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How urban impervious surface shapes bird foraging behavior in an arid city

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Wildlife behavior and interactions in urban ecosystems can vary across landscape types and species, with some birds dominating human-derived resources. This study investigates the relationship between urbanization, measured as impervious surface cover, and bird foraging behavior in the Phoenix metropolitan area in Arizona, USA. We conducted 126 feeding trials across 13 sites along a gradient of urbanization and bird interactions with anthropogenic food sources present. Trials were conducted using popcorn placed at random distances and orientations from a trash can. We recorded bird species visiting feeding stations and time to first visit during 20-minute trials and then quantified relationships among visitation timing (latency), species richness, and impervious surface coverage. Time to first visit was negatively correlated with the amount of impervious surface, with the highly urban areas having birds arrive at the feeding station the soonest. Great-tailed Grackles (*Quiscalus mexicanus*) comprised the most common visitor across all impervious surface levels. Non-native doves like Rock Pigeons (*Columbia livia*) and Eurasian Collared-doves (*Streptopelia decaocto*) were quicker to visit feeding stations compared to native doves like Mourning Doves (*Zenaida macroura*), Inca doves (*Columbina inca*), and White-winged Doves (*Z. asiatica*). Small urban-adapted generalists, like House Sparrows (*Passer domesticus*) and House Finches (*Haemorhous mexicanus*), tended to be more frequent visitors at highly urbanized sites compared to larger birds. These emphasize how species-specific foraging behaviors can differentiate resource use by birds in urban areas.

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Abstract

Wildlife behavior and interactions in urban ecosystems can vary across landscape types and species, with some birds dominating human-derived resources. This study investigates the relationship between urbanization, measured as impervious surface cover, and bird foraging behavior in the Phoenix metropolitan area in Arizona, USA. We conducted 126 feeding trials across 13 sites along a gradient of urbanization and bird interactions with anthropogenic food sources present. Trials (n=126) were conducted using popcorn placed at random distances and orientations from a trash can. We recorded bird species visiting feeding stations and time to first visit during 20-minute trials and then quantified relationships among visitation timing (latency), species richness, and impervious surface coverage. Time to first visit was negatively correlated with the amount of impervious surface, with the highly urban areas having birds arrive at the feeding station the soonest. Great-tailed Grackles (*Quiscalus mexicanus*) comprised the most common visitor across all impervious surface levels. Non-native doves like Rock Pigeons (*Columbia livia*) and Eurasian Collared-doves (*Streptopelia decaocto*) were quicker to visit feeding stations compared to native doves like Mourning Doves (*Zenaida macroura*), Inca doves (*Columbina inca*), and White-winged Doves (*Z. asiatica*). Small urban-adapted generalists, like House Sparrows (*Passer domesticus*), tended to be more frequent visitors at highly urbanized sites compared to larger birds. These findings highlight the role of urban-adapted birds in maintaining ecosystem services like trash removal and emphasize how species-specific foraging behaviors can differentiate resource use by birds in urban areas.

Introduction

As cities often overlap with areas of high species richness, wildlife habitat can be threatened by areas of rapid urban growth (Cincotta et al. 2000). However, urban green spaces can be important to support biodiversity by providing areas where wildlife and humans can coexist (Aronson et al. 2017). Metropolitan areas often contain a mix of native and non-native species, with species adapting to urban landscapes with varying levels of success (Shochat et al. 2004). Urban wildlife communities can be shaped by the availability of food and shelter among other ecological factors (Callaghan et al. 2019a). Although some species struggle to adapt to urban conditions, birds may thrive because of traits associated with novel landscapes and anthropogenic resources (Evans et al. 2011). For avifauna, habitat alterations that produce anthropogenic waste that can attract certain bird species while deterring others (García-Arroyo et al. 2023). Birds in urban environments often encounter abundant food sources, including food waste left behind by humans (Brown et al. 2022). This advantage allows "urban exploiters" to outcompete "urban avoiders" in these environments. As a result, urbanization can alter the composition and behaviors of local bird populations (Pena et al. 2023).

Behavioral responses to novel stimuli can determine how birds exploit anthropogenic food sources in urban environments. Animals can vary in response where neophilia is the attraction to a novel stimulus and neophobia is the avoidance of the stimulus (Tryjanowski et al. 2016). In cities, where food items are frequently unfamiliar or irregular, neophilic species scavenge human food waste, a trait among common and widespread urban-adapted birds (Brown et al. 2022; Pejchar et al. 2025). The heterogeneity of urban settings can desensitize birds to perceived foraging risks, encouraging bolder behavior (Tryjanowski et al. 2016). For more neophobic birds, this can suggest that individuals will quit foraging when the energetic benefits no longer outweigh the costs (Shochat et al. 2004). Consequently, smaller generalist species such as House Sparrows (*Passer domesticus*) often capitalize on feeding opportunities more quickly than larger species, which tend to assess risks differently and are more easily displaced by anthropogenic activities (Haemig et al. 2021). Together, these patterns highlight the ecological strategies birds employ to navigate the risk and rewards of the urban landscape.

