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Rapid Urbanization Alters Overwintering Abundance and Sex Ratio of the American Kestrel

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ABSTRACT.—Urbanization increasingly causes alterations in prey diversity and abundance, land cover, and human disturbance, subsequently impacting populations of even the most adaptable species. American Kestrels are currently considered urban adapters, which may be veiling the influence of urbanization on their continental population decline. We quantified overwintering abundance and sex ratios of American Kestrels throughout the past three decades in a rapidly developing region of the species' wintering range in southeast Florida to study spatial and temporal population trends relative to degree of urbanization. We detected a significant negative correlation between annual building density and kestrel abundance. Sex ratios also significantly shifted from predominantly female to predominantly male over time and in association with increased residential development. This trend suggests that developed landscapes may represent lower quality territories, as females typically occupy better quality overwintering habitat than males. These results suggest that urbanization may negatively impact overwintering American Kestrel populations in this region and should be investigated as a possible factor contributing to the overall continental population decline, particularly in the eastern flyway where urbanization is prevalent.

KEY WORDS: *Declining species*; *population density*; *sex ratio*; *survey*; *urbanization*.

LA URBANIZACIÓN RÁPIDA ALTERA LA ABUNDANCIA INVERNAL Y LA PROPORCIÓN DE SEXOS DE *FALCO SPARVERIUS*

RESUMEN.—La urbanización causa cada vez más alteraciones en la diversidad y abundancia de presas, la cobertura del suelo y la perturbación humana, impactando posteriormente en las poblaciones incluso de las especies más adaptables. *Falco sparverius* es considerada actualmente como una especie adaptada a los ambientes urbanos, lo que podría estar enmascarando la influencia de la urbanización en su declive poblacional continental. Para estudiar las tendencias poblacionales espaciales y temporales en relación con el grado de urbanización, cuantificamos la abundancia invernal y las proporciones de sexos de *F. sparverius* a lo largo de las últimas tres décadas en una región de rápido desarrollo urbano dentro del área de invernada de la especie en el sureste de Florida. Detectamos una correlación negativa significativa entre la densidad anual de edificios y la abundancia de individuos de *F. sparverius*. Con el tiempo, la proporción de sexos también cambió significativamente, desde un predominio de hembras a un predominio de machos, en relación con un mayor desarrollo residencial. Esta tendencia sugiere que los paisajes urbanizados pueden representar territorios de menor calidad, ya que las hembras suelen ocupar hábitats de invernada de mejor calidad que los machos. Estos resultados sugieren que la urbanización podría afectar negativamente a las

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poblaciones invernantes de *F. sparverius* en esta región y se debería investigar como un posible factor que contribuye al declive poblacional continental general, especialmente en la ruta migratoria oriental donde la urbanización es prevalente.

[Traducción del equipo editorial]

INTRODUCTION

Urbanization is becoming increasingly prevalent across North America, resulting in major alterations to avian community composition in urbanized habitats (Chace and Walsh 2004, Escobar-Ibáñez et al. 2019). Urbanization poses novel challenges and opportunities for organisms through fragmentation, vegetation changes, and increased human disturbance (Emlen 1974, Chace and Walsh 2004, Robinson et al. 2005). Urban sprawl generates an urbanization gradient and subsequent ecological gradient, causing the most disturbance to organisms at the center of an urbanized area (Blair 1996, McDonnell and Hahs 2008, Escobar-Ibáñez et al. 2019). Indeed, avian abundance and species diversity seem to decline as urbanization intensity increases (Clucas and Marzluff 2015, Escobar-Ibáñez et al. 2019, Planillo et al. 2020). Studying organisms along the urbanization gradient allows for categorization of species as "urban avoiders," "urban exploiters," or "urban adapters" depending on their reaction to differently urbanized landscapes (Blair 1996).

Many raptors adapt readily to urban environments, perhaps due to increased biomass of songbird and small mammal prey associated with human developments, and use of anthropogenic perching and nesting structures (reviewed in Boal and Dykstra 2018). However, threats such as increased human disturbance, collisions with man-made structures (Klem 2009), decreases in insect abundance due to nonnative plant prevalence (Tallamy 2004), and exposure to human-associated toxins (Septon and Marks 1996) may limit populations in urban environments. Due to the balance of ecological tradeoffs within urbanized landscapes, some populations may shift their level of urban tolerance depending on the degree and persistence of the urban disturbance (Cooper et al. 2021).

