Environmental Research 273 (2025) 121235

Contents lists available at ScienceDirect

Environmental Research

journal homepage: www.elsevier.com/locate/envres

City life anticipates the breeding of a bird of prey without affecting its reproductive success

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ARTICLE INFO

Keywords:
Reproductive rate
Common kestrel
Urbanisation
Raptor
Hatching success
Laying date
Fledging success

ABSTRACT

Urbanisation poses a profound threat to biodiversity, leading to the loss of natural ecosystems and changes in animal communities. Many species of birds of prey are increasingly associated with urban habitats even when they have low reproductive success. However, it is unclear if this poor reproductive performance is due to the worse environmental conditions of the cities or to the poorer quality of the nesting sites. Addressing the effects of urban habitat on reproduction under similar nesting conditions (nest-boxes of same size and material) is therefore important if we were to test a direct effect of the habitat quality on cavity-nesting raptors. To address this question, we compared life-history traits, metrics of reproductive success, and morphological traits of chicks of common kestrels (*Falco tinnunculus*) breeding in artificial nest boxes in the city of Rome, and in nearby rural and natural environments over a period of five years. We found that kestrels laid significantly earlier in the city (10 days on average) than in the natural habitat. We also found novel evidence that chicks in rural habitats had shorter wings compared to chicks raised in urban habitats (1.2 cm on average). By contrast, we did not detect any differences in clutch size, brood size at fledging, egg volume, hatching success, fledging success, and body mass, tarsus length, and body condition of chicks among breeding habitats. Our findings suggest that, despite the differences in breeding phenology, kestrels had similar reproductive performances across different habitat types. This result is in contrast with previous studies on the same species carried out in other European cities, indicating that some urban habitats might be optimal for sustaining viable bird populations.

1. Introduction

Urbanisation is one of the most pervasive forms of land-cover changes on our planet because it dramatically affects resources, space, and biogeochemical and microclimatic features (Grimm et al., 2008; Chakraborty and Qian, 2024). Urbanisation can also affect the physiology (Ditchkoff et al., 2006; Birnie-Gauvin et al., 2016; Damiani et al., 2024; Giovanetti et al., 2024), behaviour (Møller, 2008; Lowry et al., 2013; Biondi et al., 2024), life-history (Bailly et al., 2016; Sepp et al., 2018; Capilla-Lasheras et al., 2022), and morphology (e.g. Iglesias-Carrasco et al., 2017; Putman and Tippie, 2020) of a number of organisms. These changes are not necessarily detrimental in terms of fitness, as cities may benefit adaptable and generalist species (Bonier et al., 2007; Sorace and Gustin, 2009; Møller, 2012; Palacio, 2020).

Birds are common in cities and present different sensitivities to urbanisation (Zuniga-Palacios et al., 2021; Grünwald et al., 2024a, 2024b). They can be classified as urban adapters, urban exploiters or urban avoiders, depending on their capability to thrive in urban environments (Tryjanowski et al., 2020). Urban birds may benefit from the local abundance of food (Chamberlain et al., 2009; Kettel et al., 2019), availability of nesting sites on buildings (Sumasgutner et al., 2014b; James Reynolds et al., 2019), warmer climate (Sumasgutner et al., 2023), or absence of predators (Chamberlain et al., 2009; Møller, 2012). As a consequence, urban bird populations may show better reproduction or survival compared to conspecific non-urban bird populations (e.g. Kettel et al., 2018). On the other hand, many bird species are declining or even disappearing from certain urban areas (Chamberlain et al., 2009; James Reynolds et al., 2019; Zuniga-Palacios et al., 2021), due to several factors as pollution (Kekkonen, 2017) or the limitation of food resources (Seress et al., 2020). Urban bird populations may also differ noticeably from non-urban bird conspecific populations in a number of life-history or phenotypic traits, such as time of breeding (Chamberlain et al., 2009; Capilla-Lasheras et al., 2022), clutch size (Chamberlain et al., 2009), or body size of chicks (Chamberlain et al., 2009).

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https://doi.org/10.1016/j.envres.2025.121235
Received 19 November 2024; Received in revised form 24 February 2025; Accepted 25 February 2025
Available online 25 February 2025

Another relevant type of anthropogenic effect on animal populations is the conversion of natural environments in rural areas. Although moderate farming may increase for birds the availability of sites for feeding or reproduction (Stoate et al., 2009), intensive farming may result in dramatic abiotic changes and loss of biodiversity (DeStefano and DeGraaf, 2003; Tudi et al., 2021). Despite this, possible divergences in life-history traits between urban, rural, and natural conspecific populations, and the potential underlying tradeoffs are relatively understudied at the level of single species (e.g. Bonier et al., 2007; Capilla-Lasheras et al., 2022; Grünwald et al., 2024a, 2024b).

