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No difference in reproductive investment or success across urban and rural breeding pairs in an urban-adapted songbird

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ABSTRACT

Species classified as "urban-adapters" are often assumed to thrive in cities because they are commonly found across the urbanization gradient. However, urban-living populations of many urban-adapted species have been found to have lower reproductive success relative to their rural counterparts. *Sturnus vulgaris* (European Starling) is a common urban-adapted species found across most of the globe. While *S. vulgaris* have lowered reproductive success in urban areas in their native range, less is known about how urbanization impacts reproduction in their invasive ranges. We tested for differences in reproductive investment and success across urban and rural *S. vulgaris* populations in Georgia, which is part of their North American invasive range. We found few differences in reproductive output for urban vs. rural *S. vulgaris*—clutch size, egg mass, egg volume, incubation behavior, provisioning rates, brooding behavior, and nestling wing chord were all similar across *S. vulgaris* populations from more urban and more rural study sites. Although urban birds produced a higher number of hatchlings and rural birds produced young in higher body condition, neither of these factors influenced reproductive success because the number of fledglings produced were similar for urban and rural breeding *S. vulgaris*. Overall, *S. vulgaris* in their invasive range performed similarly well in more urban vs. more rural habitats. Future work should explore whether urbanization affects other components of fitness in starlings (e.g., adult survival).

Keywords: clutch size, European Starling, fledglings, parental care, *Sturnus vulgaris*, urbanization

How to Cite

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LAY SUMMARY

- Birds living in urban centers can sometimes produce fewer chicks in their nests, though it is not always clear why.
- We monitored nests of a common bird—*Sturnus vulgaris* (European Starling)—at 2 urban and 2 rural sites in metro Atlanta, Georgia, USA.
- We counted (1) the number of eggs in each nest, egg mass, and volume, as well as the amount of time parents spent keeping their eggs warm; (2) the number of nestlings that hatched in each nest, their wing length, and body condition, as well as the amount of food the parents delivered to the nest; and (3) the number of nestlings that fledged each nest successfully.
- While we expected nests from urban sites to have fewer or smaller eggs and nestlings, we found that rural and urban nests were statistically the same with a few exceptions. Urban *S. vulgaris* hatched more of their eggs into nestlings, and rural birds had nestlings in superior body condition.
- Ultimately, because urban and rural nests had the same number of chicks surviving to the age of leaving the nest, it appears that *S. vulgaris* breed similarly well in urban and rural areas in metro Atlanta.
- We suggest that future studies could look at where chicks choose to live or breed in the future, as well as how urban life affects adult condition and survival rather than just nestlings.

Pas de différence dans l'investissement ou le succès reproductif entre les couples nicheurs urbains et ruraux chez un oiseau chanteur adapté à la ville

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RÉSUMÉ

Les espèces classées comme « adaptées à la ville » sont souvent présumées prospérer dans les villes parce qu'elles sont communément observées sur tout le gradient d'urbanization. Cependant, on a constaté que les populations urbaines de nombreuses espèces adaptées à la ville ont un succès reproductif inférieur à celui de leurs congénères ruraux. *Sturnus vulgaris* est une espèce commune adaptée à la ville que l'on trouve dans la plupart des régions du monde. Alors que *S. vulgaris* a un succès reproductif plus faible dans les zones urbaines de son aire de répartition naturelle, on en sait moins sur la façon dont l'urbanization affecte la reproduction dans ses aires de répartition invasives. Nous avons testé les différences d'investissement et de succès reproductif entre les populations urbaines et rurales de *S. vulgaris* en Géorgie, qui fait partie de son aire de répartition invasive en Amérique du Nord. Nous avons trouvé peu de différences dans les paramètres de reproduction de *S. vulgaris* en milieu urbain et en milieu rural: la taille de couvée, la masse des œufs, le volume des œufs, le comportement de couvaison des œufs, le taux de nourrissage, le comportement de couvaison des jeunes et la corde de l'aile des oisillons étaient tous similaires dans les populations de *S. vulgaris* des sites d'étude les plus urbains et les plus ruraux. Bien que les oiseaux urbains aient produit un plus grand nombre d'oisillons à l'éclosion et que les oiseaux ruraux aient produit des jeunes en meilleure condition physique, aucun de ces facteurs n'a influencé le succès reproductif car le nombre d'oisillons à l'envol produits était similaire pour *S. vulgaris* se reproduisant en milieu urbain et en milieu rural. Dans l'ensemble, *S. vulgaris* a eu un succès similaire dans les habitats plus urbains et les habitats plus ruraux de son aire de répartition invasive. Les futures recherches devraient explorer si l'urbanization affecte d'autres composantes de la condition physique chez cette espèce (p. ex., la survie des adultes).

Mots-clés: taille de couvée, oisillons à l'envol, soins parentaux, *Sturnus vulgaris*, urbanisation

INTRODUCTION

Over half of the world's human population lives in urban centers, which is expected to increase in the coming decade (United Nations 2018). The density of humans paired with the built-up environment in cities can have a profound impact on the wildlife that live there, too (Moll et al. 2019). Understanding how urbanization impacts the success of wildlife is critical in order to predict population trends and manage these organisms. Different species vary greatly in their ability to exist in urban centers, and can be categorized according to their abundance along urbanization gradients (Schoeman 2016, Martin and Bonier 2018, Injaian et al. 2020, Palacio 2020, Neate-Clegg et al. 2023). "Urban-avoiders" are species that are found rarely in urban habitats—they are typically excluded from cities because critical resources are lacking and they cannot survive or breed in these habitats. In contrast, "urban-adapters" (Blair 1996, McKinney 2002; sometimes called "urban-dwellers," Fischer et al. 2015) are species commonly found in urban areas and beyond. While we might assume that urban-adapted species are distributed across the urbanization gradient because they can thrive in cities, many such species have been declining (Stracey et al. 2010, Rosenberg et al. 2019) or show reduced reproductive success in urban habitats (Peach et al. 2008, Seress et al. 2012). It is thus not clear the extent to which urban-adapted species truly thrive in cities.

Even for species that commonly live in urban areas, urbanization is generally thought to have a negative impact on wildlife health (Murray et al. 2019; but see Iglesias-Carrasco et al. 2020). Such altered health for animals living in cities would be expected to lead to lowered reproductive success or survival in these habitats. For example, urban-breeding *Passer domesticus* (House Sparrow) had lower body mass, and the nestlings of urban parents suffered from nutritional stress (Meillère et al. 2015). For other species, urbanization can lead to novel sources of food and does not negatively affect body mass (Bókony et al. 2012). As a result, the impacts of urbanization on condition are complex and not fully understood. Nevertheless, in birds—a well-studied taxa in urban ecology research (Magle et al. 2012)—a recent meta-analysis showed that urban-living populations produce fewer young than their rural counterparts (Capilla-Lasheras et al. 2022).

