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Title	Breeding performance of an apex predator, the peregrine falcon, across urban and rural landscapes
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Publication date	2018-09-08
Original Citation	Kettel, E.F., Gentle, L.K., Yarnell, R.W. and Quinn, J.L., 2019. Breeding performance of an apex predator, the peregrine falcon, across urban and rural landscapes. Urban Ecosystems, 22(1), (9pp). DOI:10.1007/s11252-018-0799-x
Type of publication	Article (peer-reviewed)
Link to publisher's version	https://link.springer.com/article/10.1007%2Fs11252-018-0799-x - 10.1007/s11252-018-0799-x
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Download date	2026-11-16 09:56:42
Item downloaded from	https://hdl.handle.net/10468/8665

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Urban Ecosystems (2019) 22:117–125
https://doi.org/10.1007/s11252-018-0799-x

Breeding performance of an apex predator, the peregrine falcon, across urban and rural landscapes

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Published online: 8 September 2018
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Abstract
Urban environments present wildlife with major challenges and yet surprising numbers of species have colonised towns and cities globally. Despite the growing realisation that urban centres can be important habitats for wildlife, why some species do better than others in urban environments remains poorly understood. Here, we compare the breeding performance of an apex predator, the peregrine falcon (*Falco peregrinus*), in urban and rural environments, and test whether variation in reproductive success between and within environments is driven by prey. Historical breeding data were collected from raptor study groups across Great Britain between 2006 and 2016, from 22 urban and 58 rural nest sites, involving 101 and 326 nesting attempts, respectively. Prey density, biomass and diversity around the individual nests was estimated using modelled estimates from a national bird census. Urban peregrines produced more fledglings and had a higher overall nesting success (i.e. whether a nesting attempt was successful or unsuccessful) than rural peregrines. Prey density and biomass were significantly higher, and diversity significantly lower, in the urban sites, and explained the variation in reproductive success within both the urban and rural environments. Therefore, urban environments in Great Britain appear to provide peregrine falcons with superior habitats in terms of prey availability compared to rural habitats. We conclude that some apex predators can benefit from urban environments and that urban planning has the potential to benefit biodiversity across many trophic levels.

Key words *Falco peregrinus* · Urban predator · Urbanisation · Productivity · Breeding Bird Survey

Introduction

Urbanisation is increasing rapidly, causing profound and irreversible changes to natural landscapes (Gaston 2010). These changes represent major challenges for some wildlife populations through associated habitat loss and fragmentation (McKinney 2006), barriers to dispersal (Erritzoe et al. 2003; Bishop and Brogan 2013), increased disease (Dhondt et al. 2007), noise and light pollution (Fuller et al. 2007; Kempenaers et al. 2010), human disturbance (Schlesinger et al. 2008), increased mortality due to road traffic accidents and collisions (Erritzoe et al. 2003), and high densities of domesticated predators such as cats (*Felis catus*) (Schlesinger et al. 2008). Although many species are unable to persist in urban environments, others are able to colonise and reproduce successfully in even the most extreme urban environments (Blair 1996; Marzluff 2001). Why this variation between species occurs has become a major question in current ecology (e.g. Brand and Snodgrass 2010; Bonnington et al. 2015; Orros et al. 2015; Russo and Ancillotto 2015; Demeyrier et al. 2016; Rautio et al. 2016).

Key factors that are likely to explain how well species can persist in urban environments include whether the species is a specialist or a generalist, how well they tolerate human disturbance, the availability of suitable habitat, their exposure to predation, and food availability (Shultz et al. 2005; Fuller et al. 2008; Sims et al. 2008; Evans et al. 2009, 2010, 2011; Pettett et al. 2017). Even when species persist and manage to reproduce in urban environments, their breeding performance relative to traditional habitats can be highly variable across and within species (e.g. Chamberlain et al. 2009; Kettel et al. 2018). In some cases, urban populations do worse than those in traditional environments (e.g. Mennechez and

