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The population density of an urban raptor is inextricably tied to human cultural practices

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Human socio-cultural factors are recognized as fundamental drivers of urban ecological processes, but their effect on wildlife is still poorly known. In particular, human cultural aspects may differ substantially between the extensively studied urban settings of temperate regions and the poorly studied cities of the tropics, which may offer profoundly different niches for urban wildlife. Here, we report how the population levels of a scavenging raptor which breeds in the megacity of Delhi, the black kite *Milvus migrans*, depend on spatial variation in human subsidies, mainly in the form of philanthropic offerings of meat given for religious purposes. This tight connection with human culture, which generated the largest raptor concentration in the world, was modulated further by breeding-site availability. The latter constrained the level of resource-tracking by the kites and their potential ecosystem service, and could be used as a density-management tool. Similar ties between animal population densities, key anthropogenic resources and human beliefs may occur in thousands of cities all over the globe and may fit poorly with our current understanding of urban ecosystem functioning. For many urban animals, key resources are inextricably linked with human culture, an aspect that has been largely overlooked.

1. Introduction

Urbanization is one of the most rapidly expanding land uses worldwide [1,2], with profound consequences for animal individuals, populations and communities [3,4]. As a result, research in urban ecology is in rapid expansion (e.g. [5]), but three aspects have received very limited attention. First, current knowledge is heavily biased towards urban systems of Europe and North America, despite the fact that a major share of urban sprawl is taking place in tropical countries [2,6] and that these may present profoundly different human and ecological settings from their temperate counterparts. Thus, there have been many calls highlighting the urgent need for more studies from tropical cities, but with limited progress (e.g. [7,8]). Second, despite the fact that humans are, for obvious reasons, the dominant species in the urban ecosystem, few studies have incorporated explicit human socio-cultural aspects in their research. Such factors are increasingly recognized as essential components of the urban ecosystem, leading to an urgent need for more insight into their ecological consequences [9–11]. In particular, while some studies have reported biodiversity, or individual-level behavioural responses by urban animals to human socio-cultural factors (e.g. [12,13]), it is virtually unknown whether these translate into

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Figure 1. The black kites of Delhi depend heavily on human subsidies offered for religious reasons: (*a*) a man with his sons ritually feeds kites with the typical, compact chunks of red meat (red circle); (*b*) large numbers of kites, sometimes into the hundreds, may congregate at such feeding events; (*c*) the ritual offerings are taken to the nests; (*d*) a parent kite is about to feed its fledgling with a ritual meat chunk. More than 90% of the diet in this population is composed of ritual offerings, which explains the tight link between breeding density and ready access to human cultural subsidies (photo credit for all images: F. Sergio). (Online version in colour.)

population-level consequences. Third, while much research has focused on the relationship between animal abundance and urbanization, this has been framed mainly as: (i) comparisons of population density between urban and rural sites; or (ii) evaluations of the landscape predictors of density measured within small vegetation patches (e.g. parks) embedded within the urban matrix of impervious surfaces (reviews in [3–5]). In the latter case, the small size of these fragments enforced that density could only be studied for small-bodied species, such as many songbirds. Both these approaches are obviously valuable to tackle the factors that allow certain species to colonize or persist in urban environments, but miss important information on: (i) density variations within the urban matrix and within the fully urban core of a city landscape, which is still typically heterogeneous [14] and could impose further internal variations in density; and (ii) density variations of wide-ranging species, such as raptors, whose populations may respond to integrated components of the landscape that include both the urban matrix and its embedded patches of 'natural' habitats, but may not fit well a simplistic classification such as urban versus rural.

Thus, there is a need for studies from tropical areas that investigate whether the density of wide-ranging species capable of urban colonization responds to variation in urban configuration and human socio-cultural factors. To fill this gap of knowledge, here we examine how the population abundance of a raptor, the black kite *Milvus migrans*, breeding in a tropical megacity responds to variation in landscape features and human cultural factors that mediate food and nest-site availability.