Birds of prey are valuable indicators of the health of the environment because they are at the top of the food chain, and their breeding is highly influenced by the availability of nest sites, particularly for cavity-nesting raptors. Thus, raptors may act as sentinels of environmental changes (Kettel et al., 2018). However, the life-history and physiological responses of birds of prey to urbanisation vary significantly among species (Chace and Walsh, 2006; Kettel et al., 2018). For example, specialist diurnal bird predators tend to have a higher breeding performance (clutch size, brood size, number to fledge and nest success) than those that predate on small mammals in urban areas (Sumasgutner et al., 2014a; Kettel et al., 2018). Studies on barn owls, Cooper's hawks and northern goshawks found that they produce larger brood sizes in urban than non-urban habitats (Boal and Mannan, 1999; Salvati et al., 2002; Solonen, 2008). Moreover, smaller Australian raptors have greater urban tolerance than larger Australian raptors (Headland et al., 2023). Thus, factors like prey availability and species attributes appear to drive the capacity of birds of prey to exploit the urban environment.

The common kestrel (*Falco tinnunculus*) is a small bird of prey highly common across different habitat types, including cites. Studies carried out in urban areas of central Europe showed that kestrels may be negatively affected by city life (e.g. Sumasgutner et al., 2014a; Kettel et al., 2018). However, it is unclear whether the poor reproductive performance of urban kestrels is due to habitat-related effects or quality of the nesting sites (e.g. cavities in cites, nests of corvids outside the

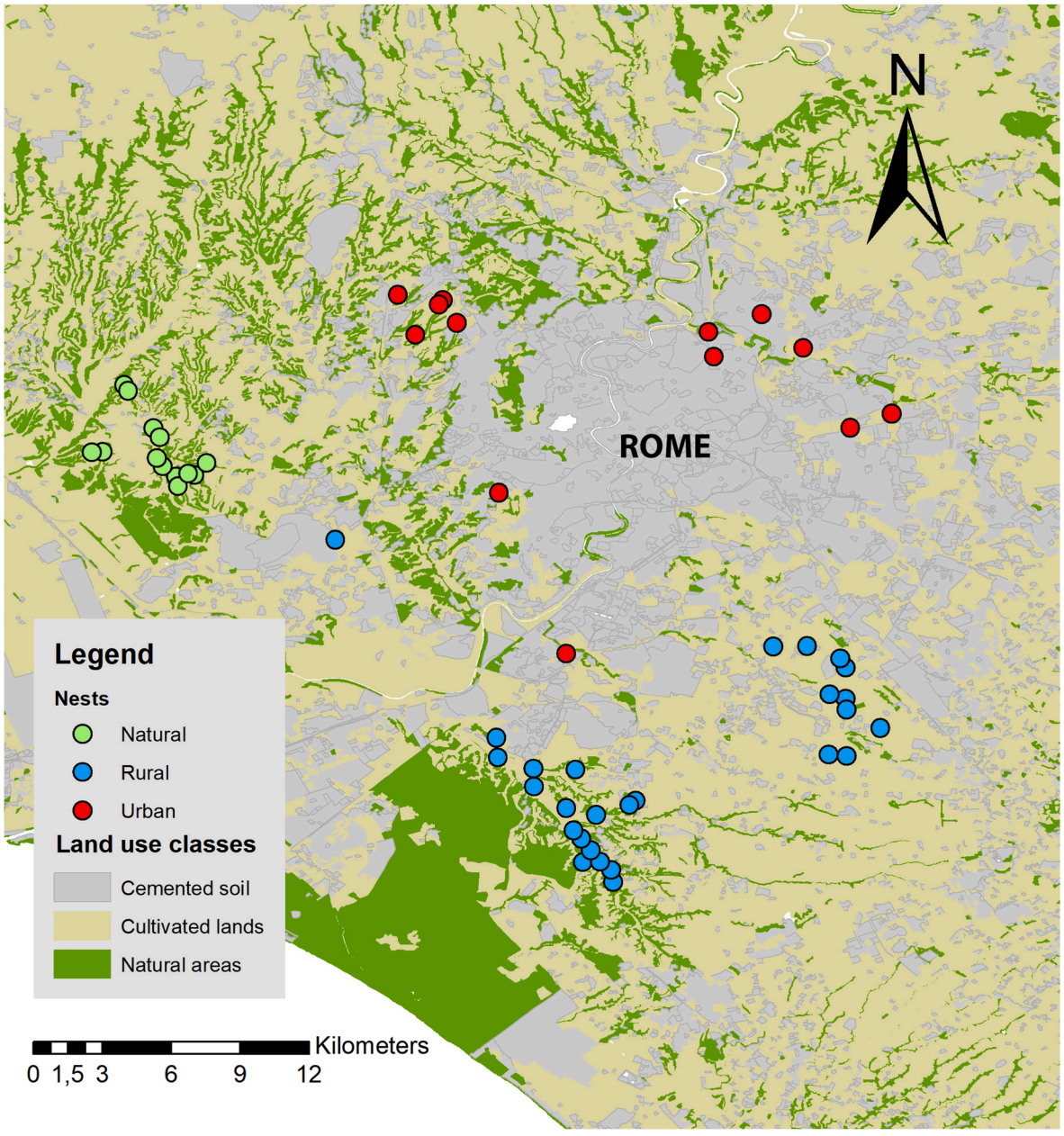

Fig. 1. The image illustrates the study areas in and around the city of Rome, with the monitored nests used for the analysis, highlighted as: urban = red; rural = light blue; natural = green. Main land use classes are reported: cemented soil (grey); cultivated lands (light yellow); natural areas (green).

cities), which can influence the reproductive investment and success of birds (e.g. Álvarez and Barba, 2011; Costantini and Dell'Omo, 2020). Addressing this gap in the data is important if we were to test the direct effect of habitat quality on cavity-nesting birds independently from the influence of the quality of the nesting site.