Urban landscape characteristics, such as the density of buildings, pavements, and impervious surfaces, play a crucial role in shaping the presence and behaviors of wildlife species. These features can alter the availability of essential resources like food, water, and shelter

73 (Callaghan et al. 2019a) and even influence the presence of wildlife diseases (Hernandez et al.

74 2016). Specifically, impervious surfaces are key indicators of urbanization-driven habitat loss

75 associated with reduced presence, abundance, and diversity of wildlife taxa, especially among

76 bird species (Aronson et al. 2017; Haight et al., in press). Urbanization is also characterized by a

77 reduction in vegetation cover, as measured by NDVI (normalized difference vegetation index)

78 which is inversely related to the amount of impervious surface area (Weng and Lu 2008).

79 Therefore, impervious surfaces could affect the foraging behaviors of birds in urban

80 environments by altering resources and vegetation density, which may influence the types of

81 birds that visit these areas.

82   In this study, we conducted a field experiment to investigate how bird foraging behavior

83 can vary across an urban gradient, defined by proportion of impervious surface. We specifically

84 assessed: time (latency) for birds to visit a feeding station across a gradient of impervious

85 surface. We then considered species- or guild-specific likelihood of visits to feeding stations

86 across impervious surface levels. In general, we predicted that non-native birds would visit

87 stations sooner and at locations with higher levels of impervious surface. We hypothesized that

88 smaller species, such as the House Sparrow, would visit feeding stations sooner in high-

89 impervious areas, while larger species and species associated with expanding their range into

90 mesic habitats like the Great-tailed Grackle (*Quiscalus mexicanus*), would visit feeding stations

91 sooner in areas with lower impervious surface.

92

Materials & Methods

93

94 *Study Area*

95   This study was conducted in the Phoenix metropolitan area (metro Phoenix; Figure 1),

96 characterized by its location within the Sonoran Desert ecosystem (Comus et al. 2015). This

97 desert environment is known for its hot and arid climate, sparse natural shrubland vegetation, and

98 landscapes transformed by urbanization, including the creation of impervious surfaces such as

99 buildings and roads. The urbanized and agricultural environments of metro Phoenix are also

100 characterized by extensive year-round irrigation practices that support greater vegetation cover

101 and productivity than that of natural desert habitats (Buyantuyev and Wu 2009).

102

103 *Feeding Trials*

104   We assessed bird foraging behavior by establishing feeding stations at 13 sites across a

105   gradient of urbanization. Feeding stations were placed randomly within 13 sites across the

106   metropolitan Phoenix area and were selected for public accessibility and with a range of (24% to

107   90%) urbanization levels (Figure 1). Sites included the Rio Salado Audubon Center in Phoenix,

108   Kiwanis Park in Tempe, the Queen Creek Olive Mill, Veterans Oasis Park in Chandler, Base and

109   Meridian Wildlife Area in Avondale, Schnepf Farms in Queen Creek, the ASU Polytechnic

110   Campus in Mesa, the Mesa Community College Red Mountain Campus, the ASU West Valley

111   Campus in Glendale, Civic Space Park in Phoenix, the ASU Tempe Campus, Santan Village

112   Mall in Gilbert, and Tempe Marketplace. Levels of impervious surface at each site were

113   calculated post-selection using i-Tree Canopy, an online tool that provides estimates based on

114   satellite imagery (explanatory variable described in landscape variables).

115   Time to first visit was recorded during 6-16 trials per site to observe bird behavior near

116   anthropogenic waste sources (a total of 126 feeding trials). Trash cans were the primary starting

117   points for positioning feeding stations because they are ubiquitous in the urban area, represent

118   places of resources for urban wildlife (García-Arroyo et al. 2023), and to maximize geographical

119   coverage at each site. We did not include large dumpsters in this study. In areas with limited or

120   no trash cans, alternative human-made structures (e.g., benches or signs) or visible trash on the

121   ground were used as starting points, these made up fewer than 8% of trials. Although most sites

122   had 10 feeding stations, smaller sites had fewer than 10 (i.e., Mesa Community College Red

123   Mountain Campus had six, Civic Space Park and the Base and Meridian Wildlife Area each had

124   seven), and one large site had more than 10 stations (i.e., the ASU Tempe Campus had 16 trials).

125   Once a starting point was chosen, a feeding station was established by adding a handful

126   (15 pieces) of minimally processed and unseasoned popcorn placed on the ground. The observer

127   walked away (approximately 25 m away) from the station and used binoculars for observations.

128   We positioned feeding stations at a random distance (5-20 meters, using a random number

129   generator) with a random orientation from the starting point. Random orientations were chosen

130   by dividing the area around the trash can into 12 directional segments (e.g., a clock with N at

131   12:00) and used a random number generator to select one. For the safety of observers, we

132   avoided establishing a feeding station in a parking lot and therefore truncated the orientation to

133   avoid these areas   .

