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Urban House Sparrow (*Passer domesticus*) populations decline in North America

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ABSTRACT—House Sparrow (*Passer domesticus*) populations declined across much of their global range in the late 20th century. Most research examining this decline is conducted in the species' native European range, but Europe encompasses a small portion of the species' current distribution. House Sparrow population trends in the United States and Canada, and the potential mechanisms driving these trends, remain relatively unexplored. We use 21 years of data from Project FeederWatch, a large-scale citizen science project, to investigate House Sparrow population trends in North America. We found winter flocks in urbanized areas were larger than flocks in rural areas, with widespread spatial heterogeneity in local population trends. Despite greater abundance in developed areas, House Sparrow populations declined in developed areas from 1995 to 2016 while remaining stable in rural areas. House Sparrow population declines coincide with an increase in populations and expansion of the winter distributions of *Accipiter* hawks, which are known predators of House Sparrows. However, we do not find a direct connection between the presence of *Accipiter* hawks at count sites and House Sparrow population declines in winter. These results expand our knowledge of widespread House Sparrow declines to North America and provide context for continuing research on House Sparrow declines in the introduced range. *Received 30 January 2019. Accepted 16 July 2020.*

Key words: *Accipiter*, citizen science, Project FeederWatch, urban ecology.

Decline de las poblaciones urbanas del gorrión *Passer domesticus* en Norteamérica

RESUMEN (Spanish)—Las poblaciones del gorrión *Passer domesticus* han declinado en gran parte de su rango de distribución global desde finales del siglo XX. La mayoría de las investigaciones que examinan este decline se han llevado a cabo en su rango de distribución nativa en Europa, aunque esta región representa solo una pequeña porción de su distribución actual. Las tendencias poblacionales de este gorrión en los Estados Unidos y Canadá, y los posibles mecanismos que operan estas tendencias, permanecen relativamente inexplorados. Utilizamos 21 años de datos del Project FeederWatch, un proyecto de ciencia ciudadana de gran escala, para investigar sus tendencias poblacionales en Norteamérica. Encontramos que las parvadas invernales tuvieron mayor tamaño que aquellas de áreas rurales, con una amplia heterogeneidad espacial en tendencias de las poblacionales locales. Si bien las áreas con mayor desarrollo urbano tuvieron abundancias mayores, las poblaciones de este gorrión declinaron en las mismas de 1995–2016 y permanecieron estables en zonas rurales. Los declines poblacionales de este gorrión coinciden con un incremento poblacional y expansión de las poblaciones invernales de gavilanes *Accipiter*, los cuales son conocidos depredadores de los gorriones. Sin embargo, no encontramos una conexión directa entre la presencia de gavilanes *Accipiter* en los sitios de conteo y los declines poblacionales de los gorriones en el invierno. Estos resultados aumentan nuestro conocimiento sobre los amplios declines del gorrión en Norteamérica y proveen contexto para continuar investigándolos en su rango introducido.

Palabras clave: *Accipiter*, ciencia ciudadana, ecología urbana, Project FeederWatch.

The House Sparrow (*Passer domesticus*) is one of the most ubiquitous passerines globally with a range including parts of 6 continents. First introduced to the United States in Brooklyn, New York, in 1851, House Sparrows rapidly spread across North America (Barrows 1889, Moulton et al. 2010). Today, the House Sparrow is one of North America's most common birds (estimated 82 million individuals; Partners in Flight Science Committee 2013). House Sparrow populations, however, are declining in many parts of the world (Europe: DeLaet and Summers-Smith 2007; Canada: Lepage and Francis 2002, Erksine 2006; Australia: Olsen et al. 2003).

In Europe, House Sparrow population declines began significantly earlier in rural areas than in developed areas, suggesting that population trends are influenced by habitat (Robinson et al. 2005). In rural areas, agricultural intensification is often cited as a factor contributing to declines because modern agricultural practices reduce food availability for largely granivorous species like House Sparrows (DeLaet and Summers-Smith 2007). The most dramatic declines in Europe, however, have occurred in developed areas where decreases in greenspace (Chamberlain et al. 2007) and the lack of potential nesting sites in newer buildings (Wotton et al. 2002) are cited as contributing factors. Additionally, research suggests that the increasing population of Eurasian Sparrowhawks (*Accipiter nisus*) contributes to sparrow population declines (MacLeod et al. 2006, Bell et al. 2010).

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Rural House Sparrow populations in Europe stabilized in the mid-1990s, but House Sparrows continued to decline in developed areas (Summers-Smith 2003). The decline in developed areas, much like the decline in rural areas (Hole et al. 2002), is heterogeneous with some populations remaining stable (DeLaet and Summers-Smith 2007). This heterogeneity is believed to be the product of the House Sparrow's short dispersal range, which prevents House Sparrows from quickly recolonizing areas following local extirpation (Hole et al. 2002). This trend of heterogeneous urban population decline has recently led researchers to focus on the drivers of House Sparrow declines in developed areas, particularly by investigating factors that might affect fledging success (Shaw et al. 2008, Seress et al. 2012, Peach et al. 2014).

Recent House Sparrow population trends are relatively poorly studied in their nonnative range. Breeding Bird Survey trends suggest that House Sparrows are declining at a rate of ~3% per year across North America (Sauer et al. 2017), and declines have also been observed in a number of research studies (Bergtold 1921, Duncan 1996b, Lowther and Cink 2006). Little research has been done on potential mechanisms influencing these trends. Some of the same factors contributing to House Sparrow population declines in Europe may also be contributing to declines in North America, including the intensification of agriculture, reduction of green space in cities, and the resurgence of *Accipiter* hawk populations.