Populations of the small, partially migratory, American Kestrel (*Falco sparverius*; hereafter kestrel) have been steadily declining since the 1970s possibly due in part to degradation of winter territories (Smallwood et al. 2009). Kestrels are currently considered urban adapters since they readily nest in human-made structures, benefit from increased songbird and small mammal abundance in urban environments, and hunt from anthropogenic structures such as powerlines (Brack et al. 1985, Berry et al. 1998, Chace and Walsh 2004). Indeed, some studies describe populations of kestrels residing exclusively in urban habitats year-round, likely capitalizing on these urban benefits (Buckley et al. 2018). However, urban migratory stopovers and wintering areas may hold some migratory individuals that are not necessarily adapted to urban conditions at any other point in their annual cycle (Smallwood et al. 2009). It is therefore important to test whether kestrels are urban adapters at all points in their full annual cycle to evaluate whether urbanization may be contributing to population declines.

Intraspecific competition between sexes may also increase as urbanization leads to decreased availability of undisturbed territories. Female kestrels typically occupy winter territories of higher quality than male kestrels (Ardia and Bildstein 1997, Pandolfino et al. 2011), likely due to the dominance status provided by sexual size dimorphism (female kestrels are typically 10–15% heavier than males; Bird 1988). Female kestrels also generally arrive at wintering grounds before males, allowing females to select preferred territories (Smallwood 1988). This sexual segregation may allow for assessment of habitat preferences, as female kestrels' territories may represent preferred habitat characteristics compared to male kestrels' territories. Population sex ratios could therefore provide inference into habitat quality (Mills 1976, Marra 2000). Subsequently, alterations in population sex ratios may indicate alterations in habitat quality, with an increasingly female-dominated sex ratio suggesting increased availability of high quality habitat and an increasingly male-dominated sex ratio suggesting diminishing availability of high quality habitat.

During the majority of our survey years (1994 through 2021), the human population in the United States grew more rapidly in the southern states than in any other region (Reynolds 2001). With the population of Florida doubling every 20 yr during the 20th century, urban development is dramatically increasing to meet demands (Reynolds 2001). Among this increase in urban development is the growth of residential communities like those found in Cape Coral, Florida, USA, a known wintering ground for kestrels. Cape Coral is one of the fastest-growing cities in Florida and expanded to cover about 480 km^2 since its founding in 1957 (Cape Coral Florida [CCF] 2021). In the 1980s, paved roads and powerlines were

