavioral data collection:

(1) Urban flock provisioning experiment:

To collect data on ibis density during experimental feeding events, we mounted a GoPro camera on a self-standing frame approximately 5m above the ground and baited an ibis flock (defined here as a distinct group of birds who travel and interact together) using bread (Set-up shown in Supplemental Figure A1). We baited the ibis flock to the camera area and once the flock was under the camera, threw bread directly under the camera for five minutes while recording. Videos were collected at 4 urban sites during June and July 2019, February 2021, and July 2021. Individual ibis were tracked using ImageJ Manual Tracking Plugin (Schneider et al. 2012) for the duration of the video in which they were in frame. Birds were excluded if they were in the frame for less than 30 seconds. Frames were approximately 33 sq. m in area. For each tracked focal individual, density estimates were recorded by counting the number of individuals within a 1m radius of the focal bird, at five equally spaced time points during the duration of the video in which the entire 1m radius around the focal bird was in frame (i.e., the bird was not close to the edge of the frame).

(2) Urban flock observational study:

We conducted 10-minute behavioral observations (hereafter referred to as 'focal follows') of adult ibis using the iOS application Animal Observer when flocks were not actively being fed by humans. Focal follows were conducted by selecting an individual adult ibis in a flock to observe. Caution was taken to avoid observing the same individual more than once during a day. Focal follows with less than two-minute durations were excluded from analysis. Most focal follows were conducted between 08:00-10:00 each morning. Each site was sampled across 2-3 observation days, with repeat visits in subsequent weeks on different weekdays. If a member of the public started to feed the ibis, focal follows were stopped and were not started again until approximately 10 minutes after feeding concluded to allow the flocks to return to normal behaviors.

State behaviors recorded during focal follows included drinking, flying, foraging, grooming, sleeping or resting, vigilance, walking, and response to disturbances (Table 3.1). Additionally, we recorded the number of other ibis within a 1m radius of the focal bird at the start and end of the observation interval, and any direct contact events that occurred during the focal follow. We also recorded flock size multiple times (approximately every 30 minutes) while conducting focal follows and recorded the number of individual people and the number of groups of people that we observed feeding the ibis with bread, crackers, etc. We calculated the provisioning frequency for each site and observation day by dividing the number of groups observed feeding ibis by the total observation time. Qualitative notes were taken on the duration of feeding and type of anthropogenic food.

(3) Urban vs wetland flock observations*:*

To determine whether activity budgets differ between urban and natural wetlands, behavioral data were collected using scan sampling (Altmann 1974). Scans were collected at the three natural sites and corresponding observations were taken at an urban site directly following the natural scan or the next day at approximately the same time of day. Three urban sites were chosen for a balanced comparison and sites were selected based on feasibility for conducting scan sampling. All scans were collected between 08:30-17:30 and were carried out every 10 minutes until the flock was no longer visible (e.g., hidden by the landscape or flushed from the area). This resulted in 1-8 scans per observation period.

Scans were conducted by recording the activity of all visible ibis over a 30-120 sec interval depending on the size of the flock. Behaviors were recorded via dictation to notetaker or voice recording, and included grooming, foraging, being vigilant, resting (bill tucked under feathers), walking, bathing and other (Table 3.1). We imposed a 5-sec delay before recording vigilance or walking behaviors to ensure the individual was not actually foraging, grooming, or resting. All scans were collected by one observer to prevent observer bias and flocks were observed from a distance (typically at least 15m) to avoid influencing the birds' behavior.

Statistical Analyses:

All data analyses were performed using R version 4.1.2 (R Core Team 2021). For the urban flock provisioning experiment, we predicted that density in ibis flocks would increase when the flock is actively being fed compared to when ibis are foraging naturally in the environment. To test this hypothesis, we compared flock densities while ibis were 'behaving naturally' (i.e., not actively being provisioned) during focal follows and when ibis were actively being fed during video recordings. We averaged 1m density estimates for each focal individual and compared the mean number of individuals within 1 m radius of each focal bird for provisioned and not provisioned birds. We used a Wilcoxon rank sum test because it does not assume a normal distribution or equal variance among groups. Although Wilcoxon rank sum tests do not allow us to account for other potential covariates (e.g., total density in a flock, or time of day), we compared actively provisioned observations and 'natural foraging' focal follow observations for the same sites during similar times of day to control for potential differences.

We focused our analysis of urban flock observational data on the extent to which flock size and provisioning influence the three most common behaviors: foraging, grooming, and vigilance. We modeled the time spent performing each behavior as a function of the covariates, using zero-inflated negative binomial generalized linear mixed models with a log link function. Fixed covariates were *flock size* (continuous) and *provisioning frequency* (continuous), and their interaction (*flock size x provisioning)*. Because flock size was recorded multiple times during an observation period, we paired each focal follow with the flock size measurement taken at the time closest to the start of the focal follow. To adjust for differences in the duration of time an individual was observed, an offset term of *observation duration* was included in the regression equation to model each behavior as a proportion of total observation time. The zero-inflation portion of the model was set to ~1 to assume a constant probability for obtaining a false zero, because false zeros are likely due to the experimental design (e.g., birds were not observed for enough time to observe all behaviors rather than birds truly never performing a specific behavior). To control for inherent differences in ibis behavior at different urban sites not attributed to flock size or provisioning, we used *site* as a random intercept effect. Exploratory analyses revealed that using *site* as a random effect had no impact on model comparison ranking, so we elected to include it in all models despite it only having 5 levels. Predictor variables were standardized for ease of effect comparison. Models were fitted using R package `glmmTMB` (Brooks et al. 2017).

We used the Akaike information criterion (AIC) to select best fitting candidate models for each response variable (Table 3.2). All models within two AIC values of the best fitting models were considered best fit models and results for these models are reported in Supplemental Table A1 when the best fit model was not the null model. Model assumptions were verified by plotting residuals versus fitted values and versus each covariate in the model using R package `DHARMa` (Hartig 2022). Model validation indicated no problems for the two top performing foraging models. We obtained coefficient estimates, standard deviations, z-values, and p-values for each parameter in the top performing foraging models (Supplemental Table A1).

To compare ibis activity budgets in urban parks and natural wetlands, we first calculated the average proportion of the flock doing each behavior by averaging scans for each observation period. We performed a two-sample t-test on each of the behaviors to determine whether behaviors differed by site type (urban or natural) if the assumptions of the statistical test were met. If the data were not normally distributed with equal variance, we conducted a Wilcoxon rank sum exact test. Significance was set at alpha = 0.05 with Bonferroni corrections applied to correct for multiple comparisons.

Results

(1) Experimental feeding in urban parks:

Density estimates for 117 individual birds from 17 provisioning trial videos were combined with 164 individual bird density observations from urban park focal follows.

Analysis showed significantly more conspecifics within 1m of focal birds while being actively provisioned (Wilcoxon rank-sum test, $Z=-10.24$, $P < 0.0005$, Figure 3.2). On average, ibis density increased by 205% when ibis were provisioned, or from 2 ibis within 1m of a focal bird to 7 ibis within 1m of a focal bird.

(2) Urban site focal follows:

Excluding focal follows lasting less than 2 minutes and without corresponding provisioning data resulted in 150 focal follows spanning a total duration of 22.22 hours (average of 8.88 minutes per follow). At least two different behaviors were observed during any given focal follow, and on average, each bird performed 3.8 different behaviors during an observation. Cumulatively, ibis spent the most time being vigilant, foraging, and grooming.

We built a series of statistical models to determine whether flock size, provisioning frequency, or their two-way interaction influenced foraging, grooming, or vigilance time. The two top performing models for foraging time both included flock size and provisioning as main effects, and one of the two models included the interaction between flock size and provisioning (Table 3.2). Foraging models showed that as provisioning frequency and flock sizes increase, time spent foraging decreases (Figure 3.3, Supplemental Table A1). In contrast, the null model (comprising only the random effect *site*) was the best fitting model for both grooming and vigilance (Table 3.2), with no evidence for effects of provisioning and flock size.

(3) Urban vs wetland site flock scans:

Flock sizes recorded from scans in urban (n = 9) and natural wetland (n = 8) sites ranged from 5 to 134, with an average of 30.24 birds per flock. Flock sizes did not differ between site types (unpaired two-sample Wilcoxon rank sum exact test, Z= -0.59, p = 0.28).

Ibis were most frequently observed foraging, grooming, and being vigilant at both urban and natural wetland sites (Figure 3.4, panel 6). We found no site-type differences in the proportion of ibis in a flock observed foraging (Welch Two-sample t-test with Bonferroni correction, t = 1.81, p-adjusted = 0.49), grooming (Welch Two-sample t-test with Bonferroni correction, t = -0.72, p-adjusted = 1.00), resting (Wilcoxon rank sum exact test with Bonferroni, Z= 0.24, p-adjusted = 1.00), or being vigilant (Welch Two-sample t-test with Bonferroni correction, t = -2.40, p-adjusted = 0.16). A larger proportion of urban birds were observed walking relative to wetland birds (Wilcoxon rank sum exact test with Bonferroni, Z= -2.83, p-adjusted = 0.01).

Discussion

Within urban parks, white ibis flock densities more than doubled during short intervals when birds were actively provisioned with food. In contrast, among urban sites with varying levels of food provisioning by park visitors, the effects of provisioning on site-level differences in behavior were less pronounced. Time spent foraging decreased with flock size and provisioning levels, but we observed no change in other behaviors measured here. When comparing activity budgets and flock sizes in provisioned urban sites to natural wetland settings, we observed minimal to no differences between site types. Taken together, these findings suggest that food provisioning by humans influences ibis aggregation and foraging activity over short timescales, with potential implications for the transmission of close-contact parasites – but has not yet resulted in significant long-term changes in ibis flock sizes or daily activity budgets.