The effect of *Accipiter* hawks on House Sparrow populations is of particular interest because of the rapid recovery of *Accipiter* populations in both Europe and North America. *Accipiter* hawks regularly depredate House Sparrows (Dunn and Tessaglia 1994), and the resurgence of *A. nisus* in Europe is closely correlated with House Sparrow declines (Bell et al. 2010). *Accipiter* populations (particularly *A. cooperi*) in the United States are increasing (Curtis et al. 2006, Bildstein et al. 2008), suggesting that increased predation could negatively affect House Sparrow populations in the United States. The threat of predation in winter may be particularly strong because increasing numbers of *Accipiter* hawks are foregoing migration to Central America and staying in North America year-round (Duncan 1996a, Viverette et al. 1996).

Citizen science projects provide a useful avenue for tracking the abundance of House Sparrows at large spatial and temporal scales. Project FeederWatch, a citizen science project in which people use a standardized protocol to count birds at supplementary feeding stations in North America, offers a particularly good dataset for exploring this question because both House Sparrows and accipiters are frequently found in the proximity of supplementary feeding stations. The FeederWatch dataset is particularly good for longitudinal analyses because it is designed to capture repeated counts at thousands of fixed locations over decades, providing a robust dataset for identifying population trends. Previous research demonstrates strong correlations between Project FeederWatch trends and those from the Christmas Bird Count (Lepage and Francis 2002), and FeederWatch data are widely used in studies of bird populations (e.g., Bonter et al. 2010, Zuckerberg et al. 2011, Greig et al. 2017). While citizen science datasets are often useful for identifying patterns, linking those patterns to process is difficult.

The goal of the current study was not to suggest a definitive cause of House Sparrow declines, but to establish the population trend in North America and provide context for future research on potential factors driving the trends. Specifically, our objectives were to (1) quantify long-term trends in House Sparrow populations at supplementary feeding stations in the United States and Canada, (2) test for variability in population trends depending upon landscape context (rural vs. developed), and (3) explore the potential association of increasing *Accipiter* hawk populations with House Sparrow abundance. Based on findings in the species' native range, we predicted that North American House Sparrow populations would be declining, that declines would be most rapid in developed landscapes, and that declines would be associated with the recent recovery and year-round presence of *Accipiter* hawks in the northern portion of their ranges.

Methods

Bird observations

Data on the abundance and distribution of House Sparrows and *Accipiter* hawks (Sharp-shinned Hawk [*A. striatus*] and Cooper's Hawk [*A. cooperii*]) are from Project FeederWatch

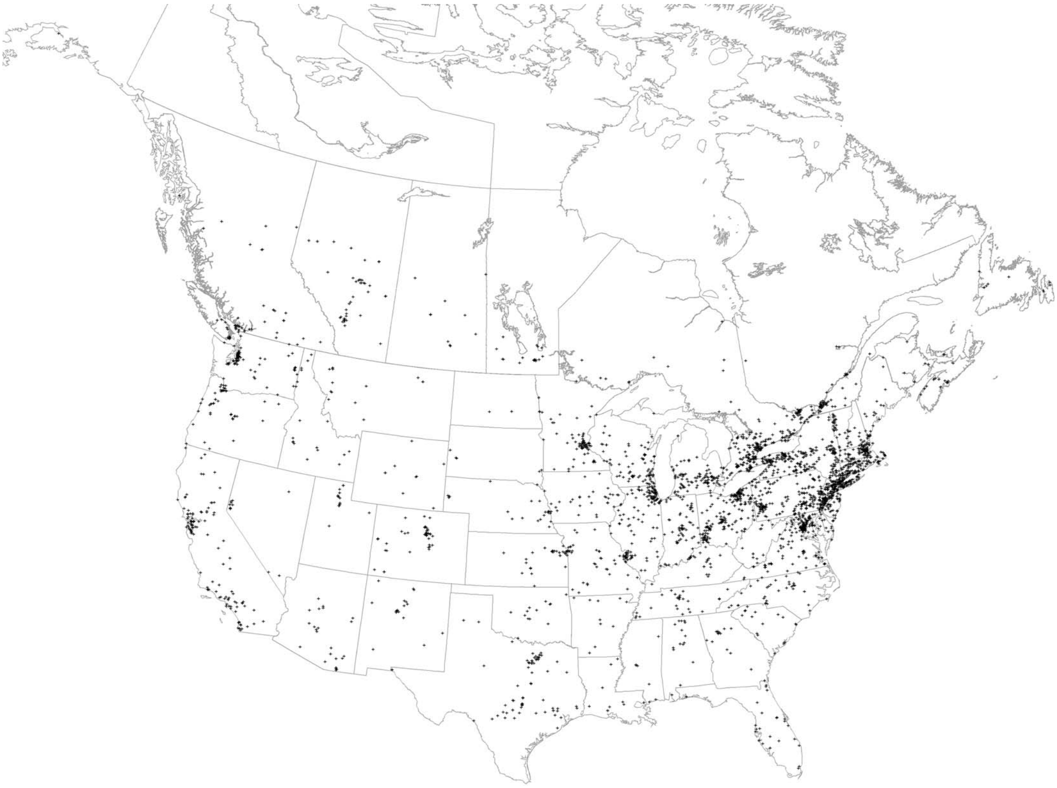

Figure 1. Portions of North America included in the study area. Symbols indicate the locations of Project FeederWatch sites included in the analyses.