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Clergeau 2006; Peach et al. 2008; Pollock et al. 2017). In others they are just as successful (e.g. Conway et al. 2006; Suri et al. 2017) and in others, still, urban do better than traditional populations (e.g. Solonen 2008; Rebolo-Ifrán et al. 2017). It is suggested that higher temperatures and food availability, and a reduced level of predation from natural predators, are likely to be the key reasons why populations sometimes do better in urban environments (e.g. Newhouse et al. 2008). The generality of this conclusion remains unclear, however, not least because most research in this area comes from low trophic-level species. Higher trophic-level (apex) predatory species are likely to show very different patterns because they often have large home ranges and require an abundance of suitable prey, factors not often associated with urban environments (Fischer et al. 2012). However, some mammalian, avian and reptile (notably snake) predators have exploited urban environments very effectively (Fischer et al. 2012), where their densities can be relatively high when food availability is high (Ordeñana et al. 2010; Šálek et al. 2014). Urban centres are often associated with an abundant and stable food supply in the form of discarded human food (Maciusik et al. 2010), or food that is deliberately provided in gardens and greenspaces (Jones and Reynolds 2008; Rautio et al. 2016). Nevertheless, the predictability of food may be harder in urban environments, and the quality of food may not necessarily be optimal (e.g. Heiss et al. 2012; Meillère et al. 2015). Consequently, clear evidence that differences in prey availability may be driving the high reproductive success sometimes reported among urban predators is lacking (Bateman and Fleming 2012).

Avian predators provide a good model for understanding the effects of urbanisation because they are readily detectable and their ecology is generally well known. Kettel et al. (2018) highlight that while the breeding performance of small mammal-eating raptors tends to be reduced in urban environments (e.g. Tella et al. 1996; Liven-Schulman et al. 2004; Charter et al. 2007), the opposite is true for bird-eating raptors (e.g. Boal and Mannan 1999; Solonen 2008; Lin et al. 2015). Again, it has been suggested that prey availability plays a key role because native small mammal densities are known to decline with urbanisation (Baker et al. 2003), whilst bird densities increase (Blair 1996; Tratalos et al. 2007). Indeed, low small-mammal prey availability has been linked to reduced breeding performance in urban predators (Sumasgutner et al. 2014), and high avian prey availability is thought to have a positive effect on the health of urban raptor nestlings (Suri et al. 2017). To date, however, no studies have directly linked high avian prey density to an improved breeding performance of an urban predator.

Our aim was to examine the breeding performance of an apex predator, the peregrine falcon (*Falco peregrinus;* hereafter 'peregrine'), in urban and rural environments in relation to prey availability. Peregrines are specialist bird-eating raptors found in cities globally (Altwegg et al. 2014; Wilson et al. 2018), an environment in which some potential prey species of peregrines are especially abundant. Despite being one of the best-known urban predators, it is unclear whether the peregrine is benefitting from nesting in urban environments. We predicted that breeding success would be relatively high in urban environments and that this would be explained by higher prey availability in urban centres.

Methods

Breeding data

Reproductive success data were collected from 2006 – 2016 by amateur raptor and bird study groups, conservation organisations, peregrine researchers, and organisations involved in the maintenance of peregrine web-cameras (in urban locations). Data comprised 101 nesting attempts over 22 nest sites in urban environments, and 326 nesting attempts over 58 sites in rural environments. Data for urban nests were less extensive due to the relatively recent colonisation of urban areas in the UK by peregrines (Wilson et al. 2018). 'Urban' sites were defined as nests located in towns or cities, and contained at least 50% urban or suburban land-cover (using the Land Cover Map 2007) within a 2-km radius of the nest. 'Rural' sites included inland, natural nest-sites or quarries (either used or disused), outside of towns or cityscapes, and containing no more than 10% urban or suburban land-cover within a 2-km radius of the nest. Sites located on grouse moorland, where persecution leads to reduced breeding performance (Amar et al. 2012), were excluded. Data obtained included nest location and number of young fledged (to reach fledging age or actually leave the nest), for each nesting attempt.

Urban nests ($n = 22$) were located across England ($n = 21$), with one site in Wales, whereas rural nests ($n = 58$) were only located in Derbyshire ($n = 21$), Gloucestershire ($n = 13$), Leicestershire ($n = 1$), Shropshire ($n = 22$) and Staffordshire ($n = 1$), in England (Fig. 1). The disparity in nest locations across regions is explained in part by the natural distribution of peregrines. For example, in low-lying eastern England natural nest sites are relatively rare (Ratcliffe 2010; Balmer et al. 2013).