In addition to health disparities across the urbanization gradient, differences in parental care are a possible explanation for reduced offspring production in urban habitats: for example, urban females spent less time incubating their eggs per day than rural ones (Heppner and Ouyang 2021), urban parents brought fewer preferred prey to their nestlings (Sinkovics et al. 2021), and urban parents were less coordinated in their parental care (Baldan and Ouyang 2020). Despite many studies and meta-analyses on how urbanization affects reproductive output in birds, there remains a lot of variation from 1 species to the next (Birnie-Gauvin et al. 2016, Zuñiga-Palacios et al. 2021); as a result, it is difficult to predict how urbanization ultimately shapes avian reproduction let alone other demographic parameters (e.g., immigration, emigration, survivorship, etc.).

In this study, we explored the impact of urbanization on the reproductive investment and success of a common urban-adapted songbird, *Sturnus vulgaris* (European Starling; hereafter "starlings"). *Sturnus vulgaris* are native to Europe and Asia where they are distributed across the urbanization gradient (e.g., Mennechez and Clergeau 2001). In addition, starlings have successfully established invasive populations across many parts of the world including in the Americas, Australia, New Zealand, and South Africa (Feare and Craig 1998, Feare 1984). In their invasive ranges, starlings have a history of being introduced in urban areas but have successfully expanded into rural habitats as well (Zufiaurre et al. 2016, Jernelöv 2017). Starlings can represent a species of management concern (Clergeau et al. 2001, Clucas and Marzluff 2012); their roosting or nesting in human structures, their use of animal feed lots, their flocking at airports, and their competition with native birds all contribute to their perception as a nuisance. Not only would understanding the impacts of urbanization on starling reproductive success contribute to the field of urban ecology, but it could also contribute to this species' management plan.

In their native range, starlings are distributed similarly across the urbanization gradient which is often attributed to their flexibility in roost or nest site selection (Clergeau and Quenot 2007) and in their diet (Mennechez and Clergeau 2001). Nevertheless, within their native range, urban starlings show reduced reproductive success compared to their counterparts in rural habitats (Mennechez and Clergeau 2006). Urbanization appears to lower reproductive success via reduced prey availability to feed the young, resulting in lower body condition of urban-raised nestlings (Mennechez and Clergeau 2006); indeed, urban nestlings were fed fewer insects and more human refuse (Mennechez and Clergeau 2001). In their invasive range, populations of starlings have also been declining (Rosenberg et al. 2019) with some datasets

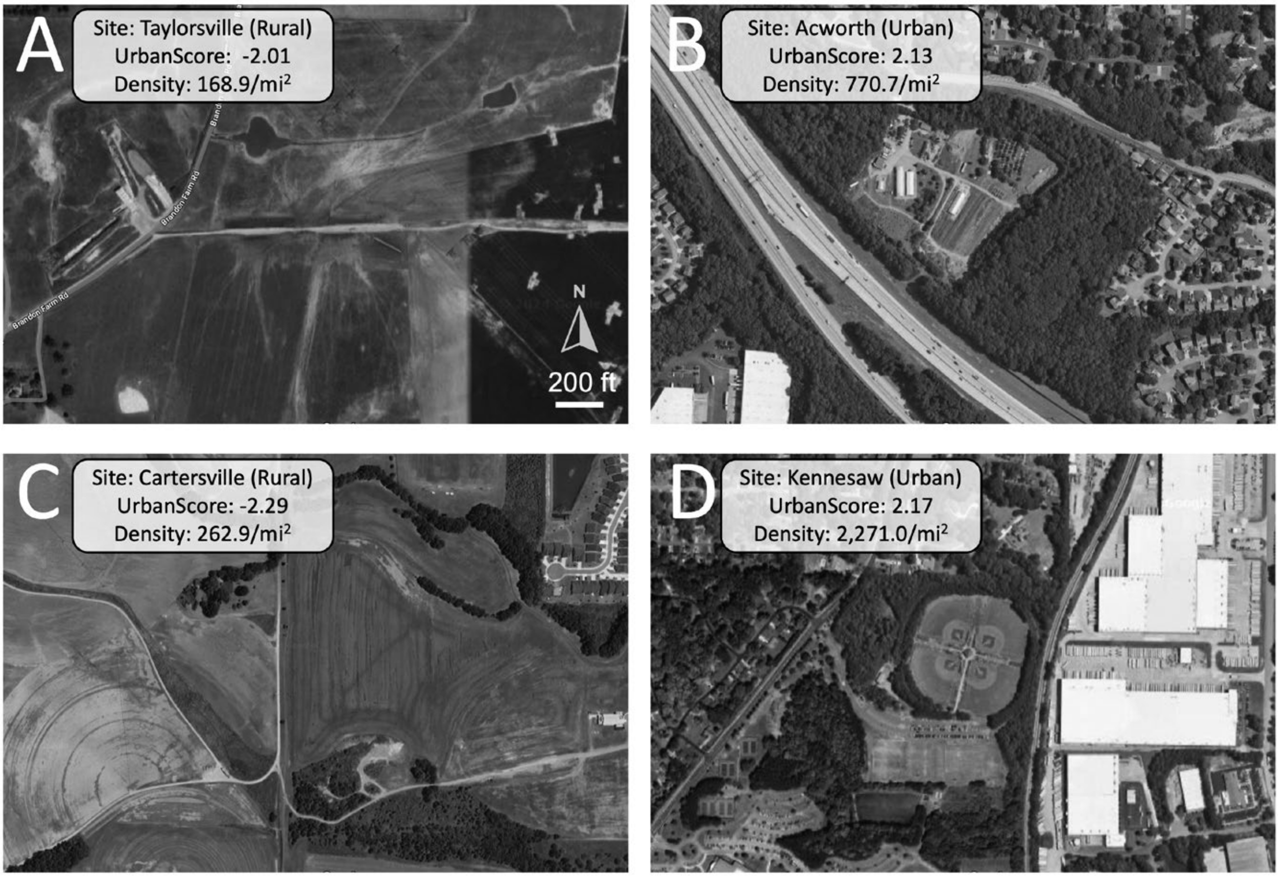

FIGURE 1. Satellite images of the 4 study sites, which include (**A**) a rural farm, (**B**) an urban farm, (**C**) a rural park, and (**D**) an urban park. Each panel is labeled with the site's city, the UrbanizationScore, and the human population density from the 2020 U.S. census. Panel (**A**) also includes the North arrow and a scale bar that is standardized for all 4 panels.

suggesting these declines may be greater in urban compared to rural areas (Barton et al. 2020). However, less is known about possible differences in reproductive success along the urbanization gradient for invasive populations of starlings.