134   Observations lasted for 20 minutes during early morning hours (6:00-9:30 AM, although

135   some surveys exceed this range) to maximize bird activity in a hot, arid environment. We

136   recorded bird species visiting feeding stations through visual identification (based on Sibley

137   2022) during the 20-minute trial periods. All birds landing at or approaching the feeding stations

138   were noted. For stations with no visitors, a maximum time of 20 minutes (1200 seconds) was

139   recorded as the first visit time. We primarily focused on recording the first bird visitor to the

140   station. After the first month of surveys, we also recorded birds that arrived after the first visit

141   within the 20-minute period (82% or 106 of 129). Field data collection occurred over a 14-week

142   period, from 7 July 2024 to 13 October 2024. This period overlapped with bird migrations, such

143   as the White-winged Doves (*Zenaida asiatica*) migrating from Arizona to Mexico in the fall.

144   However, most bird visitors were non-migratory, resident species. ASU Institutional Animal

145   Care and Use committee approved methods for this research (23-2016T).

146

147   *Landscape Variables*

148   We related bird foraging behavior, species richness, and likelihood that individual species

149   or guilds would visit a station to levels of urbanization by quantifying percent impervious

150   surface. We quantified landscape characteristics at each site using the i-Tree Canopy tool (2024),

151   which estimates impervious surface cover and vegetation features based on satellite imagery.

152   The tool produced by the US Department of Agriculture utilizes imagery datasets from Google

153   Earth. First, a bounding box was drawn around the sampling areas for each site. Then, 50 random

154   land cover sampling points were placed across the sampling area (manually drawn grid and

155   bounded site by roads), and each point was manually characterized by its land surface cover

156   (e.g., impervious road, impervious buildings, tree/shrub, grass/herbaceous vegetation). We

157   combined the resulting percentages of each land surface cover type to define impervious surface

158   as including roads, buildings, and other impermeable land cover types (e.g., concrete sidewalks).

159

160   *Data Analysis*

161   We investigated research questions by modeling the likelihood that individual species or

162   guilds would visit a feeding station, the time to first visit, and species richness in relation to

163   impervious surface levels. Feeding station-level response variables included whether or not a

164   species or guild visited a station, latency or time to first visitation, and species richness (total

165 number of species that visited a station). We quantified relationships of each response variable

166 with impervious surface area, day-of-year (DOY; Julian date of feeding trials at each site)

167 using generalized linear mixed models (GLMMs) fit within the R programming language 4. 1

168 using the *glmmTMB* package (Brooks et al. 2017; R Core Team 2024). We modeled the

169 responses of whether or not a species or guild visited, latency, and species richness as having

170 binomial (logit-link), normal (Gaussian-link), and Poisson (log-link) distributions, respectively.

171 We fit GLMMs for each response variable with two sets of fixed effects (impervious surface area

172 only, and impervious surface area and DOY) and study site as a random effect (intercept). We

173 compared the relative quality of models with and without the DOY fixed effect by using the R

174 package *performance* to calculate marginal R^2 values for fixed effects and the Akaike

175 Information Criterion adjusted for low sample size (AICc), regarding the lower-AICc model as

176 being the better model (Anderson and Burnham 2002). Impervious surface area and DOY did not

177 demonstrate significant collinearity across 13 sites (r = 0.115, p = 0.709).

178

179 **Results**

180 *Bird Visitors*

181 Across all trials, a total of 15 bird species were observed visiting feeding stations

182 (Supplementary Table 1). Out of 126 trials, 64 trials had no visitors (50.8%) and 62 (49.2%) had

183 visitors. Of the trials with visitors, the first visits were recorded as follows: 41.9% were Great-

184 tailed Grackles, 12.9% were native doves (Inca Dove, *Columbia inca*; White-winged Dove; and

185 Mourning Dove), 11.3% were House Sparrows, 11.3% were House Finches (*Haemorhous*

186 *mexicanus*), 8.1% were non-native doves (Eurasian Collared-dove, *Streptopelia decaocto*, and

187 Rock Pigeon, *Columbia livia*), and 3.2% were Abert's Towhees (*Pipilo aberti*). The following

188 species were recorded only once as the first visitor: Rock Wren (*Salpinctes obsoletus*), Cactus

189 Wren (*Campylorhynchus brunneicapillus*), Northern Mockingbird (*Mimus polyglottos*), Greater

190 Roadrunner (*Geococcyx californianus*), Curve-billed Thrasher (*Toxostoma curvirostre*), and

191 European Starling (*Sturnus vulgaris*). Most trials had only a single species visit the feeding

192 station. For example, in trials where all species were counted (107 trials), the mean richness was

193 1.3 birds and 1 was the median value.