An important outcome of our study was to document the dramatic increase in ibis density during active food provisioning. Past work on other species suggested that food provisioning leads to aggregation around resources (Wright and Gompper 2005, Hidalgo-Mihart et al. 2006), and our study directly quantified these density changes associated with feeding events. Crowding around food sources can facilitate the spread of infectious diseases by increasing contact rates important for transmission (Wright and Gompper 2005). For example, songbirds captured at sites with backyard bird feeders had higher prevalence of clinical disease compared to birds captured in areas without feeders, likely due to increased density and contact at feeders (Wilcoxen et al. 2015). In white ibis, increased contact resulting from higher density could enhance the transmission of close-contact parasites like avian influenza, and fecal-oral parasites such as *Salmonella* spp., especially if flocks are continuously fed in the same area (e.g., always next to the water). This heightened transmission in urban areas could also impact ibis in more natural settings as some ibis are known to move between habitat types (Teitelbaum et al. 2020b).

A second key finding of this study was that provisioning in urban parks can reduce the amount of time ibis spend foraging, particularly at sites that have higher rates of supplemental feeding. Interestingly, the reduced foraging time does not seem to lead to significant increases in time spent doing any single behavior, such as vigilance (important for predator escape) or grooming (important for ectoparasite removal). We had initially expected that larger groups would allow individuals to rely more on the vigilance of flock mates, reducing personal vigilance investment (Pulliam 1973, Roberts 1996). However, in urban populations, ibis engage in vigilance not only to scan for predators, but also for humans who might feed them. Additionally, risk perception can affect vigilance time, which might decline as more time lapses without the appearance of a predator (Elgar 1989). Since adult ibis have few known predators, especially in urban areas, they may not remain on high alert for potential threats. Because past work showed that ibis that consumed more human-provided food had lower ectoparasite scores (Murray et al. 2018), we expected to find higher grooming activity at sites with more human-provided food. However, it is possible that other traits of urban habitats, such as warmer temperatures in urban environments (Castaño-Vázquez et al. 2018, Wemer et al. 2021), could impact ectoparasites or perhaps ibis are grooming at times of the day not captured by observational intervals in this study.

Despite the decrease in foraging time among ibis flocks in urban parks due to provisioning, we did not observe significant changes in activity budgets between urban and wetland sites. Previous studies indicated that provisioning or the presence of humans does not necessarily result in altered activity budgets among animals (Orams 2002, McKinney 2011, Back and Bicca-Marques 2019, Stofberg et al. 2019). It is possible that ibis activity budgets were largely similar between urban and natural settings owing to potential mixing between ibis groups, with birds from wetland sites also visiting urban parks at other times or days of the week (Kidd-Weaver et al. 2020, Teitelbaum et al. 2020b). Further research incorporating a wider range of wildlife species and behaviors along urban-natural gradients, especially focusing on newly urbanized and highly social animals, is needed to better understand how animals adapt or acclimate to urban habitats.

Additionally, observing animals over longer time periods might reveal subtle differences in activity budgets. In this study, we were unable to observe birds for longer durations of time due to birds flying away or moving into dense vegetation.

While provisioning can lead to short-term behavioral changes such as crowding around food resources, our results show that predicting the consequences for flock sizes and activity budgets at larger spatial and temporal scales is not straightforward. Importantly, past work on ibis movement behavior showed that birds captured at more urban sites had greater site fidelity and moved shorter distances than birds captured at less urban sites (Kidd-Weaver et al. 2020, Teitelbaum et al. 2020b). Given urban expansion and wetland degradation, we expect wading birds like ibis to increasingly use urban sites, necessitating scientifically informed guidelines to sustain wildlife and human health. Adhering to feeding guidelines, such as irregular intervals, different locations, and providing higher quality food, could help mitigate aggregation around food, limit potential disease spread, and potentially prevent further behavioral changes in this highly urbanized species (Murray et al. 2016). In conclusion, our study emphasizes the importance of urban habitats for white ibis and their ability to adapt to and utilize anthropogenic resources. However, more research is needed to understand the behavior of wildlife along urban-natural gradients to make more comprehensive comparisons and draw broader conclusions.

Data availability

The data and code that support the findings of this study are currently openly available on GitHub at https://github.com/caliwilson/Ibis_behavior.git. These materials will be deposited in DRYAD prior to final submission to the *Journal of Urban Ecology*.

Acknowledgements

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This work was reviewed and approved by the University of Georgia's Institutional Animal Care and Use Committee (Permit #: A2019 10-009-Y1-A0) and a Palm Beach County Parks and Recreation permit.

Tables and Figures:

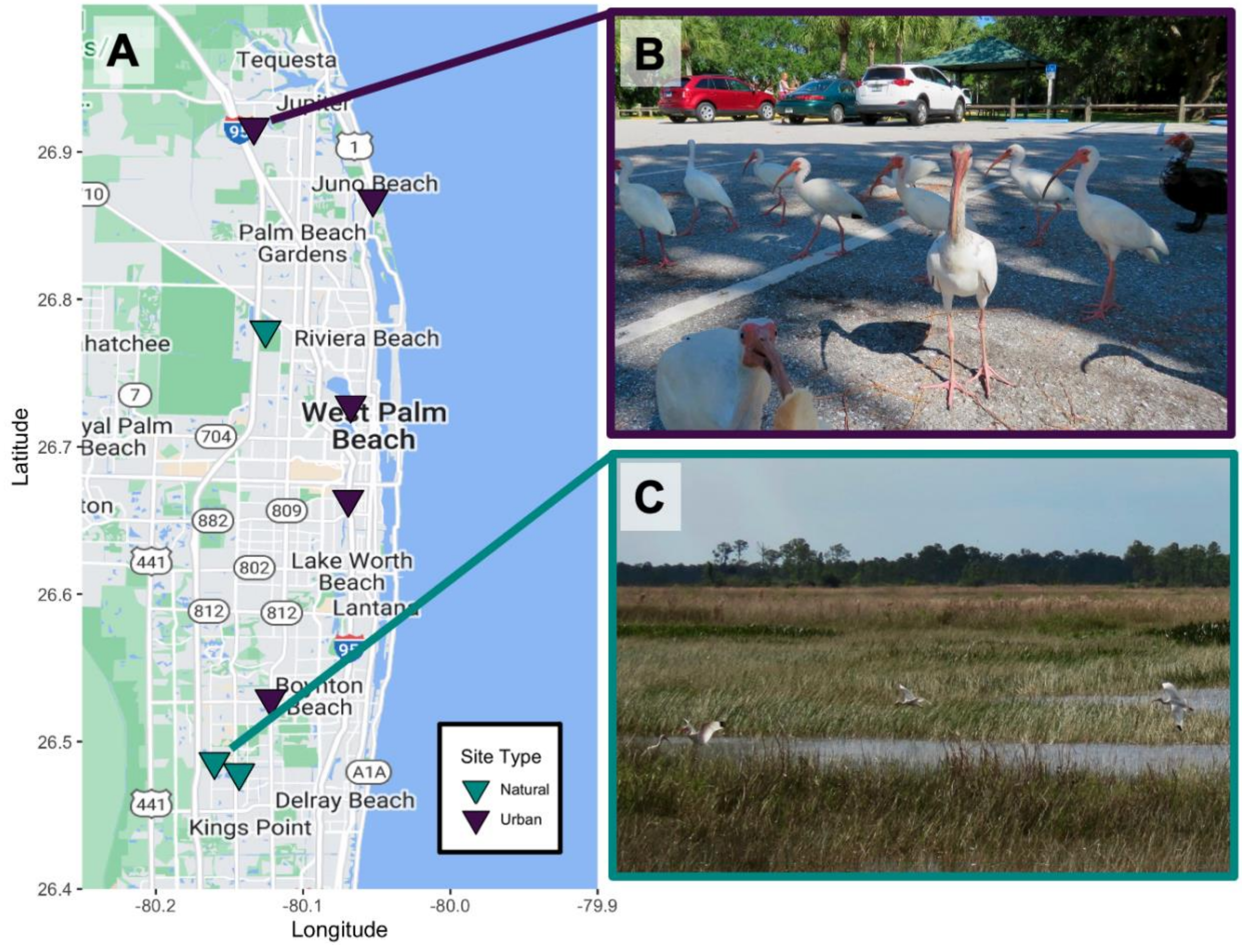

Figure 3.1 A) Map of field sites in Palm Beach County, Florida, USA. Triangle color indicates site type with natural wetland sites in teal and urban sites in purple. Examples of American white ibis flocks in B) urban and C) natural wetland sites. The urban flock (panel B) shows American white ibis along with feral muscovy ducks (*Cairina moschata*) eating bread out of the researcher's hand. The example flock in the wetland (panel C) shows American white ibis flying and foraging in the wetland.

Table 3.1 Descriptions of behaviors observed during focal follows and scan sampling of white ibis flocks.