Here, we studied breeding *S. vulgaris* across 4 years in metro Atlanta (Georgia, USA; Figure 1), which is part of their North American invasive range. We monitored breeding—from egg-laying to nestling care to fledging success—by providing nestboxes mounted at 4 sites that ranged in their degree of urbanization. As a secondary-cavity nester, starlings readily bred in the provided nestboxes that allowed us to monitor differences in reproductive investment or success across comparable nests that differed primarily in their surrounding habitat matrix. Prior work in this study system showed that urban starlings had elevated stress responses (Guindre-Parker et al. 2022), elevated cholesterol (Linkous et al. 2024), elevated heavy metal burdens (Ross et al. 2023), and experienced lowered insect prey availability (Linkous et al. 2024). Taken together, these studies suggest that starlings from urban habitats are in lowered health or physiological condition—we thus expected that urban starlings would also show lowered reproductive success. During incubation, we compared egg mass, egg volume, clutch size, and incubation behavior for urban vs. rural breeding starlings. After hatching, we compared the body condition, size, and number of hatchlings produced, as well as parental care behavior and the number of young that fledged successfully from urban vs. rural nests. Despite being an urban-adapted species commonly found across the urbanization gradient, we expected that urban starlings in Georgia would invest in smaller or fewer eggs, produce fewer young, and provide less parental care. This study contributes to our understanding of the complex ways in which urbanization shapes reproductive success and focuses on an invasive species of important management concern.

METHODS

Study Sites

We studied *S. vulgaris* nestlings from 4 sites in Georgia (Figure 1), where we mounted nest boxes for starlings to nest in. The study sites had similar numbers and placement of nest boxes ($n = 35–45$ boxes), but differed in their surrounding degree of urbanization: the rural farm site was in Taylorsville (latitude: 34.0914, longitude: −84.9079; mean human density = 168.9 mile^{-2} [U.S. Census Bureau 2020]), the rural park site was located in Cartersville (latitude: 34.1289, longitude: −84.8233; mean human density = 262.9 mile^{-2} [U.S. Census Bureau 2020]), the urban park site was in Kennesaw (latitude: 34.0031, longitude: −84.6195; mean human density = 2,271.0 mile^{-2} [U.S. Census Bureau 2020]), and the urban farm site was in Acworth (latitude: 34.0621, longitude: −84.6038; mean human density = 770.7 mile^{-2} [U.S. Census Bureau 2020]). We collected data at the rural farm in 2020 and 2021, and when the property underwent renovations, we relocated these nest boxes to a nearby rural park for 2022 and 2023. We collected data at the urban farm from 2020 to 2023 and added the urban park site in 2021 to increase our urban sample size (studied from 2021 to 2023). To rank the degree of urbanization at these 4 sites, we used the *UrbanizationScore* software (Lipovits et al. 2015)—an automatic urbanization scoring tool that yields a relative ranking of sites. This tool yields relative urbanization scores by incorporating information about vegetation, buildings, and impervious surfaces where a higher score indicates a more urban site. The rural sites were indeed more rural and the urban sites were indeed more urban: the urbanization score for the rural farm was –2.29, for the rural park was –2.01, for the urban farm was 2.13, and for the urban park was 2.17. Because our 2 more urban sites and our 2 more rural sites clustered so closely together, we pooled sites into a dichotomous "urbanization status" (i.e., urban vs. rural) in our subsequent analyses (as in Ross et al. 2024).

Reproductive Investment and Success

In Georgia, *S. vulgaris* are multi-brooded and begin nesting around March, and continue re-nesting until June. We checked nest boxes every few days during the breeding season (March to June) across 4 years in order to monitor reproductive investment and outcomes across sites. We labeled new eggs found in each nest to determine the maximum number of eggs laid in a nest or the clutch size. We weighed each new egg within 2 days of its lay date using a small digital scale and measured the length and width of each egg at its widest part using digital calipers. We calculated the volume of *S. vulgaris* eggs using the following formula: egg volume = $0.51 \times \text{length} \times \text{width}^2$ (Hoyt 1979). We also monitored the number of eggs that successfully hatched and measured the nestlings around 16 days of age (range: 14 to 19 days, mean: 16.4 days). We banded each nestling with a uniquely numbered band from the United States Geological Survey, and we recorded nestling mass, tarsus length, and wing chord. We calculated nestling body condition using the residuals of a linear model with mass as the dependent variable and tarsus length as the independent variable (Guindre-Parker et al. 2022). All nestlings were then returned to the nest. Finally, we monitored the number of nestlings deemed to fledge successfully from each nest. Predation events were differentiated from fledging by the following features: nests had been damaged, dead nestlings, or blood were present in or near the nest, or when previously healthy nestlings were suddenly missing earlier than the typical fledging age which is ~21 days for *S. vulgaris* (Cornell et al. 2017). Starvation was determined when nestlings were found dead in the nest, underweight, and lacking other signs of harm. In the absence of evidence for predation, when nestlings known to have survived over the age of 20 days were no longer found in the nest, they were deemed as having fledged successfully. We did not observe any evidence to suggest that our nestling measurements resulted in forced fledging, as nestlings were always in the nest the day following their measurements and banding.

Parental Care Videos

During the breeding seasons of 2020 to 2022, we monitored parental care using small video cameras temporarily mounted to each nest box. We did not collect videos in 2023 because we had a reduced field crew. We filmed nest boxes during 2 stages: incubation and nestling care. Incubation videos were collected, on average, 9.9 days after the first egg was laid (range: 4 to 29 days) and nestling care videos were collected when chicks were, on average, 7.3 days of age (range: 1 to 15 days of age with 1 outlier being 22 days of age). For both stages, each nest was recorded for ~30 min (range: 25 to 65 min, mean: 32.8 min) in the morning (between 8:00 AM and 12:00 PM). Video cameras were mounted to film the only nest entrance so that birds entering or leaving the nest could be observed from the video files. Cameras were mounted to the nest box at least 15 min prior to starting recording in order to give starling parents time to habituate to the equipment. In 2020, we observed nest boxes after mounting the cameras and found that all birds returned to the nest within 15 min which we interpreted to mean this habituation time was sufficient. At a later time, we watched the videos to calculate parental care behaviors. One person watched all incubation videos, while a second person watched all provisioning videos, such that no observer effects should be present. Incubation behavior was calculated as the sum of the number of minutes a bird spent inside the nest containing eggs (whether this occurred in 1 bout or across multiple visits) divided by the length of the video recording. This yields incubation behavior as a percentage of the time the eggs were incubated by a parent. The videos collected while chicks were in the nest were used to calculate 2 offspring care behaviors: provisioning and brooding. The provisioning rate was calculated as the number of trips where a starling delivered food into the nest per hour. Brooding behavior was calculated as the percentage of time a bird spent inside the nest containing nestlings (similarly to incubation behavior). While male and female starlings show sexual dimorphism during breeding by differing in the color at the base of their bill, we were unable to sex the parent in many appearances on camera due to the speed with which starlings entered the nestbox. As a result, incubation behavior, provisioning rate, and brooding behavior were calculated for the nest by pooling care performed by both sexes of a breeding pair. During provisioning, the majority of nests received care by the male and female starlings: males were observed in the videos at 69% of nests and females were observed in the videos at 70% of nests (at 18% of nests, a parent was observed but could not be sexed). These measurements of parental care thus represent the total care the eggs or nestlings received regardless of whether that care was divided evenly among the male and female at a nest or whether a single parent performed all the care alone. For cases when we were able to identify the sex of the parent entering the nest, our data support prior work suggesting that starlings can engage in biparental care of both the eggs and the nestlings (Wright and Cuthill 1990, Smith et al. 1995, Sandell et al. 1996).