Raptors are upper-trophic-level, wide-ranging predators. Many species of this avian group have recently been shown to be able to colonize and even thrive in urban areas, by attraction to abundant prey supplies usually directly or indirectly promoted by human subsidies [15]. Raptor populations are typically limited by food and nest-sites [16], both of which are likely to depend in urban areas on structural landscape features and human socio-economic processes. However, it is virtually unknown whether the population levels of these species vary among different types of urban configuration, or in response to human cultural factors. Such a lack of knowledge is probably caused by the low density of these species and the consequent challenges to survey enough study areas of sufficient size to investigate variations in density and link them to urban features.

The model species of this study, the black kite (hereafter 'kite'), is a medium-sized, opportunistic predator and facultative scavenger. In India, the resident subspecies *M. m. govinda* is synurbic [17], i.e. it occurs almost exclusively in close association with humans in towns and cities [18]. In Delhi, where this study was conducted, kites breed throughout the city, often a few metres from human habitation, thanks to the exploitation of human food subsidies facilitated by inefficient refuse disposal and by religious kite-feeding practices (figure 1 [19,20]; see details below). While kites prefer breeding sites with ready access to such subsidies [20], it is currently unknown whether this generates heterogeneity in breeding distribution at the population level, especially once controlling for nest-site availability. Overall, the large area of this megacity and the magnitude of its food subsidies for kites generate one of the largest raptor concentrations in the world [19]. In turn, this offers a unique opportunity to examine how a predator population density varies among city-sectors which differ in access to religious subsidies, landscape configuration and availability of nesting structures.

This study expands and complements a previous evaluation of the effect of urban structure and anthropogenic subsidies on kite nest-site selection [20]. In that study, we focused on the habitat choices and performance of individual pairs, while here we employ a larger number of study areas to examine the collective response of this population to variations in landscape structure, nest-site abundance and food availability. This new analysis further allowed us to: (i) test the effect of food subsidies while controlling for nest-site availability (which was impossible by the modelling-design of [20]; and (ii) investigate whether individual-level decisions translated into population effects, an aspect that is rarely tested and that provides a key link by which urban development may impact individuals and populations at multiple spatial scales. In particular, based on published studies on this and other urban bird species, we hypothesized that kite density would: (i) increase with higher access to human subsidies; and (ii) respond to the abundance of potential breeding sites, as modulated by plot-level urban architecture. Finally, the potential for nest-site availability to constrain population-responses to food abundance has been scarcely investigated, despite its importance and management implications (reviews in [21,22], see further details in the Discussion). Thus, we further tested whether nest availability could limit the capability of kites to track spatial variation in food availability.

2. Methods

(a) Study area

Delhi is a megacity of more than 16 million inhabitants, covering an area of 1500 km^2 and in constant expansion (http://censusindia.gov.in/2011census). Three aspects of Delhi are important for kites. First, much of the city is characterized by poor solid waste management, which affords plenty of food to kites in the form of carrion or refuse. Second, many people engage in the centuries-old religious practice of feeding meat scraps to kites (hereafter termed 'ritualized-feeding'), typically offered by throwing meat into the air for the birds to catch (figure 1). These offerings are made for a variety of reasons, such as asking for blessings and relief from sins and worries [23,24]. While meat-offering is practiced by a number of communities, in Delhi it is especially prevalent among members of the Islamic faith, whose numbers are concentrated in well-defined portions of the city (hereafter 'Muslim colonies') where large quantities of meat are tossed to kites at predictable hours each day, sometimes causing hundreds of kites to congregate. Third, Delhi still retains reasonable green cover, thus providing abundant nesting habitat for kites [25]. However, tree-cover is also being rapidly lost [25], which calls for the need to forecast the potential ecological consequences of such changes.

