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Research Article

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Nesting in urban areas affects *Falco sparverius* (American Kestrel) home range size and adult female health

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ABSTRACT

Current rates of urbanization are unprecedented and wildlife must adapt or face population declines. *Falco sparverius* (American Kestrel) inhabit urban areas; however, whether human-dominated landscapes impact their space-use, survival, and reproductive success is largely unknown. We monitored *F. sparverius* nest boxes along a gradient of urbanization, measured using impervious surface area (ISA), and deployed 108 GPS loggers on breeding adults to examine the relationship between urbanization, home range size, and adult and nestling health during the 2021–2023 breeding seasons. Male home ranges ($n = 29$) were 9.14 times larger than those of females ($n = 44$), and home range sizes decreased as ISA increased for both sexes. Adult females lost weight at twice the rate of adult males; and, although there was no relationship between weight loss and home range size, females lost more weight as ISA increased. The effect of female home range size on individual nestling weight and the weight variation within broods depended on ISA. In less urbanized areas, larger home ranges led to higher nestling weight and lower within-brood weight variation, but this relationship was reversed in more urbanized areas, where larger home ranges led to lower nestling weight and higher variation compared to smaller home ranges with similar ISA. Male home range size did not explain nestling weight but showed a similar, dependent effect on within-brood weight variation as the female home range size. Results suggest that smaller home range sizes in urban areas may be adaptive for *F. sparverius*. However, the effects of urbanization on adult female weight loss shows that while they can successfully breed in urban areas, it could come at a cost to female health and potentially survival. *Falco sparverius* may be more sensitive to urbanization than previously reported.

Keywords: American Kestrel, breeding season, *Falco sparverius*, GPS logger, home range, raptor, urban ecology

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LAY SUMMARY

- The urban landscape is growing faster than ever and wildlife must adapt or face population declines.
- We studied *Falco sparverius* (American Krestrel) nesting along an urban gradient, from wildland to commercial areas, to examine the effect of landscape on home range size, seasonal weight change of the adults, nestling mass, and variation in nestling weight within broods.
- *Falco sparverius* had smaller home ranges in more urban areas, and adult females lost more weight as urbanization increased. On the other hand, male weight loss was consistent across the urban gradient.
- Only the home range size of the adult females affected nestling weight, and the effect depended on the level of urbanization. In less urbanized areas, larger female home ranges led to heavier nestlings. Conversely, in more urbanized areas, larger home ranges led to lighter nestlings.
- Both adult female and adult male home ranges affected the variation of nestling weight within broods. In areas with higher urbanization, variation was higher as the home range size increased.
- *Falco sparverius* breeding in urban areas tended to have smaller home ranges, but females in these areas lost more weight during the breeding season. If this added cost decreases overwinter survival or future productivity, *F. sparverius* may be more sensitive to urbanization than previously reported.

La nidificación en áreas urbanas afecta el tamaño del área de campeo y la salud de las hembras adultas de *Falco sparverius*

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RESUMEN

Las tasas actuales de urbanización no tienen precedentes y la fauna silvestre debe adaptarse o enfrentar declives poblacionales. *Falco sparverius* habita áreas urbanas; sin embargo, en gran medida se desconoce si los paisajes dominados por el ser humano afectan su uso del espacio, supervivencia y éxito reproductivo. Monitoreamos cajas nido de *F. sparverius* a lo largo de un gradiente de urbanización, medido mediante el área de superficie impermeable (ASI), y colocamos 108 marcadores GPS en adultos reproductivos para examinar la relación entre urbanización, tamaño del área de campeo y la salud de adultos y polluelos durante las temporadas reproductivas 2021–2023. Las áreas de campeo de los machos (n = 29) fueron 9,14 veces mayores que las de las hembras (n = 44), y el tamaño del área de campeo disminuyó a medida que aumentó el ASI en ambos sexos. Las hembras adultas perdieron peso al doble de la tasa de los machos adultos; y, aunque no hubo relación entre la pérdida de peso y el tamaño del área de campeo, las hembras perdieron más peso a medida que aumentó el ASI. El efecto del tamaño del área de campeo de las hembras sobre el peso individual de los polluelos y la variación de peso dentro de las nidadas dependió del ASI. En áreas menos urbanizadas, áreas de campeo más grandes generaron pichones más pesados y una menor variación de peso dentro de la nidada, pero esta relación se invirtió en áreas más urbanizadas, donde áreas de campeo más grandes generaron pichones de menor peso y una mayor variación en comparación con áreas de campeo más pequeñas con ASI similar. El tamaño del área de campeo de los machos no explicó el peso de los polluelos, pero mostró un efecto dependiente similar sobre la variación de peso dentro de la nidada, comparable al del área de campeo de las hembras. Los resultados sugieren que tamaños de área de campeo más pequeños en áreas urbanas pueden ser adaptativos para *F. sparverius*. Sin embargo, los efectos de la urbanización sobre la pérdida de peso de las hembras adultas muestran que, si bien pueden reproducirse con éxito en áreas urbanas, esto podría implicar un costo para la salud de las hembras y potencialmente para su supervivencia. *Falco sparverius* podría ser más sensible a la urbanización de lo que se había reportado previamente.

