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Research article

Human-provided food increases aggregation but does not change activity budgets in an urban wading bird

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Abstract

In urban areas, animals often aggregate at higher densities, 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, e.g. 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.

Key words: food provisioning; urbanization; wildlife behavior; American white ibis; infectious disease

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, e.g. 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 year-round resident populations in Spain where birds now feed 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). Lastly, habituation to human contact (as facilitated by regular feeding) can increase negative human-wildlife interactions, including increased aggression or attacks on people and their domestic animals, stealing of food and non-food items, property damage and exposure to contaminants and pathogens through increased deposition of feces (Altmann and Muruthi 1988, Orams 2002, Carlos et al. 2009, Cox and Gaston 2018).

Supplemental food can influence behavioral activity budgets in wildlife both directly, and indirectly through changes in conspecific density. Predictable access to resources can drastically decrease the time animals spend foraging; e.g. suburban Florida Scrub-Jays (*Aphelocoma coerulescens*) utilizing anthropogenic food spent less time foraging, and foraged more efficiently, than wildland birds (Fleischer et al. 2003). Activity budgets are also mediated by density, with higher conspecific density associated with individual reductions in vigilance in flocking species such as European Starlings (*Sturnus vulgaris*) (Powell 1974) and moderate reductions in vigilance across diverse mammal taxa (Beauchamp et al. 2021). Therefore, food subsidies that attract higher densities may allow individuals to reduce time spent being vigilant. Increased foraging efficiency and density mediated effects on vigilance could potentially reduce tradeoffs with other maintenance

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activities such as grooming and resting (Fleischer et al. 2003, Agostini et al. 2023).

These behavioral responses of wildlife to food subsidies can alter the transmission of pathogens in opposite directions (Bradley and Altizer 2007, Becker et al. 2015, Murray et al. 2016) and influence the risk of pathogen spillover between wildlife and humans (Plowright et al. 2015). Instantaneous responses to food (e.g. increased aggregation around resources) (Flint et al. 2016) 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. 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.

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. These birds 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). Ibis interactions in urban settings are of human health concern as ibis host a variety of microbes, including avian influenza virus (Bahnson et al. 2020, Christie et al. 2021) and West Nile virus (Silva Seixas et al. 2022). Additionally, parasite prevalence and burden in white ibis is not uniform across the landscape; 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.

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 for feeding wildlife that reduce pathogen transmission risk in wildlife, and therefore human exposure to pathogens at feeding sites.

Methods

Study sites

Field data were collected from eight locations in Palm Beach County, Florida (Fig. 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

Urban flock provisioning experiment

To collect data on ibis density during experimental feeding events, we mounted a GoPro camera on a self-standing frame ∼5 m 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 Fig. S1). We baited the ibis flock to the camera area and once the flock was positioned beneath it, threw bread directly under the camera for five minutes while recording. Videos were collected at four 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 <30 s. Frames were ∼33 sq. m in area. For each tracked focal individual, density estimates were recorded by counting the number of individuals within a 1 m radius of the focal bird, at five equally spaced time points during the duration of the video in which the entire 1 m radius around the focal bird was in frame (e.g. the bird was not close to the edge of the frame).