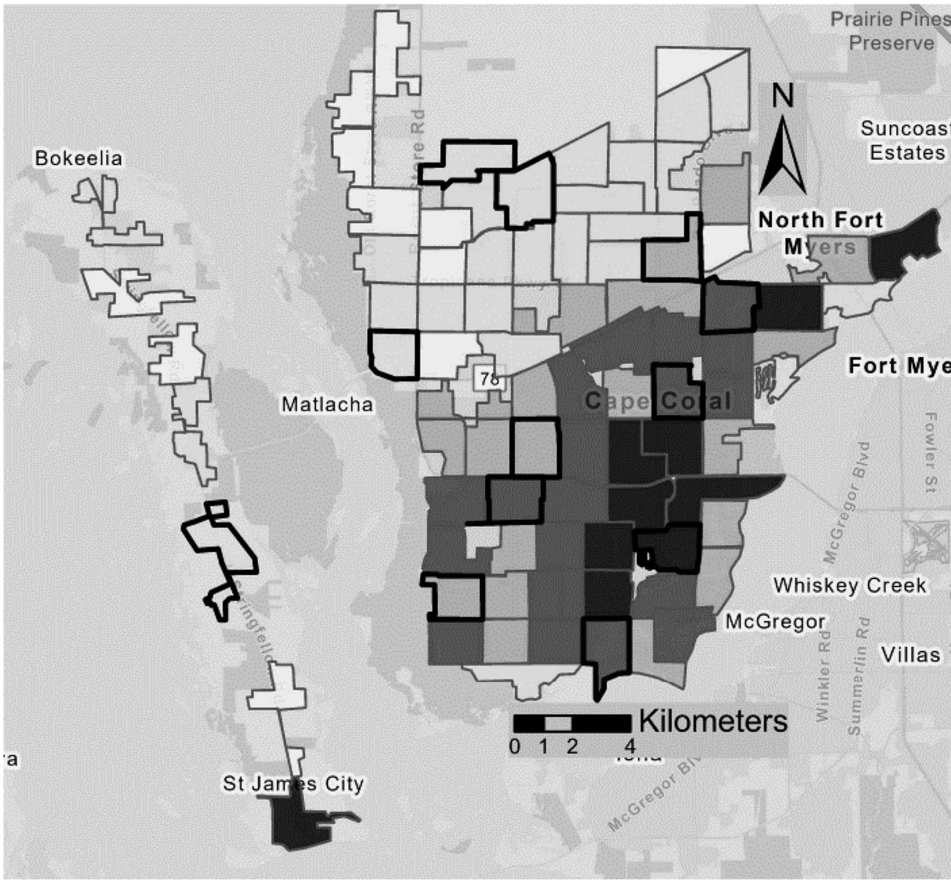

Figure 1. Map of survey blocks latitudinally dispersed throughout the study area in Cape Coral, Florida. Gradient of dark to light grey indicates high to low building density respectively in 2021. Survey blocks outlined in black indicate subset surveyed in 2021.

installed, but housing developments occurred slowly (S. Robertson, L. Goodrich, unpubl. data). This produced vast stretches of grassy meadows with powerlines, which is ideal habitat for kestrels (S. Robertson, L. Goodrich, unpubl. data). Shortly thereafter, residential development accelerated across the Cape, resulting in residential single-family homes as the current primary land use (CCF 2021). Despite increasing habitat change, many kestrels migrate to Cape Coral during the winter (Hinnebusch et al. 2010).

Using road survey data on the overwintering kestrel population in Cape Coral collected in the past three decades, we aimed to (1) quantify the annual abundance of the population, (2) assess patterns of kestrel abundance in response to urbanization, and (3) document changes in sex ratios of the population over time to gain insight into habitat quality, based on the assumption of sexual segregation of habitat use. Based on long-term surveys spanning a period of urbanization, our data provide the opportunity to test whether kestrels are truly adaptable to the urban conditions of this region and to identify potential threats to kestrel populations that may not readily adapt to urban territories. We evaluated several models testing hypotheses about kestrel population trends in our study system relative to time, urbanization, and habitat quality, including the null of no relationship.

METHODS

Data Collection. *Kestrel surveys.* We divided the entire Cape Coral region into 87 quadrilateral blocks following contours of roads and canals (Fig. 1). We arranged blocks in tiers latitudinally to account for heterogeneity in building density between northern and southern regions of Cape Coral. Blocks ranged from 1.4 km^2 to 3.9 km^2 and area was noted for each block for subsequent analyses. We systematically surveyed every road in each block (approximately 275 km^2 of land) for wintering kestrels by driving <25 km/hr on the same transecting roadways each winter (1 Dec–15 Mar). We surveyed each block once per winter from 1994 to 1999 and from 2006 to 2007 using the same two surveyors (authors BR and SR). During the winters of 2019, 2020, and 2021, we surveyed a representative subset of these same areas (~20% of blocks, stratified across the sampling area using a random number generator within a tier-based framework to ensure equal latitudinal distribution) utilizing the same methods (two surveyors, authors MM and JFT or authors KF and JFT).

Because kestrels prefer prominent perches such as powerlines and telephone poles (Hinnebusch et al. 2010), detection and sex determination were straightforward. We also surveyed other potential perches, including trees, rooftops, fences, and ground stubble. To avoid double-counting individuals, we mapped each kestrel location and sex upon detection, trapped and color-banded kestrels when possible, and surveyed roads only once per year. Wintering kestrels in Cape Coral maintain static non-overlapping territories and are highly site-faithful (unpublished data from color-banding and resighting), allowing road surveys to be conducted across a span of time without encountering individuals at multiple sites (Hinnebusch et al. 2010).

Land use data. We quantified building density within each block using the count function in a geographic information system (ArcGIS Pro 2.9.1, Esri 2021) on a "building footprints" data layer (Lee County Florida GIS 2022). Because lot size is relatively homogeneous throughout the study area, building density reliably describes the amount of developed land (and conversely, undeveloped land). We filtered building data points by year to create annual building maps, and subsequently, building count estimates for each year during the study period. We divided counts of buildings by the area of the block surveyed, resulting in number of buildings/km^2, a building density estimate for each block. To assess whether building density had increased over time, we created a linear model containing year as a predictor variable and building density as the response.