Using data collected across five years from common kestrels breeding in nest-boxes in the city of Rome, and in nearby rural and natural environments, we address whether urban and non-urban kestrels differ in (i) the key life-history traits of laying date, clutch size, brood size at fledging, and egg volume, (ii) hatching and fledging success, and (iii) the body mass, tarsus length, wing length, and body condition index of their chicks. In order to control for nest quality (e.g. size of the nesting site), we relied on data collected from kestrels breeding in nest boxes. If kestrels were adaptively adjusting their life-history strategies to their breeding environmental conditions, we would expect differences in life-history traits, but not in reproductive success. If one particular environment is found to be suboptimal for kestrels, we would expect lower reproductive success in that environment when compared to others. If reproductive success is similar across different environments, any morphological differences among chicks from different habitats might indicate adjustments of their growth patterns (e.g. developmental plasticity) to the prevailing local conditions, expression of genetic variation, or degree of hatching synchrony as indicated by previous work on birds (e.g. Merilä, 1997; Caizergues et al., 2021).

2. Methods

2.1. Study area

We carried out the fieldwork in central Italy from 2020 to 2024. The study area included the urban area of Rome (URB) and the nearby rural (RUR) and natural (NAT) areas (Fig. 1). The urban area is characterized by an anthropogenic matrix (e.g. buildings, cemented areas), with small green areas (e.g. urban parks, gardens) scattered around the city. The urban area is within the great ring junction, which is the core area of the metropolitan city of Rome. Both natural and rural habitats (with the exception of two nests) are outside the great ring junction. The rural area is dominated by the agricultural/rural landscape, with cultivated lands and a few Mediterranean trees (*Quercus* sp.). The natural area is mainly characterized by shrubs, pastures, and Mediterranean forests.

To support our categorization, we calculated an urbanisation index as the percentage of three main land use classes (cemented and sealed soil, cultivated lands, and natural areas) within 500 m radius from each nest (Kübler et al., 2005; Sumasgutner et al., 2014a; Giovanetti et al., 2024; Damiani et al., 2024) in order to encompass the home-range of kestrels (Damiani et al., 2022). To evaluate the land use classes, we used levels 1 and 2 of the CORINE Land Cover with 20-m-pixel resolution and 100 m of accuracy (Fig. 1). As cut-off points, we used 0–3% of cemented area for NAT, 5–10% for RUR, and >15% for URB, following de Satgé et al. (2019). To better differentiate NAT and RUR, we also relied on the percentage of cultivated lands: <50% for NAT and >50% for RUR. To measure the land use classes, we used QGIS v3.10. Our categorization of habitat type does not change if a radius of 1 Km is used.

2.2. Data collection

Kestrels bred in nest boxes installed on high voltage power lines (Terna s.p.a.). All nest boxes were made of marine plywood with a size of 50 × 30 × 30 cm (L × W × H), and a roof 60 cm long. Their orientation was South-South/East-South/West. We monitored on a weekly basis the nest boxes in the URB, RUR and NAT habitat (25, 66 and 47 respectively), in order to record the laying date, the clutch size, the egg volume (calculated as $length*width^2*0.51$; Hoyt, 1979), hatching date, and the number of hatched eggs, and the number of chicks, which we measured (tarsus length and wing length with a caliper; body mass with a pesola) before fledging at the age of 25 days. Each nest was visited 1 to 3 times per week from March to July of each year (2020–2024). Biometric parameters of the chicks were collected during the breeding seasons 2023–2024. We summarized the sample sizes per year in Table S1. The body condition index was derived by including the body mass as a dependent variable and the tarsus length (proxy of body size) as a covariate in the statistical models (García-Berthou, 2001, Table 1). This is because the ratio between body mass and wing or tarsus length, or the use of residuals obtained from a linear regression of body mass on wing or tarsus length have many drawbacks (García-Berthou, 2001). The age of chicks on the sampling day did not differ among the habitat types ($F = 0.21$, $p = 0.81$). In the case of missing reproductive data, we excluded the nest from further analysis.