Statistical Analyses

Overall, we sampled 23 nests from urban sites and 123 nests from rural sites: this included monitoring 82 urban eggs and 470 rural eggs, as well as 34 urban chicks and 167 rural chicks. We sampled 42 nests in 2020, 51 in 2021, 22 in 2022, and 31 in 2023.

We tested whether *S. vulgaris* breeding in more rural vs. more urban habitats differed in the mass or volume of the eggs they laid using 2 general linear models (n = 1,134 eggs across 136 nesting attempts): 1 model included egg mass as the dependent variable and the other considered egg volume as the dependent variable. Both models included the following predictor terms: urbanization status (urban vs. rural), the egg age in days (days since it was laid), Julian lay date, the nest attempt number (as starlings are multi-brooded within a breeding season), the clutch size, and year. Though preliminary analyses suggested there was no difference in the timing of breeding across urban vs. rural nest (Welch 2 sample *t*-test: $t = 0.11$, df = 26.1, *p*-value = 0.91), we included Julian lay date in the model to control for possible season effects. These models also included a random effect of nestbox ID, since multiple eggs were measured from the same nest. When a breeding pair renested, they typically did so in the same nestbox so control for nestbox ID also controls for the identity of the breeding pair. We did not have birds return to breed in our nest boxes in multiple years. Note that for these models (and future models described below) we chose to include year as a fixed effect rather than a random 1 because we had relatively few levels (i.e., 4 years).

Next, we examined whether urban vs. rural starlings differed in the number of eggs, hatchings, or fledglings produced in a nesting attempt ($n = 143$ nesting attempts). We built 3 generalized linear mixed models with a Poisson distribution with either clutch size, the number of hatchlings, or the number of fledglings as the dependent variables. For all 3 models, we included urbanization status, nest attempt, Julian lay date, and year as predictor variables. We also included a random effect of nestbox ID to account for the non-independence of parent starlings renesting more than once. For the hatchling and fledgling models, we found that high rates of nesting failure resulted in many observations of 0—both these models thus included a zero-inflation parameter. Finally, the hatchling and fledgling models included an offset term for clutch size, which controls for the possibility that nests with more eggs have the potential to produce more chicks than ones with smaller clutches. The offset term is included in *nlme* and *glmmTMB* packages via the "offset" argument.

We examined whether nestlings raised in more urban vs. more rural nests differed in their body condition or wing chord length ($n = 199$ nestlings), where both of these indices of size are important predictors of future survival (Morrison et al. 2009, Jones et al. 2017). We used 2 linear mixed models with either body condition or wing chord length as the dependent variables. These models included urbanization status, chick age at measurement (days since the hatch date), Julian date, the nest attempt number, brood size, and year as predictor variables along with a random effect of nest ID to control for the non-independence of sampling multiple nestlings from the same nest. These analyses represent a single measurement per nestling, when chicks were sampled at an average age of 16.4 days (range: 14 to 19 days).

Finally, we used 3 generalized linear mixed effect models to test for differences in egg or chick care behaviors in parents raising their young at more urban vs. more rural sites. We built 3 models for incubation behavior (percentage of time on eggs), provisioning rate (trips per hour), and brooding behavior (percentage of time on chicks) as the dependent variables ($N_{\text{incubation}} = 65$ nesting attempts and $N_{\text{provisioning and brooding}} = 61$ nesting attempts). We included urbanization status, Julian lay date, the nest attempt number, and year as predictor variables. We included clutch or brood size as well as clutch age or brood age in each model, depending on whether the nest contained eggs or chicks at the time of video collection. We also included a random effect of nestbox ID to account for parents that nested more than once. All 3 models used a negative binomial distribution due to the large variance of the dependent variables, and the provisioning rate model also included a zero-inflation parameter because many nestling care videos captures parents brooding but not provisioning their young (via the *glmmTMB* package's "ziformula" parameter).

For all models, we considered adding site as a nested random effect with nestbox ID to control for there being 2 urban and 2 rural sites. However, we found that models with nestbox ID as the random effect were always 2 or more AIC_c values lower than the same model with nestbox ID nested within site, suggesting the simpler random effect structure was an adequate and preferred model (models with a random effect for site are presented in Supplementary Material Tables 1, 2, 3, and 4). Because adding a more complex random effect structure did not improve model fit and did not change the qualitative results of the study, we did not include site as a random effect. All analyses were performed in R (v.4.3.1) (R Core Team 2021). General linear models were performed using the *nlme* package (v.3.1-162) and model diagnostic plots showed normally distributed and non-heteroscedastic residuals. Generalized linear models were performed using the *glmmTMB* package (v.1.1.7).

RESULTS

This study explored whether reproductive investment and success differed for birds breeding in more urban ves. more rural habitats in *S. vulgaris* in the metro-Atlanta area. In total, we monitored 146 nesting attempts; 23 at the urban sites and 123 at the rural sites. Despite providing the same numbers of nest boxes across all sites, we had higher starling occupancy at the rural sites—while the urban sites had a mean occupancy rate of 0.11 nesting attempts per box provided, the rural sites had a mean occupancy rate of 0.86 attempts per box.

When comparing how urban and rural birds invested in the production of their eggs, we found that neither egg mass nor egg volume was associated with urbanization status (Figure 2). Egg mass decreased with egg age and with Julian date (Table 1). Egg mass also increased as parents undertook more nesting attempts, and varied from year to year. Like egg mass, egg volume decreased with Julian date and varied across years (Table 1).