Palabras clave: área de campeo, ave rapaz, ecología urbana, Falco sparverius, marcador GPS, temporada reproductiva

INTRODUCTION

Urbanization is happening at an unprecedented rate and poses a significant threat to biodiversity (Brown and Laband 2006, Aronson 2014). Urban landscapes present challenges for wildlife, including human disturbance (Strasser and Heath 2013), collisions (Loss et al. 2014, Cusa et al. 2015), disease (Hernández-Téllez et al. 2023), and toxicants (Badry et al. 2021). Urban landscapes can also provide benefits, such as novel prey (Fleming and Bateman 2018), perches (DeCandido and Allen 2006), nesting sites (Stout et al. 2006), or release from native predators (Gering and Blair 1999). Understanding how species adapt in urban spaces is key to maximizing biodiversity and population persistence in this rapidly growing environment.

Bird species inhabit urban spaces with varying success. Species that do well in urban areas often exhibit high behavioral plasticity or take advantage of resources that mimic their natural resources (Lowry et al. 2013). Many raptor species show plasticity in both diet (Steenhof and Kochert 1988) and home range size (Marquiss and Newton 1982, Pfeiffer and Meyburg 2015) as the types and availability of prey change, and some suggest raptors do well in urban environments because of their flexibility (Chace and Walsh 2006). However, not all raptor species thrive in urban areas. For example, even though *Falco tinnunculus* (Eurasian Kestrel) in Vienna nested at higher densities in the city center compared to suburban outskirts, it was likely due to cavity availability rather than overall habitat quality, because nest success and number of fledged young were lower in the city center compared to the suburbs (Sumasgutner et al. 2014). Further, the body mass index of *F. tinnunculus* nestlings was inversely correlated with urbanization because of low access to quality prey (Wemer et al. 2021).

Raptors can have either smaller (Dykstra et al. 2001, Rutz 2006) or larger (Catry et al. 2013, Lövy and Riegert 2013) home ranges in urban areas compared to their rural conspecifics. Home range size is often linked to habitat quality (Marzluff et al. 1997, Lourenço et al. 2015), with individuals having smaller home ranges in areas with more or higher-quality prey. Yet, Hinam and Clair (2008) associated smaller breeding home ranges with lower productivity in *Aegolius acadicus* (Northern Saw-whet Owls), suggesting home range size alone may not adequately assess habitat quality in all cases. Pairing home range size with metrics of health or productivity (Pfeiffer and Meyburg 2015) along a gradient of urbanization (Corsini et al. 2021) can inform how well a species adapts to urban environments.

Falco sparverius (American Kestrel) inhabit urban areas and are ubiquitous across the landscape. Many populations are in decline, and the causes are still unknown (Smallwood et al. 2009, McClure et al. 2017, Oleyar et al. 2023). *Falco sparverius* are cavity nesters and readily take to human-made nesting structures, including nest boxes, along an urban gradient from rural environments to urban centers. However, how nesting in different landscape types impacts kestrel survival, reproduction, and home range size is largely unknown. Strasser and Heath (2013) documented increased rates of nest abandonment in areas with a higher human disturbance score and linked it to higher levels of stress hormones in adult females. Home range associations are largely unstudied because, until recently, modern tracking devices were too heavy to deploy on these small falcons. To date, there is only one published study of *F. sparverius* home ranges using high-resolution tracking data for females (Kolowski et al. 2023). Understanding the relationships between urbanization, home range size, and health would provide insight into the potential impacts and environmental risks urbanization poses to *F. sparverius* and other wildlife and highlight areas for future research.

Our objective was to study the breeding ranges of *F. sparverius* pairs to assess the impacts of increased urbanization on home range size and adult and nestling health. We deployed GPS trackers on *F. sparverius* to estimate home ranges for adults nesting along an urban gradient during the 2021–2023 breeding seasons. We also measured adult weight change during the breeding season and nestling weight at fledging. If urban areas provided poorer habitat quality for *F. sparverius*, we expected a combination of larger home range sizes, increased weight loss in adults, and decreased nestling weight in more urban areas. If urban areas provided better habitat quality, we expected to see the opposite. If *F. sparverius* were able to adjust to urban environments, we predicted that home range sizes would differ between urban and rural environments, but there would be no difference in adult or nestling health, reflected in weight-related metrics, along the urban gradient.

METHODS

Study Area

Our study area had ~500 nest boxes interspersed throughout 5 counties in the greater Salt Lake area along the Wasatch Range in northern Utah, USA (Figure 1). The study area spanned ~130 km north to south and ~70 km east to west, centered around Salt Lake City (40.7609°N, 111.8910°W). Box locations included parks, backyards, commercial complexes, and roadside utility poles. Nest box height, orientation, and attachment substrate varied throughout the study area. For this study, we included a subset of the ~120 nest boxes occupied by *F. sparverius* each year, where we were able to deploy GPS units. We attempted to disperse included nests evenly over a range of urbanization (from undeveloped wildlands to urban commercial parks) and in a variety of box locations (e.g., city parks and residential areas) that were geographically representative of the study area.