Sampling Type	**Behavior**	**Description**
Focal follows	Disturbance Response	Moving away from disturbance via flying up and away or walking/running away
Focal follows	Drinking	Taking sip of water and tipping head back to swallow
Focal follows	Flying	Flying
Focal follows; scan sampling	Foraging	Eating behavior; probing with bill
Focal follows; scan sampling	Grooming	Using feet or bill to scratch body or run bill through feathers to clean AND/OR submerging body in water and shaking clean
Focal follows; scan sampling	Asleep/Resting	Sitting on legs and/or bill tucked into body; eyes may be closed
Focal follows; scan sampling	Vigilant	Not moving but head is up and alert
Focal follows; scan sampling	Walking	Walking while not probing for food items

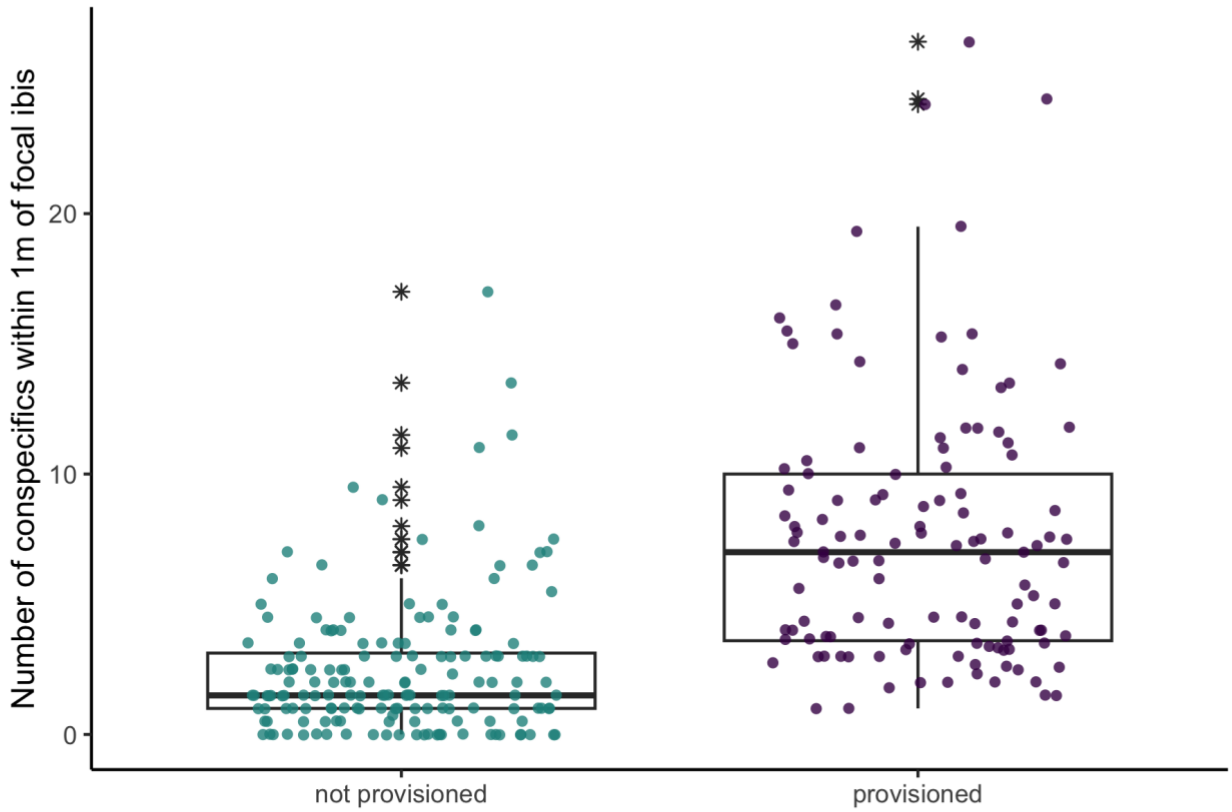

Figure 3.2 Number of conspecifics within 1m of a focal bird while ibis are provisioned (right, purple) or not provisioned (left, blue). The thicker horizontal line indicates the median, the box encompasses the first and third quartiles, the whiskers extend to 1.5 times the interquartile range, and outliers are detonated with asterisks.

Table 3.2 Complete list of zero-inflated negative binomial generalized linear mixed effect models testing the effect of provisioning and flock size on each behavior, with *site* as a random effect (best performing models did not differ and estimates were similar when site was excluded). Null models contain only the random effect *site*.

Foraging Candidate Models

Model	K	AIC	Δ AIC	ModelLik	AICWt	LogLik	Cum.Wt
provisioning + flock size + (1|site)	6	1567.219	0.000000	1.0000000	0.4603299	-777.6095	0.4603299
provisioning * flock size + (1|site)	7	1569.121	1.901545	0.3864425	0.1778910	-777.5603	0.6382209
flock size + (1|site)	5	1569.594	2.374851	0.3050054	0.1404031	-779.7969	0.7786240
provisioning + (1|site)	5	1569.842	2.623076	0.2694053	0.1240153	-779.9211	0.9026393
null + (1|site)	4	1570.326	3.107042	0.2115019	0.0973607	-781.1630	1.0000000

Grooming Candidate Models

Model	K	AIC	Δ AIC	ModelLik	AICWt	LogLik	Cum.Wt
null + (1|site)	4	1545.776	0.0000000	1.0000000	0.4200894	-768.8879	0.4200894
flock size + (1|site)	5	1546.623	0.8474312	0.6546100	0.2749948	-768.3116	0.6950842
provisioning + (1|site)	5	1547.742	1.9657806	0.3742279	0.1572092	-768.8708	0.8522934
provisioning + flock size + (1|site)	6	1548.494	2.7177867	0.2569450	0.1079399	-768.2468	0.9602332
provisioning * flock size + (1|site)	7	1550.491	4.7148714	0.0946627	0.0397668	-768.2454	1.0000000

Vigilance Candidate Models

Model	K	AIC	Δ AIC	ModelLik	AICWt	LogLik	Cum.Wt
null + (1|site)	4	1796.749	0.0000000	1.0000000	0.3405399	-894.3743	0.3405399
provisioning + (1|site)	5	1796.914	0.1650839	0.9207728	0.3135599	-893.4569	0.6540997
flock size + (1|site)	5	1798.384	1.6356869	0.4413825	0.1503083	-894.1922	0.8044081
provisioning + flock size + (1|site)	6	1798.500	1.7508891	0.4166767	0.1418950	-893.2498	0.9463031
provisioning * flock size + (1|site)	7	1800.443	3.6943541	0.1576817	0.0536969	-893.2215	1.0000000

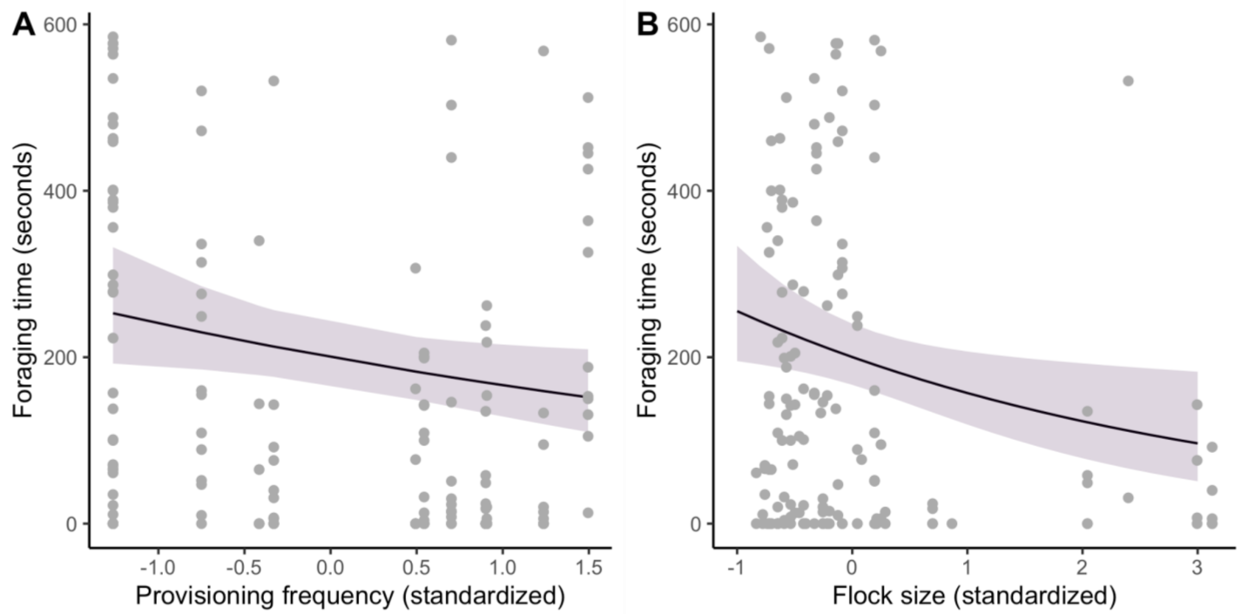

Figure 3.3 Results of the best fit zero-inflated negative binomial GLMM testing the effect of provisioning frequency (panel A) and flock size (panel B) on foraging time. Gray points show observed foraging values, solid line shows model output predictions, and purple shading shows model 90% confidence intervals.