Statistical Analysis. To evaluate trends in kestrel density, we used zero-inflated negative binomial generalized linear mixed models with raw kestrel count as the response variable, survey block ID as a random variable, and area of the survey block as an offset term. Our data contained a prevalence of zeros (1.5% to 44% of surveys annually), requiring us to use zero-inflated models (based on maximum likelihood) that are suitable for count data. To evaluate the importance of each of our predictors, we created competing models using scaled values of building density, year, building density * year, and building density + year and compared AIC values. Preference toward single-predictor models of building density or year indicate the predictor has a stronger influence on kestrel population metrics singly than when combined with other predictors. In models containing both year and building density, both predictors play a role in influencing population metrics, with building density being associated with the kestrel population response over and above temporal trends in kestrel populations. Building density and year were related based on linear models, but were minimally correlated (correlation coefficient < 0.5), allowing for model creation without impacts of collinearity.

We determined annual sex ratios for each survey block by dividing the number of female kestrels sighted by the total number of kestrels sighted to achieve a proportional sex ratio. We followed a similar modeling approach to evaluate trends in kestrel sex ratio, but used a proportional binomial generalized linear mixed model with kestrel sex ratio as the response variable, survey block number as a random effect, and each of the described combinations of fixed effects to create competing models. All analyses were done in R version 2022.12.0 (R Core Team 2022).

RESULTS

Throughout the 11 survey years, we surveyed the study area of approximately 275 km^2 11 times (for a total of 2117 km^2), resulting in 2215 kestrel sightings. Building density values ranged from 0 to 653.1 buildings/km^2 (average of 261.3 buildings/km^2) and linearly increased over time throughout the study period (slope = 8.30, $F_{(1,\ 912)} = 243.02$, $P < 0.001$; Fig. 2).

Among competing models, the building density * year interaction best explained variation in kestrel abundance (Table 1). Both building density (estimate = −0.622, SE = 0.089, $P < 0.001$) and year (estimate = −0.373, SE = 0.067, $P < 0.001$) were negatively related to kestrel abundance (Fig. 3). The building density * year interaction was also negative (estimate = −0.379, SE = 0.079, $P < 0.001$), indicating that the negative impact of building density increased over time. The model including the building density * year interaction also was the best to explain patterns in sex ratio (Table 2). Effect estimates for both building density (estimate = −0.642, SE = 0.091, $P < 0.001$)

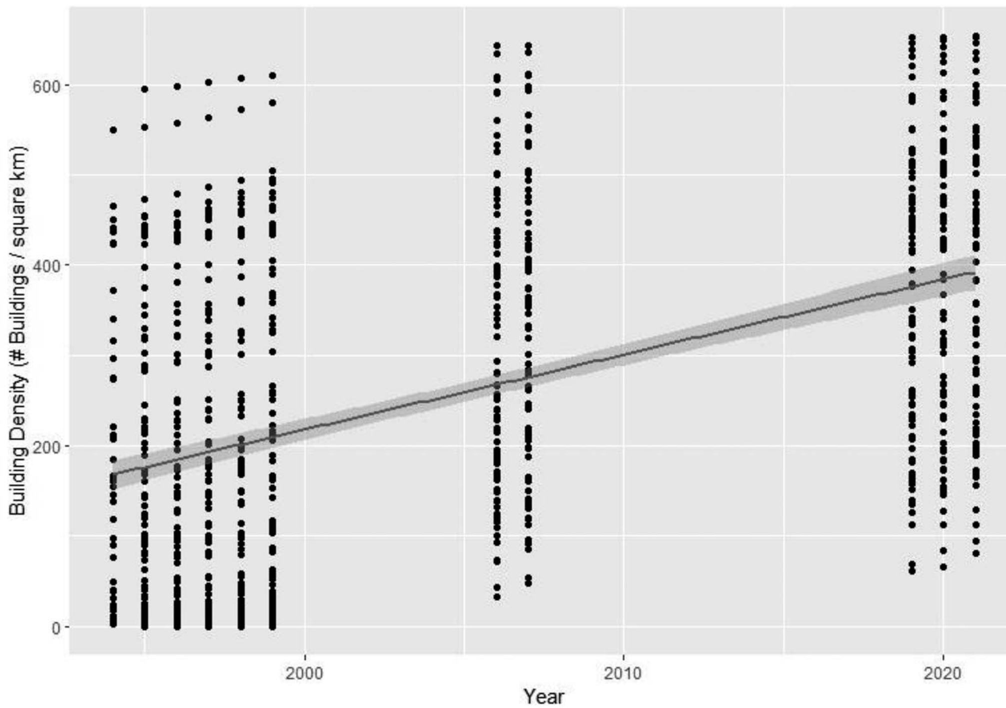

Figure 2. Building density over time across survey blocks throughout the study area in Cape Coral, Florida.