194 Visitation behaviors at feeding stations varied among bird species. Great-tailed Grackles

195 were the largest proportion of first birds to visit feeding stations and averaged 318.0 seconds

196   (58.45 SE) to arrive (Figure 2). Among the common groups of birds that visited, native doves

197   took the longest to arrive and averaged 451.3 seconds (145.98 SE), then House Finches averaged

198   285.7 seconds (91.50 SE), and House Sparrows averaged 242.0 seconds (91.53 SE). Non-native

199   doves were the quickest to visit feeding stations and averaged 222.6 seconds (87.86 SE; Figure

200   2). Smaller birds were not significantly associated with shorter visitation times (slope = 0.895

201   seconds per gram, R^2 = 0.145, r = 0.012, p = 0.200, n = 13).

202

203   *Bird Behavior Related to Impervious Surface*

204   Bird visitation to feeding stations occurred across a gradient of 24% to 90% impervious

205   surface area. Across all response variables, the best model was the one including the fixed effect

206   of impervious surface area (β_{ISA}) but excluded DOY (Supplementary Table 2). Three species or

207   guilds differed in their likelihood to visit stations across levels of impervious surface. Native

208   doves were marginally more likely to visit less urbanized feeding stations (p=0.098, β_{ISA} = -1.10,

209   95% CI: -2.41, 0.20). More urbanized feeding stations were more likely to be visited by House

210   Finches (p = 0.041, β_{ISA} = 1.10, 95% CI: 0.05, 2.16) and by House Sparrows (β_{ISA} = 0.153, p =

211   0.028, 95% CI: 0.17, 2.90). Impervious surface area had no significant relationship with whether

212   or not sites were visited by Great-tailed Grackles (p = 0.243, β_{ISA} = 0.30, 95% CI: -0.21, 0.81) or

213   introduced doves (p = 0.807, β_{ISA} = -0.09, 95% CI: -0.81, 0.63). The best model for latency

214   indicated that birds visited feeding stations faster in areas with high levels of impervious surface

215   (0.001, β_{ISA} = -118.52, 95% CI: -188.78, -48.26; R^2 = 0.152; Figure 3). The average time for

216   the first visitor to arrive at feeding stations with the highest impervious surface was 2.7 times

217   shorter in areas with lowest impervious surface (Figure 3A). Latency time demonstrated no

218   substantial relationship with DOY, as indicated by the relatively low quality of models

219   containing the DOY fixed effect (Supplementary Figure 1; Supplementary Table 2). We detected

220   no significant relationship between species richness and impervious surface (p = 0.778, β_{ISA} =

221   0.034, 95% CI: -0.20, 0.27).

222

223   **Discussion**

224   We explored urban bird foraging behavior by conducting a field experiment establishing

225   feeding stations across a range of impervious surface levels in the greater Phoenix metropolitan

226   area. About half of the stations had bird visitors and species richness was low with only a single

227 species visiting during most trials. In places with high amounts of impervious surface, birds visit
228 feeding stations sooner compared to places with less impervious surface. Great-tailed Grackles
229 were the most common first visitor (over 40%). Other species, such as native doves, took longer
230 to arrive; whereas, non-native doves were the quickest to visit. Bird species also varied in
231 foraging behavior across the urban landscape. The likelihood of native doves visiting stations
232 had a negative relationship with impervious surface amount; whereas, House Finches and House
233 Sparrows had the opposite pattern and were more likely to visit stations with high levels of
234 impervious surface.

235   Urbanized environments can be advantageous for birds with generalist feeding behaviors,
236 especially species that can utilize anthropogenic food sources (Seress and Liker 2015). In our
237 study, feeding stations in more urbanized areas were visited quickly by urban-adapted, generalist
238 species (e.g., Great-tailed Grackle, non-native doves, House Sparrows). These results are
239 consistent with others showing that urbanization tends to select bird species with more flexible,
240 generalist diets (Hahs et al. 2023). Great-tailed Grackles, although considered native to North
241 America, are a species that have thrived in landscapes converted to agriculture and irrigated
242 vegetation in dryland ecosystems. The species has expanded its range in North America since the
243 late 19th century due to human-driven landscape changes by thriving in urban areas by
244 exploiting anthropogenic food sources like waste grain and discarded food (Wehtje 2003).
245 Grackle presence in the Phoenix metropolitan area is linked to cultivated lands and wetland
246 environments within urban areas where they have benefited from reduced nest predation and
247 stable food supplies (Wehtje 2003). Grackles' ability to exploit novel food sources, including
248 livestock feedlots, allows them to thrive in urban environments, making them well-adapted to
249 human-altered landscapes in arid lands (Pandolfino and Handel 2018).