(www.feederwatch.org), a citizen science project managed by the Cornell Lab of Ornithology and Birds Canada. FeederWatch participants count the maximum number of each species seen simultaneously in the proximity of a supplementary feeding station during 2 d observation periods, with observations repeated as often as weekly between early November and April annually. Reports are filtered through standard data validation tools (Bonter and Cooper 2012) and only data from valid checklists are included in these analyses. FeederWatch data are scientifically robust and have been used to track changes in the abundances and distributions of birds (e.g., Wells et al. 1998, Bonter and Harvey 2008, Davis et al. 2013), the dynamics of species invasions (Bonter et al. 2010, Koenig et al. 2013, Davis et al. 2014), and the influence of climate change (Zuckerberg et al. 2011, Princé and Zuckerberg 2014, Zuckerberg et al. 2015) and disease on bird populations (Hochachka and Dhondt 2000, Hartup et al. 2001).

For analysis of House Sparrow trends, we limited the FeederWatch dataset to observations submitted during the nonbreeding season (Nov, Dec, and Jan) when individuals tend to congregate in flocks. Data were zero-filled (zero added for FeederWatch submissions where House Sparrows were not recorded) and limited to observations from November 1995 to January 2016 because of missing data on observer effort during the early years of the project. Data were further limited to locations with at least 3 counts reported. Because data entry or computerized data scanning errors can occasionally result in obvious errors such as extremely high counts, we deleted all observations where >200 House Sparrows were reported (<0.001% of all observations), resulting in a final dataset of 1,356,478 observations (Fig. 1). House Sparrows were reported on 44% of those observations. The number of House Sparrows present

Table 1. Model selection results testing for the influence of year, presence of *Accipiter* hawks, and location on mean House Sparrow flock size. Regression coefficients are shown if the variable was included in the model. Effort was included and location was used as a repeated variable in all models. $n = 531{,}322$ observations from 32,313 locations. Lowest AIC_c value = 4,051,793.

Year	Year^2	Accipiter[a]	Latitude	Longitude	ΔAIC_c	Model likelihood	w_i
−25.69	0.006	0.809	0.160	−0.035	0	1.00	1.00
−25.51	0.006	0.810	0.166		50	0.00	0.00
−25.93	0.006	0.810		−0.037	88	0.00	0.00
−25.73	0.006	0.807			145	0.00	0.00
−24.76	0.006		0.159	−0.035	317	0.00	0.00
−24.61	0.006		0.164		367	0.00	0.00
−25.01	0.006			−0.037	403	0.00	0.00
−24.82	0.006				460	0.00	0.00

[a] Accipiter is a categorical variable and the coefficient is related to the presence of an *Accipiter* hawk.

during an observation will hereafter be referred to as flock size (counts reporting zero House Sparrows were eliminated from calculations of mean flock size).

Data on *Accipiter* hawks combined all reports of Sharp-shinned Hawk, Cooper's Hawk, and "unknown *Accipiter*" because both species depredate House Sparrows and similarities between the species often make definitive identification challenging. Data were coded as presence/absence of an *Accipiter* hawk during a given observation period because almost all reports of *Accipiter* hawks are of a single individual; accipiters were reported on 122,194 (9%) of the 1,356,478 observation periods.

Statistical analyses

To identify which predictor variables best explained year-to-year changes in flock sizes of House Sparrows we evaluated a set of candidate models using AIC_c scores (Burnham and Anderson 2002). The full model (Table 1) was [flock size = year + year^2 + Accipiter + latitude + longitude + effort], where year = the FeederWatch season (continuous), Accipiter = the detection of an *Accipiter* hawk during the count period (binary), effort = observation effort during the 2 d count period (categorical scale: <1, 1–4, 4–8, and >8 h), and the latitude and longitude of each observation site to test for potential spatial trends in abundance. Because counts were conducted at the same locations over time, we included the unique location identifier as a random (repeated) variable in the analyses (PROC MIXED in SAS 9.4; SAS Institute 2012). We included observation effort in all candidate models due to prior research demonstrating the importance of including effort when analyzing FeederWatch data (Bonter et al. 2010). After we deleted zero counts, flock size analyses were based on data from 531,322 observations from 32,313 locations.

Because changes in abundance could be reflected in changes in flock size or changes in the proportion of locations hosting the species, we further tested for trends in the proportion of counts on which House Sparrows were observed. We translated abundance data into presence/absence data and calculated the proportion of counts per FeederWatch season on which House Sparrows (or *Accipiter* hawks) were reported at each location. This proportion was then used as the response variable in a model (PROC GLIMMIX with distribution = beta and link = logit) with year, year^2, and number of counts per site/year combination as explanatory variables.

To test for differences in trends among habitats, the dataset was trimmed to only include locations established after the year 2000 that were plotted with online mapping tools allowing for accurate placement of counting locations (previous location information was geolocated to the centroid of postal codes). Data were further limited to sites in the continental United States due to the geographical limits of the National Land Cover Data 2011 (NLCD) dataset (Homer et al. 2015). After trimming, the dataset included 212,186 observations from 12,485 sites. The NLCD dataset divides the United States into 30×30 m cells, each with a single land cover classification based on the predominant land cover type within that cell. We used ArcGIS 10.4.1 (ESRI 2015) to draw a 1 km buffer around each location and quantify the proportion of the buffer that overlapped with each NLCD category. The 1 km buffer distance is based on the likely radius of a House Sparrow home range (Summers-Smith 2003). We then aggregated NLCD categories to create a "proportion urban" variable, which included land cover categories defined as "developed" by the NLCD based on an estimation of impervious surface. The "developed" category therefore included NLCD categories 21 (developed, open space), 22 (20–49% impervious), 23 (50–79% impervious), and 24 (80–100% impervious), as a proportion of the total landscape within the buffered area. All other land cover types, which include various forest and agricultural categories, were classified as "rural." We then tested for potential habitat-based differences in House Sparrow population trends with the models [flock size = year + habitat + year*habitat + effort] and [proportion of counts with House Sparrows = year + habitat + year*habitat + effort] with site included as a random variable.