Monitoring Nests

We worked with a team of biologists and volunteers to monitor nest boxes every 7–10 days from mid-March through July in

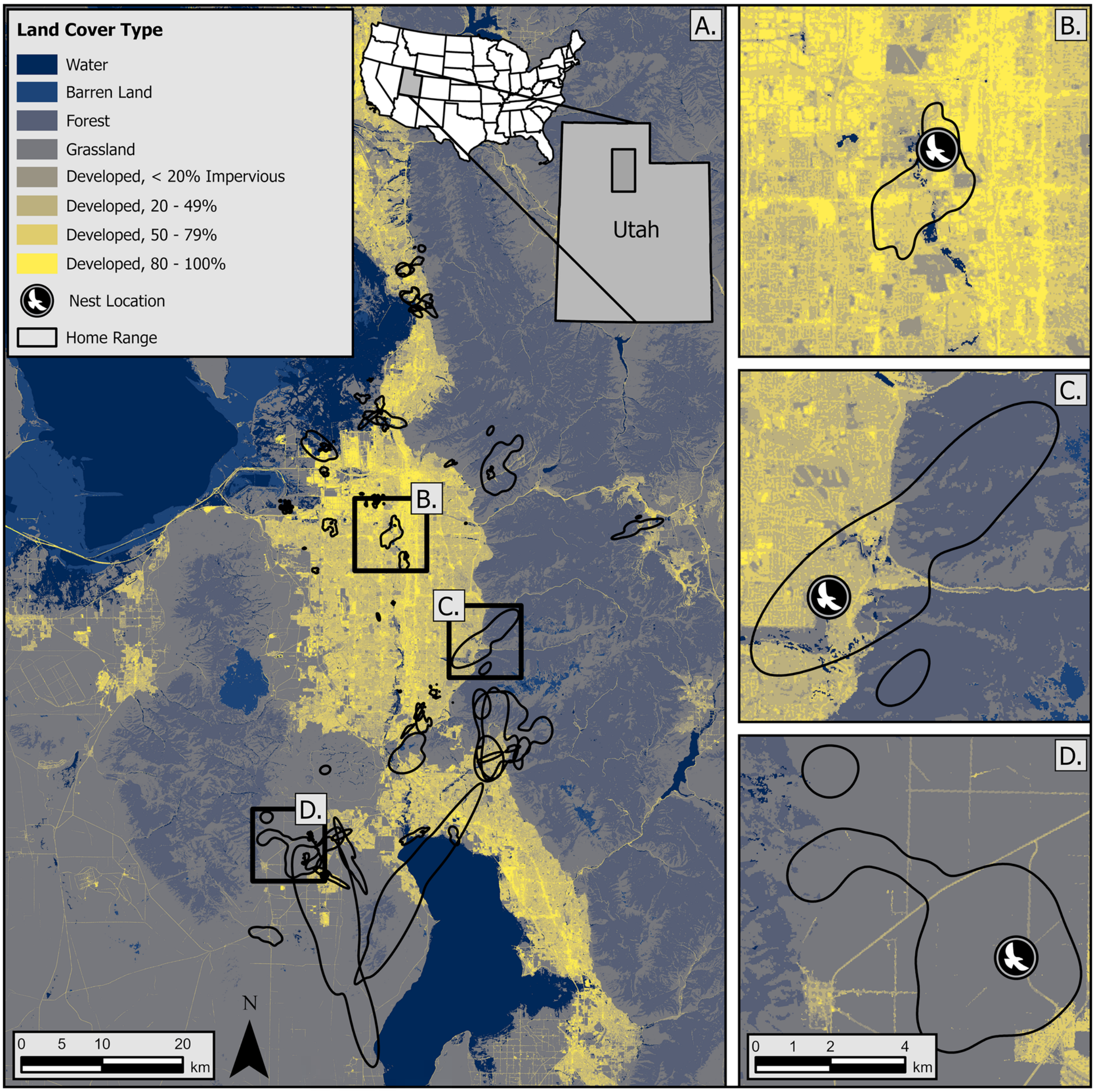

FIGURE 1. Study area and home ranges of breeding *Falco sparverius* (American Kestrels) across a range of urbanization, represented by impervious surface area. Panel (**A**) shows the home ranges (95% autocorrelated kernel density estimates) of all 73 individuals tracked during the 2021–2023 breeding seasons. Individuals were tracked during the 2021–2023 breeding seasons, and not tracked for more than one season. The panels on the right depict the home range of individual adults nesting in areas with high (**B**), medium (**C**), and low (**D**) imperviousness.

2021, 2022, and 2023. A researcher on a ladder looked directly inside the boxes or used a camera attached to a paint pole and recorded observations using a digital data entry form. We estimated the full clutch date by either observing the nest during the egg-laying period and assuming one egg was laid every other day or by backdating from the hatch date and assuming a 30-day incubation period (Bird and Palmer 1988). We estimated the hatch date by either observing the nest during the hatching process or backdating from the nestling age based on plumage using an aging guide (Klucsarits and Rusbuldt 2007).

Capture and Tracking

We deployed GPS store-on-board loggers on *F. sparverius* throughout the three breeding seasons. We targeted one adult from each nest in the first season and after confirming that the transmitters worked effectively, we targeted breeding pairs in subsequent seasons. However, we were often unable to deploy loggers on or retrieve loggers from both adults. *Falco sparverius* are sexually size dimorphic, and females are larger than males (Snyder and Wiley 1976). With few exceptions, we attempted to capture the males first because (a) they spend less time in the nest box and are therefore more difficult to catch and (b) some males did not meet the weight requirement (3% of the individual's body weight for the combined weight of the logger, harness, and bands) to carry the GPS units (Katzner and Young 2024). In these cases, we did not deploy loggers on either adult and selected alternate nests for the study. We initially captured the adults by hand after blocking the box entrance when parents were incubating or brooding. Many of the adults in our study were previously banded with a USGS band and a color band. If the bird was not already banded, we did so, and fit a GPS unit with a backpack-style harness made of 2.54 mm Spectra (Bally Ribbon Mills, Bally, Pennsylvania, USA). Adults received 1 of 2 models of trackers: Lotek PinPoint 50 GPS logger (PP50) or Technosmart Gypsy XS GPS logger (GXS). The PP50 loggers stored data onboard and had to be retrieved to download the data. These loggers did not have a solar panel and the battery was depleted after ~500 location fixes. The GXS units had solar panels, and the data were downloaded with a receiver from a distance of ~100 m. To recapture adults with loggers, we used either an animatronic owl in front of a mist net placed near the nest, a mist net placed directly in front of the box entrance, or a Bal-chatri with a mouse or sparrow. We started recapture attempts when the nestlings were ~21 days old. We weighed each adult at capture and recapture and noted if there was anything in their crop. We banded and weighed the nestlings at ~21 days or older when their body mass growth reached an asymptote (Smallwood and Bird 2020).