250   During our trials, we observed that first visitors often monopolized the feeding station,
251 preventing access to other birds. Although this behavior was not limited to a single species, it
252 was commonly observed from Great-tailed Grackles, similar to other feeding studies (Fronimos
253 et al. 2011). The tendency of first visitors to dominate the feeding station and prevent access to
254 others may help explain the lack of differences in species richness across sites. In our study, all
255 visitors were birds. Perhaps sampling rural to urban areas with increase the presence of other
256 taxa, as in small mammals found in the study by Swartz et al. (2024). Future studies could
257 investigate how dominance hierarchies or non-avian species structure urban bird communities.

258   Non-native doves like Rock Pigeons and Eurasian Collared-doves were associated with
259   more urbanized areas in this study compared to native doves like Mourning Doves, Inca doves,
260   and White-winged Doves. Generalist species, like non-native doves, are more urban-tolerant due
261   to their broader ecological niches and behavioral flexibility (Callaghan et al. 2019b). Urban-
262   exploiting species have been associated with areas having high density of restaurants and
263   discarded food waste (Brown et al. 2022). Research has shown that urban birds generally display
264   higher neophilic tendencies than rural birds, enabling them to take advantage of unpredictable
265   resources in urban areas (Tryjanowski et al. 2016). Thus, urbanization may shape avian
266   community composition. As urbanization continues to alter resource availability, species with
267   high behavioral flexibility and generalist feeding strategies are likely to dominate, potentially
268   outcompeting more specialized native species over time.
269   Sonoran Desert birds, such as Cactus Wrens and Curve-billed Thrashers and winter
270   migratory species such as White-crowned Sparrows (*Zonotrichia leucophrys*), were rarely
271   observed at feeding stations in this study, suggesting that urbanization may exclude some species
272   from anthropogenic food resources. One way the methods in this study could have excluded
273   species was the choice of food at feeding stations. Some insectivorous species may not have
274   viewed popcorn as a food source. Future studies could use a different food to determine how
275   insectivorous birds relate to novel food sources in urban areas.
276   The relationship between urbanization and bird foraging behavior has implications for
277   balancing the coexistence of humans and wildlife in cities. Birds play a wide range of social-
278   ecological roles in urban ecosystems, and their traits and behaviors can influence human well-
279   being. The species that are more likely to scavenge food waste in urbanized settings (e.g., Great-
280   tailed Grackles, House Sparrows) are commonly characterized as "messy" birds with unpleasant
281   appearance or sound (Brown et al. 2022), traits associated with negative attitudes toward and
282   diminished appreciation of their ecosystem services (Andrade et al. 2022). Although many
283   studies assess the value of wildlife (Von Döhren et al. 2015), understanding these relationships
284   can better manage urban ecosystems to promote coexistence and tolerance of urban wildlife.
285

286 **Conclusion**

287   Overall, this field-based investigation found that urban birds utilize anthropogenic
288   food resources quickest in places with high impervious surfaces. The species composition

289 includes both native and non-native species and the most common species, Great-tailed Grackles,

290 are a common urban adaptor in arid land systems. For humans and wildlife to coexist in urban

291 systems, it is important to consider that some urban adaptors are associated with human sourced

292 food or trash and may have undesirable traits such as 'noisy' or 'messy' which could be viewed

293 negatively (Andrade et al. 2022). For humans and wildlife to coexist in urban systems, it is

294 essential to consider the nuanced positive and negative impacts of species traits and biodiversity

295 on human well-being. By acknowledging these complexities, we can promote coexistence and

296 tolerance of urban wildlife.

297

298

299 **Acknowledgements**

302

303

304 **References**

305 Anderson DR, Burnham KP. 2002. Avoiding pitfalls when using information-theoretic methods.

306 *The Journal of Wildlife Management* (2002):912-918.

307

308 Andrade R, Larson KL, Franklin J, Lerman SB, Bateman HL, Warren PS. 2022. Species traits

309 explain public perceptions of human–bird interactions. *Ecological Applications* **32**(8):e2676.

310 https://doi.org/10.1002/eap.2676

311

312 Aronson MFJ, Lepczyk CA, Evans KL, Goddard MA, Lerman SB, MacIvor JS, Nilon CH,

313 Vargo T. 2017. Biodiversity in the City: Key Challenges for Urban Green Space Management.

314 Frontiers *in Ecology and the Environment* **15**:189-196

315

316 Brooks ME, Kristensen K, Benthem KJ van, Magnusson A, Berg CW, Nielsen A, Skaug HJ,

317 Maechler M, Bolker BM. 2017. glmmTMB Balances Speed and Flexibility Among Packages for

318 Zero-inflated Generalized Linear Mixed Modeling. *The R Journal* 9:378–400. https://doi-org

319 /10.32614/RJ-2017-066.