Prey data

Here we use the term 'prey data' to refer generally to prey density, prey biomass and prey diversity, collectively. Prey data were gathered for each peregrine nest using data from the Breeding Bird Survey (BBS) (Harris et al. 2016) because it provides a smaller-scale (1-km) resolution than other national surveys (e.g. Bird Atlas). The BBS is a volunteer-based annual survey that is organised by the British Trust for Ornithology (BTO) and aims to monitor population trends of the UK's

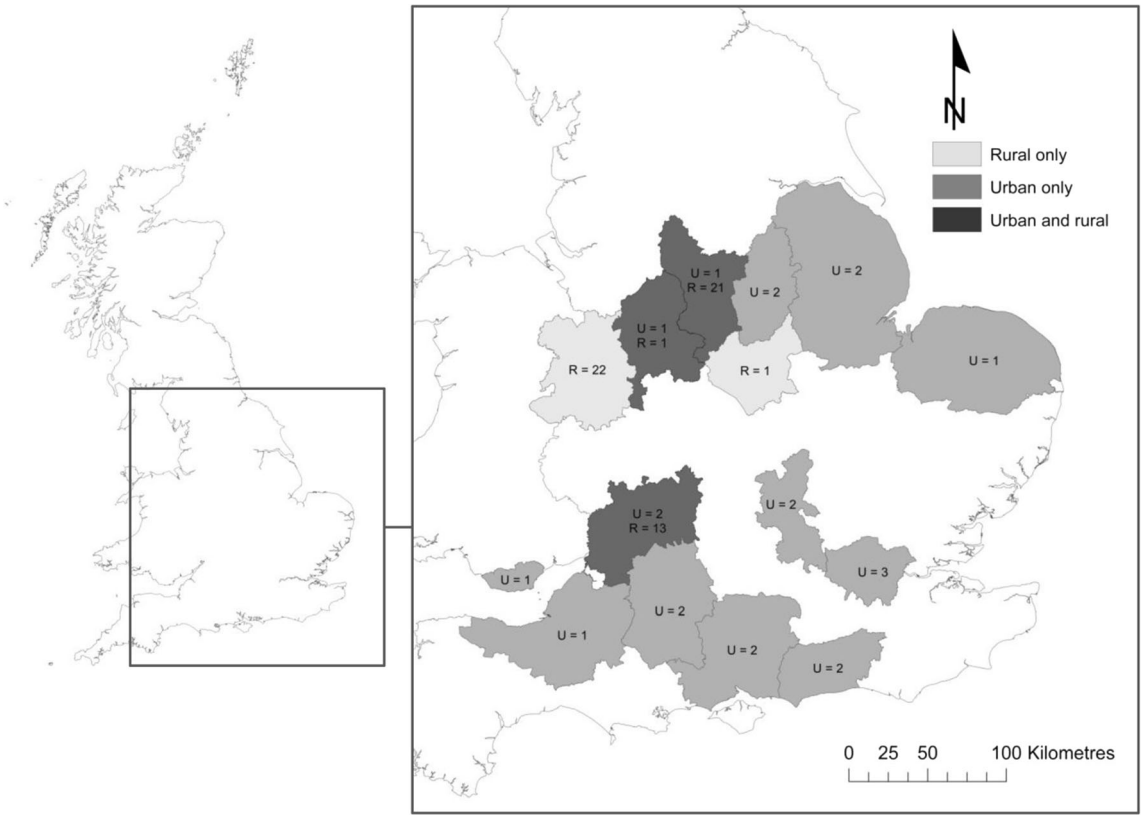


Fig. 1 The counties in England and Wales where peregrine breeding data were obtained. Light grey shading shows where data for rural peregrines were obtained, dark grey shading shows where data for urban peregrines were obtained, and black shading shows where data for both urban and rural peregrines were obtained. Sample sizes for urban (u) and rural (r) are shown for each county.