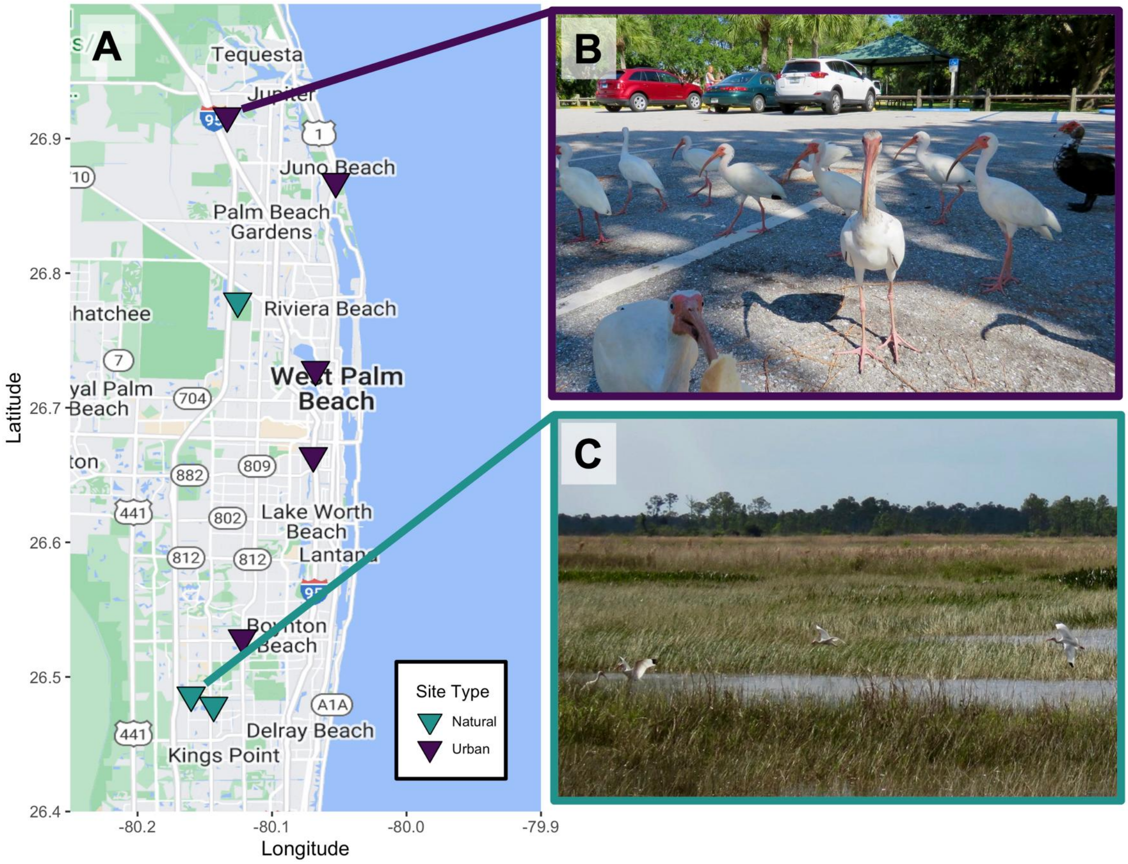

Figure 1. (A) Map of field sites in Palm Beach County, Florida, USA. Triangle color indicates site type with natural wetland sites in teal and urban sites in purple. Examples of American white ibis flocks in (B) urban and (C) natural wetland sites. The urban flock (panel B) shows American white ibis 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. Photos by C. Wilson.

Table 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

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. Based on differences in plumage, bare parts coloration, position in the flock, and the relative proportion of birds within a flock being observed, we felt confident that repeated observations of the same individual within a day were unlikely. Focal follows with <2-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 ~10 min 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 1). Additionally, we recorded the number of other ibis within a 1 m radius of the focal bird at the start and end of the focal follow observation interval, and any direct contact events that occurred during the focal follow. We also recorded flock size multiple times (approximately every 30 min) while conducting focal follows and recorded the number of 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.

Urban vs wetland flock observations

To determine whether activity budgets differ between urban and natural wetlands, 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 min 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. An observation period for scan sampling is defined as all individual scans taken at a site on a specific day.

Scans were conducted by recording the activity of all visible ibis over a 30–120 s 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 1). We imposed a 5-second 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 15 m) 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 hypothesized 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 in urban sites and when ibis were actively being fed in urban sites during video recordings. We averaged 1 m density estimates for each focal individual and compared the mean number of individuals within 1 m radius of each focal bird for birds being actively provisioned and birds not being actively provisioned. 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 not actively provisioned 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 frequency 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 at a site during the time period when focal follows were being conducted, 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. 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 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 S1 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 was performed, and coefficient estimates, standard deviations, z-values, and p-values were obtained for each parameter in the models.