and year (estimate = −0.784, SE = 0.080, $P < 0.001$) were negatively correlated with the proportion of females in the kestrel population (Fig. 4). The interaction effect was positive (estimate = 0.256, SE = 0.10, $P = 0.014$), which indicated that as the study progressed (year increased), housing density did not influence kestrel sex ratio as strongly as it did in the earlier years.

DISCUSSION

From our findings, increasing density of building developments appear associated with decreased abundance of wintering kestrels in Cape Coral, Florida. Although some previous literature suggests that kestrels readily adapt to urbanization, our results suggest that kestrels may not be as urban-adaptable as previously thought, at least in our study area where urbanization increased significantly over a short period. For many avian species, population density within a habitat is constrained by that habitat's availability of resources, such as food and territory space (Sherry and Holmes 1996). As we surveyed the same habitat over a period of urbanization, the consistent decrease in kestrel abundance overall would suggest that resource availability and habitat quality has diminished over time, potentially due to the continuous conversion of open grassy land to manicured, fragmented developments

Table 1. Competing models to explain abundance trends in overwintering American Kestrel populations in Cape Coral, FL, USA, from 1994 to 2021. Marginal R^2 is calculated based on likelihood ratio tests.

Model	AIC	ΔAIC	AIC Weight	Log-likelihood	Marginal R^2
Building Density * Year	2782.9	0.00	0.9999886	−1384 (df = 4)	0.058
Building Density + Year	2805.7	22.76	0.0000114	−1396 (df = 3)	0.039
Building Density	2826.9	43.68	3.272×10^{-10}	−1408 (df = 2)	0.065
Year	2837.9	54.95	1.169×10^{-12}	−1414 (df = 2)	0.023
~ 1 (null)	2919.6	136.69	2.077×10^{-30}	−1455 (df = 1)	0.000

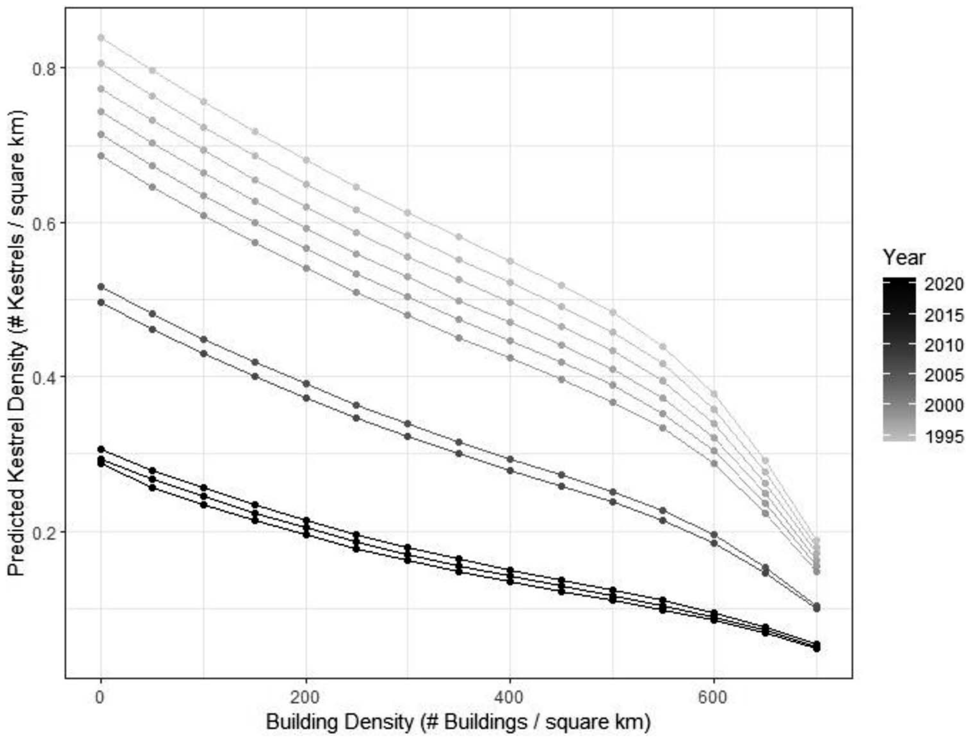

Figure 3. Predicted American Kestrel density (kestrels per km^2) in response to building density (buildings per km^2) using top-ranked model of building density * year. Year is signified by grey shade with lines connecting points of the same year.