breeding birds. Volunteers visit randomly-allocated 1-km squares during the breeding season, recording all birds heard or seen along two parallel transects within the square. Few of the squares surveyed overlapped with the peregrine sites; therefore, modelled densities provided by the BTO (following Massimino et al. 2015), based on BBS data from 2007 and 2009, were used as our prey densities, and we assumed that modelled densities reflected the raw data accurately. We also assumed this partial 3-year temporal overlap with the breeding data led to no bias in the patterns reported below. The predicted density (hereafter 'density') of each prey species per 1-km grid was estimated using Generalised Additive Models with land-use, elevation, and eastings and northings (to account for spatial variation across different regions) as explanatory factors (full methodology described in Massimino et al. 2015). Though the peregrine's diet can be dominated by medium-sized prey, such as feral pigeons (*Columba livia*) and wader species, they are generalist predators of birds and often take prey from the smallest species up to 500g (Drewitt and Dixon 2008; Ratcliffe 2010). We therefore chose to include the density of 49 individual bird species known to be depredated by peregrines (Ratcliffe 2010; Table 1). Data were only available for these 49 species as they were the most common birds observed during the BBS, providing enough data to model their density (Massimino, pers. comms.). Densities were calculated for each 1-km grid square contained within a 2-km radius of a known peregrine nest. All urban nests were included in analyses but volunteers provided the exact locations of only 27 rural nests (because of the sensitivity of the data), reducing the sample. A 2-km radius was chosen as this is considered to be the approximate core range of a breeding female peregrine in GB (Mearns 1985; Ratcliffe 2010). The 2-km radius included all 1-km squares within, and touching, the boundary around the peregrine's nest. Thus, the number of 1-km squares varied slightly among nest sites.

The total biomass of each prey species per 1-km grid square was calculated by multiplying the expected density estimates by average species biomass (from Snow and Perrins 1997) for each of the 49 species. The low sampling resolution of the species data did not allow analyses for individual species or groups of species to be conducted; thus, data were summed to produce a total prey biomass estimate for the nest area. Prey diversity in each 1-km grid square within the 2-km radius was also calculated using Simpson's diversity index, which takes into account both species richness and abundance (Simpson 1949). Overall density (i.e. the number of all birds of all 49 species per 1-km grid square), biomass and diversity were calculated by taking the average of the values obtained for each of the 1-km grid squares within the 2-km radius of each site, giving an average value per 1-km for each site.

Table 1 Species included in the prey data analyses, using data derived from the BTO's Breeding Bird Survey

Common name	Scientific name	Common name	Scientific name
Blackbird	*Turdus merula*	Lapwing	*Vanellus vanellus*
Blackcap	*Sylvia atricapilla*	Linnet	*Linaria cannabina*
Blue tit	*Cyanistes caeruleus*	Long-tailed tit	*Aegithalos caudatus*
Bullfinch	*Pyrrhula pyrrhula*	Magpie	*Pica pica*
Carrion crow	*Corvus corone*	Mallard	*Anas platyrhynchos*
Chaffinch	*Fringilla coelebs*	Meadow pipit	*Anthus pratensis*
Chiffchaff	*Phylloscopus collybita*	Mistle thrush	*Turdus viscivorus*
Coal tit	*Periparus ater*	Moorhen	*Gallinula chloropus*
Collared dove	*Streptopelia decaocto*	Nuthatch	*Sitta europaea*
Cuckoo	*Cuculus canorus*	Pied wagtail	*Motacilla alba*
Curlew	*Numenius arquata*	Reed bunting	*Emberiza schoeniclus*
Dunnock	*Prunella modularis*	Robin	*Erithacus rubecula*
Feral pigeon	*Columba livia domestica*	Rook	*Corvus frugilegus*
Garden warbler	*Sylvia borin*	Skylark	*Alauda arvensis*
Goldcrest	*Regulus regulus*	Song thrush	*Turdus philomelos*
Goldfinch	*Carduelis carduelis*	Starling	*Sturnus vulgaris*
Great spotted woodpecker	*Dendrocopos major*	Stock dove	*Columba oenas*
Great tit	*Parus major*	Swallow	*Hirundo rustica*
Green woodpecker	*Picus viridis*	Swift	*Apus apus*
Greenfinch	*Carduelis chloris*	Whitethroat	*Sylvia communis*
House martin	*Delichon urbica*	Willow warbler	*Phylloscopus trochilus*
House sparrow	*Passer domesticus*	Woodpigeon	*Columba palumbus*
Jackdaw	*Corvus monedula*	Wren	*Troglodytes troglodytes*
Jay	*Garrulus glandarius*	Yellowhammer	*Emberiza citrinella*
Kestrel	*Falco tinnunculus*		