2.3. Statistical analyses

We performed Generalized Linear Mixed-Effects Models (GLMER) or Linear Mixed-Effects Models (LMER) using the package "lme 4" (Bates et al., 2015). In each model (see Table 1), we included the nest-box identity as a random factor because siblings are not independent from each other, and the habitat type (three levels: URB, RUR, and NAT) as a

Table 1
The table summarises the best-fitting models used in this study. We did the within-year centering of laying date when this was included as a covariate. The body condition index was analysed by including the body mass as response variable and the tarsus length as explanatory variable following previous studies (García-Berthou, 2001; Costantini et al. 2009). Nest in the models indicates the nest-box identity.

Model	Response variable	Explanatory variables	Years
Linear Mixed-Effects model	$\log_{10}$(laying date)	habitat + 1|nest	2020–2024
Generalized Linear Mixed-Effects model (Poisson model with a log link function)<	clutch size	habitat + year + laying date + 1| nest	2020–2024
Linear Mixed-Effects model	egg volume ($length*width^2*0.51$)<	habitat + year + laying date + clutch size + 1| nest	2022–2024
Generalized Linear Mixed-Effects model (Poisson model with a log link function)<	brood size	habitat + year + laying date + 1| nest	2020–2024
Generalized Linear Mixed-Effects model	Hatching success (cbind hatched-unhatched eggs)<	habitat + year + laying date + 1| nest	2020–2024
Generalized Linear Mixed-Effects model	Fledging success (cbind fledged-dead chicks)<	habitat + year + laying date + 1| nest	2020–2024
Linear Mixed-Effects model	body mass of chicks (25 days old)<	habitat + year + laying date + brood size + 1| nest	2023–2024
Linear Mixed-Effects model	$\log_{10}$(tarsus length of chicks) (25 days old)	habitat + year + laying date + brood size + 1| nest	2023–2024
Linear Mixed-Effects model	wing length of chicks (25 days old)<	habitat + year + laying date + brood size + 1| nest	2023–2024
Linear Mixed-Effects model	body condition index of chicks (25 days old)<	habitat + year + laying date + brood size + tarsus length + 1|nest	2023–2024

fixed factor. We used the number of successfully (i) hatched and unhatched eggs per clutch and (ii) fledged and dead chicks per nest as the response variables for hatching and fledging success, respectively, by applying the function "cbind". To determine the best model to use for each single variable, we relied on AICc values obtained with the function "AICc" (Burnham and Anderson, 2004), selecting those models with the lowest AICc. We assessed whether there was spatial autocorrelation in our data using the Autocorrelation Function (ACF, Venables and Ripley, 2002) and Linear Models (*lm* function), with each response variable as dependent variable, and both latitude and longitude as covariates. The outcomes showed that there was no significant spatial autocorrelation among nests, so that this factor was no longer considered. Statistical analyses were conducted using the software R studio v4.2.1.

3. Results

We found that urban kestrels laid significantly earlier (10 days on average) than natural kestrels (19th April vs. 29th April; Tables 2 and 3, Fig. 2). By contrast, the laying period of rural kestrels did not differ from that of urban or natural kestrels. Kestrels laid clutches of similar size and eggs of similar size across all the three areas (Fig. 2, Tables 2 and 3); the size of clutches and the size of eggs laid later in the season were significantly smaller and larger, respectively than those laid earlier in the season, (Table 3). Brood size at fledging, hatching success, and fledging success were similar among habitat types (Fig. 2, Table 2), and did not vary across the season (Table 3).

Chicks from the three habitat types measured at 25 days of age were similar in terms of body mass, tarsus length, and body condition index (Fig. 3, Tables 2 and 3). These three morphological traits were also not influenced by the time of the season nor the brood size (Table 3). By contrast, urban chicks had significantly longer wings (+1.2 cm on average, Table 2) than RUR chicks; there was also a tendency for natural chicks to have longer wings than rural chicks (Fig. 3, Tables 2 and 3). Finally, chicks from larger brood sizes had longer wings than those from smaller brood sizes, and we found differences in the wing length among different years (Table 3).

4. Discussion

We found significant evidence for differentiation in laying date between common kestrels breeding in urban and natural habitats. We also found evidence for significant differences in wing length of chicks between common kestrels breeding in urban and rural habitats. By contrast, the variation in clutch size, egg volume, brood size, hatching success, fledging success, body condition index, and tarsus length was not significantly associated with the breeding habitat. Finally, we found that earlier breeders laid larger clutch sizes with eggs of smaller volume, and chicks from larger broods had longer wings. There was little variation in traits between the study years.

Urban kestrels laid significantly earlier than natural kestrels, indicating that the urban conditions influence their breeding decisions. We did not find any evidence for an influence of urban conditions on clutch size. Recent meta-analyses have shown that urban kestrels reproduce earlier and lay smaller clutches than non-urban conspecifics, suggesting that city life might not be optimal for reproduction (Capilla-Lasheras et al., 2022). Whereas our findings suggest that the earlier start of breeding in urban kestrels might reflect a plastic response to the prevailing environmental conditions of the city (e.g. warmer temperatures and availability of food throughout the year; Chamberlain et al., 2009). However, hatching and fledging success were not lower in the urban habitat, so that we can exclude any short-term detrimental effects of city life. In addition, urban kestrels laid eggs of size similar to natural or rural kestrels. Thus, in our study area kestrels adjusted their breeding phenology to the different habitat conditions, without any detrimental consequences for their short-term reproductive outcomes.