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 the proportion of the flock performing 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 = .05 with Bonferroni corrections applied to correct for multiple comparisons.

Results

Experimental feeding in urban parks

Density estimates in a 1 m radius around 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 1 m of focal birds while being actively provisioned (Wilcoxon rank-sum test, $Z = -10.24$, $P < .0005$, Fig. 2). On average, ibis density increased by 205% when ibis were provisioned, or from 2 ibis within 1 m of a focal bird to 7 ibis within 1 m of a focal bird.

Urban site focal follows

Excluding focal follows lasting <2 min resulted in 150 focal follows spanning a total duration of 22.22 h (average of 8.88 min per follow). At least two different behaviors were observed during any given focal follow, and on average, each bird performed 3.8

Table 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).[a]

Foraging candidate models

Model	K	AIC	ΔAIC	ModelLik	AICWt	LogLik	Cum.Wt
provisioning + flock size + (1|site)	6	1567.22	0.00	1.00	0.46	−777.61	0.46
*provisioning * flock size + (1|site)*	7	1569.12	1.90	0.39	0.18	−777.56	0.64
flock size + (1|site)	5	1569.59	2.37	0.31	0.14	−779.80	0.78
provisioning + (1|site)	5	1569.84	2.62	0.27	0.12	−779.92	0.90
null + (1|site)	4	1570.33	3.11	0.21	0.10	−781.16	1.00

Grooming candidate models

Model	K	AIC	ΔAIC	ModelLik	AICWt	LogLik	Cum.Wt
null + (1|site)	4	1545.78	0.00	1.00	0.42	−768.89	0.42
flock size + (1|site)	5	1546.62	0.85	0.65	0.27	−768.31	0.70
provisioning + (1|site)	5	1547.74	1.97	0.37	0.16	−768.87	0.85
provisioning + flock size + (1|site)	6	1548.49	2.72	0.26	0.11	−768.25	0.96
*provisioning * flock size + (1|site)*	7	1550.49	4.71	0.09	0.04	−768.25	1.00

Vigilance candidate models

Model	K	AIC	ΔAIC	ModelLik	AICWt	LogLik	Cum.Wt
null + (1|site)	4	1796.75	0.00	1.00	0.34	−894.37	0.34
provisioning + (1|site)	5	1796.91	0.17	0.92	0.31	−893.46	0.65
flock size + (1|site)	5	1798.38	1.64	0.44	0.15	−894.19	0.80
provisioning + flock size + (1|site)	6	1798.50	1.75	0.42	0.14	−893.25	0.95
*provisioning * flock size + (1|site)*	7	1800.44	3.69	0.16	0.05	−893.22	1.00

[a] Null models contain only the random effect *site*.