Statistical analyses

Breeding performance across urban and rural landscapes Generalised linear mixed models (GLMMs) were used to test the effect of landscape type (urban or rural) and geographical location (county), which we took to represent a range of measures including regional climate, on three breeding parameter responses. Number of fledglings from all nesting attempts (i.e. including sites that attempted to fledge young but may or may not have produced young to fledge in a given year), number of fledglings from successful nesting attempts only (i.e. sites that only produced at least one young to fledge), and whether the nesting attempt was successful (binary response: successful or unsuccessful), were fitted as response variables in separate models. Year and site were fitted as random terms in each model, and landscape type and county were fitted as fixed effects. Interactive terms between landscape type and county could not be fitted as only three out of the fifteen counties had data for both urban and rural sites. Binomial error structures with a probit link function were used to test the probability of nest success. Quasi-Poisson error structures with a log link function were used to test for effects on number to fledge from all nesting attempts and number to fledge from successful nesting attempts. Quasi-Poisson structures were chosen to control for overdispersion.

Variation in prey across urban and rural landscapes A principal component analysis was carried out to reduce the dimensionality of the interrelated variables related to prey (prey density, prey biomass and prey diversity), creating a single new prey component that captured 77.5% of the variance amongst the variables. This component correlated positively with prey density and prey biomass, and negatively with prey diversity. Hence, it can be interpreted as a measure of 'prey availability'.

A general linear model (GLM) with a log link function was fitted to test the effect of landscape type (urban or rural) on the prey component, where landscape type was fitted as a fixed effect.

Effects of prey on peregrine breeding performance GLMMs were fitted to test the effects of the prey component on breeding performance. Both the number of fledglings from successful nests (Poisson error structure with sqrt link function) and nest success (binomial error structure

with probit link function), were fitted as response variables in two different models. The prey component and landscape type were fitted as fixed effects in each model, with year and site fitted as random terms. Interactive terms between landscape type (urban or rural) and the prey component were also included in the models.

To obtain the best fitting models, the error distributions and link functions of all models were changed and compared using an information theoretic approach via AIC comparison. The model with the lowest AIC value was chosen as the best fitting model. All statistical analyses were performed using R (version 3.2.2).

Results

Breeding performance in urban and rural landscapes

Peregrines nesting in urban sites produced approximately one more chick to fledge from all nesting attempts, and from successful nesting attempts only, than those nesting in rural sites (Table 2; Fig. 2a). Furthermore, the probability that a nesting attempt would be successful was higher at urban sites (94 % successful) compared to rural sites (78 % successful; Table 2; Fig. 2b). There was no effect of county on any of the breeding parameters, suggesting climate or other local factors was unlikely to cause the difference between breeding performance in urban and rural sites (Table 2).

Variation in prey availability across urban and rural landscapes

There was a significant effect of landscape type on the prey component ($X^2_{(304)} = 12128$, $p < 0.001$), where urban sites had a higher prey component (i.e. high prey density and biomass, but low prey diversity per 1-km^2) compared to rural sites (Fig. 3).

Breeding performance in relation to prey

The prey component had a significant positive effect on the number of young to fledge ($X^2_{(304)} = 320.63$, $p < 0.001$; Fig. 4a); i.e. the higher the prey density and biomass, and lower the prey diversity per 1-km^2, the greater the number of young to fledge. There was no significant interaction between landscape type and the prey component ($X^2_{(304)} = 99.61$, $p = 0.66$) on the number of young to fledge.

The prey component also had a significant positive effect on the probability of nest success ($X^2_{(304)} = 253.83$, $p < 0.001$; Fig. 4b). Again, there was no significant interaction between landscape type and the prey component ($X^2_{(304)} = 250.47$, $p = 0.30$) on nest success.