Previous work in other European cities found lower productivity of kestrels breeding in cities compared to those breeding in the countryside (Charter et al., 2007; Sumasgutner et al., 2014a; Kettel et al., 2018). One possible reason for this result might lie in the different abundance and quality of prey between urban and non-urban environments. For example, it has been suggested that a trophic shift from voles to birds in northern Europe could lead to a lower productivity of kestrels within urban areas (e.g. Sumasgutner et al., 2014). On the other hand, in the Mediterranean region, kestrels feed mainly on insects and reptiles (Costantini et al., 2005), which are abundant in both urban and non-urban environments (Vignoli et al., 2009). Another explanation for this discrepancy between these studies and our work might lie in the variation in the quality of the nesting site. Studies reporting lower reproductive success in cities involved pairs nesting in a variety of conditions, including cavities on old buildings, deserted corvid nests, or nest boxes. For example, pairs breeding in open nests have lower productivity than pairs breeding in closed nests (Kreiderits et al., 2016). While it is important to determine the impact of nesting site quality on reproductive outcomes, this can hide possible habitat-related variation in life-history strategies. Another reason for these differences between studies might be related to the features of the city. In Rome, the fledging success was 90%, which is higher than that reported for kestrels in Israeli cities (78%, Charter et al., 2007) or Wien (67%, Sumasgutner et al., 2014a). This higher reproductive success seen in Rome when compared to other cities might be due to the availability of green areas that characterize Rome, one of the "greenest" European cities (Quatrini et al., 2019; Gratani, 2020). The urban landscape can be variegated and patchy, and cities with more green areas can offer suitable habitat and prey to kestrels, which tend to select nesting sites close to backyards and urban green areas (Sandström et al., 2006; Sumasgutner et al., 2014b; Tzortzakaki et al., 2018). Nest boxes in Rome are surrounded by less cemented and sealed soil than nests in other European cities (Sumasgutner et al., 2014a) owing to the large green areas of the city (Quatrini et al., 2019; Gratani, 2020). These green patches might have a buffering effect against possible detrimental effects of urbanization on reproduction and offer prey more typical of the Mediterranean area, such as insects and lizards (Costantini and Dell'Omo, 2020), which are not much represented in the diet of kestrels living in other European cities. The quality of the local habitat might also explain why, in contrast to other European sites, kestrels are rather sedentary in our study region (Damiani et al., 2022). Studies on birds showed that the habitat quality can stimulate birds to be sedentary (Taylor and Norris, 2007), and year-round residents might exploit local resources better than migrating individuals.

Finally, prior work in norther European cities suggested that diet changes could play a key role in the adaptation of birds to city life, and that urban kestrels prey more on passerines and less on rodents compared to kestrels living in the countryside (Kübler et al., 2005;

Table 2
Descriptive statistics (untransformed mean ± SD) of all life-history and morphological traits of kestrels collected from the three habitat types included in this study. Sample sizes are also reported.

	Urban	Rural	Natural	Sample size
Laying date (from 1st January)	109 ± 15	116 ± 13	119 ± 13	138 nests
Clutch size	4.8 ± 0.8	4.4 ± 1.0	4.2 ± 1.1	138 nests
Egg volume (cm^3)	19.7 ± 1.7	19.0 ± 1.7	19.8 ± 1.9	334 eggs
Brood size	3.8 ± 1.0	3.8 ± 1.2	3.4 ± 1.5	124 nests
Hatching success (%)	79.5 ± 29.2	72.1 ± 37.4	75.8 ± 33.1	124 nests
Fledging success (%)	91.9 ± 16.5	92.9 ± 15.6	91.8 ± 27.0	124 nests
Body mass of chicks (g)	204 ± 27	199 ± 21	214 ± 18	135 chicks
Tarsus length of chicks (mm)	48.0 ± 1.8	47.4 ± 1.5	48.2 ± 2.1	135 chicks
Wing length of chicks (cm)	14.7 ± 2.2	13.5 ± 1.5	14.7 ± 1.5	135 chicks

Table 3
Outcomes of Generalized Linear Mixed-Effects Models (GLMER) and Linear Mixed-Effects Models (LMER) used to analyze differences among natural, rural and urban kestrels in life-history traits, reproductive success, and metrics of chicks. Reference level indicates the level of a given fixed factor against which the other levels are compared to. Estimates of fixed effects are reported. Sample sizes of each habitat type are also reported. Significant results are shown in bold. URB = urban; NAT = natural; RUR = rural.