In 2021, we programmed GPS units to obtain location fixes during daylight hours (7:00–21:00 MDT) at 20- or 60-min intervals during the nestling period (from hatch to fledge). For the PP50 units, we found that 60-min intervals would last ~30 days before the battery died, whereas the 20-min intervals lasted ~12 days. The GXS units would usually charge enough to handle 15- or 20-min intervals once the females were consistently out of the box. We, therefore, adjusted the schedules in 2022 and 2023 to 60-min intervals for all PP50 units and either 15-, 20-, or 60-min intervals for the GXS units, depending on the charge. Although we usually deployed GPS units when the adults were on eggs, we programmed them to start collecting location points when the eggs had hatched (based on the estimated hatch date) to capture as many points as possible during the nestling period before the battery died. We tracked each individual for one breeding season.

Analysis

Home range and weight calculations

We excluded GPS locations collected from females before the nestlings were 10 days old, which is when *F. sparverius* females do the primary share of the brooding and are mostly in the box (Bird and Palmer 1988). We also excluded points collected 30 min before sunset or later to avoid including potential roost locations. We removed all data for a nest where the eggs did not hatch, and the points from another nest following a predation event when the nestlings were ~13 days old. To estimate home range size, we used continuous-time movement models that describe movement as a stochastic process in continuous time and account for temporal autocorrelation. We fit movement data for each bird to 4 candidate movement models: Brownian motion (BM), Ornstein-Uhlenbeck process (OU), Ornstein-Uhlenbeck forage process (OUF), and uncorrelated, independent data (IID) (Fleming et al. 2014). We selected the model that best described movement patterns for each individual using the lowest Akaike Information Criterion corrected for small sample size (AIC_c; Akaike 2003). We fit models using the auto-correlated kernel density estimator (aKDE) available in the *amt* package (Signer et al. 2019) in program R version 4.2.2 (R Core Team 2023). We used the top model to calculate the 95% home range isopleths and mean area for all birds (Fleming et al. 2015).

We determined adult weight change by calculating the percentage of the initial body weight lost each day to account for variation in the number of days between capture and recapture for each individual (percentage daily weight loss = (initial weight − recapture weight)/days between captures/initial weight * 100). We excluded any individual with food in their crop from this analysis ($n = 10$). We also excluded individuals recaptured in the winter or during the following breeding season ($n = 6$). We did not account for differences in the initial weight because it was not influenced by urbanization (Supplementary Material Figure 1, see Online Supplementary Material for a color version of this figure).

We wanted to capture effects on both the individual weight of nestlings in each brood, but also within-brood weight variation because some broods had one or more nestlings that were underweight, while other nestlings in the brood were at or above average. Therefore, we used a single weight for each nestling and calculated the coefficient of variation (CV) for nestlings in each brood.

Predictor variables

We used percent impervious surface area (ISA) from the 2021 National Land Cover Database (Dewitz 2023) as a proxy for urbanization. We estimated ISA within a circular buffer with a 5-km radius around the nest box, which was large enough to capture the urbanization of the landscape and to encompass 88% of *F. sparverius* home ranges in our study. We expected males and females to have different home range sizes and that resources may be poorer later in the nesting season (Callery et al. 2022). Additionally, we expected potential intraspecific competition and calculated a weighted inverse distance to all other occupied nests to account for the density of neighboring *F. sparverius* pairs. We calculated neighbor density by summing the inverse distances to all other known *F. sparverius* nests in the same season, which gives closer nests more weight and a higher value (Cruz et al. 2019).

Models

We assessed how urbanization (ISA) influenced home range size using a Bayesian mixed-effect model with a Gamma distribution. We included adult sex, neighbor density, nest phenology (i.e., hatch date), and an interaction between sex and urbanization as predictors in the model. We examined the influence of urbanization (ISA) on adult weight change using a Bayesian mixed-effect model with a Gaussian distribution and included home range size, nest phenology, the number of fledged young, sex, and an interaction between sex and urbanization in the model.

To examine the influence of urbanization and parent home range size on nestling weight, we fit a Bayesian mixed-effect model with a Gamma distribution. We included nest phenology, the number of fledged young, nestling sex, and an interaction between urbanization and home range size as predictors in the model. Separately, we modeled the CV of nestling weights in each nest using a Beta distribution. Because we did not have the paired adults from each nest, we used the female and male home range sizes as predictors in separate models for both the individual nestling weight and the CV of weight models. In the weight variance model, we replaced nestling sex with the percent of whichever sex was in the majority to account for variation between sexes and removed three nests with a single nestling.