(b) Field procedures

We surveyed kite nests systematically in 2013–2018 at 28 plots of approximately 1 km^2. These were plotted randomly within Delhi (1500 km^2) so as to cover all its possible urban settings, from semi-natural to extremely built-up sites (details in [19]). We surveyed each plot by walking slowly and carefully inspecting all potential nest-structures (trees, poles, towers, etc.). Structures were classified as active nest-sites when a kite individual or pair was observed to perch on a nest or its immediate surroundings, or to add material to a nest. Each plot was surveyed greater than or equal to three successive times each year during the breeding season, separated by greater than or equal to 20 days until we were reasonably confident to have detected all territorial pairs. This generated an overall sample of 79 plot-years available for analysis. To measure nest-site availability for each plot, we: (i) digitized all large-enough trees clearly visible in Google Earth imagery; and (ii) visited each plot and mapped any additional trees that were not visible in Google Earth (e.g. because of low quality, blurred imagery for some sectors of Delhi) and all potential anthropogenic nest-structures (e.g. poles, towers) that were typically too difficult to detect in Google Earth. Because more than 90% of the available nest-structures were trees, we summed trees and artificial structures into a single cumulative estimate of breeding-site availability.

(c) Statistical analyses

To investigate the predictors of kite population density, for each plot we collected a number of landscape and human variables (electronic supplementary material, table S1) chosen on the basis of our knowledge of kite ecology and of previous analyses of the factors that affect habitat preferences, breeding success and behavioural performance by Delhi kites [20,26]. These variables characterized each plot in terms of its landscape structure, food availability (e.g. local availability of organic waste, access to Muslim ritual subsidies) and nest-site availability (details in the electronic supplementary material, table S1). We further hypothesized that the effect of food availability could interact with nest availability in shaping density (e.g. [22]) and thus also modelled the interaction of nest availability with Muslim subsidies or with refuse availability. We then tested the effect of the above variables on kite density as follows. Because density could be spatially autocorrelated, we initially modelled it through a spatial linear mixed model (LMM) by means of a Bayesian approach, as outlined in [27]. However, such a model gave poor support to the presence of spatial autocorrelation and gave the same conceptual results (electronic supplementary material, appendix S1). Thus, we repeated the analysis by means of an LMM with normal errors and an identity link [28], where plot-identity and year were fitted as random factors. The LMM was built through a backwards stepwise procedure following [28]: all explanatory variables were fitted to a maximal model, extracted one at a time, and the associated change in model deviance was assessed by the significance of a likelihood-ratio test; the procedure was repeated until we obtained a final model which only included significant variables [28]. The R^2 of the LMM was calculated following [29]. Variables were standardized before fitting them to the models and all analyses were performed through R 3.4.3 [30].

3. Results

The average density in Delhi was 19.02 breeding pairs km^{-2} (s.e. = 7.43, $n = 28$ independent plots). Kite density increased with deteriorating sanitation levels (i.e. more human refuse in the streets) and depended on the interaction between access to Muslim subsidies and nest-site availability (table 1): density increased more steeply with Muslim subsidies when breeding sites were abundant than when they were in poor supply (figure 2). These explanatory variables explained 89.9% of the variation in density.

4. Discussion

Kite density was tied to spatial variation in human subsidies, in the form of human refuse, ritual offerings and their ready

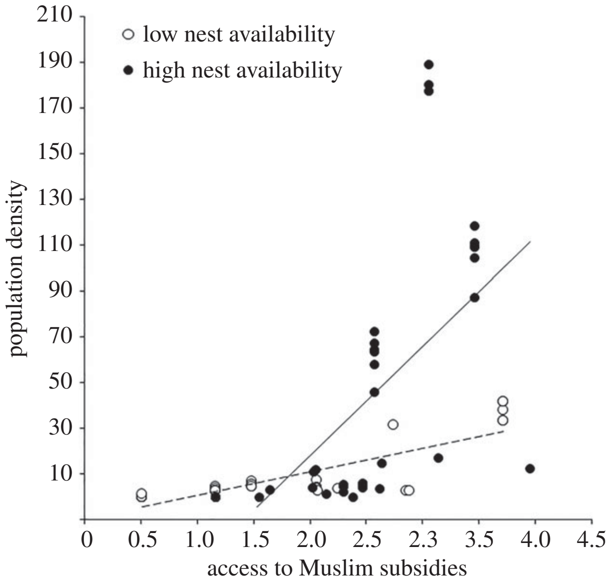

Figure 2. The population density of black kites in the megacity of Delhi (India) increases with food availability (access to Muslim subsidies), but such a relationship is modulated by the availability of breeding sites. For clarity of visualization, nest availability is here depicted as high (above the median value of nest availability: black dots, continuous line) or low (below the median value: white dots, hatched line).