320

321 Brown JA, Lerman SB, Basile AJ, Bateman HL, Deviche P, Warren PS, Sweazea KL. 2022. No

322 fry zones: How restaurant distribution and abundance influence avian communities in the

323 Phoenix, AZ metropolitan area. *PloS one* **17**(10):p.e0269334.

324

325   Buyantuyev A, Wu J. 2009. Urbanization alters spatiotemporal patterns of ecosystem primary
326   production: A case study of the Phoenix metropolitan region, USA. *Journal of Arid*
327   *Environments* **73**:512-520. https://doi.org/10.1016/j.jaridenv.2008.12.015

328

329   Callaghan CT, Bino G, Major RE, Martin JM, Lyons MB, Kingsford RT. 2019a. Heterogeneous
330   urban green areas are bird diversity hotspots: insights using continental-scale citizen science
331   data. *Landscape Ecology* **34**:1231-1246.

332

333   Callaghan CT, Major RE, Wilshire JH, Martin JM, Kingsford RT, Cornwell WK. 2019b.
334   Generalists are the most urban-tolerant of birds: a phylogenetically controlled analysis of
335   ecological and life history traits using a novel continuous measure of bird responses to
336   urbanization. *Oikos* **128**:845-858

337

338   Cincotta RP, Wisnewski J, Engelman R. 2000. Human population in the biodiversity hotspots.
339   *Nature* **404**(6781):990–992.

340

341   Comus PW, Phillips SJ, Dimmitt MA, Brewer LM. (eds) 2015. *A natural history of the Sonoran*
342   *Desert*. Univ of California Press.

343

344

345   Evans KL, Chamberlain DE, Hatchwell BJ, Gregory RD, Gaston KJ. 2011. What makes an
346   urban bird? *Global Change Biology* **17**(1):32-44.

347

348   García-Arroyo M, Gómez-Martínez MA, MacGregor-Fors I. 2023. Litter buffet: On the use of
349   trash bins by birds in six boreal urban settlements. *Avian Research* **14**: p.100094.

350

351   Haemig PD, De Luna SS, Blank H. 2021. Dynamic Table-Visiting Behavior of Birds at Outdoor
352   Restaurants and Cafés, *Ethology* **127**:505-516.

353

354   Haight JD, de Albuquerque FS, Bateman HL, Frazier AE, Larson KL (*In Press*). Regional
355   urbanization and climate dynamics drive long-term changes in avian diversity and associated
356   ecosystem services in the Sonoran Desert, USA. *Ecological Applications*, May 2025.

357

358   Hahs AK, Fournier B, Aronson MFJ, Nilon CH, Herrera-Montes A, Salisbury AB, Threlfall CG,
359   Rega-Brodsky CC, Lepczyk CA, La Sorte FA, MacGregor-Fors I, Scott MacIvor J, Jung K,
360   Piana MR, Williams NSG, Knapp S, Vergnes A, Acevedo AA, Gainsbury AM, Moretti M. 2023.
361   Urbanisation generates multiple trait syndromes for terrestrial animal taxa worldwide. *Nature*
362   *Communications* **14**(1):4751. https://doi.org/10.1038/s41467-023-39746-1

363

364 Hernandez SM, Welch CN, Peters VE, Lipp EK, Curry S, Yabsley MJ, Sanchez S, Presotto A,
365 Gerner-Smidt P, Hise KB, Hammond E. 2016. Urbanized white ibises (*Eudocimus albus*) as
366 carriers of Salmonella enterica of significance to public health and wildlife. *PLoS One*, **11**(10),
367 p.e0164402.

369 i-Tree. (2024 Oct 10). i-Tree Landscape (version 4.6.0) [Web application].

371 Pandolfino ER, Handel CM. 2018. Population trends of birds wintering in the Central Valley of
372 California, in Trends and traditions: Avifaunal change in western North America (Shuford WD,
373 Gill Jr., RE, Handel CM, eds.), pp. 215–235. *Studies of Western Birds 3. Western Field*
374 *Ornithologists*, Camarillo, CA; doi 10.21199/SWB3.12.

375 Pejchar L, Rega-Brodsky CC, Vázquez L, MacGregor-Fors I. 2025. Bird-mediated ecosystem
376 services and disservices in cities and towns. *Frontiers in Ecology and the Environment* e2835.
377 https://doi.org/10.1002/fee.2835

378 Pena JC, Ovaskainen O, MacGregor-Fors I, Teixeira CP, Ribeiro MC. 2023. The relationships
379 between urbanization and bird functional traits across the streetscape. *Landscape and Urban*
380 *Planning* **232**:104685. https://doi.org/10.1016/j.landurbplan.2023.104685

381 Seress G, Liker A. 2015. Habitat urbanization and its effects on birds. Acta Zoologica
382 Academiae Scientiarum Hungaricae **61**(4):373-408. https://doi.org/10.17109/AZH.61.4.373.2015

383 Shochat E, Lerman SB, Katti M, Lewis DB. 2004. Linking optimal foraging behavior to bird
384 community structure in an urban-desert landscape: field experiments with artificial food patches.
385 *The American Naturalist* **164**(2):232-243.

386 Sibley DA. 2022. *The Sibley field guide to birds of western North America*. Knopf.

387 Swartz TM, Blaney AR, Behm JE. 2024. Crumb bums? Context dependence in ecosystem
388 services supplied by common urban animals. *Ecosphere* **15**(10):p.e70014.