To generate a map for visualizing the spatial patterns of changes in sparrow populations, we limited the dataset to "long-term" sites with at least 3 counts during November, December, and January for at least 10 FeederWatch seasons ($N =$ 3,236 locations). We then modeled flock size at these "long-term" sites as a function of observer effort (categorical), the presence or absence of an *Accipiter* (binary), and year (continuous) using PROC GLM in SAS. Using the beta estimates for the year variable, we generated an interpolated map using inverse distance weighting (Spatial Analyst toolbox, ArcGIS 10.4.1; ESRI 2015).

Finally, we examined whether House Sparrow flock sizes declined more rapidly within a season at sites with *Accipiter* hawks than at sites where these predators were not observed. We identified sites as "*Accipiter* present" if an *Accipiter* hawk was reported at least once during January and February. We then calculated the mean monthly flock size for each location by year and the proportion change from the November mean (i.e., monthly mean/November mean) for each location and year combination (n = 95,940 location/year combinations). To graphically illustrate seasonal declines in House Sparrow abundance, we then plotted the mean monthly proportions by the presence or absence of *Accipiter* hawks.

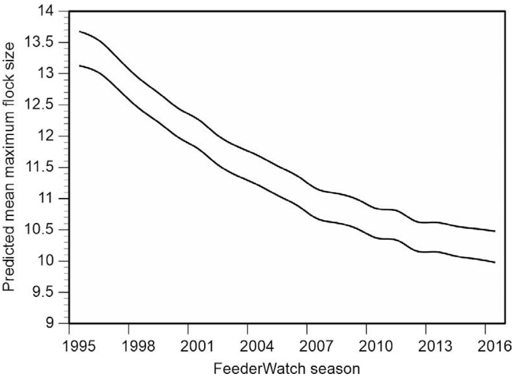

Figure 2. Decline in mean flock size over time across FeederWatch locations in the United States and Canada. Data indicate the predicted mean (95% confidence interval) from the best-fitting model (see Table 1).

Results

House Sparrow winter flock sizes declined across the United States and Canada from 1995 to 2016 (Fig. 2). Model selection results indicated that the full model containing year, year^2, presence of *Accipiter* hawks, latitude, longitude, and observer effort was best supported by the data (Table 1). According to this model, the maximum flock size of House Sparrows on a count decreased over time ($\beta = -25.692 \pm 2.530$; Fig. 2), decreased from east to west across the United States and Canada ($\beta = -0.035 \pm 0.005$), increased from south to north ($\beta = 0.160 \pm 0.016$), and increased when an *Accipiter* hawk was present ($\beta = 0.809 \pm 0.045$). House Sparrow winter flock sizes were 9.7% greater on counts where *Accipiter* hawks were reported (mean 12.05 $\pm$ 0.006) than on counts where *Accipiter* hawks were not seen (10.98 $\pm$ 0.002). The proportion of sites reporting House Sparrows decreased from 1995 to 2016 by 7.5% while the proportion of sites reporting accipiters increased by 14.4%.

Examining the relationship between anthropogenic development and trends in House Sparrow flock sizes, we found larger flock sizes in more developed landscapes ($\beta = 219.12 \pm 38.49$; Fig. 3). Although larger flocks were found in developed landscapes, House Sparrow flocks decreased in size over time in developed landscapes while remaining stable in rural landscapes (year $\times$ habitat interaction: $\beta = -0.11 \pm 0.02$; Fig. 4). The model predicted that the proportion of counts on which

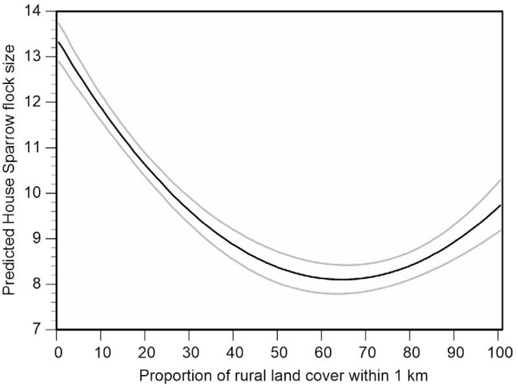

Figure 3. Predicted mean House Sparrow flock sizes based on the percentage of the 1 km radius landscape surrounding a count site that was defined as "rural". Values represent mean (95% CI) predicted maximum flock sizes from a mixed model where mean flock size was modeled as a function of habitat type and (habitat type)^2 with site identifier as a random variable.

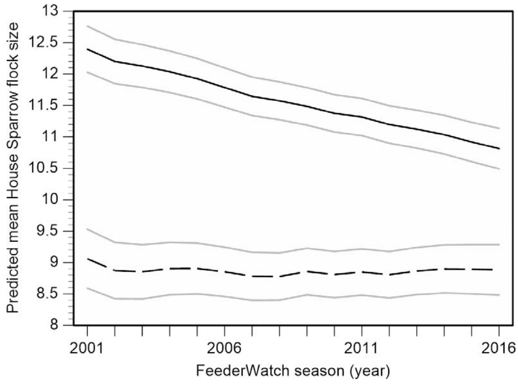

Figure 4. Trends in House Sparrow flock sizes in developed (solid line) and rural (dashed line) landscapes. Values represent mean predicted values (95% CI) from the model (flock size = year + year^2 + Accipiter + proportion_developed + year*proportion_developed + latitude + effort) with location as a random variable. For graphical representation only, "rural" sites show those where the developed proportion of the landscape <30% and "developed" sites show those where the developed proportion of the landscape >70%.