accessibility. Because kite breeding pairs were previously shown to select sites with these same characteristics [20], individual-level habitat selection scaled up to population-level consequences. However, the subsidy-effect on density was more complex, because it was also modulated by breeding-site availability. Higher nest-site availability allowed the population to increase more steeply and reach higher densities in response to religious subsidies (figure 2). Conversely, lower nest availability constrained the breeding population to a weaker response to religious subsidies (figure 1). Thus, the availability of nesting structures modulated the capability of the population to track its food resources. As a consequence, only the combination of high availability of both human subsidies and urban nesting structures (trees, artificial poles and towers) allowed the population to reach the extremely high densities that generate what is probably the largest raptor concentration in the world.

The above results are important for two reasons. First, most of the support for the limitation of animal populations by breeding-site availability is given by experimental studies based on nest-box addition-removals (reviews in [21,22]). For species that build their own nests, demonstrations of the importance of nest availability are scarcer, probably because measuring the availability of nesting structures is often difficult or very time-consuming. In urban settings in particular, we are not aware of previous studies showing links between population density and breeding-site availability, despite their obvious importance for management in the highly 'engineered' landscape of urban ecosystems. Second, while the importance of human subsidies for predator populations is well established (e.g. [31,32]), the fact that breeding-site availability can mediate their population effect is, to our knowledge, reported here for the first time, and could be exploited for management purposes (see below).

Table 1. LMM with normal errors and an identity link function testing the effect of landscape and human variables on the population density of black kites in the megacity of Delhi (India); $n = 79$ plot-years from 28 independent plots.

variable	$B \pm$ s.e.	t	p-value
access to Muslim subsidies	6.07 ± 4.25	1.43	0.166
refuse availability score	16.18 ± 6.80	2.38	0.025
nest-site availability	29.87 ± 5.57	5.36	<0.001
access to Muslim subsidies $\times$ nest-site availability	13.10 ± 4.90	2.67	0.010
intercept	13.19 ± 3.53	3.74	<0.001

Overall, our results showed how the density of an urban raptor was limited by food and nest-sites, whichever was in shorter supply. This suggested the action of processes of population functioning in urban settings broadly similar to those observed in more natural habitats (e.g. [16,21,22]), but their modality and underlying mechanism stood out strikingly in that food was dictated by the spatial zoning of human socio-religious and cultural practices. This stresses the importance of human behaviours and culture as an interactive component of the urban ecosystem [10]. In fact, for synanthropic species that have closely coexisted with man in cities for centuries and are thus in the mature stages of urban colonization, humans can become a targeted resource and the leading component of their ecological niche, rather than a constraint to avoid or withstand. For example, in our population, more than 90% of the diet was dominated by ritual subsidies (data from greater than 1000 prey items from camera-trapping at 40 nests; N. Kumar, Y. V. Jhala, Q. Qureshi, F. Sergio 2017–2018, unpublished data).