Response variable	Factor	Reference level	Level	Estimate	Standard error	*t*-value	*p*-value
Laying date $n_{urb} = 23$, $n_{nat} = 49$, $n_{rur} = 66<$	**Habitat**	**Urban**	**Natural**	**0.044**	**0.016**	**2.673**	**0.011**
	Habitat	Urban	Rural	0.025	0.015	1.695	0.096
	Habitat	Natural	Rural	−0.019	0.013	−1.453	0.154
Clutch size $n_{urb} = 23$, $n_{nat} = 49$, $n_{rur} = 66<$	Habitat	Urban	Natural	−0.076	0.122	−0.617	0.537
	Habitat	Urban	Rural	−0.030	0.114	−0.260	0.795
	Habitat	Natural	Rural	0.046	0.092	0.499	0.618
	Year	2020	2021	−0.096	0.150	−0.640	0.522
	Year	2020	2022	−0.100	0.141	−0.708	0.479
	Year	2020	2023	−0.086	0.143	−0.602	0.547
	Year	2020	2024	−0.106	0.127	−0.831	0.406
	Laying date			**−0.104**	**0.044**	**−2.371**	**0.018**
Egg volume $n_{urb} = 80$, $n_{nat} = 94$, $n_{rur} = 160<$	Habitat	Urban	Natural	−0.035	0.669	−0.052	0.958
	Habitat	Urban	Rural	−0.516	0.545	−0.947	0.348
	Habitat	Natural	Rural	−0.481	0.569	−0.845	0.402
	Year	2022	2023	0.303	0.213	1.427	0.155
	Year	2022	2024	0.137	0.203	0.674	0.501
	Year	2023	2024	−0.167	0.171	−0.977	0.329
	Laying date			**0.237**	**0.118**	**2.015**	**0.045**
	Clutch size			0.154	0.143	1.075	0.283
Brood size $n_{urb} = 20$, $n_{nat} = 39$, $n_{rur} = 47<$	Habitat	Urban	Natural	−0.086	0.151	−0.567	0.571
	Habitat	Urban	Rural	0.029	0.139	0.206	0.836
	Habitat	Natural	Rural	0.114	0.119	0.964	0.335
	Year	2020	2021	−0.342	0.212	−1.609	0.108
	Year	2020	2022	−0.053	0.181	−0.295	0.768
	Year	2020	2023	−0.119	0.174	−0.685	0.493
	Year	2020	2024	−0.274	0.162	−1.696	0.089
	Laying date			−0.095	0.057	−1.670	0.095
Hatching success $n_{urb} = 22$, $n_{nat} = 44$, $n_{rur} = 57<$	Habitat	Urban	Natural	−0.282	0.685	−0.412	0.680
	Habitat	Urban	Rural	−0.374	0.591	−0.633	0.527
	Habitat	Natural	Rural	−0.092	0.537	−0.171	0.864
	Year	**2020**	**2021**	**−1.658**	**0.502**	**−3.307**	**<0.001**
	Year	**2020**	**2022**	**−0.889**	**0.451**	**−1.973**	**0.049**
	Year	2020	2023	0.102	0.466	0.218	0.827
	Year	2020	2024	−0.309	0.425	−0.727	0.467
	Laying date			0.265	0.186	1.424	0.155
Fledging success $n_{urb} = 20$, $n_{nat} = 39$, $n_{rur} = 47<$	Habitat	Urban	Natural	−0.739	1.146	−0.645	0.519
	Habitat	Urban	Rural	−0.219	1.002	−0.218	0.827
	Habitat	Natural	Rural	0.484	0.972	0.498	0.618
	Year	**2020**	**2021**	**−3.072**	**1.408**	**−2.182**	**0.029**
	Year	2020	2022	−0.495	1.611	−0.307	0.759
	Year	2020	2023	−1.571	1.318	−1.192	0.233
	Year	**2020**	**2024**	**−3.499**	**1.267**	**−2.762**	**0.006**
	Laying date			0.336	0.336	0.999	0.318
Body mass of chicks $n_{urb} = 41$, $n_{nat} = 32$, $n_{rur} = 62<$	Habitat	Urban	Natural	6.154	8.878	0.701	0.490
	Habitat	Urban	Rural	−6.057	6.843	−0.885	0.383
	Habitat	Natural	Rural	−12.211	8.086	−1.510	0.143
	Year	2023	2024	−1.067	5.687	−0.188	0.852
	Laying date			1.525	3.202	0.476	0.637
	Brood size			−1.136	2.466	−0.461	0.647
Tarsus length of chicks $n_{urb} = 41$, $n_{nat} = 32$, $n_{rur} = 62<$	Habitat	Urban	Natural	0.0002	0.0048	0.045	0.964
	Habitat	Urban	Rural	−0.0055	0.0039	−1.426	0.165
	Habitat	Natural	Rural	−0.0057	0.0044	−1.293	0.208
	Year	2023	2024	0.0020	0.0038	0.537	0.593
	Laying date			0.0021	0.0019	1.110	0.275
	Brood size			0.0002	0.0016	0.110	0.913
Wing length of chicks $n_{urb} = 41$, $n_{nat} = 32$, $n_{rur} = 62<$	Habitat	Urban	Natural	−0.096	0.704	−0.136	0.893
	Habitat	**Urban**	**Rural**	**−1.149**	**0.543**	**−2.116**	**0.042**
	Habitat	Natural	Rural	−1.053	0.649	−1.623	0.117
	Year	**2023**	**2024**	**1.227**	**0.426**	**2.872**	**0.005**
	Laying date			0.420	0.254	1.653	0.108
	Brood size			**0.566**	**0.189**	**2.999**	**0.004**
Body condition of chicks $n_{urb} = 41$, $n_{nat} = 32$, $n_{rur} = 62<$	Habitat	Urban	Natural	5.464	7.587	0.720	0.479
	Habitat	Urban	Rural	−3.458	5.950	−0.581	0.566
	Habitat	Natural	Rural	−8.921	7.008	−1.273	0.215
	Year	2023	2024	−1.332	5.045	−0.264	0.792
	Laying date			0.749	2.784	0.269	0.790
	Brood size			−0.832	2.172	−0.383	0.703
	Tarsus length			**5.089**	**0.911**	**5.584**	**<0.001**