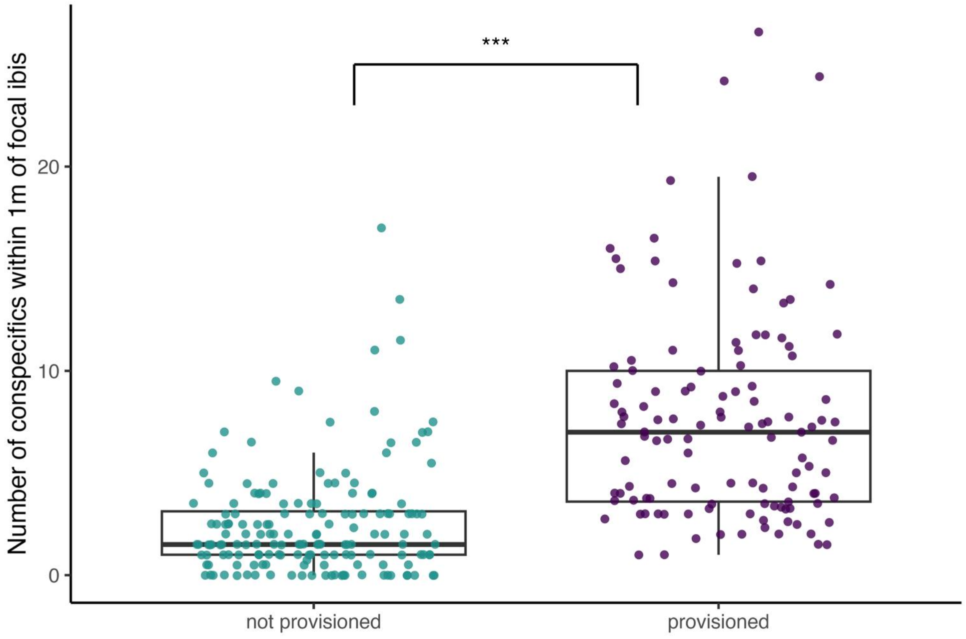

Figure 2. Number of conspecifics within 1 m of a focal bird while ibis are actively provisioned (right, purple) or not actively provisioned (left, blue) in urban parks. The thicker horizontal line indicates the median, the box encompasses the first and third quartiles, the whiskers extend to 1.5 times the interquartile range, and data points beyond the whiskers are considered outliers. Asterisks (***) denote significant differences (*P*-values < .05) between groups.

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 were *flock size + provisioning* and *flock size x provisioning* (Table 2). Foraging models showed that as provisioning frequency and flock sizes increase, time spent foraging decreases (Fig. 3, Supplemental Table S1). In contrast, the null model (comprising only the random effect *site*) was the best fitting model for both grooming and vigilance (Table 2), with no evidence for effects of provisioning and flock size.