To date, other studies have reported the effect of human socio-economic factors on the behaviour of the individuals of certain species (e.g. [13,26,33]), or on the biodiversity of gardens and parks embedded in the urban matrix (e.g. [12,34]). Here, we show that these individual and local effects can scale up to population-level responses. This highlights how human practices and culture, which are often spatially clustered in cities for socio-economic and historical reasons [12], can structure the urban landscape, ultimately creating ecologically relevant social gradients which are independent and overlaid over more classical gradients based on urban physical structures (e.g. housing density) or position along an urban–rural transition. Such socio-cultural gradients are often challenging to detect and to measure, because they may not be reflected by any strikingly visible or physical feature [35]. However, the fact that their modelling explained nearly 90% of the variation in kite density and that diet was so dominated by religious offerings provides compelling support for the often stressed need to incorporate a sociological perspective into studies in urban ecology [3,6,10,11]. In particular, we emphasize that some form of socio-economic and cultural gradient is likely to be present in most cities of the world. In the much studied cities of Europe and North America, such gradients often reflect differences in income and social status (e.g. [12]), while our study completes this picture by showing gradients based on religious factors, sanitary conditions and refuse management. These latter types of gradients are likely to be commonplace over large portions of southern Asia, Africa and South America, where most of the urban growth is currently concentrated [2]. In many of these regions, poor sanitary conditions in urban areas promote social acceptance of species that offer ecosystem services through refuse consumption, such as many scavengers [36–39]. Because sanitary conditions are usually tied to poverty, which is typically heterogeneously distributed within cities [40], the stage is set for socially generated variation in subsidies and resources, as well as human perceptions and responses to wildlife. Finally, the effect shown here of socio-cultural factors on wildlife populations implies that geographical variation in human cultural aspects can generate marked variation in the basic functioning of urban ecosystems from different regions. This stresses the urgency of completing our views of urban ecology through more studies on the strongly overlooked cities of the so-called developing world.

(a) Implications for management and conservation

Interestingly, both the factors that seemed to limit the kite population (food and breeding sites) were already directly or indirectly managed by humans. In particular, nest availability could easily be exploited through tree addition or removal in order to increase or constrain local predator density. For example, density could be enhanced close to urban areas with poor sanitation infrastructures in order to boost the ecosystem service function of kites, while density could be reduced in areas with conflictive pairs that attack humans for nest defence or to steal food [26]. Because urban ecosystems are typically temporally dynamic, a good understanding of the factors underlying local abundance is key to forecast or minimize the future impacts of such changes. For example, urban development in Delhi is currently causing rapid and often dramatic erosion of tree-cover [25]. This could cause a progressive decline in the ecosystem service offered by kites, with potential repercussions even on human health, for example, through an increase in rotting organic waste or in populations of feral dogs. The latter are a major source of rabies for humans in India and have been shown to increase in response to declines of scavenging birds [41]. On the other hand, kites are aggressive raptors that frequently harass and steal food from other species and their very high densities in Delhi could prevent urban colonization or lower the populations of other possibly more endangered species. While no such effect is currently demonstrated for Delhi, the human subsidies that promote such high densities could indirectly lead to faunal homogenization (i.e. community domination by a few 'weedy' species), a widespread phenomenon in urban environments [42]. However, the current levels of heterogeneity in food and nest availability should leave enough refugia with low kite density to enable the presence of less dominant species.

In conclusion, human socio-cultural factors may represent a widely overlooked force in urban ecology and conservation, and their impact may be even greater than currently appreciated in the poverty-structured cities of the developing world, where social inequalities and cultural beliefs may be tied to human subsidies and wildlife perceptions. The massive food-base so generated may have population impacts further modulated by anthropogenic structures that provide safe breeding, roosting and resting sites, whose availability could be easily exploited as a management tool. Thus, for many urban animals, key resources are inextricably linked to human culture.

Ethics. Fieldwork was conducted under permit CF/LC/105/07/HQ/10504-8 from the office of the Additional Principal Chief Conservator of Forests (APCCF) and the Government of National Capital Territory of Delhi under the provisions of the Wildlife Protection Act, 1972. The Training, Research and Academic Council (TRAC) of the Wildlife Institute of India, Dehradum (WII), gave bioethical approval for all research activities.

Data accessibility. The dataset supporting this article is available in the electronic supplementary material.

Competing interests. We declare we have no competing interests.