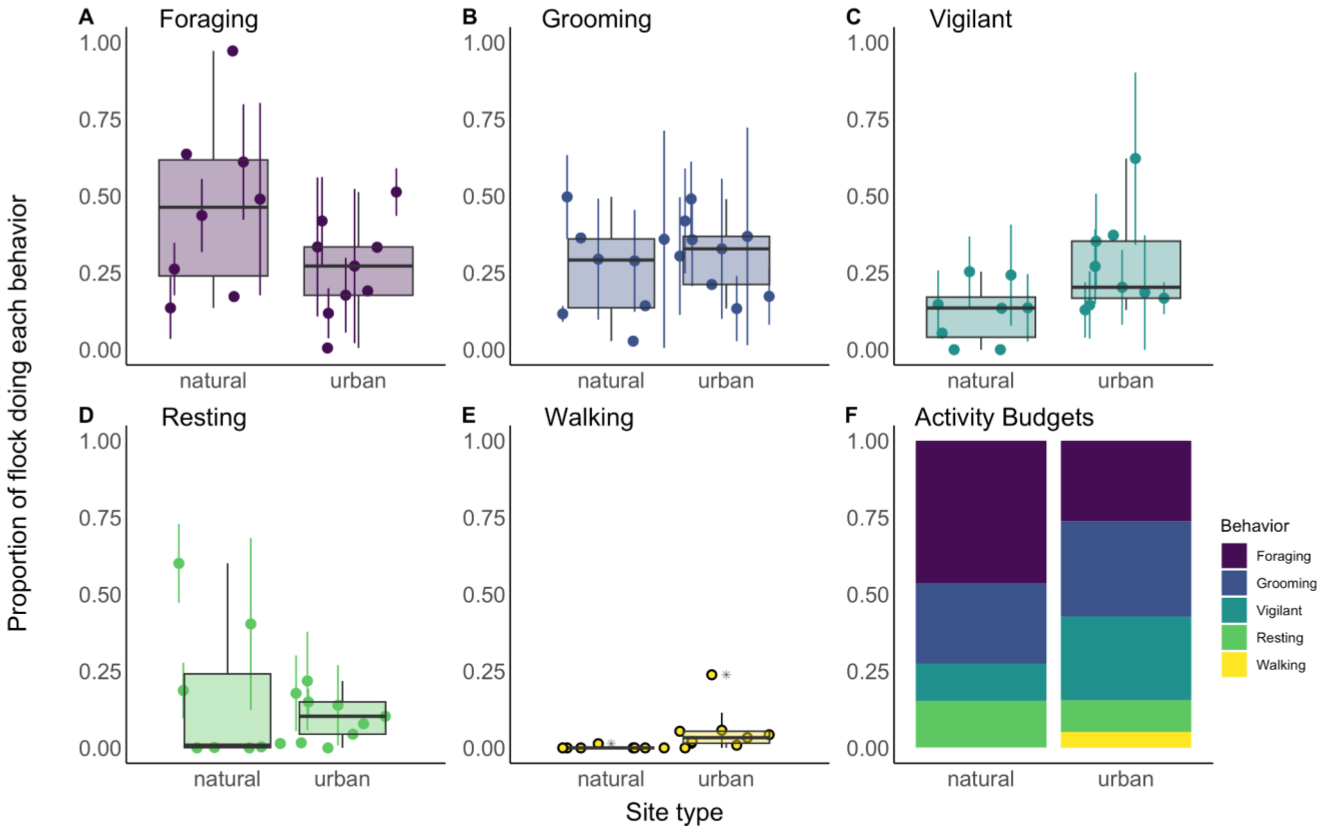

Figure 3.4 Proportion of flock observed performing each behavior (panels A through E) at natural wetland sites or urban sites. Individual points represent mean values and bars indicate standard deviation for each day/site combination. Panel A through E box plots where the thicker horizontal line indicates the median, the box encompasses the first and third quartiles, the whiskers extend to 1.5 times the interquartile range, and outliers are detonated with asterisks. Last panel (F) shows the average proportion of the flock observed doing each behavior in natural (left) and urban (right) settings. Colors represent each behavior.

CHAPTER 4

ANTHROPOGENIC FOOD PROVISIONING DRIVES AGGRESSION IN AN URBAN-DWELLING WADING BIRD[3]

[3]Wilson CA, Weil JN, Altizer S, Hall RJ.

To be submitted to *IBIS*.

Abstract

Urbanization has dramatically altered natural habitats worldwide, having profound effects on wildlife health, behavior, and human-wildlife interactions. Animals with certain behavioral types (e.g., bold or exploratory individuals) may be better suited to the stressors of urban environments and better able to exploit anthropogenic resources, such as human-provided food. Additionally, human-provided food can drastically alter wildlife interactions by changing time spent foraging, increase human-wildlife interactions, and lead to aggregations around resources. Both urbanization and food provisioning are often associated with increased aggression, but the drivers behind these mechanisms are not well understood. In this study, we explored drivers of aggression in urban American white ibis (*Eudocimus albus*), a waterbird that has recently habituated to urban habitats and feeds on human-provided food in south Florida. We used a combination of observational field data and experimental feeding trials to quantify aggressive interactions while ibis are foraging in urban areas and when they are actively being provisioned with anthropogenic food. We found significantly more aggressive interactions per second and a higher percentage of total birds observed being aggressive when actively being fed compared to when birds were not actively being fed. We then asked whether density immediately surrounding a focal bird, total flock density, an individual's distance from the anthropogenic food, or the interaction between these variables best predicted the frequency of aggression. We found that distance from anthropogenic food and density (either flock or local) were the best predictors of aggression in urban ibis. Our results indicate that even short-duration and well-intentioned provisioning of wildlife in urban settings increases the frequency of

aggressive behaviors that could negatively impact wildlife and lead to human-wildlife conflict.

Introduction

Urban areas are expanding, resulting in loss and fragmentation of wildlife habitat, as well as creating new environments for wildlife to inhabit. The stable resources and milder climates of urban areas can be attractive to some wildlife, but to access these benefits, they must also adapt to novel stressors such as light pollution and mortality hazards such as glass buildings and traffic (Longcore and Rich 2004, Andrade et al. 2021, Farnsworth et al. 2024). Animals with certain behavioral types (e.g., bold or exploratory individuals) may be better suited to the stressors of urban environments (Lowry et al. 2013), but these behaviors can also lead to negative interactions with people, including damage to plantings and property, aggression towards people and pets, and human exposure to pathogens (Blackwell et al. 2016, Honda et al. 2018). Understanding how wildlife behaviors are shaped by aspects of the urban environment is therefore critical for predicting how wildlife can persist in human-modified landscapes and for reducing human-wildlife conflicts.

One way in which urbanization impacts wildlife is through the availability of anthropogenic food, either provided intentionally through people feeding wildlife in parks and backyards or unintentionally through access to trash cans and landfills. People feeding wildlife is common and widespread in urban settings, with over half of US households regularly providing food for wildlife (Martinson and Flaspohler 2003, Robb et al. 2008, Oro et al. 2013). Feeding wildlife can allow humans to have meaningful interactions with wildlife (Dayer et al. 2024) and wildlife can benefit when natural food is scarce. However, anthropogenic food can drastically alter wildlife ecology in ways that can negatively impact wildlife health (Murray et al. 2019). The consumption of anthropogenic food can negatively impact body condition and potentially expose wildlife to toxicants and pathogens (Blanco et al. 2017, Murray et al. 2019). Accessing human-provided food often brings individuals into extremely close contact with conspecifics and leads to novel species interactions (Polis et al. 1997, Oro et al. 2013). Aggregation around food sources can have a range of negative impacts on individuals, from competitive interactions to increased risk of predation or infection (Wright and Gompper 2005). These interactions may be especially intense when people provide food sporadically (such as throwing bread to birds in a visit to an urban park) relative to continuous food sources such as bird feeders, but surprisingly little is known about how these short-duration feeding events influence social interactions.

Urban foraging is often associated with increased aggression (Lacy and Martins 2003, Baxter-Gilbert and Whiting 2019), but the underlying mechanisms are poorly understood. In some species, food subsidy has been proposed as a driver of elevated aggression (e.g. (Foltz et al. 2015, Fountain and McDonald 2022). Aggressive behaviors such as threat-posturing, chasing or physical contact, may arise as a plastic response to the aggregated nature of supplemental food. Aggressive behaviors may be needed for securing access to (or defending) point food sources (Lanna et al. 2017). Alternatively, social animals may have evolved elevated or reduced aggression as a response to high conspecific density in natural settings, and therefore higher densities of conspecifics due to crowding around food might be the driver of altered aggression (Parker and Nilon

2008, Łopucki et al. 2021). Finally, aggression might be driven by factors other than food or conspecific density or might be part of a fixed behavioral syndrome of urban individuals, where a combination of traits favorable to urban living (such as boldness and exploratory behavior) may be linked with aggression (Dingemanse and Réale 2005). Understanding what drives aggression around urban food subsidies could be crucial for developing management guidelines and interventions around feeding sites.

American white ibis (*Eudocimus albus*), a common wading bird of the southeastern United States, are an ideal species for exploring the effects of urbanization and provisioning on aggression. Historically, white ibis foraged on aquatic invertebrates and small fish in natural wetlands (Kushlan 1979). Over the last three decades, ibis have acclimated to feeding on carbohydrate-rich human provided food in urban parks in flocks containing tens to occasionally hundreds of birds (Kushlan 2011, Hernandez et al. 2016, Murray et al. 2018). They have become increasingly more common in urban areas in south Florida where they forage in parks, golf courses, and managed wetlands, have habituated to human presence, and will often tolerate hand feeding (Hernandez et al. 2016, Murray et al. 2018, Kidd-Weaver et al. 2020).

Here, we recorded aggressive interactions in American white ibis in urban parks, using observations of focal birds foraging naturally and video analysis of birds being actively hand-fed. We first asked whether active provisioning increased the frequency of aggressive interactions, predicting that the average aggression frequency in flocks being actively hand fed would be higher than when flocks were foraging naturally. Next, we capitalize on fine-scale video data to explore drivers of individual variation in aggression in birds being actively fed. For each focal bird in the flock being fed, we calculated two metrics of conspecific density (flock-level and local density around focal birds) and the focal bird's average distance from the food source. We hypothesized that higher flock-level and local conspecific densities, and closer proximity to food, would predict increased frequency of aggressive behavior.

Methods

<u>Study Sites:</u>

Field data were collected from five locations in Palm Beach County, Florida, where ibis flocks are regularly observed year-round and people are commonly seen feeding ibis (Figure 4.1A). The five urban sites were separated by a minimum distance of 6 km and four contained water bodies, lawns, and picnic areas. The fifth site was a shopping center parking lot containing a small pond and grass area but had similar characteristics to the four urban parks (e.g., grass, water body, regular human-provided food). Flock observational studies were done at all 5 sites; however, we were only able to collect urban provisioning video data from 4 of the 5 sites as one site did not have a large enough pavement area to set up the video apparatus without disrupting park visitor parking.