We fit all models using the *brms* R package (Bürkner 2017). We chose a Bayesian framework because it allows straightforward interpretation of complex hierarchical models and accommodates random intercepts effectively. We centered the predictors in all models at their mean and scaled by 2 standard deviations to make effect sizes comparable amongst categorical and continuous predictors and to improve model convergence (Gelman 2008). For all models except those with the CV of nestling weights as a response variable, we included the nest ID as a random intercept to account for multiple birds sampled from the same nest. We used *brms* default priors, which are flat priors for the coefficients related to the predictors and student's *t* priors for the intercepts and random intercepts. To fit each model, we ran four chains for 2,000 iterations (1,000 warm-up and 1,000 sampling iterations per chain) and assessed model convergence using visual inspection of trace plots, effective sample sizes, and the Gelman-Rubin statistic (<1.01; Gelman and Rubin 1992).

We considered predictors informative if they had a probability of direction (PD) of 90% or higher. We calculated the PD as the proportion of the posterior draws that were on the same side of zero as the median, which can be interpreted as the certainty of an effect being positive or negative (Makowski et al. 2019). We report posterior mean estimates (β), standard error (SE), and PD for all predictors. We used marginalized plots to assess the relationship between the predictor of interest and the response variable while holding other model predictors at their mean values.

RESULTS

We deployed 108 GPS units (5 GXS and 103 PP50) at 74 nests and retrieved data from 74 individuals ($n = 45$ females, $n = 29$ males) at 55 nests ($n = 19$ pairs). Most of the loggers worked as intended; however, one GXS unit failed entirely, another failed halfway through the season, and one PP50 logger failed toward the end of the season. After cleaning the data, a range of 61–860 points (mean = 270.82 ± 135.00) for each bird spanning 2–36 days (mean = 18.75 ± 7.95; Supplementary Material Figure 2, see Online Supplementary Material for a color version of this figure) contributed to home range calculations (Figure 1). Only 2 individuals had less than a week (2 and 5 days) of tracking data. Within sexes, estimated home range sizes were weakly correlated with the number of tracked days in females (Spearman's $\rho = 0.35$) but not in males ($\rho = 0.18$), indicating that variation in tracking effort was unlikely to bias home range estimates.

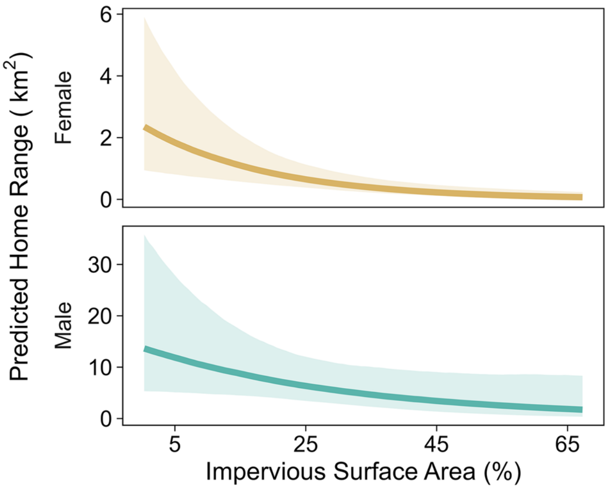

FIGURE 2. Predicted home range sizes of adult *F. sparverius* along a gradient of urbanization (impervious surface area) in northern Utah, USA from the 2021–2023 breeding seasons. Solid lines represent posterior mean estimates of home range size for females and males estimated from a Bayesian mixed-effect model with a Gamma distribution. Shaded bars represent 95% credible intervals. Predictions were made holding all other model variables at their means.

We collected weight changes for 33 females and 24 males. Time between weights ranged 9–40 days (mean = 26.84 ± 6.62). All birds lost weight throughout the nesting season, and females lost more weight than males (mean = 0.53 ± 0.23% and 0.25 ± 0.13% of initial body weight per day, respectively). We weighed 214 nestlings from 53 nests. The average nestling weight for females was 121.36 ± 14.10 g ($n = 124$) and for males 111.04 ± 13.02 g ($n = 90$).

ISA around nest boxes ranged from <1 to 67% (mean = 27 ± 19%; Supplementary Material Figure 3, see Online Supplementary Material for a color version of this figure). Hatch dates ranged from May 2 to July 6, with an average date of June 1 ± 17 days (Supplementary Material Figure 4, see Online Supplementary Material for a color version of this figure). Adults fledged 0–5 young with an average of 3.91 ± 1.32 (Supplementary Material Figure 5, see Online Supplementary Material for a color version of this figure). The summed inverse distance weights (neighbors) ranged from 3.40 to 18.18 km^{-1} (mean = 8.11 ± 3.44 km^{-1}; Supplementary Material Figure 6, see Online Supplementary Material for a color version of this figure).

Home range size decreased as ISA increased, and females had markedly smaller home ranges than males (Figure 2; Table 1). The median home range was 0.42 km^2 for females (0.01–24.40 km^2) and 3.84 km^2 for males (0.37–136.00 km^2).

TABLE 1. Posterior mean estimates (β), standard errors (SE), and probability of direction (PD) from Bayesian models describing adult home range size, adult daily weight change, nestling body weight, and the coefficient of variation (CV) of nestling weight within broods for *Falco sparverius* in northern Utah during the 2021–2023 breeding seasons.