389 Tryjanowski P, Møller AP, Morelli F, Biaduń W, Brauze T, Ciach M, Czechowski P, Czyż S,
390 Dulisz B, Goławski A, Hetmański T. 2016. Urbanization affects neophilia and risk-taking at
391 bird-feeders. *Scientific Reports* **6**(1):p.28575.

392 United States Geological Survey. 2024. Annual National Land Cover Database (NLCD)
393 Collection 1 Products [Pdf,png]. U.S. Geological Survey. https://doi.org/10.5066/P94UXNTS
394 Von Döhren P, Haase D. 2015. Ecosystem disservices research: A review of the state of the art
395 with a focus on cities. *Ecological Indicators* **52**:490-497.

396 Wehtje W. 2003. The Range Expansion of the Great-Tailed Grackle (*Quiscalus mexicanus*
397 Gmelin) in North America since 1880. *Journal of Biogeography* **30**(10):1593-1607.

398   Weng Q, Lu D. 2008. A sub-pixel analysis of urbanization effect on land surface temperature
399   and its interplay with impervious surface and vegetation coverage in Indianapolis, United States.
400   *International Journal of Applied Earth Observation and Geoinformation* **10**(1):68–83.

401   Whelan CJ, Wenny DG, Marquis RJ. 2008. Ecosystem Services Provided by Birds. *Annals of the*
402   *New York Academy of Sciences* **1134**(1):25–60. https://doi.org/10.1196/annals.1439.003
403

Figure 1

Map of feeding trial locations across range of impervious surfaces

Locations of 13 sites with feeding trials within the Phoenix metropolitan area, Arizona, USA. Impervious surface from 2021 National Land Cover Database (United States Geological Survey 2024). We characterized impervious surface using the i-Tree Canopy Tool (2024) in analyses. Study site locations ranged in longitude from -112.306 to -111.583 and in latitude from 33.221 to 33.608.
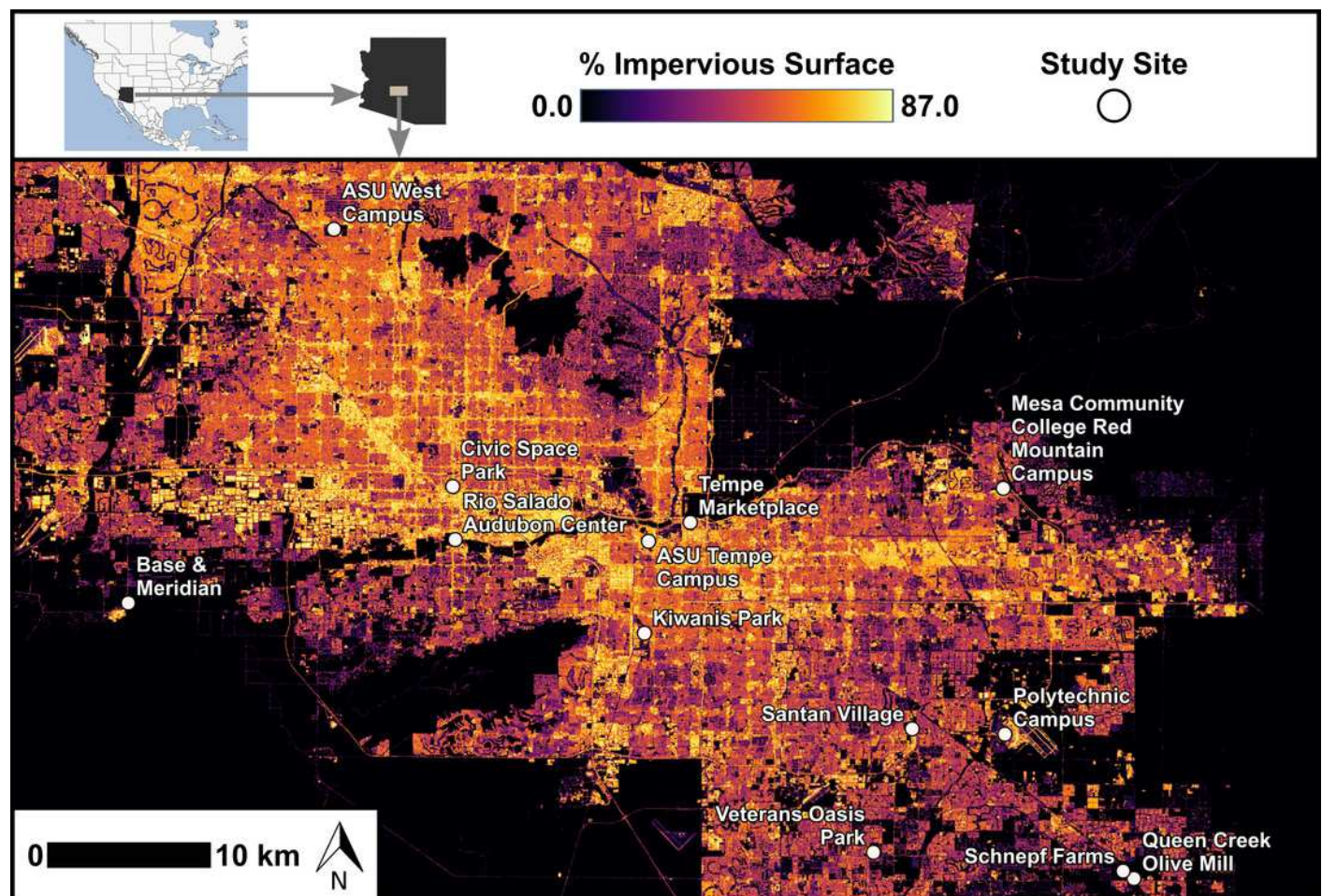
Figure 2