<u>Data Collection:</u>

(1) Urban flock observational study:

We conducted 10-minute behavioral observations (hereafter referred to as 'focal follows') of adult ibis using the iOS application Animal Observer when flocks were not actively being fed by humans. In this study, we define flock as a distinct group of birds who travel and interact together and only observe flocks greater than 5 individuals. Focal follows were conducted by selecting an individual adult ibis in a flock to observe. Caution was taken to avoid observing the same individual more than once during a day. Focal follows with less than thirty-second durations were excluded from analysis. Most focal follows were conducted between 08:00-10:00 each morning. Each site was sampled across 2-3 observation days, with repeat visits in subsequent weeks on different weekdays. If a member of the public started to feed the ibis, focal follows were stopped and were not started again until approximately 10 minutes after feeding concluded to allow the flocks to return to normal behaviors. We recorded the number of aggressive interactions instigated by the focal bird observed during the follow. Aggressive behaviors included performing threat postures, pecking, chasing, or attacking another ibis. Focal follows were conducted at all 5 urban sites (Figure 4.1A) during June and July 2019.

(2) Urban flock provisioning experiment:

To collect data on ibis aggression during experimental feeding events, we mounted a GoPro camera on a self-standing frame approximately 5m above the ground and baited an ibis flock (defined here as a distinct group of birds who travel and interact together) using bread (Figure 4.1). We baited the ibis flock to the camera area, and once the flock was under the camera, threw bread directly under the camera for five minutes while recording. Bread slides were broken up into approx. 2 inch pieces and thrown to the birds approx. every 5 seconds, which was generally how long it took for the birds to eat the piece that was previously thrown. Videos were collected at 4 urban sites (Figure 4.1A) during June and July 2019, February 2021, and July 2021. We randomly selected seven individuals to track per video by taking a screenshot of the video at the start of the bread-throwing, placing a numbered grid over the image, using a random number generator to choose which grid location to track a bird from. Individual ibis were tracked using ImageJ Manual Tracking Plugin (Schneider et al. 2012) for the duration of the video in which they were in frame. Birds were excluded if they were in the frame for less than 30 seconds. Frames were approximately 33 sq. m in area.

For each focal bird, we recorded the number of aggressive interactions instigated by the focal bird divided by the duration of time that the focal individual was in the frame of the video to estimate the number of aggressive interactions (as defined above) per second. Because we do not know at which scale ibis perceive conspecific density, we calculated two metrics of density. For each tracked focal individual, we recorded local density estimates by counting the number of individuals within a 1m radius of the focal bird, at five equally spaced time points during the duration of the video in which the entire 1m radius around the focal bird was in frame (e.g., the bird was not close to the edge of the frame). Flock-level density was calculated by counting the total number of birds in frame divided by the area of the entire frame at each of the same five time points described above. We then calculated the average flock and average local density per bird as the mean of the five-point estimates of flock and local density.

To calculate the average distance each bird was from the food, we converted the ibis videos into image sequences set at 15 frames per second. Using the ImageJ Manual Tracking Plugin (Schneider et al. 2012), we tracked the position of the piece of food (bread) being thrown from the time it was thrown until it was consumed by an ibis or left the frame. Once the bread was consumed or removed from the area, another piece was thrown and tracked through time. We then calculated the Euclidean distance between the focal bird and the bread for each image slice and averaged all distances to find the average proximity to the food for each bird (Figure 4.2B).

Statistical Analyses:

All data analyses were performed using R version 4.1.2 (R Core Team 2021). At the flock level, we hypothesized that ibis would show a higher frequency of aggressive behaviors when flocks are actively being provisioned compared to when they are foraging naturally in urban environments. To test this hypothesis, we compared the proportion of focal birds observed being aggressive and the mean number of aggressive interactions per second when being actively provisioned and when ibis were behaving naturally in urban environments (e.g., not actively being provisioned). We used a chi-squared test to examine differences in the proportion of birds observed being aggressive and a Wilcoxon rank sum test to compare the mean number of aggressive interactions observed per second. A Wilcoxon rank sum test was chosen because it does not assume a normal distribution or equal variance among groups.

At the individual level, to explore potential drivers of aggression while birds are actively being fed, we modeled the number of aggressive interactions as a function of the different predictor variables using a negative binomial generalized linear model with a log link function. Predictor variables include *average distance from food*, *average local density*, and *average flock density* and pair-wise interactions between these variables. To adjust for differences in the duration of time an individual was observed, an offset term of *observation duration* was included in the regression equation to model each behavior as a proportion of total observation time. Models were fitted using R package `glmmTMB` (Brooks et al. 2017) and compared to a null intercept-only model. We used the Akaike information criterion (AIC) to select best fitting candidate models for the response variable (Table 4.1). All models within two AIC values of the best fitting models were considered best fit models. We obtained coefficient estimates, standard deviations, Z values, and P values for each parameter in all candidate models (Supplemental Table B1).

Results

Flock-level aggression provisioning comparison:

Excluding observations lasting less than 30 seconds resulted in observations of 161 focal follows of birds in naturally foraging flocks (i.e. not being provisioned), spanning a total duration of 23.0 hours (avg of 8.57 mins per follow) and 114 tracked birds in flocks being actively fed, spanning 6.36 hours (average of 3.35 mins per bird). Analysis showed significantly more aggressive interactions per second when flocks were being provisioned, with an average of 0.012 aggressive interactions per second when provisioned compared to 0.0005 aggressive interactions per second when not provisioned (Wilcoxon rank-sum test, $Z = -10.22$, $P = 2.6x10^{-10}$, Figure 4.3) than naturally foraging flocks. Similarly, the percentage of birds observed being aggressive was significantly higher in actively provisioned flocks (68.42%) compared to naturally foraging flocks (13.04%) ($\chi^2 = 88.83$, df = 1, $P = 4.29x10^{-21}$).

Predictors of individual aggression while being provisioned:

On average, birds had an average individual distance of 1.82 meters from the food while being provisioned with a minimum average distance of 0.38 meters and a maximum of 9.36 meters. The average flock density was 1.31 birds per square meter while average local density was 2.11 birds per square meter. We built a series of statistical models to determine whether distance from food, average local density, average flock density, or the interaction between these variables best predicted the average number of aggressive interactions observed while ibis were being provisioned. The results show two top performing model which both include the interaction between average distance from food and one measure of density- either local or flock density (Table 4.1). These models showed that ibis that were closer to the food (Figure 4.4A,C) and in higher flock (Figure 4.4C) or local (Figure 4.4D) density situations on average had more aggressive interactions. Average local density and average flock density did not do better than a random intercept null model at predicting average aggression (Table 4.1).

Discussion

Exploiting urban resources is associated with shifts in wildlife behavior including aggression, but how aggression is influenced by short-duration provisioning events, and what drives this response, is frequently unknown. Using focal follows and video tracking, we explored flock-level differences in aggression between naturally foraging and actively provisioned flocks, and further examined the roles of density and proximity to food in driving individual variation in aggression within flocks. We found that active provisioning increased aggression in flocks (both the frequency of aggressive interactions and the proportion of birds showing aggressive behaviors). Additionally, our model results show that aggression is higher for individuals that are closer to the food and when density (either flock or local) is high. Together, these results suggest that instantaneous provisioning can increase aggression, with implications for conservation and management of urban wildlife. However, further research is needed to untangle whether individual aggression responses to provisioned food are plastic or fixed behavioral attributes.

Our finding that feeding increases aggression frequency aligns with prior work in multiple taxa, but the role of conspecific density in driving aggression may be more system specific. For example, sporadic food provisioning in Congo tilapia (*Tilapia rendalli*) increased aggressive interactions by more than six times in comparison to a typically unprovisioned and lower density control population (Pereira and Bessa 2022). When ibis are being actively provisioned in parks, their local densities increase by 205% (Wilson et al. 2024, in revision, see Chapter 3) even though the total flock sizes are unchanged from when they are naturally foraging in these locations. Increased aggression associated with proximity to provisioned food and density could have wider consequences for wildlife health. Aggression is costly; aggressive events can result in physical injury, create opportunities for infectious disease transmission (Hamede et al. 2013), take time away from beneficial activities such as foraging or grooming, and lead to other physiological costs such as immunosuppression (Takahashi et al. 2018). However, provisioning may reduce energetic costs associated with aggression, and time constraints on foraging might not be as important when ample food is present, which may explain increased aggression found during active provisioning. Further studies are needed to understand how supplemental feeding influences the energetic costs of aggression and physiological changes.

Distance from food and density together being a main driver of aggression in ibis can help inform feeding management guidelines to mitigate human-wildlife conflict. Our findings support previous recommendations to spread out food provided at feeding stations for hunting, conservation or recreation (e.g., Murray et al. 2016). Our findings also suggest that direct hand-feeding of waterfowl in urban parks should be discouraged, since it could result in a higher frequency of aggressive interactions between ibis and other species or with people, potentially facilitating opportunities for cross-species disease transmission (Lonsdorf et al. 2011) and ibis are known reservoirs of zoonotic pathogens (Hernandez et al. 2016, Bahnson et al. 2020, Christie et al. 2021). In a related species with similar ecology, the Australian white ibis (*Threskiornis molucca*), habituation to foraging on anthropogenic food in cities has led to ibis being considered a nuisance species (Ross 2004, Martin et al. 2007), begging for food at cafes, obstructing aircrafts (Shaw 1999), and likely facilitating pathogen transmission between ibis and humans (Epstein et al. 2006). As American white ibis and other waterbirds, such as Wood Storks (*Mycteria americana*) (Picardi et al. 2020), are increasingly using urban sites, it is vital to provide the public with information about appropriate actions around urban wildlife to prevent them from becoming pest species.