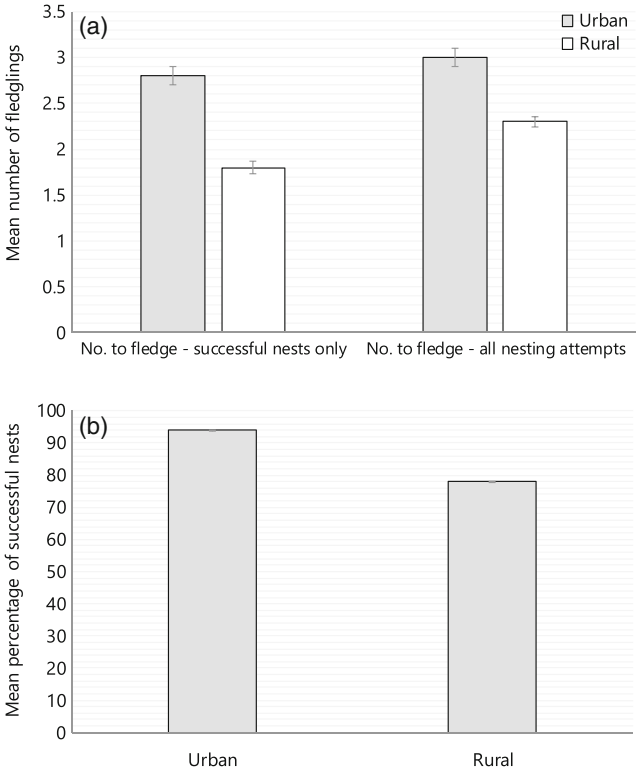


Fig. 2 Mean (±1 SE) number of chicks to fledge from (**a**) successful nests only, number of chicks to fledge from all nesting attempts and (**b**) percentage of successful nesting attempts at urban and rural sites between 2006 and 2016. Sample sizes are shown in Table 2

Discussion

Here, we provide evidence that the breeding performance of an apex predator is positively influenced by urbanisation on a national scale. Peregrines in urban environments across Great

Table 2 GLMMs exploring the effect of landscape type (urban versus rural) and county on the breeding parameters of peregrine falcons between 2006 and 2016. *=significant effect

Response variable	Fixed effect	N urban/rural	X^2	*P* value
Number to fledge from successful nests only	Landscape type	94/256	11.84	< 0.001*
	County		0.22	0.637
Number to fledge from all nesting attempts	Landscape type	101/326	39.91	< 0.001*
	County		20.71	0.110
Nest success	Landscape type	101/326	19.01	< 0.001*
	County		11.96	0.597

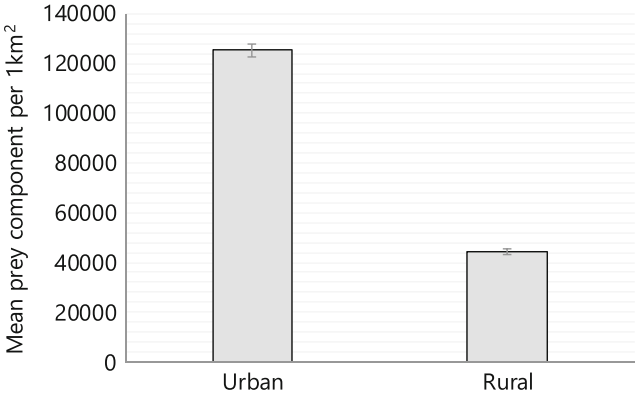


Fig. 3 Mean (±1 SE) prey component per 1-km^2 within a 2-km radius of urban and rural peregrine nests. The higher the number for prey availability, the higher the prey density and biomass, and the lower the prey diversity. *n* urban = 22, *n* rural = 27. Data derived from the BTO's Breeding Bird Survey