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References

1. United Nations. 2014 *World urbanization prospects: the 2014 revision highlights*. New York, NY: United Nations.
2. Malakoff D, Wigginton NS, Fahrenkamp J, Wible B. 2016 Rise of the urban planet. *Science* (doi:10.1126/science.aaf5729)
3. Marzluff JM, Shulenberger E, Endlicher W, Alberti M, Bradley G, Ryan C, Simon U, ZumBrunnen C (eds) 2008 *Urban ecology: an international perspective on the interaction between humans and nature*. New York, NY, Berlin, Germany: Springer Science.
4. Gaston KJ (ed.) 2010 *Urban ecology*. Cambridge, UK: Cambridge University Press.
5. Niemelä J (ed.) 2011 *Urban ecology: patterns, processes and applications*. Oxford, UK: Oxford University Press.
6. Grimm NB, Faeth SH, Golubiewski NE, Redman CL, Wu J, Bai X, Briggs JM. 2008 Global change and ecology of cities. *Science* **319**, 756–760. (doi:10.1126/science.1150195)
7. Magle SB, Hunt VM, Vernon M, Crooks KR. 2012 Urban wildlife research: past, present, and future. *Biol. Conserv.* **155**, 23–32. (doi:10.1016/j.biocon.2012.06.018)
8. Marzluff JM. 2016 A decadal review of urban ornithology and a prospectus for the future. *Ibis* **159**, 1–13. (doi:10.1111/ibi.12430)