House Sparrows were detected was, on average, 30.8% greater in developed areas than in rural areas ($\beta_{habitat}$ = 9.76 ± 1.30). The predicted proportion of counts with House Sparrow detections, however, decreased in developed landscapes by 6.9% between 2001 and 2016 while increasing by 10.1% in rural landscapes ($\beta_{year*habitat}$ = –0.005 ± 0.001).

Temporal trends in flock size at long-term sites indicated that the spatial pattern was heterogeneous, with populations increasing in some areas while decreasing in nearby locations. The largest declines tended to be associated with developed areas (Fig. 5).

Patterns of interannual change in House Sparrow flock sizes did not vary between sites where accipiters were reported and sites that lacked accipiters. Flock sizes increased from November to December, presumably as winter flocks continued to form, and then decreased to 90% of November sizes by March (Fig. 6).

Discussion

In the United States and Canada, the proportion of sites reporting House Sparrows declined by 7.5% and mean flock sizes declined by 22% from 1995 to 2016. These declines are comparable to those observed in the similar Garden Bird Feeder Survey in Britain (58% population decline from 1970 to 2000; Robinson et al. 2005). The declines we detected in North America were spatially heterogeneous with reductions in highly developed landscapes while rural populations were stable. Our results, therefore, do not suggest a connection between contemporary agricultural intensification and House Sparrow declines in the United States and Canada, although such changes could have affected sparrow populations in the past. Although our counts are limited to those areas where feeders are present, we believe that the widespread use of feeders in both urban and rural areas has provided accurate insight into a decline that differs based on land cover type. Our results are spatially consistent with recent House Sparrow declines in Europe, which have occurred almost exclusively in developed areas since the mid-1990s (Summers-Smith 2003).

Contrary to our expectations, we found flock sizes of House Sparrows to be higher at sites at which *Accipiter* hawks were reported. Although we anticipated that the presence of bird-eating hawks would lead to reduced House Sparrow abundance as individuals are lost to predation, the contrary result could be a function of changes in sparrow behavior instigated by perceived predation pressure. It is possible that, when a hawk is seen near a feeder, the birds in the area form larger

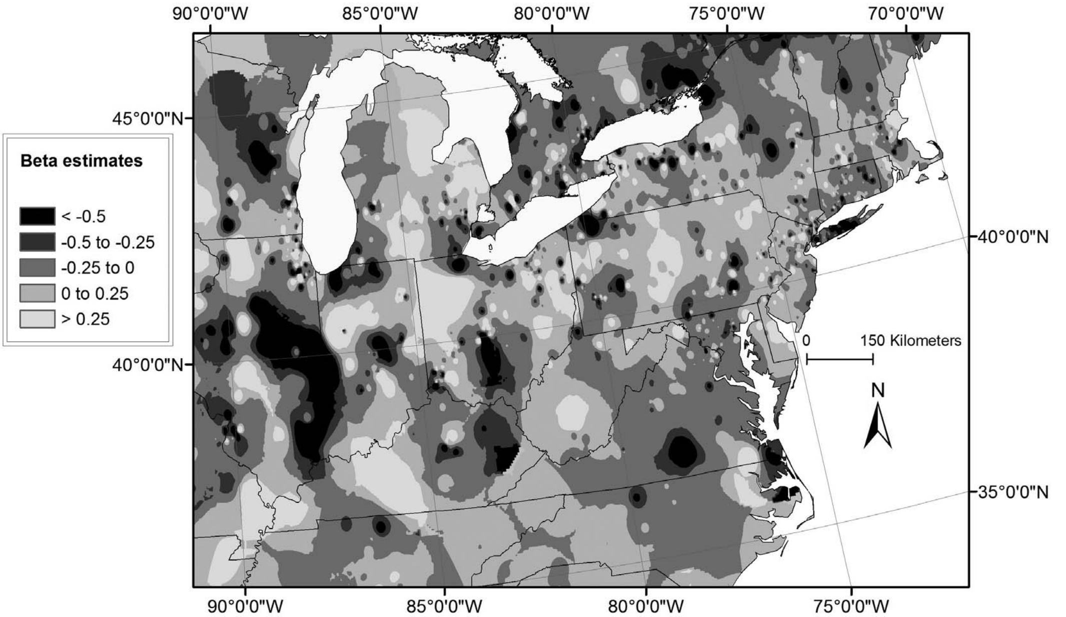

Figure 5. Heterogeneous spatial patterns in House Sparrow population trends at long-term sites (≥10 year). Data represent beta estimates of the linear trend in mean flock size over time for 3,236 sites from the model [flock size = year + effort + Accipiter]. The maps were created using inverse distance weighting in ArcGIS. The northeastern United States is shown because the abundance of sites in the region allowed for interpolation.