Home range size	**β**	**SE**	**PD (%)**
Intercept	–0.47	0.27	95.67
Sex	2.30	0.31	100
ISA	–1.96	0.52	100
Hatch date	0.37	0.47	77.70
Delta (neighbors)	–0.33	0.46	76.33
Sex × ISA	0.80	0.66	89.03

Daily weight change	**β**	**SE**	**PD (%)**
Intercept	–0.53	0.04	100
Sex	0.29	0.05	100
Home range size	0.01	0.06	57.50
ISA	–0.16	0.07	99.15
Hatch date	–0.05	0.06	81.55
Fledge	–0.11	0.06	97.58
Sex × ISA	0.16	0.10	94.12

	Female home range			**Male home range**		
Nestling weight	**β**	**SE**	**PD (%)**	**β**	**SE**	**PD (%)**
Intercept	4.78	0.02	100	4.83	0.02	100
Nestling sex	–0.10	0.02	100	–0.09	0.01	100
Home range size	–0.08	0.06	93.30	0.01	0.04	56.00
ISA	–0.04	0.05	79.12	–0.03	0.04	75.48
Hatch date	–0.07	0.03	98.28	–0.05	0.03	91.60
Fledge	0.03	0.03	83.45	0.04	0.03	91.22
Home range × ISA	–0.36	0.24	92.90	–0.01	0.11	51.48

	Female home range			**Male home range**		
CV of nestling weight	**β**	**SE**	**PD (%)**	**β**	**SE**	**PD (%)**
Intercept	–2.46	0.14	100	–2.60	0.10	100
% Majority sex	–0.56	0.25	98.75	–0.42	0.25	95.50
Home range size	0.68	0.32	97.35	0.57	0.24	98.67
ISA	0.61	0.37	95.25	0.70	0.22	99.90
Hatch date	0.00	0.24	50.40	0.01	0.22	51.38
Fledge	0.20	0.29	75.20	0.07	0.27	59.82
Home range × ISA	2.20	1.66	91.70	2.19	0.85	99.55

We used females as the reference category for sex and only report fixed effects. We fit nestling weight models separately using female or male home range size as predictors.

Hatch date, neighbor density, and the interaction between sex and ISA had small effect sizes with high variability and were not considered informative.

The effect of ISA on adult weight loss depended on sex. Adult females lost more weight as ISA increased, whereas ISA did not influence male weight change (Figure 3; Table 1). Adults also lost more weight as the number of fledglings increased. Home range size and hatch date did not influence adult weight change.

The nestling weight model with female home range size as a predictor included 179 individuals from 44 nests, and the model with male home range size included 117 individuals from 28 nests. The effect of female home range size on nestling weight depended on ISA, but male home range was not influential (Figure 4; Table 1). At low ISA, nestling weight increased as female home range size increased; and at high ISA, nestling weight decreased as female home range size increased. Female nestlings weighed more than male nestlings in both models. Hatch date predicted nestling weight in both models. Nestlings that hatched late in the season tended to weigh less than those hatched early in the season. The number of fledged young also had a weak relationship with home range size in the male model and was not influential in the female model.

We calculated the CV of nesting weight for 50 nests and we used 42 of these nests in the model with female home range size and 26 in the model with male home range size. Variation in nestling weights within a brood varied with the adult home range size of adult males and females, although the effect depended on the degree of urbanization at the nest site (Figure 4, Table 1). At high ISA, variation in nestling weight within broods was higher as home range size increased, and at low ISA, variation was lower as home range size increased. The proportion of same-sex nestlings within a brood predicted the CV of nestling weight in both models. Hatch date was not influential in either model, nor was the number of fledged young.

DISCUSSION

Falco sparverius home range size was highly variable, but changed with the intensity of development for both males and females. Both sexes had smaller home ranges in more highly urbanized areas. Over the breeding season, the rate of weight loss was twice as high in adult females compared to adult males, and females lost more weight in more urbanized areas than in less developed landscapes. Male home range size did not predict individual nestling weight, whereas the effect of female home range size on nestling weight depended on ISA. Nestling weight was highest in areas with low ISA and large female home ranges, but this relationship was reversed in areas with high ISA, where smaller female home ranges led to higher nestling weight relative to larger home ranges. Both male and female home range size influenced the within-brood variation in nestling weight and also depended on ISA. Variation was highest in areas with high ISA and large home ranges. Overall, this suggests that smaller home ranges in urban areas may be adaptive; however, it still incurs a cost for adult females. We predicted if *F. sparverius* were well-adapted to urban environments, home range sizes would differ between urban and rural environments, but there would be no difference in adult or nestling health along the urban gradient. While *F. sparverius* breed successfully in urban areas, it comes with added weight loss to females. If this added cost decreases overwinter survival or future productivity, *F. sparverius* may be more sensitive to urbanization than previously reported (Chace and Walsh 2006).

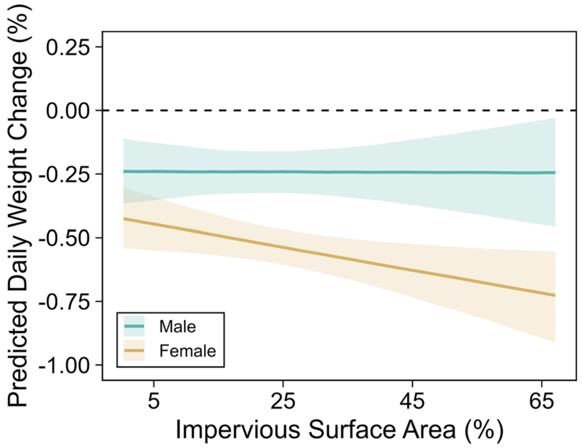

FIGURE 3. Predicted daily weight change in response to urbanization (impervious surface area) for adult *F. sparverius* during the 2021–2023 breeding seasons. Solid lines represent posterior mean estimates of daily weight change (as a percentage of initial weight) estimated from a Bayesian mixed-effects model with a Gaussian distribution. Shaded bars represent 95% credible intervals. Predictions were made holding all other model variables at their means.