Next we explored proxies for reproductive success in urban vs. rural breeding starlings via clutch size, the number of hatchlings, and the number of fledglings produced. We found that clutch size was unrelated to urbanization status, number of prior nest attempts undertaken, Julian date, and year (Table 2). We found that urban breeding starlings typically produced a greater number of hatchlings than rural ones (Figure 3), with the median number of urban hatchlings being 4 and the median number of rural hatchlings being 3. We also found that the number of hatchlings in a nest decreased with subsequent nesting attempts, increased with Julian date, and varied across years. We found that the number of fledglings from urban and rural nests did not differ. The fledgling count was unrelated to the number of prior nesting attempts or Julian date but did vary from year to year (Table 2). At urban sites, 39% of nests fledged, and at the rural sites, 45% of

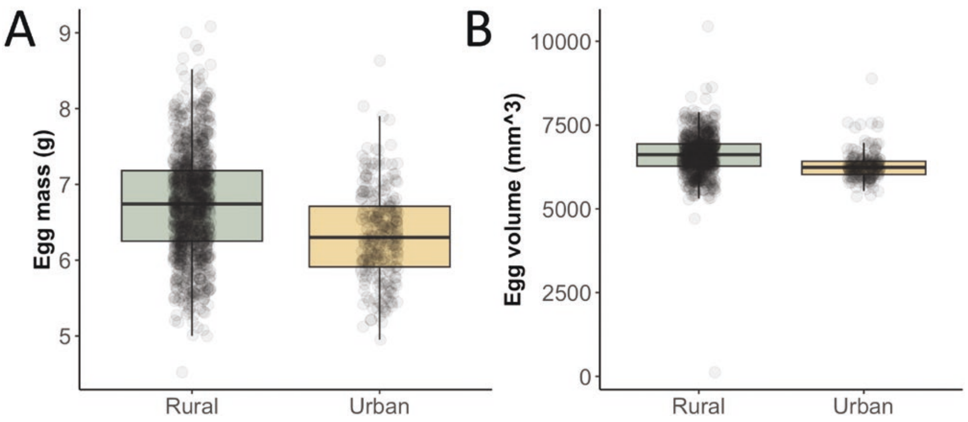

FIGURE 2. There were no differences in the (**A**) mass or (**B**) volume of eggs laid by *S. vulgaris* breeding at more rural (green) vs. more urban (yellow) sites. Figures depict box and whisker plots and gray circles represent individual data points (*n* = 552 eggs across 146 nesting attempts). The bolded line is the median, the box indicates first and third quartiles, and the whiskers indicate a confidence interval encompassing 1.5 times the interquartile range.

TABLE 1. We tested for differences in egg mass (g) and volume (mm^3) in urban vs. rural breeding starlings using linear mixed models. Asterisks and bolding denote significant predictor variables where the *P*-value was below or equal to 0.05. SE means standard error and SD means standard deviation.

	Egg mass			Egg volume		
Fixed effects	Estimate ± SE	*t*-value	*P*-value	Estimate ± SE	*t*-value	*P*-value
Intercept	**240.5 ± 53.0**	**4.54**	**<0.001***	**154787.8 ± 63737**	**2.43**	**0.02***
Urbanization status	−0.20 ± 0.15	−1.33	0.19	−229.0 ± 182	−1.26	0.21
Egg age	**−0.05 ± 0.004**	**−13.8**	**<0.001***	8.52 ± 5.42	1.57	0.12
Julian date	**−0.01 ± 0.003**	**−4.40**	**<0.001***	**−8.10 ± 3.48**	**−2.33**	**0.02***
Nest attempt	**0.23 ± 0.12**	**1.94**	**0.05***	240.3 ± 145	1.65	0.10
Clutch size	−0.06 ± 0.04	−1.70	0.09	18.46 ± 45.8	0.40	0.69
Year (2021)	**4.96 ± 1.11**	**4.45**	**<0.001***	**3377.4 ± 1339**	**2.52**	**0.01***
Year (2022)	**9.27 ± 2.14**	**4.32**	**<0.001***	**6132.4 ± 2579**	**2.38**	**0.02***
Year (2023)	**14.37 ± 3.24**	**4.44**	**<0.001***	**9332.0 ± 3886**	**2.40**	**0.02***
Random effects	SD		Residual	SD		Residual
Nest ID	0.57		0.31	721.1		292.3

nests fledged 1 or more young. When we could assign a cause of failure to fledge, 9% of urban nests and 3% of rural nests failed due to nestling starvation and 9% of urban nests and 15% of rural nests failed due to nest predation. It is difficult to use these observations more than anecdotally because we could not always ascribe the cause of nest failure, but these percentages suggest that urban nests may be more susceptible to nestling starvation whereas the rural ones are more susceptible to nest predation. Future work on the topic could focus on predator surveys across site types along with camera traps to better study variation in predator pressure across urban and rural nests.

While starling nests from urban and rural sites fledged similar number of young, there could exist differences in the quality and survival of these chicks post-fledge. To test this possibility, we compared indices of nestling size across chicks from more urban and more rural nests: body condition and wing chord length. We found that rural chicks were in better body condition than urban ones (Figure 4). Nestling body condition also declined with Julian date, decline with brood size, and varied across years (Table 3). Conversely, nestling wing chord length was unrelated to urbanization status. However, we found that wing chord increased as chicks aged (Table 3).

Finally, we compared parental care behavior for starlings raising their young at more urban vs. more rural sites. We did not find any differences in incubation behavior, provisioning rate, or brooding behavior for urban and rural starling parents (Figure 5). None of the egg and nestling care behaviors were associated with the number of prior nesting attempts, to Julian date or to year (Table 4). Incubation behavior was unrelated to clutch size or clutch age, while provisioning and brooding behaviors were unrelated to brood size or chick age (Table 4).

DISCUSSION

This study explored whether more urban-living *S. vulgaris* showed different reproductive investment or success compared to their rural counterparts in their invasive range.