While we were able to examine the ways in which density and distance from food predict aggressive interactions, there are some limitations in our study. In our study system it was not possible to uniquely identify all birds involved in interactions, and therefore it was impossible to detect variation in behavior associated with sex or age.

Further, limitations to automated tracking software in a natural setting with variable light conditions meant that tracks of focal birds had to be manually reconstructed. Improvements in automated tracking to simultaneously track multiple individuals combined with unique identifiers could tease apart individual consistency in these behaviors. Further, combining individual tracking with information on condition, stress and parasitism could yield further insights into the drivers and consequences of variation in aggression. Finally, for species amenable to focal follows in non-urban settings, the comparing aggression frequency between urban and natural sites could provide further insights into resource effects (for example, if food is less predictable in natural populations, food scarcity could induce aggression).

In conclusion, our results indicate that even short-duration and well-intentioned provisioning of wildlife in urban settings increases the frequency of aggressive behaviors that could negatively impact wildlife and lead to human-wildlife conflict. Given the inherent connection between these behavioral responses in wildlife and human behavior, there is an urgent need for integrated social-ecological research. This research should concurrently explore the motivations and emotional benefits to people that feed wildlife, along with the responses of responses of wildlife to establish guidelines that optimize the well-being advantages of engaging with wildlife while mitigating potential risks (Dayer et al. 2019, 2024).

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Tables and Figures

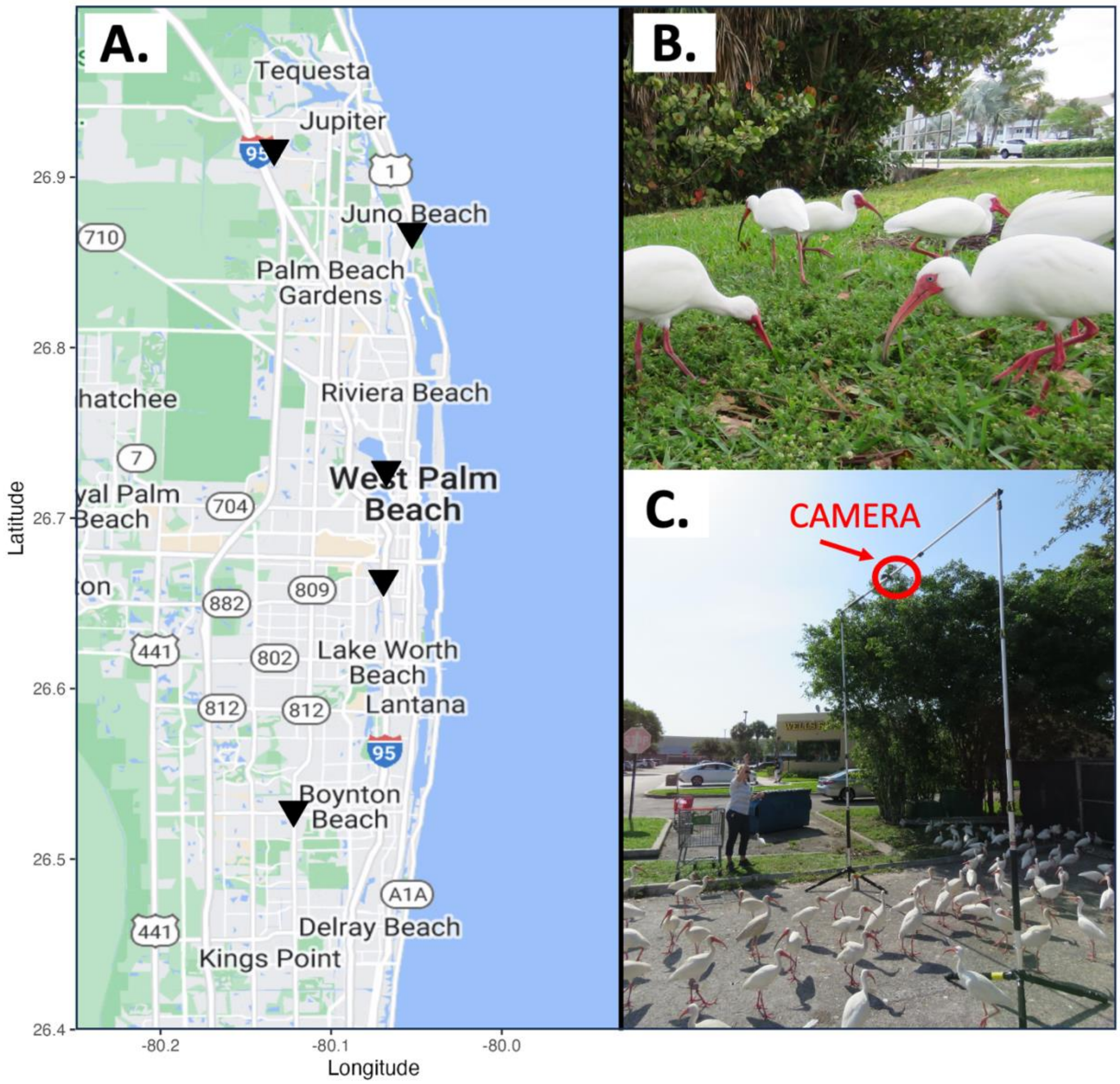

Figure 4.1. A) Map of field sites in Palm Beach County, Florida, USA. C) Photo of ibis flock foraging 'naturally' at an urban park. B) Photo of video camera set-up used to record ibis interactions while being actively provisioned.

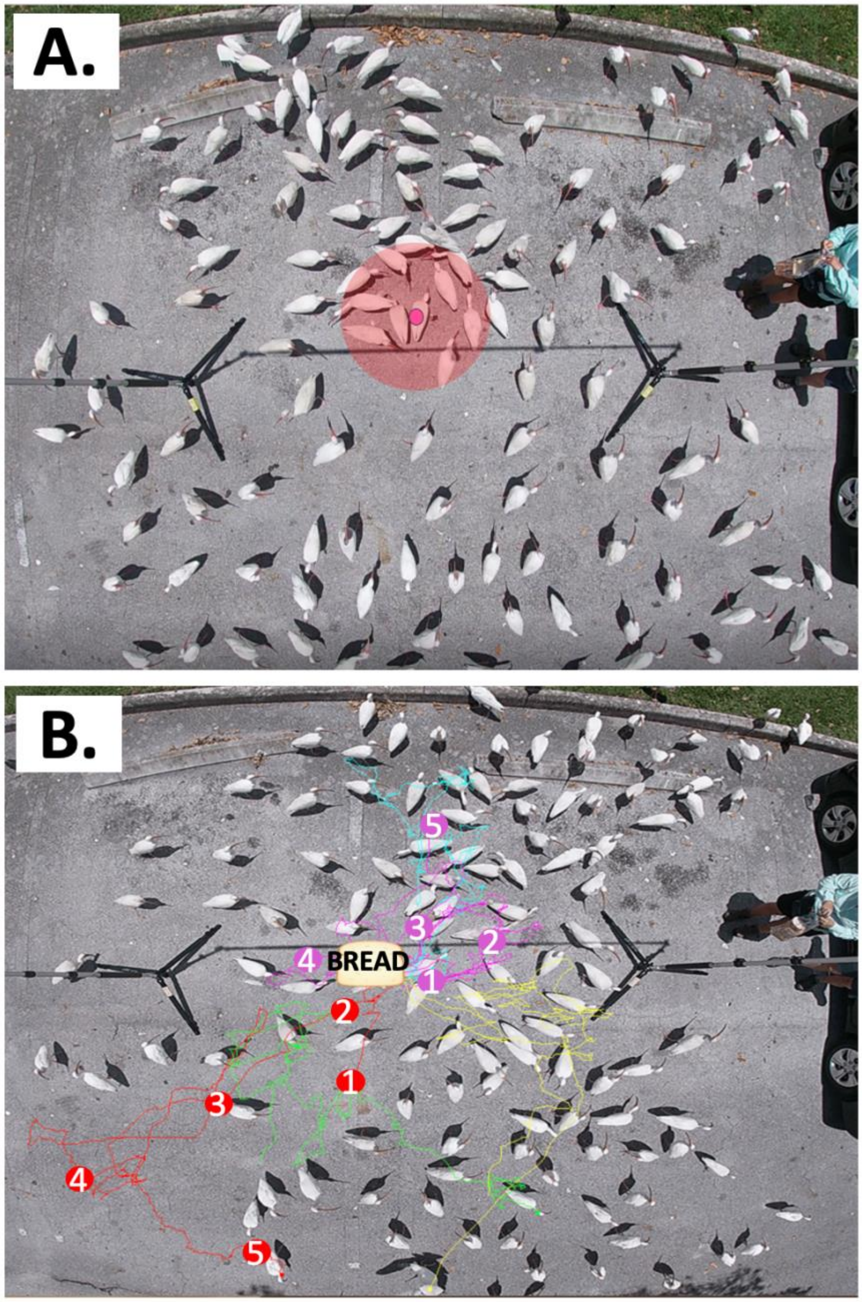

Figure 4.2. A still photo taken from the ibis provisioning videos showing A) how ibis density was quantified and B) how ibis individuals were tracked. A). Ibis local density was calculated by counting the number of individuals within a 0.5m radius around the focal bird (represented by red circle) and total flock density was calculated by counting the total number of individuals within the frame divided by the total frame area. B)

Example photo showing a snapshot of the bird tracking process where each color line represents the track of an individual bird and the colored circles with numbers represent the 5 points at which the birds distance from the bread was calculated.