The median home range size for males was 9.10 times larger than for females, even post-brooding. Of the 19 nests with GPS data from both adults, only one female had a slightly larger home range than her mate's (2.86 and 2.84 km^2 for the female and the male, respectively). Adults had high within-sex variation in home range size, and we had several individuals with home ranges greatly exceeding the median for both males and

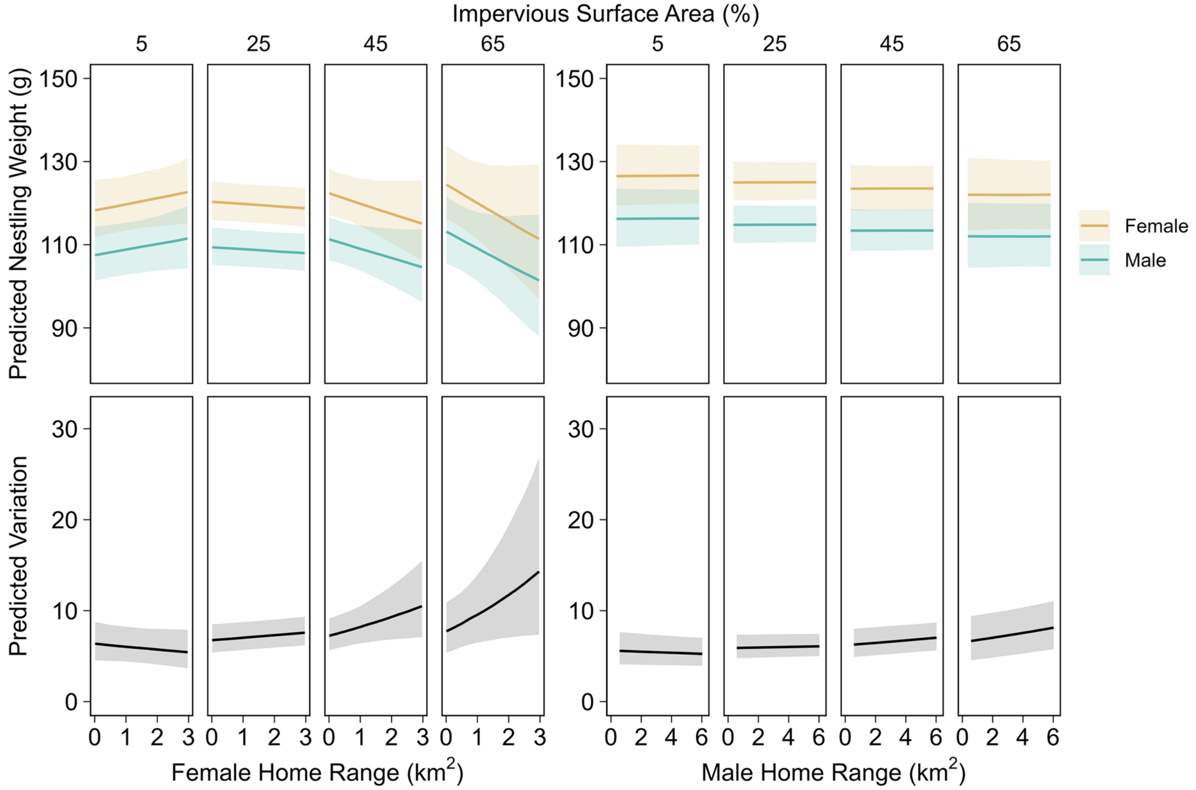

FIGURE 4. Predicted nestling weight (top) and within-brood weight variation (bottom) in response to female home range size (left), male home range size (right), and urbanization (impervious surface area) in northern Utah during the 2021–2023 breeding seasons. Solid lines represent posterior mean estimates for female and male nestlings from a Bayesian mixed-effects model using a Gamma distribution, and within-brood nestling weight variation (black) using a Beta distribution. Shaded bars represent 95% credible intervals. Predictions were made holding all other model variables at their means.

females (6 and 3 individuals with home ranges > 15 km^2, respectively). All the individuals with these large home ranges nested close to the mountains that they visited daily. Notably, 2 males with home ranges of 92.60 km^2 and 135.60 km^2 visited the same mountain ridge but nested on opposite sides of it. All kestrels with these large home ranges nested in boxes with relatively low (5–30%, mean = 16%) ISA.

Small home ranges in urban areas could be a result of increased prey availability in developed areas. Prey availability and quality are often associated with smaller home ranges (Rutz 2006, Séchaud et al. 2022), and because *F. sparverius* are dietary generalists and prey on a wide variety of taxa (Boal et al. 2021, Cornell et al. 2023), they may be able to find suitable prey in urban areas. However, adult female weight loss and nestling weights suggest that urban sites are not necessarily of higher quality compared to less developed areas. Patch size and landscape fragmentation could be alternative explanations for the negative relationship between ISA and home range size. *Buteo jamaicensis* (Red-tailed Hawk) home range size was positively associated with patch size of urban green space in Connecticut, USA (Morrison et al. 2016), and *Aegolius acadicus* had smaller home ranges and reduced provisioning to their young as forest fragmentation increased in Alberta, Canada (Hinam and Clair 2008). Human disturbance could be another factor influencing home range size. *Falco sparverius* are territorial and will actively defend their nest against intruders (Smith et al. 1972, Gard et al. 1989), potentially leading to more time spent defending against perceived threats in busy urban areas and less time foraging, resulting in a smaller home range. Future studies exploring the relationships between home range size, prey availability, patch size, disturbance, and their interactions along the urban gradient would add to our understanding of the drivers influencing *F. sparverius* space use.