Five most common species/groups seen during feeding trials at stations with visitors across 13 sites in the Phoenix metropolitan area, Arizona, USA.

Mean in seconds (and SE) to first visitor to the feeding station (popcorn). Non-native doves include Eurasian Collared-dove (*Streptopelia decaocto*) and Rock Pigeon (*Columbia livia*). Native doves include Mourning Doves (*Zenaida macroura*), Inca Dove (*Columbina inca*), and White-winged Dove (*Z. asiatica*). The most common visitor was Great-tailed Grackles (*Quiscalus mexicanus*; photo).
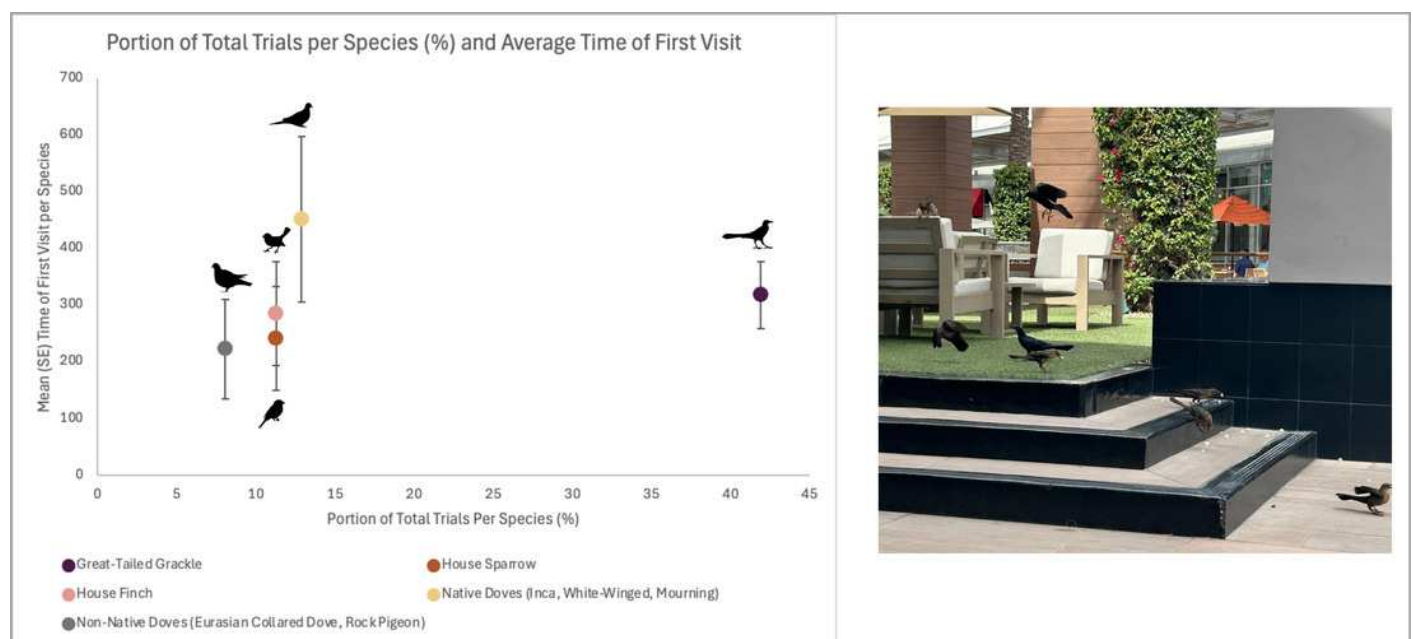
Figure 3

Relationships of impervious surface area with average time of first bird to feeding station.

The average time of first visits (in seconds) for each site (n=13) was negatively associated with sites with high percent of impervious surface. Each site had 6 to 16 feeding stations and times are averaged for each site. Total feeding stations n=126. Shaded area represents the 95% confidence interval of the trendline, as approximated by the 'geom_smooth' function in the R package 'ggplot2'.