Britain were more successful than those in rural environments in terms of number of fledglings and nesting success. Indeed, the success of urban peregrine nests in this study (94 %) is the highest reported for any urban raptor species (Kettel et al. 2018), or for rural peregrines in GB and elsewhere (e.g. Crick and Ratcliffe 1995; Amar et al. 2012; Burke et al. 2015). The prey component, including predicted prey density and biomass, was higher in urban sites, and was positively correlated with breeding performance. Thus our predictions were met because prey were more abundant in urban habitats as expected (Blair 1996; Tratalos et al. 2007), and it is well known that food abundance is typically the major driver of breeding performance among birds in particular (e.g. Martin 1987; Uttley et al. 1994; Perrig et al. 2014; Pollock et al. 2017) and animals in general (e.g. Korpimäki et al. 1991; Wauter and Lens 1995; Heesen et al. 2013)

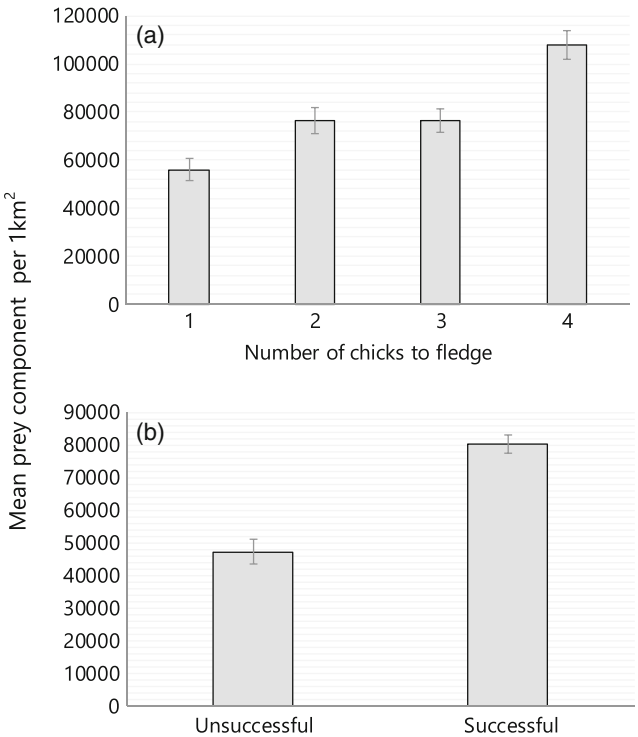


Fig. 4 Mean (±1 SE) prey component per 1-km^2 within a 2-km radius of peregrine nests in relation to (**a**) number of fledglings per successful nesting attempt and (**b**) nest success at urban and rural nests combined. The higher the number for prey availability, the higher the prey density and biomass, and the lower the prey diversity

Our results agree with another more detailed study based on a single urban raptor population in South Africa, which concluded that the stability of prey in urban environments is sufficient to maintain healthy offspring of another top avian predator (Suri et al. 2017). Furthermore, a study in Italy suggested higher densities of avian predators occurred in urban centres with higher densities of prey (Sorace 2002). In contrast, however, Gahbauer et al. (2015) found no difference in the number of young to fledge from urban and rural peregrines in northeastern North America, and suggested that habitat quality may have been similar across the two environments. The difference in findings between Gahbauer et al.'s (2015) and our study could arise for many reasons. First, for example, in Gahbauer et al.'s study, urban was defined as 'downtown core' and 'all other urban or suburban habitat, including quarries in an urban setting', whereas in our study urban nests were only located in city cores. Gahbauer et al. (2015) also included coastal habitats within the definition of 'rural' habitats, which might provide increased prey densities from aggregations of coastal birds. Thus, Gahbauer et al.'s (2015) study included a much greater diversity of urban sites in North America, which may reflect the fact that peregrines have been urbanised in North America a lot longer than in Great Britain (Cade and Bird 1990). Another reason for the difference may be that rural and urban environments in Great Britain are likely to be very different to those in North America, for example, in terms of prey availability, prey diversity, and human population density.