9. Shochat E, Warren PS, Faeth SH, McIntyre NE, Hope D. 2006 From patterns to emerging processes in mechanistic urban ecology. *Trends Ecol. Evol.* **21**, 186–191. (doi:10.1016/j.tree.2005.11.019)
10. Alberti M. 2008 *Advances in urban ecology: integrating humans and ecological processes in urban ecosystems*. New York, NY: Springer.
11. Alberti MJ, Marzluff M, Schulenberger E, Bradley G, Ryan C, Zumbrunnen C. 2003 Integrating humans into ecology: opportunities and challenges for studying urban ecosystems. *BioScience* **53**, 1169–1179. (doi:10.1641/0006-3568(2003)053[1169:IHIEOA]2.0.CO;2)
12. Kinzig AP, Warrren P, Martin C, Hope D, Madhusudan K. 2005 The effects of human socioeconomic status and cultural characteristics on urban patterns of biodiversity. *Ecol. Soc.* **10**, 23. (doi:10.5751/ES-01264-100123)
13. Kumar N, Qureshi Q, Jhala YV, Gosler AG, Sergio F. 2018 Offspring defense by an urban raptor responds to human subsidies and ritual animal-feeding practices. *PLoS ONE* **13**, e0204549. (doi:10.1371/journal.pone.020454)
14. Forman RTT. 2014 *Urban ecology: science of cities*. Cambridge, UK: Cambridge University Press.
15. Boal CW, Dykstra CR. 2018 *Urban raptors: ecology and conservation of birds of prey in cities*. Washington, DC: Island Press.
16. Newton I. 1979 *Population ecology of raptors*. Berkhamsted, UK: T&AD Poyser.
17. Francis RA, Chadwick MA. 2012 What makes a species synurbic? *Appl. Geog.* **32**, 514–521. (doi:10.1016/j.apgeog.2011.06.013)
18. Naoroji R. 2006 *Birds of prey of the Indian subcontinent*. Noida, India: OM Books International.
19. Kumar N, Mohan D, Jhala YV, Qureshi Q, Sergio F. 2014 Density, laying date, breeding success and diet of black kites *Milvus migrans govinda* in the city of Delhi (India). *Bird Study* **61**, 1–8. (doi:10.1080/00063657.2013.876972)
20. Kumar N, Gupta U, Jhala YV, Qureshi Q, Gosler AG, Sergio F. 2018 Habitat selection by an avian top predator in the tropical megacity of Delhi: human activities and socio-religious practices as prey-facilitating tools. *Urban Ecosyst.* **21**, 339–349.
21. Newton I. 1998 *Population limitation in birds*. London, UK: Academic Press.
22. Newton I. 2013 *Bird populations*. London, UK: Harper Collins.
23. Pinault D. 2008 Raw meat skyward: Pariah-kite rituals in Lahore. In *Comparative Islamic studies: notes from the fortune-telling parrot: Islam and the struggle for religious pluralism in Pakistan* (ed. D Pinault), pp. 108–121. London, UK: Equinox Publishing Ltd.
24. Taneja AV. 2015 Saintly animals: the shifting moral and ecological landscapes of North India. *Comp. Stud. S. Asia, Afr. Middle East* **35**, 204–221. (doi:10.1215/1089201x-3138988)
25. Paul S, Nagendra H. 2015 Vegetation change and fragmentation in the mega city of Delhi: mapping 25 years of change. *Appl. Geog.* **58**, 153–166. (doi:10.1016/j.apgeog.2015.02.001)
26. Kumar N, Jhala YV, Qureshi Q, Gosler AG, Sergio F. 2019 Human-attacks by an urban raptor are tied to human subsidies and religious practices. *Sci. Rep.* **9**, 2545. (doi:10.1038/s41598-019-38662-z)
27. Zuur AF, Ieno EN, Saveliev AA. 2017 *Spatial, temporal and spatial–temporal ecological data analysis with R-INLA. Volume I: using GLM and GLMM*. Newburgh, UK: Highland Statistics.
28. Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM. 2009 *Mixed effects models and extensions in ecology with R*. New York, NY: Springer.
29. Nakagawa S, Schielzeth H. 2013 A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods Ecol. Evol.* **4**, 133–142. (doi:10.1111/j.2041-210x.2012.00261.x)
30. R Development Core Team. 2017 *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
31. Oro D, Genovart M, Tavecchia G, Fowler MS, Martínez-Abraín A. 2013 Ecological and evolutionary implications of food subsidies from humans. *Ecol. Lett.* **16**, 1501–1514. (doi:10.1111/ele.12187)
32. Newsome TM, Dellinger JA, Pavey CR, Ripple WJ, Shores CR, Wirsing AJ, Dickman CR. 2014 The ecological effects of providing resource subsidies to predators. *Global Ecol. Biogeog.* **24**, 1–11. (doi:10.1111/geb.12236)
33. van Heezig Y, Hight SR. 2017 Socio-economic-driven differences in bird-feeding practices exacerbate existing inequities in opportunities to see native birds in cities. *J. Urban Ecol.* **3**, jux011. (doi: 10.1093/jue/jux011)
34. van Heezig Y, Freeman C, Porter S, Dickinson KMJ. 2013 Garden size, householder knowledge, and socio-economic status influence plant and bird diversity at the scale of individual gardens. *Ecosystems* **16**, 1442–1454 (doi:10.1007/s10021-013-9694-8)
35. Faeth SH, Warren PS, Shochat E, Marussich WA. 2005 Trophic dynamics in urban communities. *BioScience* **55**, 399–407. (doi:10.1641/0006-3568(2005)055[0399:TDIUC]2.0.CO;2)
36. Campbell M. 2009 Factors for the presence of avian scavengers in Accra and Kumasi, Ghana. *Area* **41.9**, 341–349. (doi:10.1111/j.1475-4762.2008.00870.x)
37. Barlow CR, Fulford T. 2013 Road counts of hooded vultures *Necrosyrtes monachus* over seven months in and around Banjul, coastal Gambia, in 2005. *Malimbus* **35**, 50–56.
38. Gangoso L, Agudo R, Anadón JD, de la Riva M, Suleyman AS, Porter R, Donázar JA. 2013 Reinventing mutualism between humans and wild fauna: insights from vultures as ecosystem services providers. *Conserv. Lett.* **6**, 172–179. (doi:10.1111/j.1755-263X.2012.00289.x)
39. Bildstein KL, Therrien J-F. 2018 Urban birds of prey: a lengthy history of human-raptor cohabitation. In *Urban raptors: ecology and conservation of birds of prey in cities* (eds CW Boal, CR Dykstra), pp. 3–17. Washington, DC: Island Press.
40. Kilroy A. 2009 *Intra-urban spatial inequality: cities as 'urban regions'*. Washington, DC: World Bank. https://openknowledge.worldbank.org/handle/10986/9144.
41. Markandya A, Tayor T, Longo A, Murty MN, Murty S, Dhavala K. 2008 Counting the cost of vulture decline: an appraisal of the human health and other benefits of vultures in India. *Environ. Econ.* **67**, 194–204.
42. McKinney ML. 2006 Urbanization as a major cause of biotic homogenization. *Biol. Conserv.* **127**, 247–260. (doi:10.1016/j.biocon.2005.09.005)