(Robinson et al. 2005). With fewer suitable territories and more fragmented prey populations, the urbanized habitat is likely able to support fewer individuals now than pre-urbanization.

Our model selection approach indicates that both building density and year were negatively correlated with kestrel abundance. This result may be influenced by the overall kestrel declines throughout the United States, especially in the northeastern states, where presumably most of Cape Coral's overwintering population breeds (Oleyar et al. 2023). Migratory short-stopping may also reduce the number of kestrels overwintering in Cape Coral each year (Heath et al. 2012). As kestrels follow a leap-frog migration strategy, individuals breeding in the northernmost areas typically occupy the southernmost overwintering areas. The documented decline in migration distance of kestrels breeding at the northernmost portion of their range would therefore lead to fewer overwintering birds in southern regions such as Cape Coral (Goodrich et al. 2012). Although overall abundance of kestrels overwintering in Cape

Table 2. Competing models to explain sex ratio trends in overwintering American Kestrel populations in Cape Coral, FL, USA, from 1994 to 2021. Pseudo-R^2 is calculated based on likelihood ratio tests.

Model	AIC	ΔAIC	AIC Weight	Log-likelihood	Pseudo-R^2
Building Density * Year	1359.5	0.00	0.8598	−676 (df = 4)	0.4151
Building Density + Year	1363.1	3.63	0.1402	−679 (df = 3)	0.4087
Building Density	1468.6	109.13	1.729×10^{-24}	−732 (df = 2)	0.2702
Year	1481.4	121.90	2.912×10^{-27}	−739 (df = 2)	0.2517
~ 1 (null)	1627.6	268.09	5.230×10^{-59}	−812 (df = 1)	0.0000

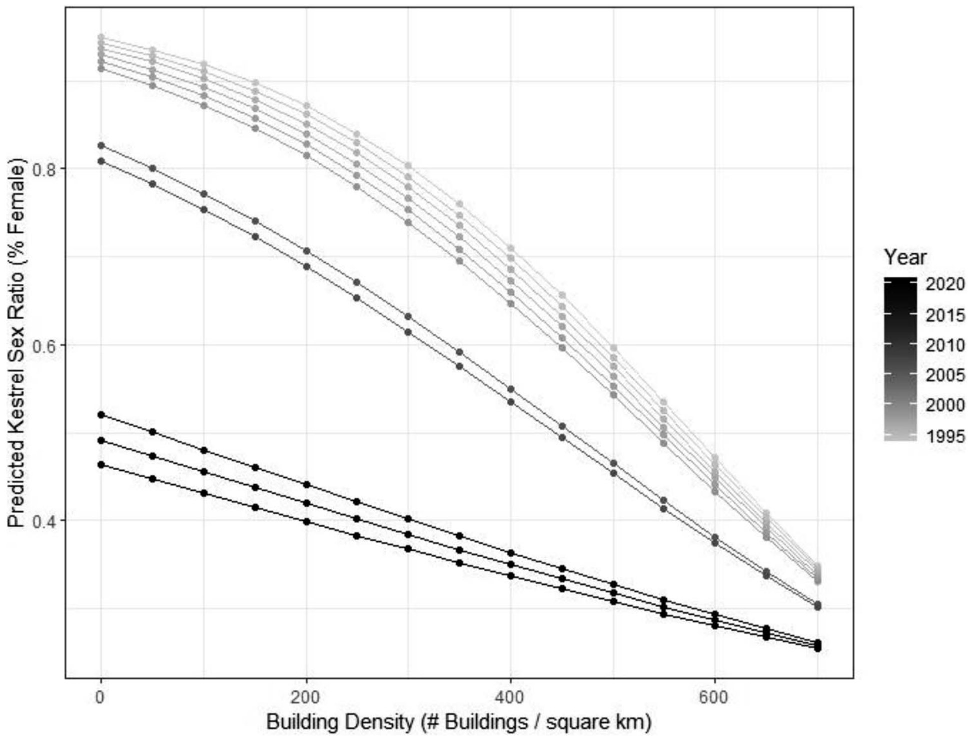

Figure 4. Predicted American Kestrel sex ratio proportion in response to building density (buildings per km^2) using top-ranked model of building density * year. Year is signified by grey shade with lines connecting points of the same year.