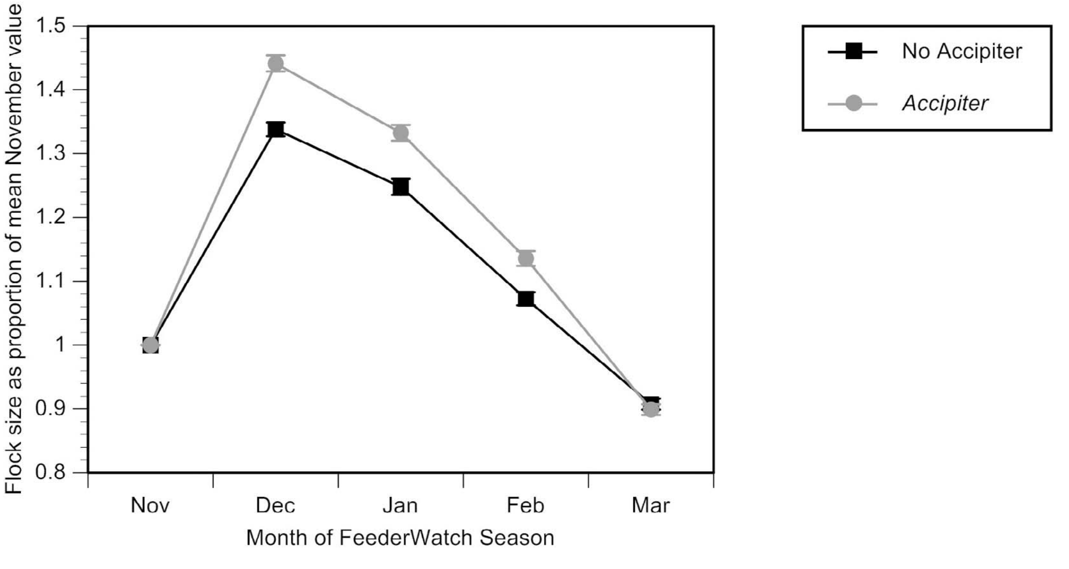

Figure 6. Seasonal changes in House Sparrow flock size as a function of whether an *Accipiter* hawk was detected at the site during the winter. Means and standard errors of the mean monthly House Sparrow flock size as a proportion of site- and year-specific November means are reported. Data across all years, 1995–2016, are combined.

flocks before undertaking risky behavior such as visiting an exposed feeder (Lima and Dill 1990). This behavioral change, therefore, would result in the detection of greater numbers of sparrows. Alternatively, the correlation between *Accipiter* presence and flock size may be due to changes in hawk behavior rather than changes in sparrow behavior. Previous research with FeederWatch data showed that hawks prefer feeding stations where birds are most abundant (Dunn and Tessaglia 1994). Thus, hawks may be selectively foraging near feeders with large numbers of birds (including House Sparrows), thereby leading to the positive relationship between the presence of a hawk and House Sparrow flock size. Finally, a third reason for the correlation between *Accipter* presence and House Sparrow abundance may be a function of the sites themselves and not an interaction between *Accipters* and sparrows; some sites may host a greater number of species overall, and this could lead to the correlation we observed.

Because predation pressure from Eurasian Sparrowhawks is positively correlated with House Sparrow declines in Europe (Bell et al. 2010), we hypothesized that increasing *Accipiter* populations in developed areas might explain the spatial pattern of declining House Sparrow populations in North America. Likewise, accipiters are implicated in contributing to declining Red-headed Woodpecker (*Melanerpes erythrocephalus*) populations (Koenig et al. 2017). *Accipiter* detections at Feederwatch sites increased from 2000 to 2016, reflecting the continued resurgence of these hawks in the United States following an early 20th century population crash (Bednarz et al. 1990, Bildstein et al. 2008). This recovery is particularly noticeable in developed areas, likely due to the abundance of preferred food sources such as doves (e.g., Mourning Dove [*Zenaida macroura*]) and European Starlings (*Sturnus vulgaris*; Boal and Mannan 1998). Contrary to the European results and to our expectations, however, roughly an equal proportion of House Sparrows disappeared from sites with and without accipiters within a season (Fig. 6). This suggests that sparrows at sites with and without these hawks experience similar rates of overwinter mortality and that accipiters are not driving declines in House Sparrow populations during the winter months. This does not rule out the possibility that accipiters are impacting House Sparrow populations during other times of the year. *Accipiter* predation may cause a decline in House Sparrows during the breeding season, for example, by reducing post-fledging survival. Predation is one of the most frequent causes of mortality in newly fledged urban birds (Whittaker and Marzluff 2009), so an increase in *Accipiter* abundance could result in significant declines in post-fledging survival. This hypothesis remains to be tested.

It is possible that an effect of accipters on House Sparrow declines could emerge if Sharp-shinned and Cooper's hawks were considered separately, because Sharp-shinned Hawks are more frequent predators of House Sparrows than are Cooper's Hawks (Dunn and Tessaglia 1994, Roth and Lima 2003). However, differentiating between these 2 species requires a level of experience that cannot be assumed in the dataset in its current form. Pursuing this line of inquiry may provide an opportunity for additional research on North American House Sparrow predation outside of a citizen science context.

There are several hypotheses for why House Sparrow populations are declining in developed areas while rural populations remain relatively unchanged. House Sparrows may encounter lower-quality habitats for nesting (Chávez-Zichinelli et al. 2010, Seress et al. 2012, Meillère et al. 2017) potentially due to the challenges of finding food sources that are high in protein (invertebrates) for their nestlings (Vincent 2005). Provisioning of supplemental insects to breeding House Sparrows in London led to a 55% increase in fledged young, indicating that insect availability is a limiting factor for rearing nestlings (Peach et al. 2014). Increases in fledging success, however, have not been correlated with increased population density (Peach et al. 2015).

Another hypothesis that could explain a decline in House Sparrows in developed areas is a decrease in the availability of nest sites. Modern architecture and construction techniques may reduce the availability of cavities and crevices within which sparrows can nest. This hypothesis is contested, however, with a study in the United Kingdom finding that breeding House Sparrows prefer older buildings to new buildings (Wotton et al. 2002), while a study in Italy found no difference (Brichetti et al. 2008). Because the importance of old buildings seems to differ depending on the location where the research is conducted, further research on nest site availability in developed areas would have to be conducted in North America to determine if this hypothesis is supported in the introduced range.

Here we establish that House Sparrow populations are, on average, declining in urbanized locations in North America. We found no support for the hypothesis that *Accipiter* hawks are causing the decline in House Sparrows, but birds face numerous other challenges in developed landscapes. For instance, survival and reproductive success may be reduced by increasing predation by cats (Churcher and Lawton 1987, Baker et al. 2005, Loss et al. 2013), changes in habitat structure (Shaw et al. 2008), window collisions (Klem 2008), and air or heavy metal pollution (Pinowski et al. 1995, Summers-Smith 2003, Vincent 2005). Exploring these potential causes might shed light on the heterogeneity of House Sparrow population declines in North America and worldwide.