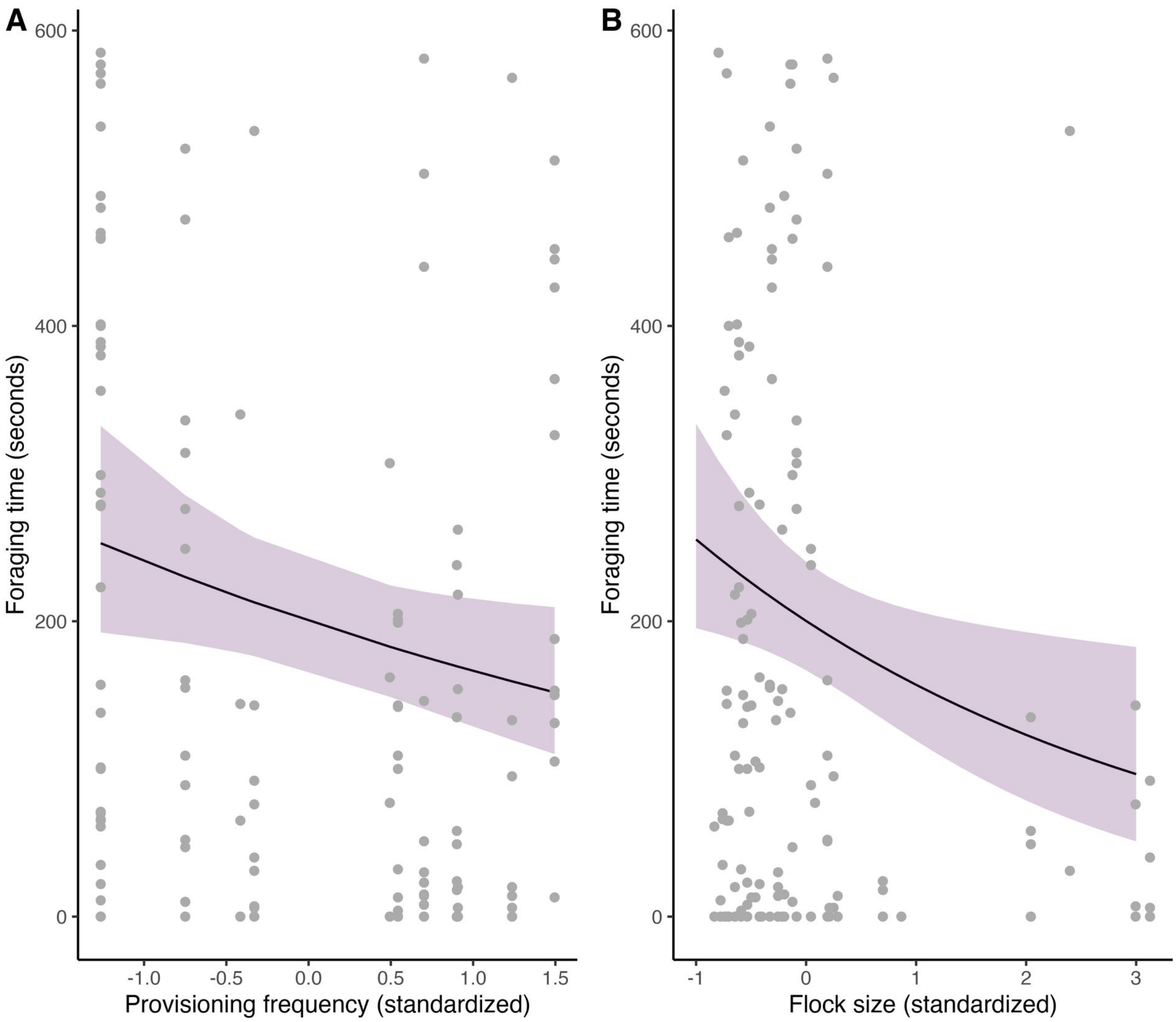

Figure 3. Results of the best fit zero-inflated negative binomial GLMM testing the effect of provisioning frequency (panel A) and flock size (panel B) on foraging time. Gray points show observed foraging values, solid line shows model output predictions, and purple shading shows model 90% confidence intervals.

Urban versus 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, $Z = -0.59$, $P = .28$).

Ibis were most frequently observed foraging, grooming, and being vigilant at both urban and natural wetland sites (Fig. 4 panel F). 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 = .49, Fig. 4A), grooming (Welch Two-sample t-test with Bonferroni correction, $t = -0.72$, P-adjusted = 1.00, Fig. 4B), resting (Wilcoxon rank sum exact test with Bonferroni, $Z = 0.24$, P-adjusted = 1.00, Fig. 4D), or being vigilant (Welch Two-sample t-test with Bonferroni correction, $t = -2.40$, P-adjusted = .16, Fig. 4C). 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, Fig. 4E).