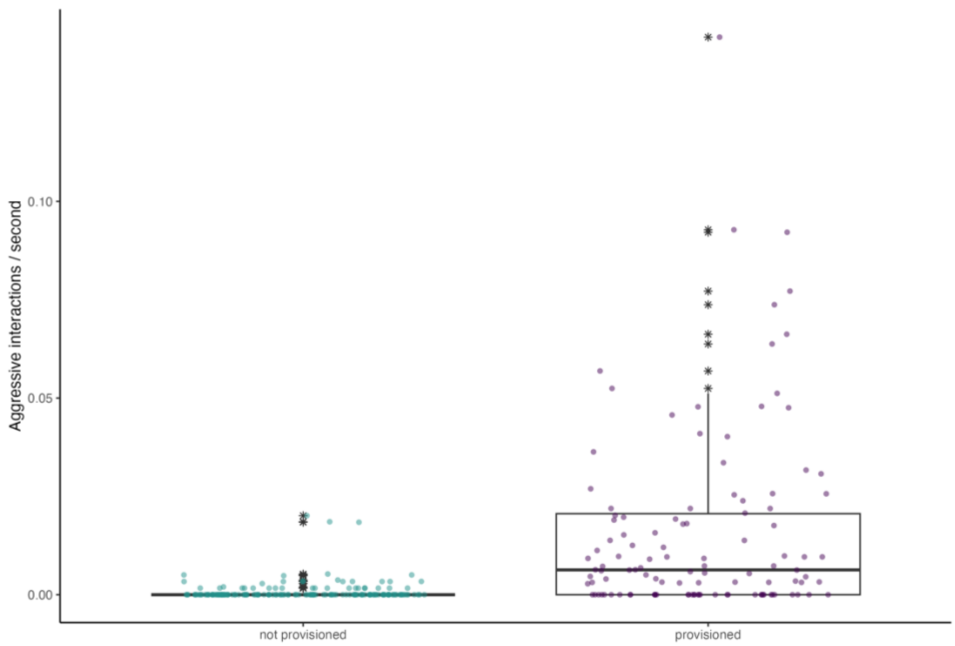

Figure 4.3. Number of aggressive interactions observed per second when birds are being actively provisioned (right, purple) and not provisioned (left, blue).

Table 4.1. List of negative binomial generalized linear models testing the effects of the average distance from food, local density, flock density, and interactions between these variables on the number of aggressive interactions observed in ibis. The null model is an intercept-only model.

Aggression Provisioning Candidate Models

	Model	K	AIC	Δ AIC	ModelLik	AICWt	LogLik	Cum.Wt
5	Average distance from food x Average flock density	5	485.42	0.00	1.00	0.66	-237.71	0.66
6	Average distance from food x Average local density	5	487.32	1.90	0.39	0.26	-238.66	0.92
4	Average distance from food	3	489.74	4.32	0.12	0.08	-241.87	0.99
7	Average flock density x Average local density	5	495.83	10.42	0.01	0.00	-242.92	1.00
1	Null (Intercept only)	2	498.37	12.95	0.00	0.00	-247.18	1.00
3	Average local density	3	499.87	14.45	0.00	0.00	-246.93	1.00
2	Average flock density	3	500.24	14.82	0.00	0.00	-247.12	1.00

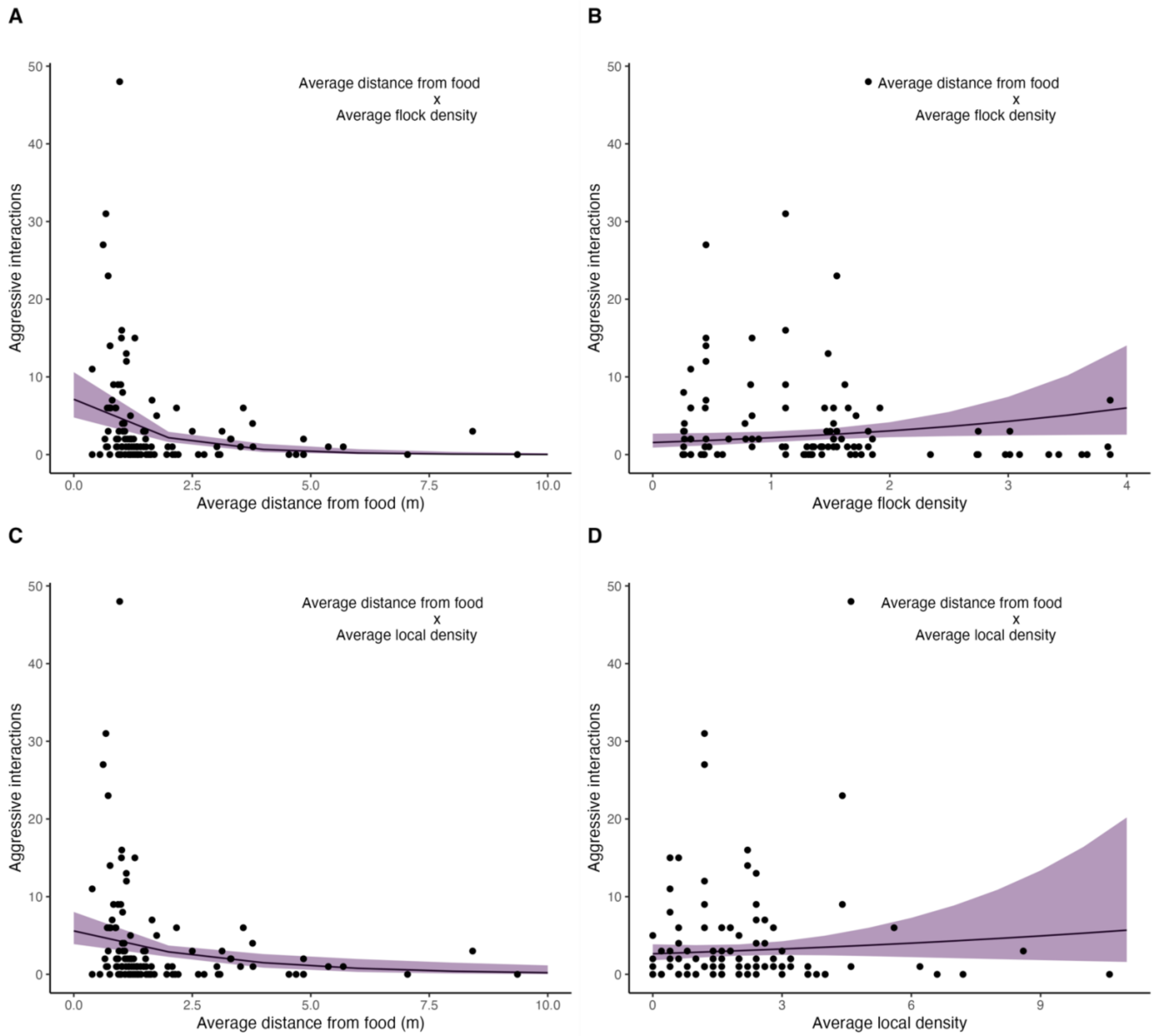

Figure 4.4. Results of the best fit negative binomial models testing the effect of average distance from food, average local density, and average flock density on aggression interactions. Black points show the observed aggressive interactions by each predictor variable, solid line shows model output predictions, and the purple shading shows the model 90% confidence intervals. Panel A and B show model outputs for the top performing model including the interaction between average distance from food (Panel A) and average flock density (Panel B). Panel C and D show model outputs for the

second top performing model including the interaction between average distance from food (Panel C) and average local density (Panel D).

CHAPTER 5

CONCLUSIONS

The overall goal of my dissertation was to investigate how urban environments affect the behavior of urban wildlife in ways that can influence the transmission of infectious diseases. I focused primarily on how anthropogenic food provisioning influences the behavior of urban wildlife, as provisioning is a common phenomenon that can impact both the health of wildlife and humans in diverse ways. I first conducted a literature review on the ways in which urbanization can influence behavioral variation relevant to infection risk and behavior-infection feedbacks, and synthesized current information to inform management guidelines and identify outstanding questions (Chapter 2). In subsequent chapters, I conducted field studies examining how urbanization and food provisioning influence American white ibis behaviors relevant to pathogen transmission at different scales, from short-duration aggregations around food provisioning events to activity budget comparisons across urban and rural sites. By studying behavior at multiple scales in a natural system, I showed that behavioral changes due to urbanization are scale- and context-dependent, and that differing responses of behaviors influencing pathogen exposure and susceptibility could have opposing outcomes for infection risk.

In Chapter 2, I synthesized recent findings of how urbanization alters diverse components of wildlife behavior and explored the consequences of these behavioral changes on host-parasite dynamics. I focused on how urbanization modifies foraging, long-distance movement, mating and off-spring rearing, and social interactions, as these behaviors can affect an individual's ability to acquire and transmit parasites, and infection can feedback to influence these behaviors. This chapter specifically demonstrates that behavioral responses to different components of urbanization can influence infection patterns in opposing ways and highlights that far fewer studies have explored how infection alters individual behavior in urban environments, with implications for host and pathogen coevolution in human-modified habitats. I outline a recent example of how research on Australian flying-fox roosting, foraging and movement behavior in relation to Hendra virus shedding has resulted in science-based guidelines to recover natural flying fox behaviors and reduce zoonotic exposure through restoration of natural habitats (Plowright et al. 2011, 2015, Eby et al. 2014, 2023). Motivated by this, I highlight behavior-based recommendations to reduce infection risk and problematic wildlife behaviors due to food provisioning and other components of urbanization. Finally, I call attention to some important knowledge gaps relating to urbanization effects on the behavior of disease-carrying vectors, parasitism in the context of multi-species interactions and microbial diversity, and the need to jointly study human and wildlife behavior in the context of pathogen sharing, especially during high-contact events such as handfeeding of wildlife.