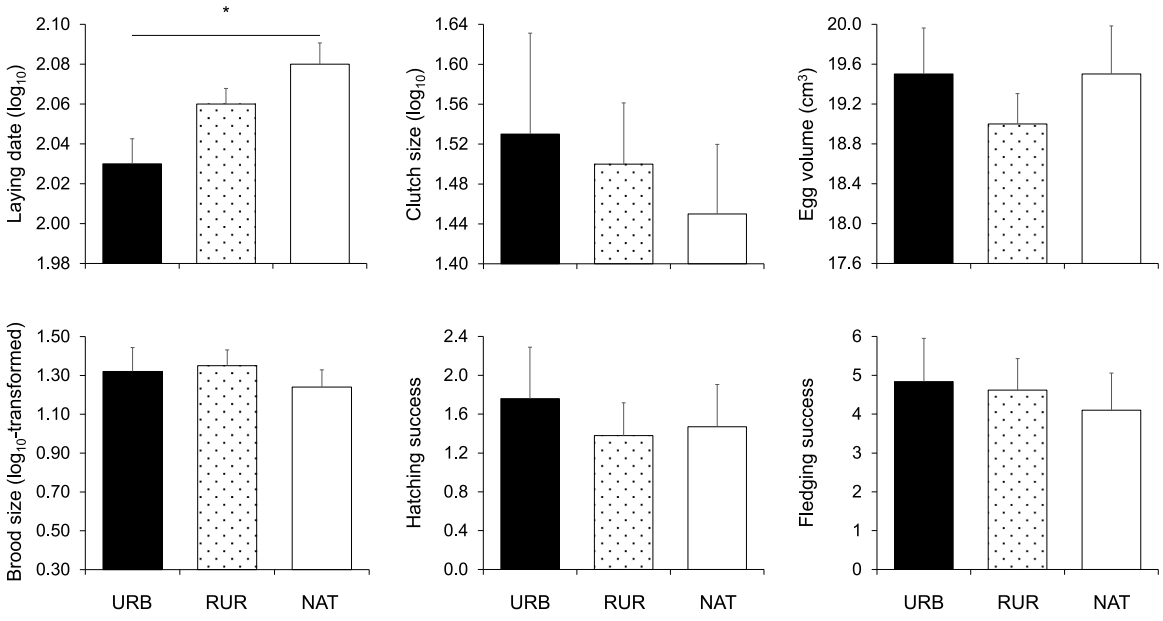

Fig. 2. Least-square means and standard error of the reproductive metrics shown for each habitat type. Significant pairwise comparisons are highlighted by an asterisk. URB = urban; RUR = rural; NAT = natural.