Coral may be declining, our models suggest that the observed numbers may reflect both time-related factors and urban development of the landscape.

The shift in sex ratio over time may also reflect urbanization influence, through habitat quality degradation, as male kestrel presence is indicative of lower quality wintering habitat (Smallwood 1988, Ardia and Bildstein 1997). Other studies have also detected correlations between sex ratio and habitat quality in kestrels (Koplin 1973, Pandolfino et al. 2011) and other species (Sherry and Holmes 1996, Marra 2000, Mettke-Hofmann et al. 2015), with the dominant sex defending the highest quality territories. Sherry and Holmes (1996) reported nonrandom sex distributions in Neotropical migrant species that forced the non-dominant sex to occupy low-quality territories, leading to decreases in wintering body mass and apparent survival. Sex-based discrepancies in individual quality due to habitat limitations could possibly influence continental population sex ratios, through the mechanism of reduction of adult male survival, resulting from unequal distribution of resources.

Another possible cause of the increase in proportion of males is the decline of kestrels throughout most regions in Cape Coral, leading to fewer females occupying territories overall. As described previously, overwintering populations of kestrels in Cape Coral may be declining due to overall continental declines and migration short-stopping. With fewer overwintering kestrels in general, male kestrels are then able to occupy territories at a higher rate than in previous years when female kestrels were more numerous overall. This hypothesis may explain observations of overall sex ratio shifts in Cape Coral, including within low building density blocks where minimal habitat change has occurred, as males are now able to occupy high quality territories that would otherwise be occupied by females.

Degradation of wintering grounds and occupation of suboptimal winter territories due to competition has implications for negative carry-over effects that may influence the continental population status of kestrels. Decreased prey abundance due to habitat fragmentation may result in reduced nutritional uptake by birds during the overwintering period, possibly leading to alterations in migration phenology and body condition (Norris and Marra 2007, González-Prieto and Hobson 2013). Negative carry-over effects due to degradation of wintering grounds may also reflect an increase in mortality on the wintering grounds, leading to decreased population levels moving into spring migration. Urban birds may experience increased mortality, due to vehicle and building collisions, higher prevalence of environmental contaminants, and greater exposure to predators (Hager 2009, Klem 2009, Calvert et al. 2013, Hindmarch et al. 2017, Dwyer et al. 2018). The implications of wintering ground degradation extend beyond the overwintering period for migratory bird species, such as the kestrel, and can help to explain otherwise unattributed reproductive failures and population declines (Norris and Marra 2007).

Although correlations between kestrel abundance and housing density seem evident from our analyses, it should be noted that the exact mechanism of these correlations should be investigated more thoroughly. Rigorous investigations of prey abundance within survey blocks of differing building density may elucidate the causal link between urbanization and kestrel abundance. Inquiry into land cover associations, beyond building density, may also reveal mechanistic links between urbanization and kestrel abundance. In this study, we were unable to distinguish lawns from natural grasses within building lots due to low-resolution land use data. Future investigations would benefit from land cover analyses using high-resolution data.

Long-term monitoring of this overwintering kestrel population demonstrated decreased abundance in urbanized habitats and an alteration in population sex ratio that suggests overwintering kestrel populations respond negatively to urbanization. These trends suggest that urbanization may negatively impact habitat features relied upon by overwintering kestrels, an effect that otherwise may be overlooked as kestrels are currently considered an urban adapter species. This study is not the first to document a kestrel population that negatively responds to urbanization or human disturbance, e.g., roads (Strasser and Heath 2013, Cooper et al. 2021); thus we suggest the current understanding of the kestrel as an urban adapter species be reconsidered. As wintering habitat quality influences individuals and populations on a larger scale and urbanization of habitats is occurring widely throughout kestrel wintering areas, it is important to understand the ecological impacts of urbanization to gain insight into its role in the ongoing kestrel population decline.

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