Increased disturbance and subsequent increased vigilance and defensive behavior around nests in urban areas may also explain increased weight loss in females. Strasser and Heath (2013) linked higher levels of stress hormones in areas with a higher human disturbance score in adult females but not adult males. Females often spend more time near the nest, while the males do the bulk of the hunting (Roest 1957, Smith et al. 1972) and may be more sensitive to disturbance near the nest than males. Additionally, weight loss may be influenced by toxicants associated with urban areas, such as anticoagulant rodenticides. We detected rodenticides in blood samples from birds in our study area (Buechley et al. 2023) and rodenticides were associated with lower body mass in *F. tinnunculus* in Spain (Martínez-Padilla et al. 2017). Understanding the impacts of rodenticides on movement and demographics are important research needs for *F. sparverius* and other urban-dwelling wildlife.

The relationships between ISA, home range size, and nestling weight could be a result of a more homogenous urban landscape. Tremblay et al. (2005) found that *Parus caeruleus* (Blue Tit) nesting in areas with poorer quality habitat and lower densities of caterpillars (their preferred prey) would travel farther to forage than individuals nesting in high-quality habitat, but they would offset the energetic cost by making fewer trips and returning with larger prey. If *F. sparverius* adults travel farther but are unable to find more or superior prey, the energy spent traveling would not be offset and these individuals might lose more weight, their young could be smaller, or there might be more size variation between siblings. Conversely, adults in wildland areas with low urbanization may be able to find higher-quality prey farther from the nest.

Male home range size affecting the variation in nestling weight within broods but not the individual nestling weight suggests that when males bring in lower quality or fewer prey, they may still provide enough to feed at least one nestling adequately, increasing the overall average nestling weight. Additionally, females may affect nestling weight more than males because of their different parental roles, where males are responsible for the primary share of the hunting and the females deliver and divide the prey for the young (Roest 1957, Smith et al. 1972). In a food supplementation experiment, Dawson and Bortolotti (2002) found that adult female *F. sparverius* decreased the frequency and biomass of prey deliveries to their young when nests were provided with *Mus musculus* (house mice), whereas the frequency and biomass of prey delivered by males did not differ between control and supplemented nests. Therefore, males may provide the baseline and females may adjust their hunting behavior in response. However, our sample may be biased toward GPS units we were able to retrieve. When adults spend less time at the nest or deliver prey infrequently, the loggers are considerably harder to retrieve. In a few cases, we did not retrieve GPS loggers from the males because these individuals were not present when we were making retrieval attempts, even after many hours over several days spent at the nest. In these cases, the effect of home range on nestling weight would be attributed entirely to the female when the absence of the male likely affected nestling weight as well.

Later hatch dates resulted in decreased nestling weight but did not influence within-brood variation, suggesting that nestlings that hatch later in the season are lighter overall. Catry et al. (2017) documented a similar trend in *F. naumanni* (Lesser Kestrel) nestlings. Additionally, Callery et al. (2022) documented that *F. sparverius* initiating nesting later in the season resulted in lower productivity. We did not include productivity because our sample was biased to nests where eggs hatched, and rates of nestling loss were low after hatching. More research examining the relationship between hatch date, nestling health, and productivity along the urban gradient would be useful.

Urbanization and wildlife responses to urbanization patterns and processes are complex phenomena, and both can be described in myriad ways and at many scales. Our results highlight this complexity of responses in nesting kestrels. Female kestrels face the costs of urban nesting far more than their mates, with larger overall weight loss during nesting, but even more so for individuals nesting in more urbanized areas. Moreover, female space use decisions also have the largest consequences on nestling and overall brood condition (as measured by weight). Notably, these consequences vary at different ends of the urban gradient. While male space use also varied along the ISA gradient with larger home ranges in less developed areas, we found no body condition cost for nesting in developed areas. This suggests that males forage maximally regardless of development intensity and that traveling farther for food or other activities has no cost as measured by weight loss. Similarly, these space use decisions by males in our study area had no impact on fledgling weight. Future work exploring whether this cost to females is a result of food distribution decisions (i.e., feeding their young versus themselves) or higher energy demands associated with increased nest defense/vigilance behavior in urban landscapes would further our understanding of urban ecology. Further, an understanding of population-level effects of these sex-specific differences in space use, such as landscape-specific male and female survival estimates, as well as survival and recruitment rates for fledged *F. sparverius* in these landscapes, could shed light on current conservation efforts focused on this once widespread and abundant species.

Supplementary material

Supplementary material is available at *Ornithological Applications* online.

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Ethics statement

Animal handling protocols were reviewed and approved by Boise State University IACUC (AC22-001). Trapping and banding efforts were approved by the Bird Banding Laboratory (Permit #21384) and Utah Division of Wildlife Resources (COR #1COLL10877-01).

Conflict of interest statement

The authors have no conflicts of interest to declare.

Author contributions

J.M.T., M.D.O., J.A.H., and J.L.W. conceived the idea, developed and designed methods, and oversaw field data collection. J.M.T. wrote the paper and M.D.O., J.A.H., and J.C. substantially edited the paper. J.M.T., J.A.H., and J.C. provided code and analyzed data. J.L.W. made the map.

Data availability

Analyses reported in this article can be reproduced using the data provided by Taylor et al. (2026).

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