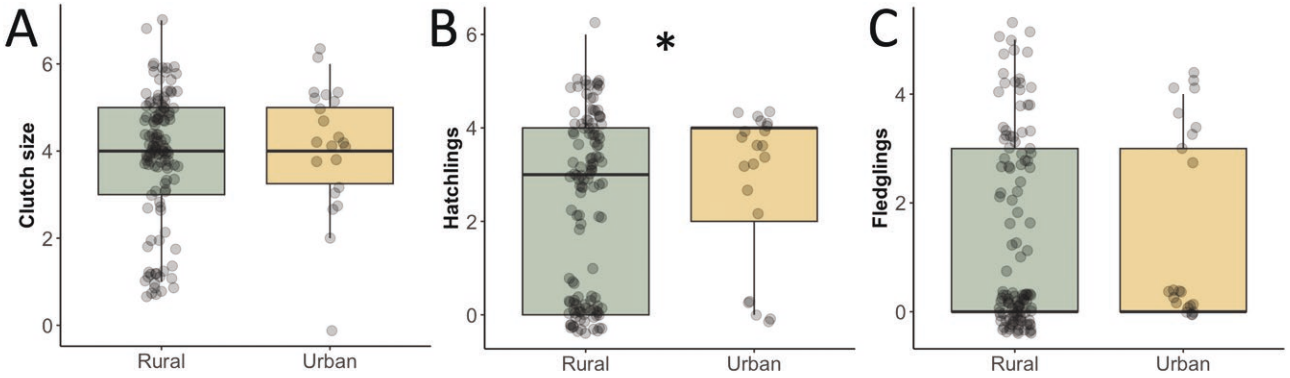

FIGURE 3. While there were no differences in the (**A**) clutch size or (**C**) number of fledglings produced in *S. vulgaris* nests from more rural (green) vs. more urban (yellow) sites, we found that (**B**) urban nests produce more hatchlings than rural ones (*z*-value = 2.71, *p*-value = 0.006). Figures depict box and whisker plots, and gray circles represent individual data points (*n* = 146 nesting attempts). The bolded line is the median, the box indicates first and third quartiles, and the whiskers indicate a confidence interval encompassing 1.5 times the interquartile range.

TABLE 2. We tested for differences in clutch size, number of hatchlings, and number of fledglings produced in urban vs. rural nests using generalized linear mixed models with a poisson distribution. The hatchling and fledglings' models are zero-inflated. Asterisks and bolding denote significant predictor variables where the *P*-value was below or equal to 0.05. No residual is shown for the random effects, as this is a generalized linear mixed model.

	Clutch size			Hatchlings			Fledglings		
Fixed effects	**Estimate ± SE**	***z*-value**	***P*-value**	**Estimate ± SE**	***z*-value**	***P*-value**	**Estimate ± SE**	***z*-value**	***P*-value**
Intercept	0.64 ± 1.43	0.45	0.65	2.12 ± 2.57	0.82	0.41	**−12.4 ± 4.64**	**−2.68**	**0.007***
Urbanization status	−0.01 ± 0.11	−0.10	0.92	**0.66 ± 0.24**	**2.71**	**0.006***	0.22 ± 0.37	0.59	0.55
Nest attempt	0.03 ± 0.10	0.31	0.76	**−0.41 ± 0.21**	**−1.94**	**0.05***	−0.22 ± 0.39	−0.55	0.58
Julian lay date	−0.61 ± 1.125	−0.53	0.66	**5.00 ± 2.04**	**2.44**	**0.01***	−6.86 ± 3.69	−1.86	0.06
Year (2021)	0.48 ± 1.08	0.45	0.66	**−3.79 ± 1.88**	**−2.01**	**0.04***	**7.04 ± 3.39**	**2.07**	**0.04***
Year (2022)	0.93 ± 2.08	0.44	0.66	**−7.89 ± 3.70**	**−2.13**	**0.03***	**13.6 ± 6.66**	**2.05**	**0.04***
Year (2023)	1.76 ± 3.14	0.56	0.58	**−13.1 ± 5.55**	**−2.36**	**0.02***	**19.3 ± 9.96**	**1.94**	**0.05***
Random effects	**Variance**	**SD**		**Variance**	**SD**		**Variance**	**SD**	
Nest ID	0.000	0.000		0.19	0.44		0.26	0.51	
Zero inflation	**Estimate ± SE**	**z-value**		**Estimate ± SE**	**z-value**		**Estimate ± SE**	**z-value**	
Parameter	NA	NA		-2.40 ± 0.46	-5.24		-0.80 ± 0.30	-2.68	

Though urban environments can lead to reduced reproductive rates in some birds (Sumasgutner et al. 2014), starlings are considered an urban-adapted bird and may thus perform similarly well or better in urban habitats than rural ones. Overall, our results suggest that very few differences in reproductive output exist between more urban and more rural breeding starlings in Georgia. Investment in eggs—including clutch size, egg mass, egg volume, and incubation behavior—were similar for starlings regardless of the urbanization status of their breeding site. As for investment in nestlings, we found that provisioning rates and brooding behavior along with the wing chord of nestlings and the number of fledglings produced were also similar for urban and rural breeding starlings. The only differences we detected between urban and rural birds were that the urban birds produced a higher number of hatchlings and that the rural birds produced young in higher body condition—though urban and rural birds fledged a similar number of young. Overall, we find little evidence that breeding in urban vs. rural habitats provides an advantage for *S. vulgaris*, which suggests that this urban-adapted bird showed similar breeding outcomes in more urban vs. more rural habitats within their invasive range.

Our finding that urban nestlings were in lower body condition than rural ones supports prior work in avian urban ecology, including in *P. domesticus* (Liker et al. 2008, Meillère et al. 2015), *Zonotrichia leucophrys* (White-crowned Sparrows; Phillips et al. 2018), and *Dumetella carolinensis* (Gray Catbird; Roux and Marra 2007). It would be possible that the differences in the number of hatchlings produced or in the body condition of nestlings across urbanization status could be explained by variation in parental care at those sites. A few lines of evidence suggest this is not the case for our study system. First, we did not find any differences in incubation behavior, provisioning rate, or brooding behavior for urban and rural starling parents. Secondly, we found few correlations among all the measures of reproductive investment or success examined in our study and none between parental

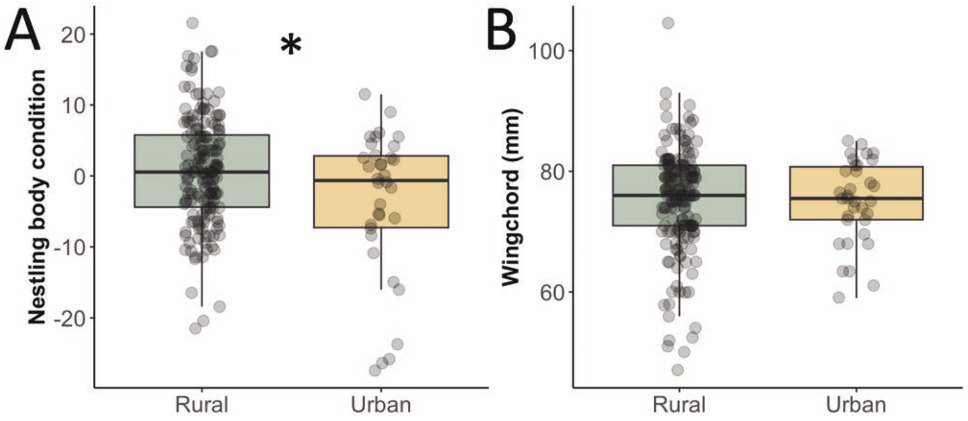

FIGURE 4. While (**A**) nestling body condition (residuals of mass on tarsus length) was higher in rural habitats (*z*-value = −3.19, *p*-value = 0.002), (**B**) we did not find a difference in wing chord length for *S. vularis* chicks growing in nests from more rural (green) vs. more urban (yellow) sites. Figures depict box and whisker plots, and gray circles represent individual data points (*n* = 201 nestlings). The bolded line is the median, the box indicates first and third quartiles, and the whiskers indicate a confidence interval encompassing 1.5 times the interquartile range.