Prey species diversity was lower in urban environments, supporting findings from other studies that bird diversity tends to decrease with urbanisation (e.g. Blair 1996; Clergeau et al. 1998; McKinney 2006; Tratalos et al. 2007), but this did not prevent peregrines from gaining a higher breeding success than rural peregrines. This is somewhat surprising because peregrines are generalist, opportunistic predators of most avian prey species (Ratcliffe 2010), and thus we would have expected that overall lower diversity could have influenced peregrine breeding success in urban centres negatively. In urban environments, however, the diet of urban peregrines typically consists of relatively few species such as pigeons and doves (Columbidae) and thrush species (Turdidae), that occur in very large numbers (Drewitt and Dixon 2008). These species have successfully colonised urban environments globally (e.g. Clergeau et al. 1998; Tratalos et al. 2007; Evans et al. 2010), and feral pigeons in particular tend to congregate around food sources in urban areas (Johnston and Janiga

1995), making them easier prey to target. The likely explanation for the lack of an effect of diversity, therefore, is that peregrines can afford to be specialists in urban environments. We were unable to test whether better predictions of reproductive success could be obtained by restricting prey availability to specific taxa. Nevertheless, although we expect that such analyses may improve the overall fit, the main effect of higher prey abundance for most prey species in urban environments will not change the main conclusion that abundance, rather than diversity, drives the success of urban peregrines.

Our results provide new evidence that urban environments may offer better habitat for some apex predators because of higher prey availability over a large spatial scale. It has been suggested that unless animals are followed throughout their lifetimes, not accounting for potential negative effects of urbanisation, for example greater exposure to disease (Krone et al. 2005; but see Suri et al. 2017), higher vehicle and building collision rates (Hager 2009), and poor food quality (Liker et al. 2008; Heiss et al. 2012; Meillère et al. 2015), may exaggerate the quality of urban environments for some species estimated from snapshot measures at single life history stages. Our estimates of quality were from the breeding season alone, and did not look at post fledgling survival, recruitment, or lifetime reproductive success, so we cannot say definitively that urban environments are better for peregrines in Great Britain. Furthermore, although the link we report with food availability in urban environments is correlational, it is based on model estimates rather than raw data, and the sampling period overlapped with a small proportion of the breeding data time series. Thus, it remains possible that the increased breeding performance may be due to other factors, for example increased temperatures or reduced persecution in urban environments (Chace and Walsh 2006), neither of which were investigated here. One reason for this high success may be a reduced threat of persecution in urban environments (Chace and Walsh 2006), which usually leads to complete failure of nesting attempts (Amar et al. 2012). However, we suspect persecution was relatively low at our rural sites as we did not include pairs nesting in habitats strongly associated with persecution, such as moorland managed for grouse shooting (Amar et al. 2012). Furthermore, the difference was detectable even when only successful pairs were included in our analyses, thus controlling for persecution. Finally, it might be expected that micro-climate differences between urban and rural sites could also be driving some of the differences in breeding performance, which remains to be tested, but including county in our analysis at least controlled for the possibility of systematic bias between geographic climatic variation and the distribution of urban and rural site.

In line with findings on other predators (e.g. Bloom and McCrary 1996; Parker 1996), our results provide evidence that the novel environments humans impose on wildlife may provide valuable habitats for some predators. They also suggest that prey availability is the key, which poses a difficult challenge for urban management because often important prey species are considered as pests in urban environments (Belant 1997; Sorace 2002). However, our results are limited for a number of reasons discussed above and not necessarily representative of all urban areas. Thus there is a clear need for future studies to focus on obtaining raw prey data at the same time as other key life history measures across individuals' lives, and across as broad a gradient of urbanisation as possible. Only then will it be possible to determine whether urban environments are sources, sinks or self-sustaining habitats for apex predators (Marzluff et al. 2001; Battin 2004; Heard et al. 2012).

Acknowledgements We thank all of the volunteers who monitored peregrine nests and provided breeding data. Special thanks go to Gloucestershire Raptor Monitoring Group (in particular G. Kirk, S. Watson and N. Wylde), Peak District Raptor Monitoring Group (in particular T. Grimshaw), Shropshire Peregrine Group (in particular J. Turner), London Peregrine Partnership, D. Pearce and G. Roberts. Thanks also go to the BTO for providing BBS data and to all of the volunteers who have carried out BBS surveys. The BBS is funded by a partnership of BTO, JNCC and RSPB. We also thank I. Barber for his comments on an earlier draft of the manuscript. This research was funded by a Nottingham Trent University Vice Chancellor's bursary scholarship.

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