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Literature cited

Baker PJ, Bentley AJ, Ansell RJ, Harris S. 2005. Impact of predation by domestic cats *Felis catus* in an urban area. Mammal Review. 35:302–312.

Barrows WB. 1889. The English Sparrow (*Passer domesticus*) in North America, especially in its relations to agriculture. Washington (DC): USDA Division of Economic Ornithology and Mammalogy. Bulletin 1.

Bednarz JC, Klem D Jr, Goodrich LJ, Senner SE. 1990. Migration counts of raptors at Hawk Mountain, Pennsylvania, as indicators of population trends, 1934–1986. Auk. 97:96–109.

Bell CP, Baker SW, Parkes NG, Brooke ML, Chamberlain DE. 2010. The role of the Eurasian Sparrowhawk (*Accipiter nisus*) in the decline of the House Sparrow (*Passer domesticus*) in Britain. Auk. 127:411–420.

Bergtold WH. 1921. The English Sparrow (*Passer domesticus*) and the motor vehicle. Auk. 38:244–250.

Bildstein KL, Smith JP, Inzunza ER, Veit RR, editors. 2008. State of North America's birds of prey. Washington (DC): American Ornithologists' Union and Cambridge (MA): Nuttall Ornithological Club. Series in Ornithology No. 3.

Boal CW, Mannan RW. 1998. Nest-site selection by Cooper's Hawks in an urban environment. Journal of Wildlife Management. 62:864–871.

Bonter DN, Cooper CB. 2012. Data validation in citizen science: A case study from Project FeederWatch. Frontiers in Ecology and the Environment. 10:305–307.

Bonter DN, Harvey MG. 2008. Winter survey data reveal rangewide decline in Evening Grosbeak populations. Condor. 110:376–381.

Bonter DN, Zuckerberg B, Dickinson JL. 2010. Invasive birds in a novel landscape: Habitat associations and effects on established species. Ecography. 33:494–502.

Brichetti P, Rubolini D, Galeotti P, Fasola M. 2008. Recent declines in urban Italian Sparrow (*Passer domesticus italiae*) populations in northern Italy. Ibis. 150:177–181.

Burnham KP, Anderson DR. 2002. Model selection and inference: A practical information-theoretic approach. New York (NY): Springer-Verlag.

Chamberlain DE, Toms MP, Cleary-McHarg R, Banks AN. 2007. House Sparrow (*Passer domesticus*) habitat use in urbanized landscapes. Journal of Ornithology. 148:453–462.

Chávez-Zichinelli CA, MacGregor-Fors I, Rohana PT, Valdéz R, Romano MC, Schondubea JE. 2010. Stress responses of the House Sparrow (*Passer domesticus*) to different urban land uses. Landscape and Urban Planning. 98:183–189.

Churcher PB, Lawton JH. 1987. Predation by domestic cats in an English village. Journal of Zoology. 212:439–455.

Curtis OE, Rosenfield RN, Bielefeldt J. 2006. Cooper's Hawk (*Accipiter cooperii*). In: Rodewald PG, editor. Birds of North America. Ithaca (NY): Cornell Lab of Ornithology.

Davis AY, Malas N, Minor ES. 2014. Substitutable habitats? The biophysical and anthropogenic drivers of an exotic bird's distribution. Biological Invasions. 16:415–427.

DeLaet J, Summers-Smith JD. 2007. The status of the urban House Sparrow *Passer domesticus* in north-western Europe: A review. Journal of Ornithology. 148:275–278.

Duncan CD. 1996a. Changes in the winter abundance of Sharp-Shinned Hawks in New England. Journal of Field Ornithology. 67:254–262.

Duncan RA. 1996b. House Sparrow (*Passer domesticus*) trends in coastal northwest Florida–Alabama based on Christmas Bird Count data. Alabama Birdlife. 42:82–83.

Dunn EH, Tessaglia DL. 1994. Predation of birds at feeders in winter. Journal of Field Ornithology. 65:8–16.

Erksine A. 2006. Recent declines of House Sparrows, *Passer domesticus*, in Canada's maritime provinces. Canadian Field-Naturalist. 120:43–49.

ESRI. 2015. ArcGIS 10.4.1. Redlands (CA): Environmental Systems Research Institute, Inc.

Greig EI, Wood EM, Bonter DN. 2017. Winter range expansion of a hummingbird is associated with urbanization and supplemental feeding. Proceedings of the Royal Society B. 284:20170256.

Hartup BK, Dhondt AA, Sydenstricker KV, Hochachka WM, Kollias GV. 2001. Host range and dynamics of mycoplasmal conjunctivitis among birds in North America. Journal of Wildlife Diseases. 37:72–81.

Hochachka WM, Dhondt AA. 2000. Density-dependent decline of host abundance resulting from a new infectious disease. Proceedings of the National Academy of Sciences USA. 97:5303–5306.

Hole DG, Whittingham MJ, Bradbury RB, Anderson GQ, Lee PLM, et al. 2002. Widespread local House-Sparrow extinctions. Nature. 418:931–932.

Homer CG, Dewitz JA, Yang L, Jin S, Danielson P, et al. 2015. Completion of the 2011 National Land Cover Database for the conterminous United States—Representing a decade of land cover change information. Photogrammetric Engineering and Remote Sensing. 81:345–354.

Klem D. 2008. Avian mortality at windows: The second largest human source of bird mortality on Earth. Proceedings of the Fourth International Partners in Flight Conference: Tundra to Tropics. p. 244–251.