In Chapter 3, I explored how urbanization and food provisioning affect the behavior of American white ibis in ways that are relevant to parasite exposure. An important outcome of our study was documenting the dramatic increase in ibis density during active food provisioning which could enhance the transmission of close contact parasites like avian influenza, and fecal-oral parasites such as *Salmonella spp*.

Mathematical models of pathogen transmission around food subsidies (e.g. Becker and Hall 2014) typically assume a constant supply of anthropogenic food and ignore temporal variation in conspecific density. This research suggests that estimates of wildlife density measured when wildlife are not being actively provisioned could underestimate transmission risk. It also highlights that incorporating short duration increases in host density due to feeding could be an important next step for developing predictive models of how active feeding of wildlife influences transmission dynamics. By comparing activity budgets of ibis in urban parks that differed in the amount of anthropogenic food provided, I found that time spent foraging decreased with increased provisioning frequency, potentially reducing exposure to environmentally acquired parasites, but did not result in an increase in anti-parasite behaviors such as grooming. Finally, I found minimal differences in activity budgets when comparing ibis behavior between urban and wetland flocks. Examining behaviors at multiple scales allowed me to consider how different components of urbanization (namely habitat type and anthropogenic food provisioning) may impact ibis in the future. My results suggest that food provisioning by humans drastically alters ibis aggregation behaviors on short timescales and suggests that these feeding events could exacerbate transmission of some pathogens. However, feeding in urban areas not yet resulted in significant long-term changes in ibis flock sizes or daily activity time budgets. It will be interesting to see whether over long time periods, easy access to anthropogenic food or elevated exposure to *Salmonella* and other pathogens will select for changes in activity budgets, especially given the recent formation of urban-breeding populations (Silva Seixas 2021).

Since I found that ibis flock density more than doubled during active food provisioning, I asked how aggressive behaviors change during provisioning in Chapter 4. As expected, I found that active provisioning increased both the number of birds observed being aggressive and the average number of aggressive interactions per bird. I also found that interactions between proximity to food and density (either flock or local) were primary drivers of aggression in ibis. My results in this study indicate that even short-duration provisioning increases aggressive behaviors, with potentially negative implications to ibis condition, stress, and parasite exposure. These results can also help inform feeding guidelines by further supporting recommendations to spread out food at feeding stations (Murray et al. 2016).

This dissertation takes a deeper dive into the behavioral changes associated with urbanization in a recently urbanized species, the American white ibis. Ibis are relatively long-lived birds and only started moving into urban habitats within the last 3 decades (Kushlan 2011), which makes them a recent urban inhabitant compared to other synanthropic species that have evolved to live close to humans over many generations. This dissertation quantified components of ibis behavior early in their use of anthropogenic food, and thus could serve as a reference point for the behavior of other wildlife that are just beginning to exploit urban food and other resources. It also allows paves the way for future comparisons – what will urban ibis behavior be like in 15 or 30 years from now? Will ibis become more of a nuisance species, like the Australian white ibis (Martin et al. 2007)? In addition to the individual-level behavioral studies conducted in this dissertation, ibis health, including immune function, physiology, and pathogen prevalence in both urban and wetland habitats has also been extensively studied in recent years (Hernandez et al. 2016, Murray et al. 2018, Bahnson et al. 2020, Cummings et al. 2020a, Christie et al. 2021). This opens the door for additional studies to examine behavior and health changes associated with urbanization over multiple decades.

In conclusion, this dissertation provides insight into key research areas at the intersection of behavioral ecology, urban ecology, and disease ecology. It synthesizes behavioral responses to urbanization in a wide range of taxa and considers how these behavioral responses can impact wildlife health and subsequently human health. It also provides insight how group-level and individual-level behaviors are affected by urbanization and quantifies variation in individual behavior in different contexts that could help identify individuals that act as superspreaders of infection. These results show that short-term feeding drastically affects individual behavior and conspecific aggregation in ways that can have profound consequences for infection risk.

Urban areas are vital habits for wildlife and will only become increasingly important as development continues. Understanding how urbanization impacts wildlife behavior is essential when designing urban areas with an eye to both human and wildlife health. Importantly, this dissertation shows that behavioral responses are not always straightforward and are context dependent. This dissertation provides a better understanding of how urbanization impacts several types of behavior in wildlife on multiple scales and provides implications of these findings for the transmission of infectious diseases.

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APPENDIX A

CHAPTER 3 SUPPLEMENTARY MATERIALS

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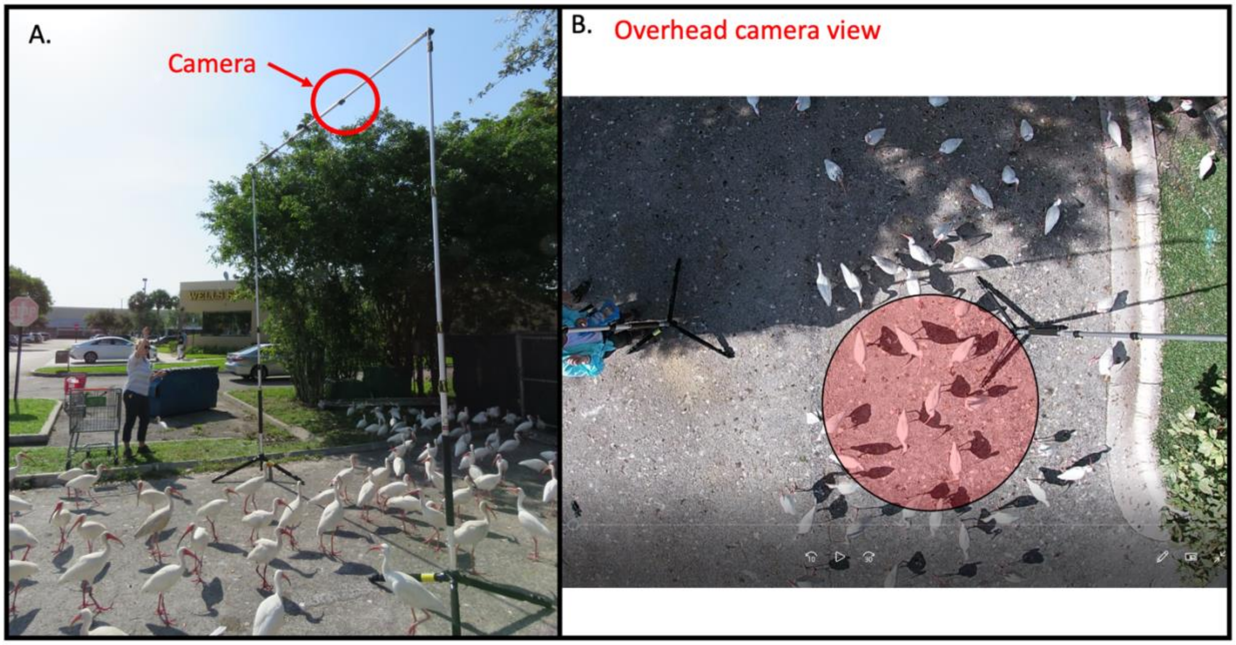
Experimental feeding in urban parks:



Supplemental Figure A1 Video camera setup (A) and example of still photo taken from video footage (B) used to examine ibis aggregation behavior while being provisioned with bread. Red circle on panel B shows an example of a 1m radius around a focal bird from which density was estimated.

Urban focal follows

Supplemental Table A1. Results of the best fit zero-inflated negative binomial GLMMs testing the effect of provisioning and flock size on foraging time. These models all include *site* as a random effect.

Response/Predictors	Estimate	Std. error	z-value	p-value
Foraging				
(Intercept)	-0.97975	0.09296	-10.53942	5.68470e-26
flocksize_nearest_s	-0.24333	0.10301	-2.36219	1.81700e-02
feedingperhour_s	-0.18472	0.08670	-2.13060	3.31200e-02
Foraging				
(Intercept)	-0.97710	0.09345	-10.45545	1.38342e-25
flocksize_nearest_s	-0.24949	0.10501	-2.37594	1.75000e-02
feedingperhour_s	-0.20032	0.09952	-2.01290	4.41300e-02
flocksize_nearest_s:feedingperhour_s	-0.05511	0.17401	-0.31668	7.51490e-01

APPENDIX B

CHAPTER 4 SUPPLEMENTARY MATERIALS

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Supplemental Table B1. Model summaries of all negative binomial generalized linear models testing the effects of the average distance from food, local density, flock density, and pairwise interactions on the number of aggressive interactions observed in ibis. The null model is an intercept-only model.

	Estimate	Standard Error	Z value	P value
Intercept	-4.09	0.12	-33.75	0.0000
Intercept	-4.02	0.22	-18.46	0.0000
Average flock density	-0.05	0.15	-0.36	0.7185
Intercept	-4.20	0.21	-20.43	0.0000
Average local density	0.06	0.08	0.70	0.4842
Intercept	-3.62	0.19	-19.45	0.0000
Average distance from food	-0.33	0.10	-3.21	0.0013
Intercept	-2.96	0.37	-7.98	0.0000
Average distance from food	-1.04	0.27	-3.86	0.0001
Average flock density	-0.29	0.22	-1.29	0.1962
Average distance from food x average flock density	0.34	0.12	2.76	0.0058
Intercept	-4.28	0.32	-13.47	0.0000
Average distance from food	-0.03	0.17	-0.16	0.8747
Average local density	0.33	0.14	2.43	0.0151
Average distance from food x average local density	-0.14	0.06	-2.23	0.0258
Intercept	-4.70	0.30	-15.53	0.0000
Average flock density	0.24	0.23	1.03	0.3022
Average local density	0.49	0.17	2.84	0.0045
Average local density x average flock density	-0.21	0.08	-2.71	0.0067