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

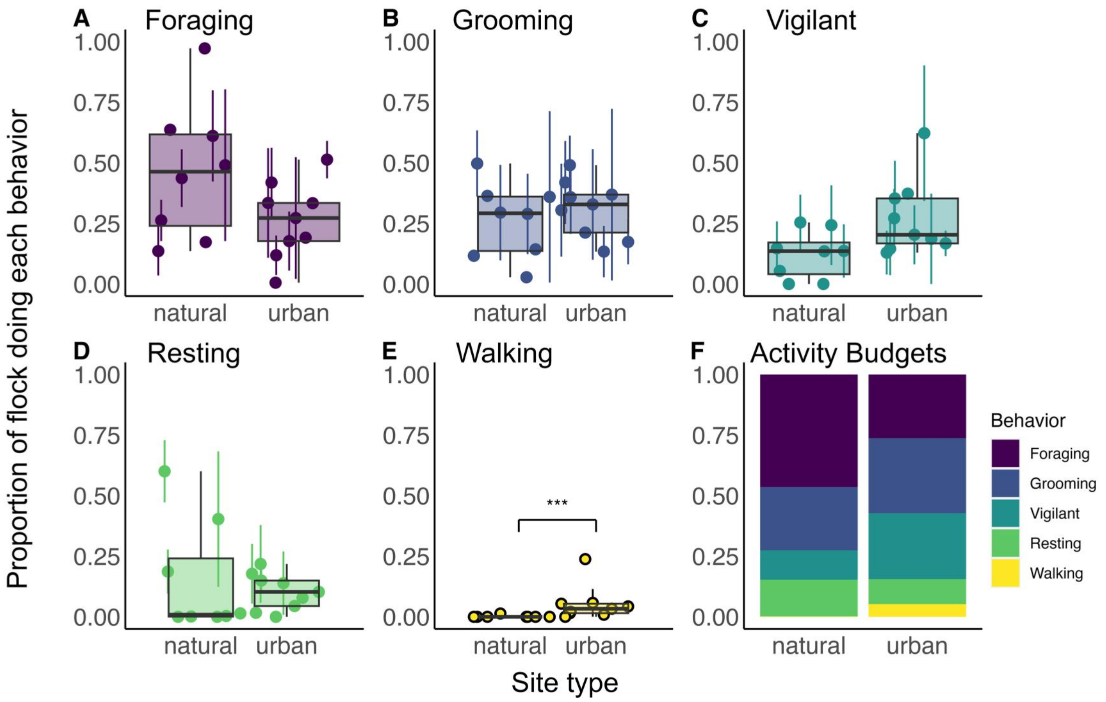

Figure 4. Proportion of flock observed performing each behavior (panels A through E) at natural wetland sites or urban sites. Individual points represent mean values and bars indicate standard deviation for each day/site combination. Panel A through E box plots where the thicker horizontal line indicates the median, the box encompasses the first and third quartiles, the whiskers extend to 1.5 times the interquartile range, and data points beyond the whiskers are considered outliers. Asterisks (***) denote significant differences (P-values < .05) between groups. 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.

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. 2020).

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. We expected to find higher grooming activity at sites with more human-provided food because past work showed that ibis that consumed more human-provided food had lower ectoparasite scores (Murray et al. 2018). 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 increased provisioning, we did not observe significant differences between urban and wetland sites in the most frequently observed behaviors (i.e. foraging, grooming, vigilance, and resting). Similar to our findings, 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 some individual birds using both urban and wetland sites over the course of a non-breeding season (Kidd-Weaver et al. 2020, Teitelbaum et al. 2020). Similarly, the natural sites being close together could lead to a more limited sampling of possible “natural” behaviors. Alternatively, small behavioral differences might exist between urban and natural settings that our scan sampling was unable to detect. In this study, we were unable to observe birds for longer durations of time due to birds flying away or moving into dense vegetation. Observing animals over longer time periods, or fitting animals with trackers and cameras that record fine-scale movement data and interactions, might reveal subtle differences in activity budgets. 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.

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. 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. 2020). This suggests that some ibis may spend more time at urban sites where they are experiencing these short-term behavioral changes like crowding. Additionally, given urban expansion and wetland degradation, we expect wading birds like ibis to increasingly use urban sites, necessitating scientifically informed guidelines for people who feed birds in parks and around their households to avoid exacerbating pathogen transmission among birds. Adhering to feeding guidelines, such as feeding at irregular intervals and 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). Recreational bird-feeding can have mixed effects on human health, with documented benefits for mental well-being (Cox and Gaston 2018), but increased exposure risk to wildlife pathogens (Lawson et al. 2014). Social science research on people engaging in backyard bird-feeding has demonstrated that people are willing to change their food provisioning activities in response to observing infected birds (Dayer et al. 2019), but policy recommendations on bird-feeding rarely account for these human behaviors associated with feeding (Dayer et al. 2024). More cross-disciplinary research is needed to understand feedbacks between human food provisioning and wildlife behaviors, and its implications for both wildlife and human health.

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Author contributions

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Supplementary data

Supplementary data are available at *JUECOL* online.

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Data availability

Data supporting the findings of this study are available upon reasonable request.

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