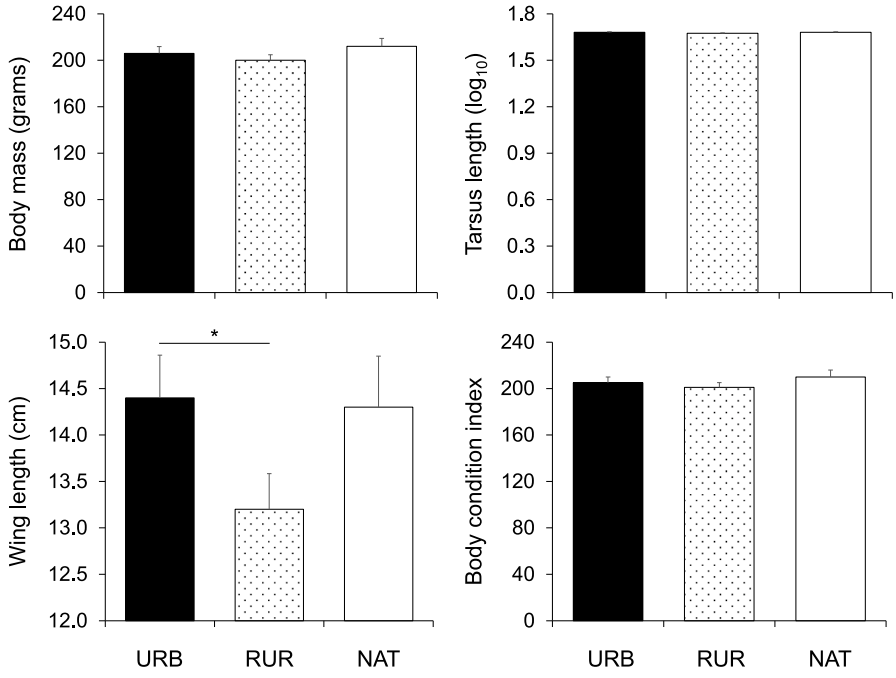

Fig. 3. Least-square means and standard error of the morphological traits of chicks shown for each habitat type. Significant pairwise comparisons are highlighted by an asterisk. URB = urban; RUR = rural; NAT = natural.

Sumasgutner et al., 2014a). This trophic shift might explain why chicks in more urbanised areas could have a lower body condition index than chicks in less urbanised areas (Wemer et al., 2021). By contrast, our study found that the body condition index of chicks was similar among the three habitat types, possibly because in our study region kestrels have a wider trophic niche than in northern regions (Costantini and Dell'Omo, 2020), and they find enough food also in urban areas. However, we found that RUR kestrel chicks had significantly shorter wings near fledging than URB kestrel chicks. Chicks were of similar age when we measured the wing length, thus this result might indicate that kestrels rely on different developmental strategies across habitats. Transcriptome analysis showed that those genes that regulate development, lipid metabolism, and insulin activity significantly differ in expression among chicks from the three habitat types (Damiani et al., 2024). Thus, kestrels might adjust their growth rate to the environmental conditions without affording significant costs. It might also be that the degree of hatching asynchrony varied among habitats, generating different levels of within-brood morphological variation as a consequence (see values of SD in Table 2). However, we do not have data on hatching synchrony, so that further studies are needed to assess

whether hatching patterns vary among habitats. Finally, the shorter wing length of rural chicks might indicate that the rural areas are not as good as the other habitat types for kestrels. However, chicks from different habitats were in similar body condition. Many studies showed that kestrels have a low reproductive performance and rear chicks in worse condition in areas impacted by intensive agriculture (Costantini et al., 2014; Sumasgutner et al., 2019). Our study area is not affected by any intensive farming, so that this difference in wing length might not indicate a suboptimality of the rural areas surrounding the city of Rome, as also suggested by the high rates of hatching or fledging success. Further work is needed to address the factors that might drive variation in morphotypes among different habitats. We do not know why the wing length differed between years. It might be that variation in weather conditions (e.g. temperature, rainfall) could have influenced hatching synchrony or food abundance, which affect growth rate of chicks. This topic deserves further study.

5. Conclusions

The results of our study show that some urban areas might not be detrimental for common kestrels. Rather, we found that kestrels in the urban environment have earlier laying dates, while maintaining similar rates of hatching and fledging success across the different breeding environments. We do not know the extent to which differences in breeding phenology between habitats are due to genetic selection or phenotypic plasticity induced by variation between habitats in key aspects of the ecology of common kestrels, such as diet, movement ecology, or parasite exposure. Overall, our study suggests that not all urban habitats are suboptimal for certain animal species as previously suggested, and particularly for common kestrels. It might be that cities similar to Rome, with extensive natural areas and a good connectivity of urban sites with nearby rural and natural areas, are optimal habitats for sustaining the reproduction of common kestrels and other generalist predators. How birds are adapting to different urban environmental conditions (e.g. temperature) deserves further in-depth research.

CRediT authorship contribution statement

Gianluca Damiani: Writing – original draft, Investigation, Data curation, Conceptualization. **Giacomo Dell'Omo:** Writing – review & editing, Supervision, Resources, Conceptualization. **David Costantini:** Writing – review & editing, Supervision, Project administration, Methodology, Conceptualization.

Funding

This research was funded by *Ornis italica* (Italy). Further support was provided by the PRIN 2020 number 2020H5JWBH. G. Damiani was supported by a PhD scholarship D.M. 117/2023 funded by 'NextGenerationEU, Piano Nazionale di Ripresa e Resilienza (PNRR) – MUR'.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank Terna s.p.a. and ACEA s.p.a. for granting access to the power lines and the nest boxes. We thank three anonymous reviewers for providing constructive comments on our work, and Marinella Nicolson for revising the language. We also thank for helping in the fieldwork: Beatrice Berardi, Sebastian Cannarella, Veronica Cippitelli, Riccardo Damiani, Francesco Di Pietro, Sarah Droghei, Giulia Forgione, Matteo Giuliani, Alice Lenzi, Nicoló Macci, Simone Messina, Luca Paoletti, Daniele Pirone, Manrico Sebastiano, and Luca Soriano. The work was authorised by the Institute for Environmental Protection and Research ISPRA (protocol n. 12495/2020 and 11640/2022) and the Regione Lazio (protocol n. G03417/2020 and G04115/2022).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envres.2025.121235.

Data availability

Data will be made available on request.

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