TABLE 3. We tested for differences in nestling body condition (residuals of mass on tarsus) and wing chord length (mm) in urban vs. rural nests using linear mixed models. Asterisks and bolding denote significant predictor variables where the *P*-value was below or equal to 0.05.

	Body condition			Wing chord length		
Fixed effects	Estimate ± SE	*t*-value	*P*-value	Estimate ± SE	*t*-value	*P*-value
Intercept	**5060 ± 1257**	**4.03**	**<0.001***	2547 ± 1542	1.65	0.10
Urbanization status	**−7.34 ± 2.20**	**−3.34**	**0.002***	−2.43 ± 2.74	−0.89	0.38
Julian date	**−0.28 ± 0.07**	**−4.01**	**<0.001***	−0.14 ± 0.08	−1.64	0.11
Nest attempt	5.12 ± 2.87	1.78	0.08	5.84 ± 3.54	1.65	0.10
Brood size	**−2.24 ± 1.06**	**−2.11**	**0.04***	1.99 ± 1.32	1.51	0.14
Chick age	0.06 ± 0.96	0.06	0.95	**3.19 ± 1.20**	**2.67**	**0.01***
Year (2021)	**105.7 ± 25.6**	**4.14**	**<0.001***	49.0 ± 31.4	1.56	0.12
Year (2022)	**197.3 ± 50.3**	**3.92**	**<0.001***	100.3 ± 61.7	1.63	0.11
Year (2023)	**305.8 ± 75.5**	**4.05**	**<0.001***	149.0 ± 92.7	1.61	0.11
Random effects	**SD**		**Residual**	**SD**		**Residual**
Nest ID	5.00		5.50	6.61		5.64

care and hatchling number or condition (see Supplementary Material Figure 1). These differences in nestling body condition could lead to differential survival of rural and urban chicks, since body condition at fledging has been associated with increased survival odds for many birds (Naef-Daenzer et al. 2001, Arizaga et al. 2015, Freeman et al. 2020, Rotics et al. 2021) including *S. vulgaris* (Krementz et al. 1989, Thompson and Flux 1991). It is important to note that the positive association between body condition in the nest and post-fledging survival may not be causative and that other traits (e.g., physiology or growth rate) may better predict survivorship in young birds (Allen et al. 2022). Nevertheless, our study found that rural nestlings were in higher body condition compared to urban nestlings, which may provide an advantage to chicks raised in more rural habitats. Interestingly, rural nestlings did not appear to receive more food from their parents, as the total provisioning rates were similar across urban and rural nests. However, it is possible that the parents in rural habitats brought different types of food or larger pieces of food to their nestlings compared to urban ones which we could not quantify from videos alone.

Prior work in this system showed that our more rural sites have higher insect availabilities (Linkous et al. 2024), suggesting that parents raising their young at more rural sites may have access to higher quality protein-rich foods whereas urban parents may use alternative food types of lower quality. Such differences in the availability of preferred prey could contribute to our findings on nestling body condition and would not be captured by provisioning rate alone. Urbanization has been shown to reduce the availability of preferred prey type for other species and thus leading to reduced reproductive output, including in *Corvus monedula* (Western Jackdaw; Meyrier et al. 2017) and *Falco tinnunculus* (Eurasian Kestrel; Sumasgutner et al. 2014). Rather than environmental causes—including differences in food availability and quality of provisioning for the nestlings—it is also possible that breeding site selection reflects genetic differences among populations or differences in the quality of individuals breeding across sites and are therefore at least partly shaped by genetic factors passed down to the nestlings. We have not found evidence that parents at rural sites are in greater body condition compared to urban ones (Kilgour et al. 2022); however, suggesting this

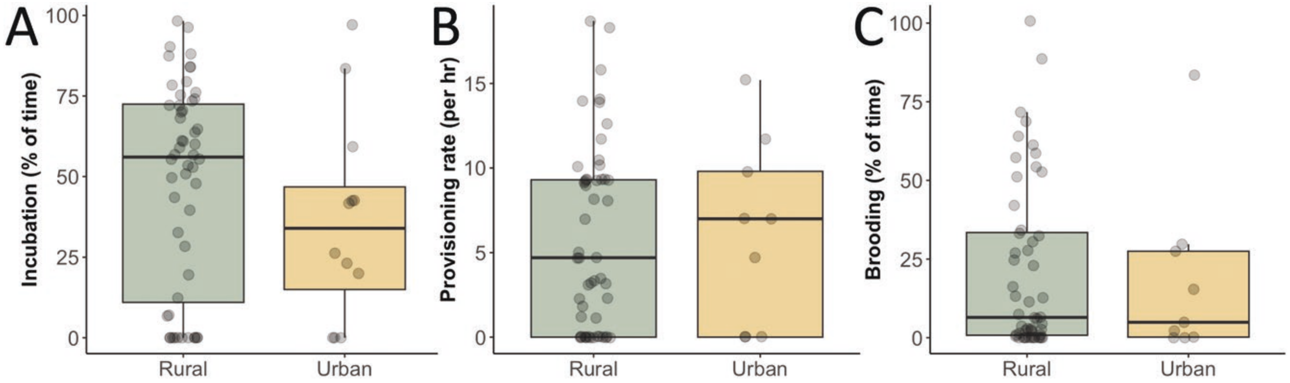

FIGURE 5. There were no differences in *S. vulgaris* (**A**) incubation behavior (% time on the eggs), (**B**) hourly rate of provisioning nestlings, or (**C**) nestling brooding (% time on the chicks) for parents breeding at more rural (green) vs. more urban (yellow) sites. Figures depict box and whisker plots, and gray circles represent individual data points ($N_{\text{incubation}}$ = 65 nesting attempts and $N_{\text{provisioning and brooding}}$ = 61 nesting attempts). The bolded line is the median, the box indicates first and third quartiles, and the whiskers indicate a confidence interval encompassing 1.5 times the interquartile range.

TABLE 4. We tested for differences in incubation behavior (percentage of time), provisioning rate (trips per hour), and brooding behavior (percentage of time) performed by parents nesting at urban vs. rural sites using generalized linear mixed models with a negative binomial distribution. The provisioning rate model was zero-inflated. No residual is shown for the random effects, as this is a generalized linear mixed model. NA means not applicable.