Koenig WD, Liebhold AM, Bonter DN, Hochachka WM, Dickinson JL. 2013. Effects of the emerald ash borer invasion on four species of birds. Biological Invasions. 15:2095–2103.

Koenig WD, Walters EL, Rodewald PG. 2017. Testing alternative hypotheses for the cause of population declines: The case of the Red-headed Woodpecker. Condor. 119:143–154.

Lepage D, Francis CM. 2002. Do feeder counts reliably indicate bird population changes? 21 years of winter bird counts in Ontario, Canada. Condor. 104:255–270.

Lima SL, Dill LM. 1990. Behavioral decisions made under the risk of predation: A review and prospectus. Canadian Journal of Zoology. 68:619–640.

Loss SR, Will T, Marra PP. 2013. The impact of free-ranging domestic cats on wildlife of the United States. Nature Communications. 4:1396.

Lowther PE, Cink CL. 2006. House Sparrow (*Passer domesticus*). In: Rodewald PG, editor. Birds of North America Online. Ithaca (NY): Cornell Lab of Ornithology.

MacLeod R, Barnett P, Clark J, Cresswell W. 2006. Mass-dependent predation risk as a mechanism for House Sparrow declines? Biology Letters. 2:43–46.

Meillère A, Brischoux F, Henry P-Y, Michaud B, Garcin R, Angelier F. 2017. Growing in a city: Consequences on body size and plumage quality in an urban dweller, the House Sparrow (*Passer domesticus*). Landscape and Urban Planning. 160:127–138.

Moulton MP, Cropper WP, Avery ML, Moulton LE. 2010. The earliest House Sparrow introductions to North America. Trends in Ecology and Evolution. 12:2955–2958.

Olsen P, Weston M, Cunningham R, Silcocks A. The state of Australia's birds 2003. Supplement to Wingspan 13.

Partners in Flight Science Committee. 2013. Population estimates database, version 2013.

Peach WJ, Mallord JW, Ockendon N, Orsman CJ, Haines WG. 2015. Invertebrate prey availability limits reproductive success but not breeding population size in suburban House Sparrows *Passer domesticus*. Ibis. 157:601–613.

Peach WJ, Sheehan DK, Kirby WB. 2014. Supplementary feeding of mealworms enhances reproductive success in garden nesting House Sparrows *Passer domesticus*. Bird Study. 61:378–385.

Pinowski J, Romanowski J, Barkowska M, Sawicka-Kapusta K, Kaminski P, Kruszewicz A. 1995. The effects of heavy metals on the development and mortality of House Sparrow (*Passer domesticus*) and Tree Sparrow (*Passer montanus*) nestlings. In: Pinowski J, Kavanagh B, Pinokska B, editors. Nestling mortality of granivorous birds due to microorganisms and toxic substances: Synthesis. Warsaw (Poland): Polish Scientific Publishers.

Princé K, Zuckerberg B. 2014. Climate change in our backyards: The reshuffling of North America's winter bird communities. Global Change Biology. 21:572–585.

Robinson RA, Siriwardena GM, Crick HQP. 2005. Size and trends of the House Sparrow *Passer domesticus* population in Great Britain. Ibis. 147:552–562.

Roth TC, Lima SL. 2003. Hunting behavior and diet of Cooper's Hawks: An urban view of the small-bird-in-winter paradigm. Condor. 105:474–483.

SAS Institute. 2012. SAS version 9.4. Cary (NC): SAS Institute.

Sauer JR, Niven DK, Hines JE, Ziolkowski DJ, Pardieck KL, et al. 2017. The North American Breeding Bird Survey, Results and Analysis 1966–2015. Version 2.07.2017. Laurel (MD): USGS Patuxent Wildlife Research Center.

Seress G, Bókony V, Pipoly I, Szép T, Nagy K, Liker A. 2012. Urbanization, nestling growth and reproductive success in a moderately declining House Sparrow population. Journal of Avian Biology. 43:403–414.

Shaw LM, Chamberlain D, Evans M. 2008. The House Sparrow *Passer domesticus* in urban areas: Reviewing a possible link between post-decline distribution and human socioeconomic status. Journal of Ornithology. 149:293–299.

Summers-Smith JD. 2003. Decline of the House Sparrow: A review. British Birds. 96:439–446.

Vincent KE. 2005. Investigating the causes of the decline of the urban House Sparrow *Passer domesticus* population in Britain [dissertation]. Leicester (UK): De Montfort University.

Viverette CB, Struve S, Goodrich LJ, Bildstein KL. 1996. Decreases in migrating Sharp-shinned Hawks (*Accipiter striatus*) at traditional raptor-migration watch sites in eastern North America. Auk. 113:32–40.

Wells JV, Rosenberg KV, Dunn EH, Tessaglia-Hymes DL, Dhondt AA. 1998. Feeder counts as indicators of spatial and temporal variation in winter abundance of resident birds. Journal of Field Ornithology. 69:577–586.

Whittaker KA, Marzluff JM. 2009. Species-specific survival and relative habitat use in an urban landscape during the postfledging period. Auk. 131:288–299.

Wotton SR, Field R, Langston RHW, Gibbons DW. 2002. Homes for birds. British Birds. 95:586–592.

Zuckerberg B, Bonter DN, Hochachka WM, Koenig WD, DeGaetano AT, Dickinson J. 2011. Climatic constraints on wintering bird distributions are modified by urbanization and weather. Journal of Animal Ecology. 80:403–413.

Zuckerberg B, Ross EJ, Prince K, Bonter DN. 2015. Climate variability on wintering grounds drives spring arrival of short-distance migrants to the upper midwestern United States. Studies in Avian Biology. 47:83–94.