	Incubation behavior			Provisioning rate			Brooding behavior		
Fixed effects	Estimate ± SE	*z*-value	*P*-value	Estimate ± SE	*z*-value	*P*-value	Estimate ± SE	*z*-value	*P*-value
Intercept	6.93 ± 8.48	0.82	0.41	−2.84 ± 4.49	−0.63	0.53	14.6 ± 9.45	1.55	0.12
Urbanization status	−0.34 ± 0.46	−0.73	0.46	−0.11 ± 0.28	−0.39	0.70	−0.63 ± 0.63	−1.00	0.32
Nest attempt	−0.06 ± 0.54	−0.12	0.91	−0.46 ± 0.26	−1.78	0.07	−1.04 ± 0.69	−1.51	0.13
Julian lay date	−2.41 ± 6.89	−0.41	0.69	−4.50 ± 3.66	−1.23	0.22	8.34 ± 7.52	1.11	0.27
Clutch size	−0.01 ± 0.21	−0.05	0.96	NA	NA	NA	NA	NA	NA
Clutch age	−0.01 ± 0.17	−0.08	0.94	NA	NA	NA	NA	NA	NA
Brood size	NA	NA	NA	0.07 ± 0.09	0.75	0.46	−0.18 ± 0.20	−0.92	0.36
Chick age	NA	NA	NA	−0.12 ± 0.13	−0.95	0.34	−0.49 ± 0.34	−1.43	0.15
Year (2021)	−2.54 ± 6.23	−0.41	0.69	4.08 ± 3.40	1.20	0.23	−20.2 ± 12.5	−1.62	0.11
Year (2022)	−4.38 ± 12.4	−0.35	0.72	8.04 ± 6.50	1.24	0.22	−0.65 ± 0.66	−1.00	0.32
Random effects	**Variance**	**SD**		**Variance**	**SD**		**Variance**	**SD**	
Nest ID	0.000	0.000		0.000	0.000		0.000	0.000	
Zero Inflation	**Estimate ± SE**	**z-value**		**Estimate ± SE**	**z-value**		**Estimate ± SE**	**z-value**	
Parameter	NA	NA		−0.89 ± 0.29	−3.13		NA	NA	

may not be supported in our system. Paired with the current study, our prior findings on adult body condition suggest that early life differences in body condition may not persist into adulthood, or that adult starlings can switch among more urban and rural sites later in life. Alternatively, early-life differences in body condition could alter recruitment into the breeding population, but our data do not allow us to test this idea. Ultimately, the consequences of these early-life differences in body condition among rural vs. urban nestlings need to be better studied, and doing so would require tracking individuals over many years to estimate their survivorship and account for their possible movements across sites.

While *S. vulgaris* breeding at more urban vs. more rural sites invested similarly in clutch and egg size, urban starlings hatched more offspring than more rural ones. Since this cannot be explained by differences in egg volume, egg mass, clutch size, or incubation investment, it is possible that urban starlings invest differently via deposits of nutrients or hormones in the yolk of their eggs. Prior work in this system suggests that there is no difference in secondary sex ratios across urban and rural nests (Kilgour et al. 2022), which provides further support that starlings invest similarly in the production of eggs across site types. However, the quality of yolk, nutrients or hormones passed down to the young remain unclear. Similarly, it is not clear why urban starlings would hatch more young than rural ones despite investing similarly in the production and care of their eggs. It is possible that urban sites have higher ambient temperatures, which would be beneficial for egg development and hatching success as suggested by work on *Troglodytes aedon* (House Wren; Heppner and Ouyang 2021) and *Turdus mandarinus* (Chinese Blackbird; Ma et al. 2023). Either way, any advantage of hatching a greater number of eggs at urban nests is canceled out by the fledging stage since there was no difference in the number of young successfully fledged from more urban vs. rural nests. This suggests that there is high nestling mortality at urban compared to rural sites, since urban nests produced more hatchlings but the same number of fledglings as rural nests. Finally, another possibility to explain differences in urban hatching rates compared to rural ones is that we had a lower sample size at urban sites which could lead to a statistical difference in the number of hatchlings observed that is not driven by a biological effect of urbanization.

Overall, our study finds that *S. vulgaris* breeding at urban and rural sites are largely similar in their reproductive investment and success. Starlings are typically designated as an urban-adapted species (sometimes urban-dwelling) (Blair 1996, McKinney 2002, Fischer et al. 2015, Fanelli et al. 2022), meaning that they are found similarly across both urban and more rural environments. At least in the greater metro-Atlanta area, the distribution of starlings across a gradient of urbanization appears to reflect similar success across these habitats. This is similar to other urban-adapted species that were similarly successful across the urbanization gradient including *Milvago chimango* (Chimango Caracara; Solaro and Sarasola 2023) and *Oenanthe oenanthe* (Wheatear; Meffert et al. 2012). It remains possible that urban-adapted species are negatively affected by city life, though these effects may only shape reproductive success indirectly or not at all: for example, starlings at more urban sites differ in their glucocorticoid physiology (Guindre-Parker et al. 2022) and in their cholesterol (Linkous et al. 2024) compared to rural starlings. It remains unclear whether adult survival differs for starlings from urban vs. rural sites, and future work monitoring adults across multiple years will reveal whether survivorship remains similar across more urban and rural starlings similarly to our results on reproductive success. Likewise, differences in emigration and immigration—in addition to reproductive success and survivorship—shape the age structure and resilience of populations. Future work characterizing starling population demography across a gradient of urbanization would help provide a greater understanding of how urban life impacts starlings. The effects of urbanization on the Darwinian fitness and behavior of wildlife remain complex, and intra-specific studies like our own paired with interspecific studies (Fanelli et al. 2022, Pharr et al. 2023) will be necessary to fully understand why some species cope with city life better than others.

Supplementary material

Supplementary material is available at *Ornithology* online.

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Ethics statement

This study monitored free-living *Sturnus vulgaris* (European Starlings) using noninvasive methods that did not harm the animals—they were released back where they were trapped after handling or observation. Research permissions were granted via the United States Geological Survey (permit 24222), the Georgia Department of Natural Resources (permit 1000974355), and KSU's Institutional Animal Care and Use Committee (protocol 20-001and 2022-0087).

Conflict of interest statement

The authors have no competing interests or conflicts of interest to declare.

Author contributions

Sarah Guindre-Parker: Conceptualization, Field data collection, Statistical analysis, Supervision, Writing (original draft). Arianna Acosta, Amberlee Cook, Joanna Corimanya, Rachel Kaplan, Denyelle Kilgour, Courtney Linkous, Michelle Ross, CareyJo Titus: Field data collection, Writing (review and editing). Cole Bourque, Trinity Smith: Video analysis, Writing (review and editing).

Data availability

Analyses reported in this article can be reproduced using the data provided by Guindre-Parker et al. (2024).

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